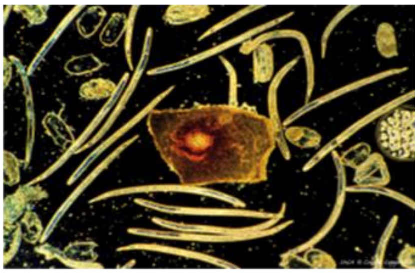
The Future Threat of PCN in Scotland

Project Final Report



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Contents

1 Executive summary

1.1 Background

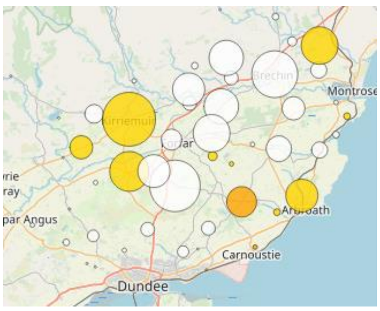
Nematodes (thread like worms) are numerically the most abundant animals on earth, and some species are parasites of plants. Nematodes are responsible for approximately 12% of crop losses worldwide and the damage has an estimated economic cost of $160 billion (Singh *et al.*, 2015). Potato cyst nematodes (PCN) are the most damaging nematodes to affect potato crops, capable of causing over 70% yield loss (Turner and Subbotin, 2006). Each cyst is a dead female worm containing approximately 400 live eggs, and so they have massive potential for reproduction. Cysts are spread with potato seed, through movement of soil and potentially by water and wind. Eggs can survive inside cysts up to 40 years making their control challenging. PCN are believed to have been introduced into Europe from South America at the end of the 19th century. Two species of PCN are present in Scotland; *Globodera rostochiensis* - the golden cyst nematode and *Globodera pallida* - the white cyst nematode. SASA estimates over 13% of the area regularly planted with potatoes in Scotland is now infested with PCN. Scotland currently produces around 70% of Great Britain's seed potatoes and is considered a high-grade region due to its low disease levels. Seed potatoes cannot be grown on land recorded as infested and ware potatoes can only be produced under an officially approved control programme. In recent years the incidence of *G. pallida* has increased markedly, with Angus the most affected county. Statutory testing data collected by SASA shows that the area of land recorded as infested with *G. pallida*, currently 6,200 ha, is doubling every 7–8 years, whilst the area of land infested with *G. rostochiensis* is relatively static at c. 14,500 ha. In the 1970s, findings of *G. pallida* represented 2–3% of the all PCN findings, whereas now they account for nearly 70%. At the current rate of increase, the widespread presence of *G. pallida* may prohibit the production of seed potatoes on PCN-free land in as little as 30 years.

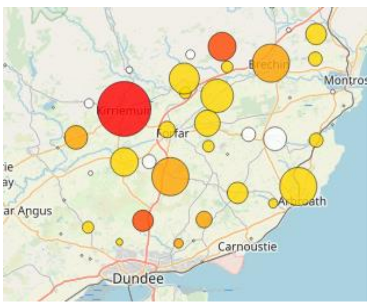
1.2 Key Research Questions

The aim of this project was to gain a better understanding of the future threat of PCN, determining the likely outcomes for PCN in Scotland. The project sought to understand control options that are available to manage PCN both in Scotland and at a wider level. We investigated what measures are currently being used to control PCN in Scotland and to what effect. We spoke to growers in order to better understand their motivations and limitations. Overall, we sought to gain an understanding of how management of this pest could be more effective.

1.3 Research undertaken and main findings

To determine how *G. pallida* has changed in the past 10 years in Angus, the most infested county in Scotland, Strathclyde University scientists used data from SASA's Seed Potato Users Database (SPUDS) to estimate the infestation by *G. pallida*. An interactive map was created to visualise these infestations (shown below), with 2010 on the left and 2018 on the right (white – no infestation, red – high infestation levels).





The area with *G. pallida* testing positive in each year was low from 1976 onwards and began to slowly increase between 2005 and 2010. This area then rose rapidly from 128 hectares in 2010 to 432 hectares in 2012. In contrast, *G. rostochiensis* was recorded from approximately 800 hectares p.a. in 1970s, but this incidence has gradually declined and is now similar to the area infested with *G. pallida* between 2005 and 2010. An exponential model captured the data well and predicted that the area testing positive each year doubles approximately every 7 years. Multiplying the loss by the acreage, an estimated £25m loss occurred in 2019 (5,000ha multiplied by £5,093 per ha loss) which is predicted to rise to £125m per year in 2040. This figure represents the opportunity loss not the actual loss, i.e. the value of potatoes that could have been grown had the land not been infested by *G. pallida*.

The spread of both *G. pallida* and *G. rostochiensis* in Scotland was mapped by BioSS scientists using results of all PCN tests from 1988 to 2019 using the SPUDS database. Animated maps of Scotland showing the spread of PCN were created from this data.

There are several options available to manage PCN. The reason for the EU PCN directive requiring land intended for the production of seed potatoes to be tested and found free from PCN is to limit the spread of PCN through seed. Nematicides can currently be used to preserve the yield of a crop, although their future availability cannot be assumed as tighter restrictions on chemicals are continually being applied. Biofumigants and trap crops may provide alternative strategies to control nematodes, but both require to be grown in place of a cash crop which limits their appeal to farmers. Tolerant varieties are capable of producing a yield despite high levels of infestation but can render the land unusable for potatoes for several years following harvest. Increasing the rotation length will decrease the population of eggs in a field when the next crop is planted, but this depends on effective control of ground keeper potatoes (potatoes left behind from the previous crop).

Resistant varieties are probably the most effective way of controlling PCN. BioSS scientists used models to predict outcomes when varieties with different resistance scores were planted to determine the potential impact of temperature changes. Predicted increases in *G. pallida* populations under increasing temperature are likely to be dwarfed by the effects of potato resistance, with resistant potatoes being shown to effectively control *G. pallida* populations. Approximately 50% of potato crops grown in Scotland are resistant to *G. rostochiensis*, which explains why infestations of land with this species have plateaued. However, less than 3% of potato crops grown in Scotland have high levels of resistance (score 7-9) for *G. pallida*. Through analysing the SPUDS database, it was possible to determine that even when infestations of *G. pallida* have been detected, 75% of ware crops planted in this land under a control programme are fully susceptible to *G. pallida*, which is only a 10% decrease from all crops planted in Scotland. For *G. rostochiensis* the baseline is better with only 43% of crops planted in Scotland being fully susceptible. However, in control programs this reduces to 33% when it could be far less than this.

In order to determine why growers were not growing resistant varieties and other potential tools available to them we surveyed a total of 35 potato farmers, (35 face to face including 8 at Potatoes in Practice). The main findings were that blackleg rather than PCN is viewed as the main concern currently in Scotland as this is responsible for most down-gradings. There was a lack of awareness about the increasing problem of *G. pallida*. While most growers were aware of their own PCN situation and whether the varieties they were growing are resistant to the species of PCN present, most growers have little say about the variety they plant. Most potatoes are grown under a contract with a potato producer. These companies sell farmers seed and buy the produce back from them, allowing a guaranteed income from the crop but limits the input in variety choice by the grower. Most conversations about which variety to grow depend on what will bring the biggest returns, what will yield well in the land and how easy the crop is to market - PCN rarely comes into the conversation. Most growers would grow resistant varieties to *G. pallida* if they were available and marketable. However, almost all

G. pallida resistant varieties are processing varieties and therefore cannot be grown for ware in Scotland. However, current restrictions on land for seed production are favouring ware production.

1.4 Recommendations and future work

The models developed by both the University of Strathclyde and BioSS would benefit from additional data. It would be helpful to look at spread of PCN within and between fields and at a national level as this might help inform the main risks of spread. Detailed estimation of losses is needed to provide more realistic estimates. Similarly, the estimation of losses in seed potato production would require a modified model that would account for recording and de-recording of land.

Protecting the seed industry for the long term in the face of a growing PCN threat is of critical importance as the ware industry relies on growing table varieties, which have a decreasing market. In order to encourage active management using resistant varieties on seed land, we propose that two options should be considered to relax the current statutory measures: a) revising PCR thresholds for positive PCN tests; and b) revising the area of land on which seed potato production is prohibited. However, such relaxations would be conditional on the availability and use of resistant varieties.

The SG PCN Control Programme allows ware to be grown in land which has been tested and found to be infested with PCN. The intention of a control programme is to reduce the population of PCN in the field. Control programmes are currently set by area offices and are advised by the AHDB PCN calculator. Growers who are renting land currently have little incentive to grow resistant varieties as they can opt for a longer rotation instead, by which time they have given the land back to the owner and is no longer their concern. We need to do more to encourage the use of resistant varieties in control programmes where possible. Also, longer rotations will only work effectively in the control of PCN where groundkeeper control is achieved. In the Netherlands crops are monitored for the presence of groundkeepers and restrictions are placed on the land where too many ground keepers are recorded.

Widespread cultivation of varieties with moderate or high levels of resistance to *G. pallida* that are suitable for the table and salad sectors is required to control *G. pallida*. Growers have said that “free” resistant varieties would be greatly beneficial as currently all *G. pallida* resistant varieties can only be grown under contract. Breeders should prioritise the development of *G. pallida* resistant varieties suitable for Scottish conditions. There is an urgent need to develop reliable markers for PCN resistance to allow rapid selection of breeding material. The industry should work closely with end markets such as processors and supermarkets to increase the demand for resistant varieties, enabling the growers to produce them profitably.

Work should be undertaken to develop novel control methods for PCN suitable to the Scottish climate. Biofumigants and trap crops are generally unsuitable for the Scottish conditions as there is not enough of a growing season to allow them to be used either before or after a main crop. Trap crops currently available are tropical species and not well adapted to cooler conditions, and in order for a trap crop to be viable it would be beneficial if they could be grown as a crop in their own right. Other potential options to control PCN include bacteria, fungi, potential predators and the use of chemicals from potato root diffusates to induce hatching. As many of the available options to control PCN are not suitable for Scottish conditions, work should be undertaken to establish alternative controls that would be suitable.

From interviews with growers it became clear that knowledge about PCN, how it multiplies, how it is spread and how to control it is limited. This is particularly true for ware growers who currently see little economic impact from PCN, as well as for landowners who rent out land to potato growers. It is important that all involved in the potato industry are aware of the impact PCN could have on the long-term sustainability of potato production in Scotland. Some growers wanted PCN test results to be more widely available, particularly where they are renting land, to know if fields or farms are infested, to have more idea where risks are and to aid with biosecurity. Many growers in the north were concerned about large ware growers moving into this area from infested areas, and a code of practice and biosecurity advice for ware growers may therefore help to alleviate some of these worries.

2 Introduction

2.1 PCN populations now and where we are heading

SASA estimates that the total area infested with PCN in Scotland is now over 13% of the area regularly planted with potatoes. Seed potatoes cannot be grown on land recorded as infested and ware potatoes can only be produced under an officially approved control programme. In recent years the incidence of *Globodera pallida* has increased markedly. Statutory testing data collected by SASA shows that the area of land recorded as infested with *G. pallida*, currently 6,200 ha, is doubling every 7–8 years, whilst the area of land infested with *G. rostochiensis* is relatively static at c. 14,500 ha. In the 1970s, findings of G. pallida represented 2–3% of all PCN findings, whereas now they account for nearly 70%. At the current rate of increase, the widespread presence of *G. pallida* may prohibit the production of seed potatoes on PCN-free land in as little as 30 years' time.

2.2 G. pallida *in Angus*

To determine how *G. pallida* has changed in the past 10 years in the most infested county in Scotland, Strathclyde University scientists used anonymised extracts from the Scottish Seed Potato Classification Database and data from SASA's Seed Potato Users Database (SPUDS) to estimate the infestation by *G. pallida* throughout Angus parishes. To visualise the spread of PCN from 2010 to 2018, an interactive map was created in R package Shiny (Fig 1). The size of the plotted circles represents the area in each parish that was tested for PCN; the colour of the circles represents the number of samples testing positive for *G. pallida* within each parish; darker circles represent parishes with a greater number of positive samples; white circles represent those with no *G. pallida* found in tested samples in a given year.

a. **b.** **c.**

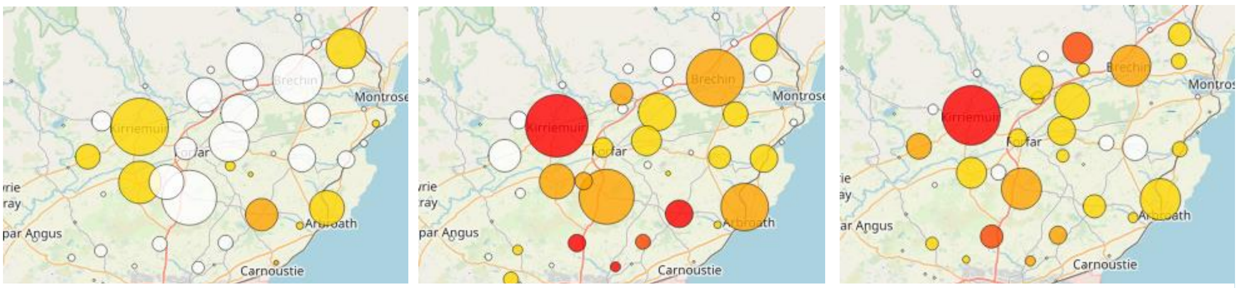


Figure 1: A map of Angus with visualisation of G. pallida positive testing. Size of circle corresponds to the area of land tested in a given year whereas colour represents the proportion of area that tested positive (white: no infestation, yellow=low infestation, red=high infestation (a.2010, b.2014, c.2018)

In 2010, most parishes in Angus had little or no land infested with *G. pallida* with the average area of infested land per parish being 1.43 hectares. By 2014, the area infested with *G. pallida* rose rapidly and the average area over the parishes reached 6.45 hectares. The pest has also spread substantially, with the number of infested parishes in Angus almost doubling over a four-year period. *G. pallida* and *G. rostochiensis* infestations in Angus were compared for the period of 1975-2018 using positive and negative testing results. The area testing positive for *G. pallida* in each year was low from 1976 onwards and began to slowly increase between 2005 and 2010. This area then rose rapidly from 128 hectares in 2010 to 432 hectares in 2012. In contrast, *G. rostochiensis* was recorded from approximately 800 hectares p.a. in 1970s, but this incidence has gradually declined and is now less than the area infested with *G. pallida* (Fig 2).

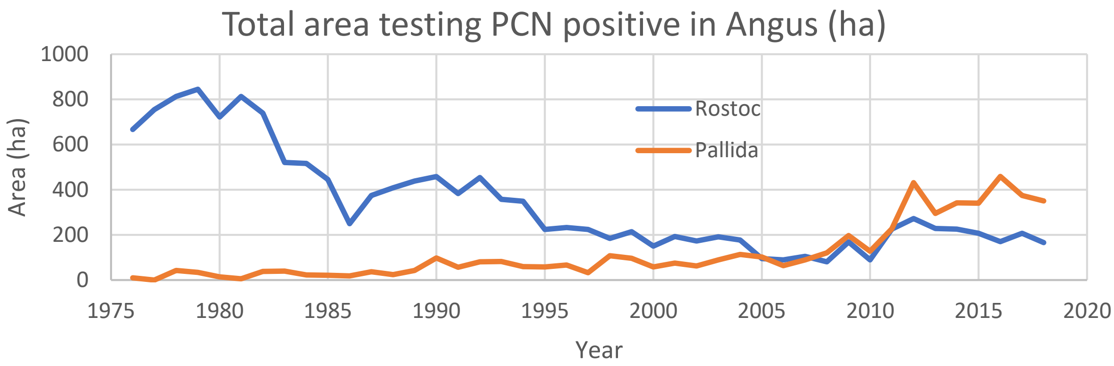


Figure 2: Total area testing positive for G. rostochiensis (Rostoc) and G. pallida (Pallida) between 1976 and 2018 in Angus

SASA data for the period 1995 to 2018 were used to estimate the parameters for a model to describe the rate at which infestation with *G. pallida* has been expanding in recent years. The exponential model captured the data well and predicted that the area testing positive each year doubles approximately every 7 years. This result was used to describe the actual cumulative acreage testing positive with *G. pallida* by treating the data shown in Figures 2 and 3 as yearly increments and calculating the sum up to a given year. This assumption ignores the process of de-recording by which land is returned to the infestation-free status. Thus, the results will provide a "worst-case" scenario.

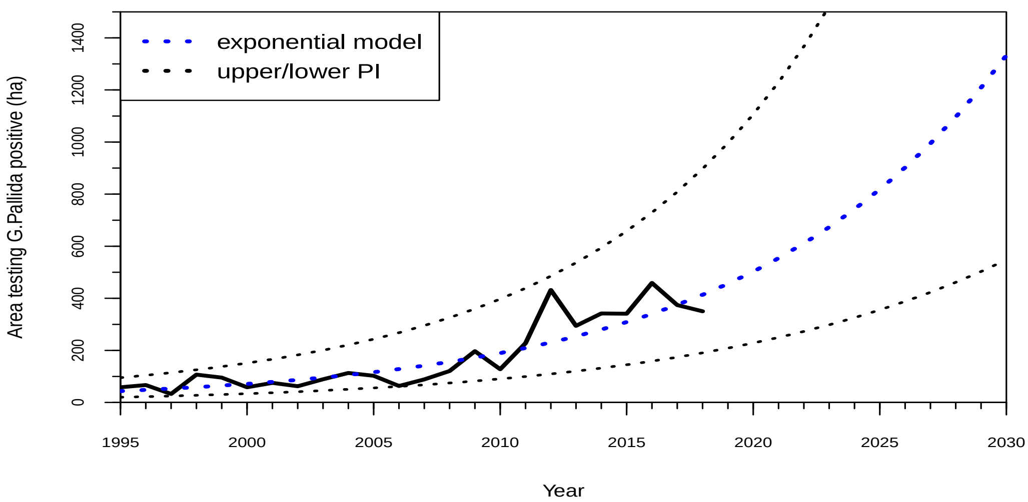


Figure 3: Increase in the area testing positive for G. pallida (solid line) compared with the model prediction (blue dotted line) and the upper and lower predictive 95% confidence intervals.

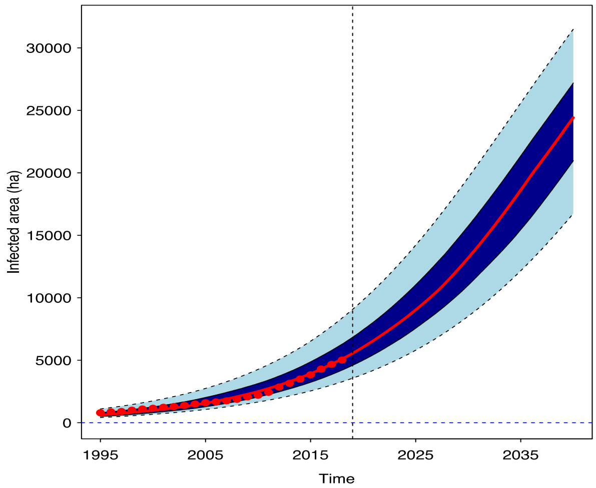


Figure 4: The cumulative area testing positive with G. pallida over time. Data (running sum of data in figure 3) are represented by points and the model outcome by red line (median), and 50% (dark blue) and 95% (light blue) confidence intervals. The prediction assumes continuing exponential growth. The code used in simulations was adapted from the model developed in the PHC project PHC2018_14

There is a good agreement between the model output and the data (Figure 4) so the model can be used to predict the levels of *G. pallida* infestation under the assumption that the current approach continues. We predict that by 2050 a large proportion of the land in Angus will be unsuitable for growing seed potatoes (the prediction is 25,000 ha of a total county area of 228,000 ha). This infestation will also limit the production of ware potatoes through loss of yield. The loss of Angus as a seed producing area threatens the overall output of Scottish seed potatoes; Angus supports 33% of the Scottish potato production area and 32% of the seed production area (SASA SPUDS data for 2010-19). This prediction currently does not consider the effect of long rotation (absence of host) or the cultivation of resistant varieties. In order to estimate the economic impact, we assumed that ware potatoes are grown in a field that has tested positively but no seed, and so the loss is a difference in price between seed and ware potatoes. Under average field conditions we estimate a yield of 45t/ha for both seed and ware potatoes. With an average price of £175/t for maincrop and £300/t for seed potatoes we arrive at the loss of ca £5000/ha (J. Nix Farm Management Handbook, 2017). Multiplying the loss by the acreage infested, yields around £25m cumulative loss in 2019 (5,000ha multiplied by £5,000 per ha loss) rising to £125m cumulative loss by 2040. This figure represents the opportunity loss not the actual loss, i.e. the value of potatoes that could have been grown had the land not been infested by *G. pallida*. Full treatment of the estimation of losses in seed potato production would require an extended model accounting for de-recording of land, as well as for the production moving to less suitable soils while the better land becomes infested with high levels of *G. pallida*.

3 Mapping PCN spread in Scotland

The spread of both *G. pallida* and *G. rostochiensis* in Scotland was mapped by BioSS scientists using the SPUDS database collected and held by SASA. Recordings of all PCN tests carried out by SASA from 1988 to 2019 were used to create a list of all fields tested for PCN over that time period. Rather than simply looking at the test results in each year, an attempt was made to accumulate information on which seed potato fields were infested over time. However, it was not possible to account fully for sub-divisions of fields.

All fields were assumed to be uninfested at the beginning of 1988 because full records of all tests were not available before that time. This assumption means that the maps produced are likely to underestimate the levels of infestation, particularly for *G. rostochiensis* for which there were more recordings before 1988 compared to *G. pallida*. However, the patterns of increase through time should remain informative. The infestation status of each field was sequentially updated each year according to the presence of positive or negative tests for that field in that year. If multiple samples were taken from a given field, then a single positive result was considered sufficient to record the field as infested. Fields not tested in a given year maintained the same status as the previous year. Data was then aggregated at a parish level and the proportion of infested fields in each parish was calculated. Any parishes for which fewer than 5 fields were tested over the full time period were excluded to prevent misleadingly high proportions based on isolated fields. Animations (available alongside this report) were produced showing that *G. pallida* infestations have spread quickly from initially low levels, whilst the proportion of fields infested with *G. rostochiensis* has increased more slowly over this time period.

4 Control options for PCN

Eradication of PCN is not considered an option except in areas where a localised infestation is detected, and measures have been taken to both eliminate the nematode and prevent its spread. In most of NW Europe, including the UK, PCN are widespread and there are reports of them surviving for as long as 40 years and to depths of 80cm (Been and Schomaker, 2013). Therefore, management to reduce the population, prevent spread and preserve yield should be undertaken by growers where possible.

4.1 Sampling

While it is a statutory requirement to test land intended for seed production for the presence of PCN, understanding the nature of infestations within fields is necessary for effective management of PCN. The primary purpose of soil testing should be detection, then once PCN are found, the species and distribution within the field should be estimated to develop an appropriate management programme. Quantification of the infestation will allow for a better understanding of the scale of the problem and help to determine the most appropriate management options. This will also allow the success of management options to be assessed. In the Netherlands it is common practice to test either 8 or 13l of soil per ha to have a greater understanding of where PCN infestations occur within a field. In contrast, in Scotland most land is tested at 400ml of soil per ha for statutory purposes only.

4.2 Use of certified seed

Restricting the production of certified seed potatoes to land that has been tested and found free from PCN helps prevent initial and further introductions of PCN into fields and is a fundamental principle underpinning the EU PCN Directive 2007/33/EC.

4.3 Control programmes

Directive 2007/33/EC prohibited seed potato production on land in which PCN are known to be present, is. However, the Directive recognizes the importance of resistant varieties in controlling PCN and the need for ware potato production on infested land, permitting this as part of an officially approved control programme aimed “at least at the suppression of” the population of PCN. In Scotland control programmes are evaluated using the AHDB PCN calculator for *G. pallida* https://potatoes.ahdb.org.uk/online-toolbox/pcn-calculator. The calculator estimates outcomes dependant on nematicide use, varietal choice and rotation length. Where *G. rostochiensis* is found, there are a wide range of commercial varieties with resistance to this species. However, there are few varieties with high levels of *G. pallida* resistance that are suitable for Scottish conditions. In the Netherlands, there are strong incentives to produce resistant ware (resistance score of 7-9) on infested land, thereby reducing the period for which seed production is prohibited from 6 to 3 years.

4.4 Varietal tolerance

The damage caused to the plant will also limit the commercial yield from the crop. Some varieties that are highly tolerant of PCN damage, e.g. Cara, can produce vigorous growth, maintaining yield at moderately high PCN populations. Such tolerant varieties also allow PCN to develop to exceptionally high population levels. The PCN population is eventually self-limiting on all varieties; if the density is high enough the host plant will die (Been & Schomaker 2006). Tolerant varieties can withstand much higher PCN population levels than intolerant cultivars. Tolerance and resistance are not related traits and they are not genetically linked.

Figure 5: AHDB SPOT farm West where land has heavy infestation of G. pallida: left panel variety Royal - highly tolerant; right panel variety Innovator - very intolerant.

4.5 Decline rates, rotation length and groundkeepers

Several studies of decline rates for PCN have been published but these have mostly concentrated on *G. rostochiensis* (Oostenbrink, 1950; Whitehead and Turner, 1998; Trudgill *et al.*, 2014). Long rotations are often used as a tool for managing PCN, taking advantage of attrition though the natural hatch and mortality of c. 20-30% of the population that occurs each year in the absence of a host plant. This decline can vary with differences in soil composition, soil type and other environmental factors, including aeration and moisture, and is therefore difficult to predict (Devine *et al.* 1999, Cole and Howard, 1962). *G. pallida* is generally thought to decline slower than *G. rostochiensis*. Taking advantage of decline rates enables rotation length to be used as a tool in the management of PCN. This is, however, dependent on removing or killing any groundkeepers as these will act as reservoirs for the nematodes, with populations increasing on susceptible varieties and potentially selecting for resistance breaking populations on resistant ones.

4.6 Nematicides

Nematicides are usually applied at planting to control the juveniles emerging from cysts in response to exudates from the roots of the growing potato crop. There are currently three granular nematicides available for use in the UK. Treatments can prevent early damage to root systems of the plants and help to achieve an economically viable yield. Nematicides reduce the initial population invading the plant roots but any successful nematodes will still undergo multiplication on susceptible hosts. Minnis *et al.* (2004) showed significant ware yield increases from 22 to 35 t/ha with granular nematicide. However, Trudgill *et al.* (2014) found that nematicides did not increase yield potential but it was noted that this was very site dependent. Fumigant nematicides are not used in Scotland.

4.7 Biofumigants

'Biofumigation' is a term used to describe the suppression of soil borne pests, using natural biocidal compounds (principally isothiocyanates). These are released in soils when glucosinolates in plant residues (predominantly brassicas) are hydrolysed. To provide the greatest benefit, crops used for biofumigation generally must be planted throughout the summer growing season for a period of approximately 12 weeks then macerated and incorporated immediately into the soil (Ngala *et al*., 2014). Along with nematicidal effects, some of the chemicals produced can inhibit hatching. The performance of biofumigation depends on which type of crop is used and a range of environmental and agronomic factors.

4.8 Trap Crops

Trap crops come in two forms, firstly a potato crop, which must be killed after only 40 days of plant growth. This has been used in the Netherlands where high infestations occur but requires the sacrifice of a potential crop. The nematodes are captured and killed within the plant prior to maturation and thus is dependent on a highly efficient plant destruction. The second method of using a trap crop is to use a crop which is related to *Solanum tuberosum* that does not allow PCN to complete its lifecycle. There have been several candidate crops studied for this and *Solanum sisymbriifolium* (sticky nightshade) shows the most potential to date (Dandurand *et al*. 2014). In such circumstances root exudates cause the eggs to hatch and whilst the juveniles attempt to invade and feed on the host, they cannot produce mature females or cysts. Despite their potential, trap crops are not widely practicable for use in Scotland as they do not establish well in the climate.

4.9 Biosecurity and knowledge

Where land is free from PCN, it is critically important to keep it that way. Cysts are sedentary and cannot move by themselves. Other than via the planting of infested seed, the most likely way for them to spread is through the movement of soil. The most effective way to prevent such spread requires thorough biosecurity. This includes ensuring soil is not moved with any farm machinery, on tyres and the soles of shoes, with all planting material, and by domestic and wild animals. A key factor in the management of PCN populations is an understanding of the biology of PCN: how they undergo their life cycle, how they are spread and how likely detection is at the county, local, farm and field levels. Understanding what the results from laboratories mean and what growers can do to prevent the spread of PCN around the farm is crucial.

4.10 Resistant varieties

Resistance is probably the most effective management tool available to control PCN. Highly resistant varieties can reduce multiplication to 1% of susceptible varieties. Resistance to PCN is scored on a 1-9 scale, with the ability to limit PCN reproduction to half of that of a variety scoring one unit less:

Table 1: Reproduction rate of PCN relative to a susceptible variety (score 2)

Resistance Score	2	3	4	5	6	7	8	9
PCN Reproduction	100%	50%	25%	12.5%	6.3%	3.1%	1.6%	0.8%

Using a scenario of an intolerant variety grown on light silt, the AHDB calculator can be used to show the rotation period between crops that is required to prevent an overall population increase following the cultivation of a crop of potatoes over the range of resistance scores. A susceptible variety (score 2) would require a 13-year rotation period, compared to 5 years for a variety of score 5 and 1 year with scores of 7 or more. If the use of a granular nematicide with an effectiveness of 70% or 50% is factored in, rotations can be reduced further. For susceptible varieties, nematicides have relatively minimal effect in managing PCN, although they are can be effective in reducing the loss of yield. Using nematicides with moderately resistant varieties (scores 4-6) has beneficial effects in controlling PCN and reducing rotation periods to less than the rotation periods that are typical for ware potato production in Scotland.

Table 2: Rotation periods required with and without nematicide treatment to prevent population increase (AHDB PCN Calculator)

Light Silt	Intolerant		20% Decline Rate					
Resistance Score	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
No Treatment	13	10	7	5	2	1	1	1
Nematicide - 70% control	11	7	4	2	1	1	1	1
Nematicide - 50% control	12	8	5	4	1	1	1	1

Using a process-based model of PCN population dynamics developed at BioSS (see Appendix), the effect of planting potatoes with a range of resistance ratings on a six-year rotation over a 30-year period is shown in Figure 6. This assumes a low initial egg density (0.1 eggs/g) and a fixed temperature typical of a Scottish field during the growing season (14°C) (Kaczmarek, Back, and Blok, 2019). For non-resistant varieties, the AHDB model predicts that rapid increases in *G. pallida* density will be observed over the first two rotations, with infestations plateauing in the range of approximately 40-100 eggs/g from the third rotation onwards. The variation in population size from the third growing season onwards (Figure 6 purple line) stems from the density-dependent processes in the model, which cause the population to fluctuate around a carrying capacity dependent on the initial egg density in each growing season. To reduce *G. pallida* population sizes with potatoes planted on a six-year rotation, a resistance of at least 6 is required if varieties of the same resistance are planted year-on-year. However, it is possible that similar or better results could be achieved by alternating between higher and lower resistance levels.

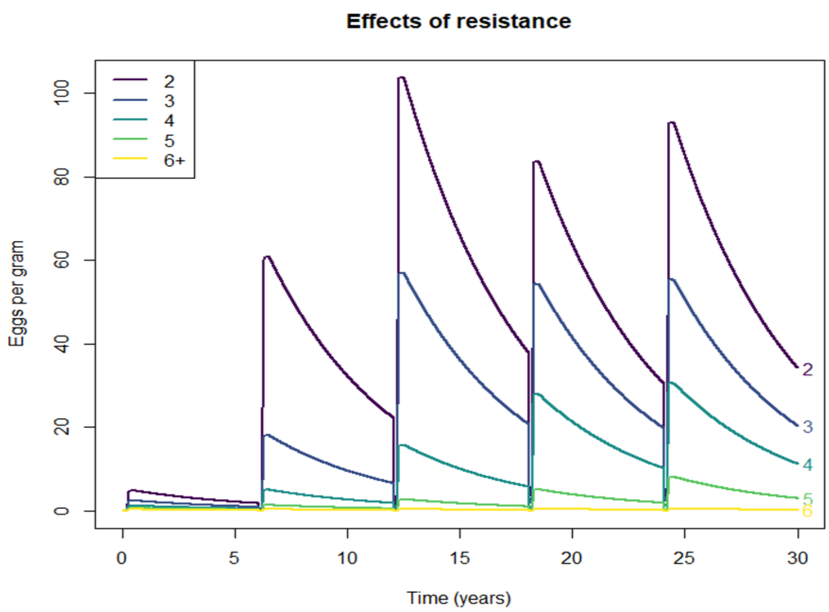


Figure 6: Predictions from a process-based model for the predicted density of G. pallida in eggs per gram for resistance ratings 2-9 (shown in the legend and on the right of the plot). The lines for resistance ratings 6 and higher are indistinguishable as the population is controlled in these cases. The drops in egg densities observed between rotations are due to the population dynamics during the growing season.

The first UK variety with resistance to PCN, Maris Piper, was released in 1966 (Norbet *et al.*, 2006). Maris Piper was been remarkably successful and is the most widely grown variety in the UK. Resistance to *G. rostochiensis* has not been observed to have been broken in the UK despite the reliance on the H1 resistance gene for decades. However, Maris Piper is fully susceptible to *G. pallida* and thus its widespread cultivation, and the use of other varieties with H1 resistance, has inadvertently led to the spread of *G. pallida* and resulted in it becoming the predominant species in the UK (Minnis *et al.*, 2002).

Figure 7: Resistance scores to G. rostochiensis of varieties grown in Scotland for seed and ware in 2019

In Scotland in 2019, varieties highly resistant to *G. rostochiensis* (resistance scores of 7-9) were grown in 50% of the area cultivated for seed potatoes and on 57% of the area used to grow ware. Susceptible varieties (resistance score = 2) were grown on 45% of seed land and 30% of ware land. The overall Scottish seed crop has an average resistance score of 5.6 to *G. rostochiensis*, whereas the ware crop has a similar average of 6.3.

Figure 8: Resistance scores to G. pallida of varieties grown in Scotland for seed and ware in 2019

Varieties highly resistant to *G. pallida* (resistance scores of 7-9) were cultivated on 5% of the area used for seed potatoes but only on 0.4% of the area used to grow ware. Varieties susceptible to *G. pallida* (resistance score = 2) were grown on 86% of both seed and ware land. The overall Scottish seed crop has an average resistance score of 2.5 to *G. pallida*, whereas the ware crop has a lower average of 2.2.

SASA recorded *G. pallida* in statutory soil tests drawn from 5352 ha between 2010-19. Whilst the cultivation of potatoes for seed is prohibited in infested land, parcels within the same field that have tested clear of PCN can be used to grow seed; and ware can be grown under a control programme on the infested parcels. Since these findings, 1485 crops of seed or ware were planted in fields with *G. pallida*. 74% of these crops were of varieties with no resistance to *G. pallida*, in comparison to an across Scotland average of 84% of susceptible potato production. This suggests that, following receipt of a positive PCN test from SASA, growers are only influenced in their choice of variety by its resistance to this species of PCN in an estimated 10% of cases. As the availability of varieties with resistance to *G. pallida* for commercial production in Scotland is limited, this result is not surprising.

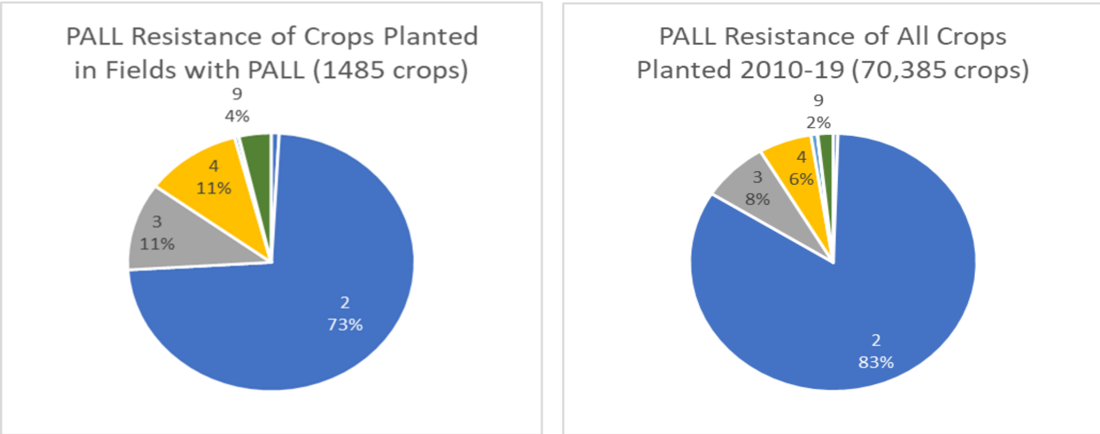


Figure 9: Resistance scores to G. pallida (PALL) of varieties grown in infested land compared to all crops

A similar situation was observed for *G. rostochiensis*, even though commercially successful varieties are widely available for most market uses. SASA recorded *G. rostochiensis* in statutory soil tests drawn from 4172 ha between 2010-19. Since these findings, 1364 crops were planted in fields with *G. rostochiensis*; 33% of these crops were of varieties with no resistance to *G. rostochiensis*, in comparison to an across Scotland average of 43% of susceptible potato production. This again suggests that, following receipt of a positive PCN test from SASA, growers are only influenced in their choice of variety by its resistance to this species of PCN only in an estimated 10% of cases. As varieties with resistance to *G. rostochiensis* are widely available for commercial production in Scotland, this suggests management of PCN is not being adequately addressed.

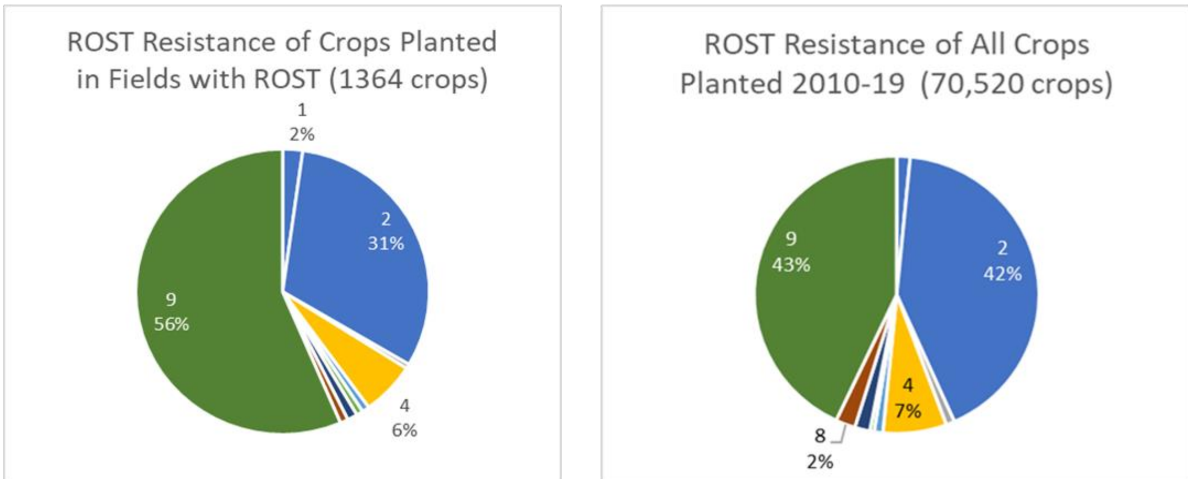


Figure 10: Resistance scores to G. rostochiensis (ROST) –of varieties grown in infested land compared to all crops

Success with breeding for resistance to *G. pallida* has lagged behind that for *G. rostochiensis*. This is partly because the two main sources of resistance used against *G. pallida* have been less amenable for breeding. Unfavourable agronomic qualities and the polygenic nature of the resistance (Gebhardt, 2013) has complicated the breeding process. However, recently varieties with resistance from both sources have been produced and these now also provide parental material for the breeder to develop further varieties.

Resistance to PCN, particularly for *G. pallida* is a high priority in potato breeding programs in Scotland. Work to combine resistance to PCN and Spraing has been prioritised due to the threat of nematicide withdrawals. Advanced lines suited for the table sector are expected to progress to National List testing in the next couple of years. There is also potential for using moderately resistant varieties in a control program to suppress multiplication of *G. pallida* when used with nematicides (Table 2).

The efficiency of breeding programs can be improved with the use of molecular markers to facilitate marker assisted selection of the progeny of crosses with resistant parents. This would replace or complement time-consuming phenotypic selection of resistant progeny. To achieve high levels of resistance to *G. pallida* that are durable (i.e. not overcome due to the reliance of a single resistance source) an approach being used by breeders is to combine, or pyramid, more than one resistance source. Used in conjunction with marker assisted selection, this is now feasible within breeding programs (See appendix for resistant varieties used in breeding programmes).

A potential complication with breeding for *G. pallida* resistance is that in the UK field populations of *G. pallida* are genetically more complex than those of *G. rostochiensis*, and thus resistance may be broken more readily. In the Netherlands, which typically has shorter rotations (3-4 years) than in the UK, breakdown of *G. pallida* resistance has been observed in starch production areas where varieties such as Innovator, have been grown for several crop cycles (Niere *et al.*, 2014). In Scotland, efficient ground-keeper control is needed so that reservoirs of PCN don't result in resistance breaking down and negate the benefits of longer rotations.

One theme that emerges from this study is that the results of SASA's PCN testing service does not influence the varieties planted in infested land. Lack of appropriate knowledge/advice on the best course of action and, secondly, a lack of choice when it comes to selecting resistant varieties are the main limiting factors. The ware sector has not embraced varieties with resistance to *G. pallida*, with the exceptions of a few varieties with low levels of resistance – average resistance of the Scottish ware crop to *G. pallida* is 2.2 compared to 6.3 for *G. rostochiensis*. The ware survey carried out to satisfy EU PCN Directive requirements indicates that the incidence of *G. pallida* in Scottish ware land is 30% compared to 11% for *G. rostochiensis* and highlights the urgency of improving the control of *G. pallida* to protect seed land

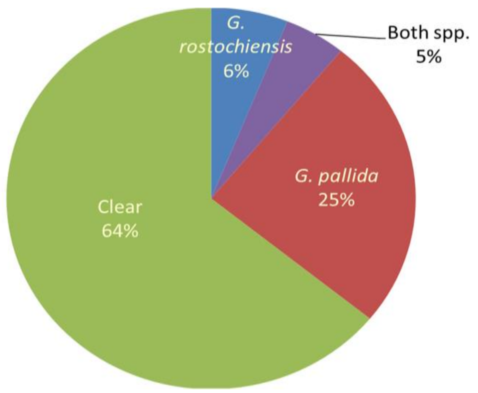


Figure 11: Results from the ware survey of 0.5% of crops grown 2010-2019

The optimal solution would be a market led drive to growing a much higher percentage of commercially successful varieties with high levels of resistance to *G. pallida* as has happened with varieties with high levels of resistance to *G. rostochiensis*, e.g. market leading varieties such as Maris Piper and Cultra. However, they need to be suitable for the Scottish climate.

4.11 Tolerant varieties

An important characteristic of a variety is tolerance to damage caused by PCN. Tolerance can be defined as the ability of the plant to withstand or recover from damage and produce a yield, whereas resistance is defined by the ability of the plant to prevent or restrict the multiplication of the nematode.

A variety is more tolerant to PCN if it's yield at a specified PCN population level is reduced by less than that of a comparable variety. One approach that has been used is to compare the yield of a variety when grown in infested plots treated with and without nematicides. In this case the yields of less tolerant varieties are reduced by a greater amount in untreated plots. Tolerance is difficult to measure as yield is influenced by a range of environmental factors, including soil type (particularly the ability of the soil to hold water) and nutrient availability. Yield loss can be minimised by irrigation and fertiliser application. Yield loss is also highly dependent upon nematode population density, and all varieties will become intolerant at high population densities. In general, the more vigorous and late maturing varieties with strong top growth are more tolerant because they can compensate for early season damage caused by nematode attack. The variety Innovator is highly resistant to and intolerant of G. pallida, so can suffer marked yield losses at low population levels. In contrast, the variety Cara has no resistance to G. pallida but is highly tolerant. Growing Innovator in land infested with G. pallida reduces the PCN population in the field for subsequent crops, but the grower is likely to suffer an economic loss in terms of yield. Growing Cara in a similar field would markedly increase the PCN population in the field for subsequent crops, but the grower is less likely to suffer a loss of yield on that year's crop. The economic impact is more likely to be experienced when the subsequent crop is planted in land with a much higher PCN population.

Because tolerance is so difficult to quantify, variety databases do not provide assessments of tolerance. Intolerant resistant varieties are sometimes discounted for PCN control, but they can be very effective in suppressing emerging infestations. In contrast, tolerant susceptible varieties can be responsible for storing up big PCN populations for future potato production.

5 The potential impact of climate change on PCN

To understand the effects of potential temperature increases on *G. pallida* population dynamics, the process-based BioSS model was run for potatoes with resistance scores of 2 (Figure 11 (a)) and 5 (Figure 11 (b)) over a range of temperatures and assuming planting on a six year rotation. Intra-annual and inter-annual temperature variations were not considered because there was no evidence of a strong seasonal pattern in soil temperatures across a growing season from the available data (Kaczmarek *et al.*, 2019). Figure 12 shows that increased temperatures are predicted to increase multiplication rates in *G. pallida*. However, this effect is small compared to the effect of the potato resistance variety. Comparison of Figure 12a with 12b shows that increasing from a resistance rating of 2 to a resistance rating of 5 results in estimated egg density dropping from a range of 60-120 eggs per gram of field soil to a range of 6-12 eggs per gram (note change in scale on y axis between Fig 12a and 12b). For non-resistant potatoes (Figure 12a) the egg density increases rapidly over the first 2-3 rotations before converging towards its carrying capacity, at which point temperature is no longer influential. For moderately resistant potatoes (Figure 12b) egg density increases much more slowly and even after 5 rotations the population has only reached approximately 5-10% of its carrying capacity, dependent on the temperature. Consequently, we see that increased temperature is an important driver of *G. pallida* multiplication rates when the population is below carrying capacity, but the resistance variety of the potatoes planted is much more influential. The planting of even moderately resistant potatoes (resistance rating of 5) in place of non-resistant potatoes is predicted to lead to an approximately ten-fold reduction in eggs per gram of soil over 5 rotations.

In the simulations in Figure 12 we assumed that development of only one generation was possible each season. If higher temperatures allowed two full generations to complete development within a season, then we would expect the carrying capacity to be reached in approximately half the number of growing seasons. However, if higher temperatures resulted in only partial completion of a second generation this may have adverse effects on nematode populations, as cysts may hatch but not complete development by the end of the season. Consequently, further work is required to better understand the potential effects of multiple generations on *G. pallida* dynamics.

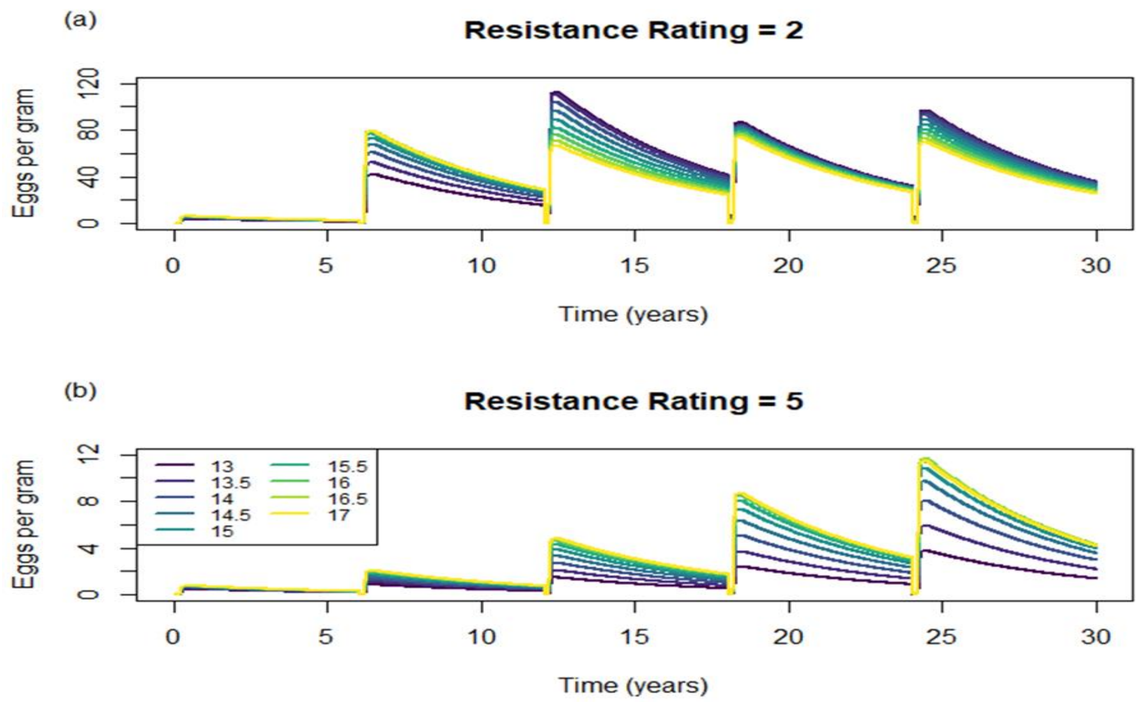


Figure 12: Predictions from a process-based model for the density of G. pallida in eggs per gram of field soil is shown for (a) non-resistant potatoes and (b) potatoes with resistance rating 5, under a range of fixed temperatures from 13 to 17 °C, with potatoes planted on a 6-year rotation.

6 Growers perception and management of PCN

In order to better understand growers' motivations towards PCN, 35 potato growers were surveyed from across all the main potato growing regions in Scotland. In total there are approximately 450 potato growers in Scotland, so this represents ca. 8% of the industry. 27 growers were contacted by telephone and face-to-face interviews arranged with them. Face-to-face interviews were complemented by a shorter paper questionnaire composed of closed-ended questions based on important factors identified during qualitative interviews. This questionnaire was used for data collection at the Potatoes in Practice event (8 August 2019, James Hutton Institute's Balruddery Farm), and 8 additional observations were collected from Scottish growers.

Table 3: Descriptive statistics of surveyed growers

	n	Min	Max	Mean	SD
Area (ha)	26	70	2000	508.3	419.4
Rotation length (years)	24	6	10	7.3	1.5
Number of varieties cultivated	27	1	23	8.5	6.2
	n	%			
Tenure					
Own most or all land	12	35.3			

Rent most or all land	14	41.2
Half owned	7	20.6
Contract grower	1	2.9
Type of production		
Seed only	22	62.9
Ware only	6	17.1
Both seed and ware	7	20.0
Presence of PCN		
G. rostochiensis only	2	6.1
G. pallida only	3	9.1
Both PCN species	13	39.4
Yes, but PCN species unknown	7	21.2
No presence of PCN detected	8	24.2

Note: S.D.: standard deviation; n = number of responses collected

Table 3 shows that the farm sizes of surveyed growers ranged from less than 100 ha to several thousand hectares. In 6 cases the farm produced ware only, in 7 they grew both ware and seed and 22 were dedicated seed growers. Most of the farmers did have PCN on their land, with many with both PCN species, although this may be historic or only in one field. In total 8 farms claimed to never have had any PCN findings. Both growers owning the land they produce on and tenants were represented, with owners seeming to favour seed production over ware.

PCN was the third most cited pest or disease as most damaging for potato crops (Figure 13) and only a minority of growers, mostly tenants, did not perceive PCN as an important threat, which demonstrates a widespread awareness of the issue across potato growers in Scotland. Most of the growers were concerned about the loss of land to PCN. However, this was mostly perceived because of current government restrictions in place, preventing the use of infested land for seed production, and not because of the effects of the PCN infestation on yields.

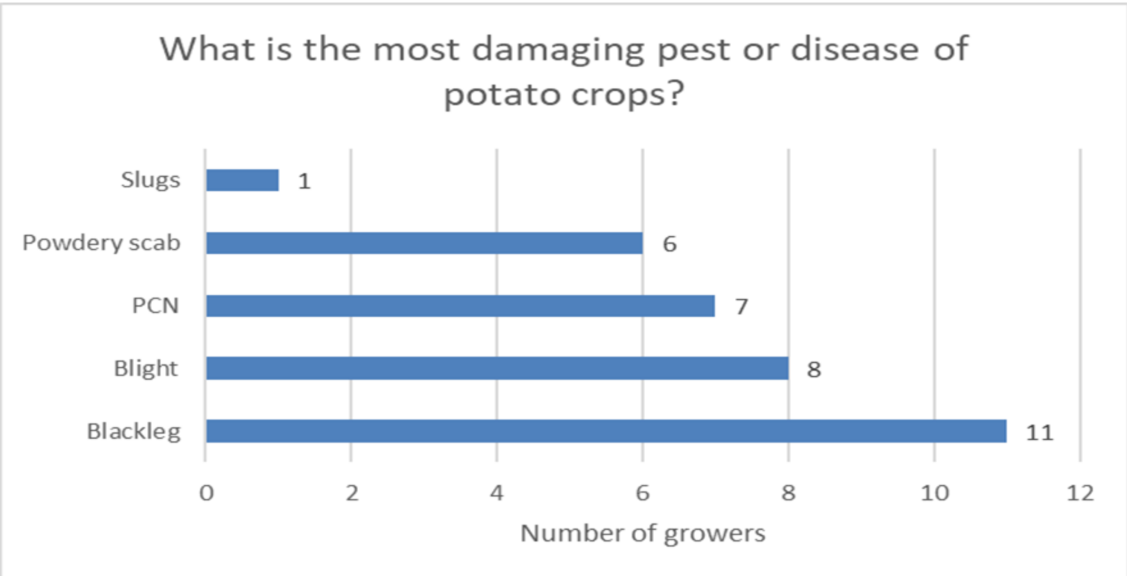


Figure 13: Chart displaying farmers opinions of the most damaging pest or pathogen

Where fields or part of fields are given a “Pass” (i.e. no PCN found in sample) result, often the current belief is that there are no PCN in this part and therefore there is no reason to manage PCN in this land. Detection of PCN is dependent on the quantity of cysts present, the size of the soil sample and the sampling protocol. Therefore, a “Pass” test result at 400ml ha-1 does not necessarily mean that there are no cysts present within that section of a field, as there is only a 50% chance of detection of a population of 3.8 million cysts ha-1 at this level of sampling (calculations based on Shomaker and Been, 1999). This appears to be an important knowledge gap for growers and where increased education is required.

On the other hand, when perceiving a risk of or identifying PCN infestation in their fields, some farmers (7 out of 33), have taken the decision to focus on ware production only, as the value of ware is potentially similar to, or greater than, the value of seed but isn't subject to the same regulation. While growing ware, growers are not required to have land tested for PCN, allowing PCN populations to grow unchecked, which could lead to losing the land for seed production indefinitely. The land tenure arrangements also contribute to push growers towards ware production, following a similar test-avoidance strategy. When renting land, landowners may preferentially rent to ware growers because there is less risk that a positive PCN test will affect the rental agreement. Ware growers are also often willing to pay more to rent land. As the Scottish climate is not conducive to achieving the dry matter content required of processing varieties, table varieties dominate the ware market and the demand for this sector is decreasing, so a shift to ware could be detrimental to the longevity of the potato industry in Scotland. The increased PCN presence and consequential switch to ware production pushes seed producers to move further afield looking for land to rent, leading to an increased biosecurity risk as machinery is moved into previously clean areas. In the north of the country there was a strong feeling that ware growers should also be testing for and acting on PCN findings.

In conclusion, current perceptions of the consequences of PCN in Scotland could be counterproductive in the management of PCN, focussing on the immediate consequences of PCN presence, i.e. the legal inability to grow seed potatoes, rather than the longer-term consequences of PCN on future potato yields, which could impact both seed and ware production. This misperception is a barrier to a pro-active management of PCN by growers. However, as described in the next paragraph, growers' management strategy is highly constrained by external forces.

Growers' management of PCN is constrained by external forces from the food chain. The most effective tool available to manage PCN infestations is to use resistant varieties of potato. These have been highly effective at restricting *G. rostochiensis* and are an integral part of any control programme. Varieties resistant to *G. pallida* only account for 3% of land grown in Scotland. Two thirds of the farmers we spoke to knew whether the varieties they were growing were resistant to PCN. However, only a couple of the growers actively sought out and used resistant varieties in rotation on their farm to control populations and alternated these with susceptible varieties. For most growers, the most important factor in a potato variety is marketability. Many growers are tied into contracts with potato marketing companies as this allows for a guaranteed income. Potato marketers/producers usually know who they can sell their products to, or they produce their own to meet market demands. The demand for varieties is therefore driven by the end processor or seller e.g. the supermarkets, crisp companies, frozen food manufacturers or fast food restaurants. They have certain requirements for their products, e.g. skin finish, fry colour. To have any influence over which varieties are being grown in the field the end market needs to be targeted and producers rather than the growers. This leaves the management of PCN using resistant varieties very challenging. A large majority of growers (26 out of 33) would be willing to use resistant varieties if available and marketable. For *G. rostochiensis*, approximately half of the crop grown in Scotland has a high level of resistance, although currently it is still not being used to maximum benefit (see page 11). Almost all potato varieties available with high levels of resistance to *G. pallida* are processing varieties, and for this reason very few varieties can be used for ware production in Scotland. Of the handful of varieties that have resistance to *G. pallida* and that are suitable for the table market the uptake of these is currently low.

This lack of control over the choice of variety pushes growers towards other management strategies. However, it should be noted that most growers would not plant potatoes in land where there is a finding of PCN (17 out of 33 who responded to this question) and would test again after another rotation. Given the rate of spread of PCN, good practices have been identified through the survey with growers. Most growers believed that increasing the length of rotation or using resistant varieties were the most effective tools available to manage PCN. Current rotation length amongst surveyed growers varied between 1 (year) in 6 (years) to 1 in 8 rotations, although in areas where higher grade seed was grown some farms grew 1 in 10. While rotations can be an effective tool in managing PCN, a few of the wheat fields we observed while passing had a large potato component from groundkeepers. There appears to be an issue with rented land where the landowner is not concerned about potatoes in the crop and ploughs them into the ground when the land is returned to them. Added to this, many farmers used to leave potatoes on the surface of the ground for the frost to kill them in the winter, although the winters now are a lot milder and so the tubers are not being killed off in the same manner. Unless groundkeepers are controlled, long rotations are broadly meaningless. Groundkeeper control is particularly important where resistant varieties are used. Resistance breaking *G. pallida* populations are already being discovered in continental Europe (Niere, 2014) and repeatedly challenging nematodes with the same resistance allows for the selection of resistance breaking populations.

We discussed the use of cover crops, or potentially biofumigants and trap crops, however the way that crop rotation in Scotland works doesn't easily allow for this. Potato crops are often harvested in September or October and the crop that immediately follows this tends to be winter wheat, which is sown immediately after the potato crop is harvested. The rotation does not have a gap in which to plant nematicidal crops such as mustards and those that are planted will not have time to establish. *Solanum sisymbriifolium* does not establish well enough in Scotland to work as a trap crop or certainly not where there would be a gap in cultivation to allow it to work as a trap crop as it really needs a warmer climate. Very few farmers would be willing to lose a summer cash crop to replace it with a biofumigant unless subsidies were provided to do this.

To reduce the spread of PCN, most growers thought that the most important factor was good hygiene and biosecurity, which included not sharing machinery. Most of the growers we spoke to use their own machinery but the ones who used contractors were concerned about the levels of cleanliness. They did tell us that although it would be preferable to clean machinery between fields this is not always practical.

In general, nematicides are not widely used in Scotland to control PCN and none of the famers we interviewed used them as they didn't have a problem producing yields. This may change in the future and with nematicides constantly under scrutiny it is possible that by the time they are needed they will not be available.

Greater communication is required about the risks of PCN and what the current situation is. Farmers who have not have PCN or who have only lost a few fields to PCN don't seem to understand that there is a risk that their land might become or may already be infested. A couple of the farmers that we interviewed knew almost nothing about PCN, and very few were fully aware of the detection thresholds and biology of PCN, including how they multiply and spread and the damage they can cause. Growers were predominantly concerned about whether they could use the land for seed because of PCN but did not always understand the potential yield losses or long-term damage PCN could cause if left unchecked. Those who have PCN on their land seem to think that if they get a negative test following a positive test that the cysts have all gone. There needs to be education about sampling and that where a famer has a patchwork pattern of results there is a low-level infestation across the farm.

7 Summary and conclusions

PCN is a major threat to the sustainability of the potato industry in Scotland. Already, as a result of SASA's statutory pre-crop testing programme, we estimate that more than 13% of the land required to produce potatoes in Scotland (estimated as 150,000 ha over a 6-year rotation) is officially recorded by SASA as infested with PCN. The annual surveys of ware potato land required by the EU PCN Directive (surveying 0.5% of the area used for potato production other than for seed p.a.) indicate that an additional 35% of an estimated 16,000 ha p.a. is infested. The area of land recorded with *G. pallida* is doubling every 7 years in line with an exponential model and now accounts for most findings in statutory testing. Modelling the cost of losses due to PCN indicates a cost of £125 million per annum by the year 2040, and, based on continuing with the control practices in current use, there could be no PCN-free land available for seed production by 2050. Control options for PCN are limited, in part due to the Scottish climate, but also due to cultural practices. Crop rotations are too short to control PCN without access to more resistant varieties and seasons are not warm enough to produce an effective trap crop or biofumigant crop. It would also be beneficial to develop trap crops and biofumigant crops that are suitable for use in Scottish climatic conditions, which preferably will also be able to generate an income. Grower interviews indicate that nematicides are currently rarely used, and they may be under threat in the longer term. Effective control of groundkeepers is lacking, undermining the benefit of rotations. Resistant varieties are the most effective tool in managing PCN populations, although for *G. pallida* most available varieties are only suitable for the processing sector and therefore not grown in Scotland. However, breeders are making progress in developing dual resistant varieties suitable for the table market. To make progress, more tools for managing PCN need to be provided to Scottish growers. Commercially viable varieties with resistance to *G. pallida* need to be available with the necessary incentives to grow them profitably.

8 Recommendations and future work

8.1 Increasing the value of the statistical and economic models

Model validation and extension for the BioSS population model would be beneficial with, ideally, more field data being added to this. We also want to examine more fully the impact of climate change on potential future scenarios, whether beneficial or detrimental. It would be helpful to look at spread of PCN within and between fields and at a national level. Grower behaviour such as rotation length, use of resistant variety and long-distance movement of PCN could provide greater depth to the model, though this may take a lot of work.

For the Strathclyde model, detailed estimation of losses is needed to provide more realistic estimates. Similarly, the estimation of losses in seed potato production would require a modified model that would account for recording and de-recording of land, as well as the production moving to less suitable soils while the better land becomes infested with high levels of *G. pallida*.

8.2 Protecting the seed potato industry in Scotland

The majority of varieties with resistance to *G. pallida* are processing varieties, which in Scotland can generally only be grown as seed. Scotland produces around 70% of Great Britain's seed potatoes and is considered a high-grade region due to its low disease levels. The lack of any requirement to test ware land for PCN allows populations to increase unchecked and will eventually lead to substantial yield losses. Scottish ware production is generally of table varieties and market demand for these varieties is decreasing. Therefore, protecting the seed industry for the long term in the face of a growing PCN threat is of critical importance. In order to encourage active management using resistant varieties on seed land, we propose that two options should be considered to relax the current statutory measures: a) revising PCR thresholds for positive PCN tests; and b) revising the area of land on which seed potato production is prohibited (see below). However, such relaxations would be conditional on the availability and use of resistant varieties.

8.3 Revising the PCR threshold

To meet the requirements of the new PCN Directive, SASA introduced DNA-based PCR to detect PCN in 2010, replacing the previous visual diagnostic method. The positive threshold was set at a CT value of <34, slightly more sensitive than visual examination criteria of a juvenile nematode with a measurable stylet. Therefore, we estimate that positives are reported for recently dead cysts (c 20% of samples previously reported as containing only dead cyst may now be PCR positive). We recommend revision of the CT threshold to bring it in line with visual assessment thus clearing more land for seed production. In addition, to enhance PCN control through encouraging the use of resistant varieties, where PCN DNA has been detected, but at a level below this revised threshold, the pre-2010 "pass resistant variety" result would be reintroduced, limiting seed production to only resistant varieties.

8.4 Revising the area of land on which seed potato production is prohibited

The EU PCN Directive states "The responsible official bodies of the Member State shall define what constitutes a field for the purposes of this Directive in order to ensure that phytosanitary conditions within a field are homogeneous as regards the risk of potato cyst nematodes." At present the Scottish interpretation is covered by SASA's PCN Soil Sampling Guidance available at http://www.sasa.gov.uk/pcn-soil-testing-documents. Currently our sampling units are a minimum of 4ha (see Figure 14 in which several fields with some units that have passed and some failed are evident). Less land could be taken out of seed production following a positive finding of PCN if these divisions were smaller, e.g. in the Netherlands, where fields tend to be smaller, fields are typically sampled in units of 0.33 ha strips and an additional buffer of 0.33 ha either side is taken out of production should PCN be found. Thus, any finding only results in 1 ha being taken out of production. In Scotland, for any units in which only one sample has tested positive for PCN, SASA could permit the re-investigation of these units to more accurately identify the infested area with a view to taking less land out of seed production. We would recommend restriction of seed production on the rest of the sampled unit to highly resistant varieties.

8.5 Permitting seed production on infested land

One proposal that has been received by SASA and voiced at seed industry meetings would be the option to permit the production of seed of highly resistant varieties on land known to be infested with PCN, with a view to marketing that seed for planting only on land known to be infested with the same species. This proposal has the advantage of opening-up the widespread cultivation of highly resistant varieties, particularly those with dual resistance to both species as an effective means of cleaning up infested land and gets around the Scottish problem of finding an end market for ware. The main disadvantages associated with this proposal are the current prohibitions set out in the EU Directive which are largely based on the risk of selecting for virulent populations, particularly of *G. pallida*. Whilst Brexit may provide the option to operate outside the constraints of the EU PCN Directive, there may be implications for export markets should Scotland adopt a practice that would be out with the norm for international seed potato production. The risk of selecting for virulent populations could be reduced by tight regulations to limit transmission with the seed, e.g. freedom from soil and monitoring of 'treated' land. At present we feel that the options proposed above provide alternatives to promote the cultivation of highly resistance varieties in a way in which we can continue to operate within the confines of the Directive.

8.6 Revision of the Scottish Government Control Programme

The SG PCN Control Programme, available at http://www.sasa.gov.uk/pcn-soil-testing-documents states: "*Under the EU PCN legislation, if PCN are found in an official PCN soil test the sampled unit will be recorded as infested. On this sampled unit no seed potatoes may be produced, either for classification or for farm saved seed. Ware potatoes may be grown,* *but only if an officially approved control programme is in place to suppress PCN and minimise the risk of spreading the pest.*"

(NB The "sampled unit" is the field or part-field from which the soil sample was taken for the PCN test. Any control programme proposed by a grower must be submitted to the local SG Area Office for approval. Control options include rotation, resistant varieties, chemical treatment and cultural options such as biofumigation and trap cropping)".

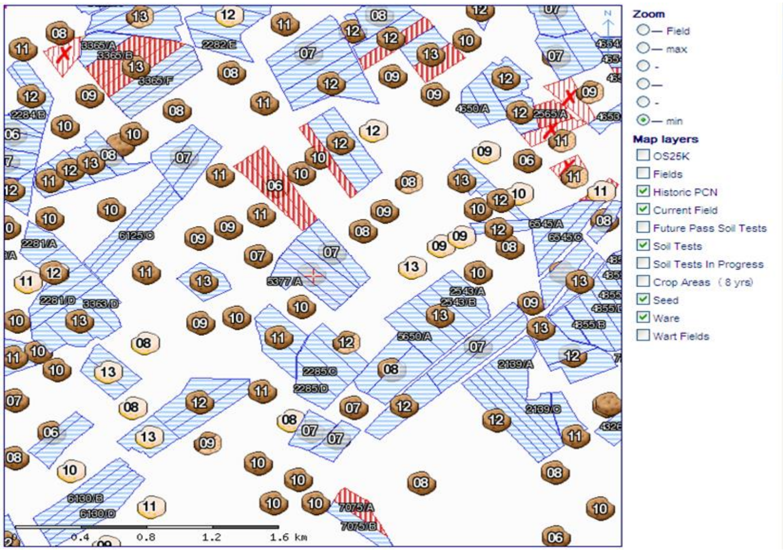


Figure 14: Map on SPUDS showing seed and ware crops and sampling units (failed units in red, passed units in blue)

8.7 Tighter control across field with more than 1 sampled unit

At present a grower can opt to have a field tested in several sampling units, each of which is currently treated as a stand-alone result (Figure 14). This enables the grower to produce seed crops in the clear units and to grow ware under a control programme in the failed unit. Production of a ware crop of a PCN susceptible variety in an infected unit within a field also used for seed production is highly likely to lead to a widespread infestation across the whole field. This practice is increasingly common in rented fields, where a grower is more concerned about maximising the commercial output from the field and less about the long-term PCN health of the whole field and farm, which will be increasingly likely to become contaminated. We recommend prohibiting the granting of a control programme for contaminated units within fields that are being used for seed production unless the ware crop is of a variety highly resistant (score 7-9) to the species of PCN present in the field.

8.8 Prohibiting options that will increase PCN populations in the short-term

Acceptance of any proposed control programme is based on the AHDB PCN calculator and currently permits a grower to plant a susceptible variety and agree to a rotation period of 12 years or more to allow the population to return to previous levels. In doing so, the risk presented by that higher population to neighbouring land and to spread further afield with any common cultivation equipment is increased. This could be increased by setting a maximum period of rotation permitted by any control programme. Prohibiting the granting of a control programme for contaminated units, which requires a rotation period of greater than 6 years for the population to return to its 'current' level, could help to address this problem.

8.9 Rotation length and better groundkeeper control

Some growers have suggested increasing current rotation lengths to manage G. pallida but, compared to other countries, Scotland already uses relatively long rotations. Without groundkeeper control, the effect of rotation in managing PCN is limited. The Dutch have a tolerance for groundkeepers which if exceeded, treats the land as a potato crop and is recorded as such. Better control of groundkeepers is required to ensure that rotation is an effective tool for managing PCN.

8.10 Increase availability of resistant varieties and demand for these varieties

More widespread cultivation of varieties with moderate or high levels of resistance to *G. pallida* that are suitable for the table and salad sectors is required to control *G. pallida*. Growers have said that "free" resistant varieties would be greatly beneficial as currently all *G. pallida* resistant varieties can only be grown under contract. Breeders should prioritise the development of *G. pallida* resistant varieties suitable for Scottish conditions. There is an urgent need to develop reliable markers for PCN resistance to allow rapid selection of breeding material. The industry needs to increase the demand for these varieties amongst the end users (processors and supermarkets), enabling the growers to produce them profitably.

8.11 Increasing knowledge

From the interviews with growers it became clear that knowledge about PCN, how it multiplies, how it is spread and how to control it is limited. This is particularly true for ware growers who currently see little economic impact from PCN, as well as for landowners who rent out land to potato growers. It is important that all involved in the potato industry are aware of the impact PCN could have on the long-term sustainability of potato production in Scotland. Some growers wanted PCN test results to be more widely available, particularly where they are renting land, to know if a particular field or farm is infested to have more idea where risks are and to aid with biosecurity. Many growers in the north were concerned about large ware growers moving in from infested areas, a code of practice and biosecurity advice for ware growers may help to alleviate some of these worries.

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Appendix - The Future Threat of PCN

Background to the mathematical model of G. pallida created by BIOSS

A process-based mathematical model predicting the seasonal dynamics of *G. pallida* was developed. This model splits the *G. pallida* life cycle into separate compartments for the larval, adult and cyst life stages and uses published data to capture the effects of temperature on growth rates and survival of each of these life stages (Kaczmarek et al., 2014; Skelsey et al., 2018; Kaczmarek et al., 2019). The model is based on a sequence of ordinary differential equations and employs the methodology of Manetsch (1976) and Vansickle (1977) to split compartments corresponding to specific life stages into multiple sub-compartments to produce realistic, temperature-dependent time delays corresponding to the time required to complete development. The effect of density-dependence on population dynamics is incorporated through variation in both the larval mortality and in the sex ratio of adults (Trudgill 1967; Jones and Perry 1978; Schans 1993). In this way we have taken published experimental data measuring the effects of biotic and abiotic processes on *G. pallida* vital rates and built a novel mathematical model that explicitly captures the effects of these processes on the *G. pallida* life cycle. The resistance rating of potatoes is assumed to affect population dynamics by altering the proportion of adults that survive to become cysts. *G. pallida* development is set to be zero in the absence of potato plants; simulations from the model over multiple years then give an understanding of the effect of different cropping strategies on nematode multiplication rates through multiple seasons.

Ideas to improve the BioSS model

1. Model validation – At present the model is validated based on relatively little field data (densities measured through one season in two fields). More field data to assess the model and, if possible, to improve estimates of some of the more uncertain parameters would be valuable. Repeated measurements of densities in multiple fields over multiple years, alongside information regarding environmental variables and potato planting schedules, would be required.
2. Multiple generations - A big concern seems to be around whether or not warmer temperatures will lead to multiple generations in a season. We assumed there would be only one generation in this case because there are a lot of question marks surrounding multiple generations such as:
   a) What happens if it gets warm enough for 1.5 generations, based on the current model that would reduce the population size but that seems unlikely?
   b) Is there a built-in diapause requirement for new cysts and, if so, how long might it take to lose that?
   c) Would the proportion of cysts that hatch for the second generation be lower than the proportion that hatched for the first one to guard against a scenario where the second generation can't complete?
   d) The model would certainly be able to incorporate multiple generations, but we chose not to explore that in this case because of constraints on time and also because of uncertainty surrounding the mechanisms.
3. Model of spread - It would be beneficial if the mathematical model could also model spread of PCN within/between fields to at least partly bridge the gap between the temporal mathematical model and the spatial spread animations. This would be a

very substantial piece of work e.g. it could potentially form the basis of a PhD project.

4. Statistical model of spread – Future statistical work could include a fuller spatial-temporal analysis to identify the major factors for spread. This would include: intensity of growing both seed and ware, use of resistant varieties in seed and ware, rotation periods, source of seed. We'd look at spatial correlation - to see the fall off in correlation by distance, but, if possible, also look at grower effects (if information exists on this).

Workings for the Strathclyde University model and economic impact table

Data between 1995 and 2018 were used to parameterise a model to estimate the rate at which infestation with *G. pallida* has been expanding in recent years. An exponential model has been used to capture the dynamics of the area testing positive in each year, $y(t)$ as a function of year,

$$y(t) = y(t_0)e^{b(t-t_0)}$$

with $t_0 = 1995$ and two parameters, $y(t_0) = 43.9 \pm 1.2$ representing the estimated area in year t_0, and $b = 0.098 \pm 0.01$ representing the exponential rate of growth. *Figure 3* shows the results of the model parameterisation.

Table 4: Breakdown of Gross Margin £/ha potatoes with yield reduction calculation

	Low	High	Average		Yield reduction	80%	
Yield (t/ha) seed	25	35	30		6		
Yield (t/ha) ware	6	6	6		1.2		
Yield (t/ha) stockfeed	2	2	2		0.4		
	33	43	38		7.6		
Seed (£220/t, £190/t)	5500	6650	6075		1230		
Ware (£45/t)	270	270	270		54		
Stockfeed (£20/t)	40	40	40		8		
Output	5810	6960	6385		1292		
Variable Costs							
Seed (£360/t)	1728	1440	1584		1584		
Fertiliser	196	196	196		196		
Sprays	515	501	508		508		
Other Expenses	2645	3405	3025		3025		
Total Variable Costs	5084	5542	5313		5313		
Gross Margin £/ha	**726**	**1418**	**1072**		**-4021**	5093	Difference

Resistant variety availability and breeding in Scotland

The predicted increases in *G. pallida* populations under increasing temperature are likely to be dwarfed by the effects of potato resistance, with resistant potatoes being shown to effectively control *G. pallida* populations. However, varieties with resistance to *G. pallida* remain scarce and are rarely grown.

The relatively newly available varieties such as Innovator and Arsenal, with high levels of *G. pallida* resistance, are not grown commercially because their end-use is predominantly the processing market and conditions in Scotland are not suitable for producing the dry-matter content required for processing. Varieties with lower levels of resistance to *G. pallida* e.g.

Harmony (score 4) and Osprey, Vivaldi, Saphire and Valor (all score 3) are more widely grown. Varieties with high levels of *G. pallida* resistance can, however, be grown as seed crops, which is increasingly the case. Innovator (score of 9) is the 8th most widely grown variety for seed, with Royal (3) 10th and Arsenal (9) 18th. These varieties contribute to keeping seed land clean. More processing and a few table varieties with high *G. pallida* resistance are in the pipeline and are likely to become available in the next couple of years.

Success with breeding for resistance to *G. pallida* has lagged behind that for *G. rostochiensis*. This is partly because the 2 main sources of resistance used for *G. pallida*, *Solanum vernei* (GpaV) and *S. tuberosum* ssp. *andigena* CPC2802 (GpaIVS adg), which have been less amenable for breeding. Unfavourable agronomic qualities and the polygenic nature of the resistance (Gebhardt 2013) has complicated the breeding process. With polygenic resistance, the reduction in multiplication of *G. pallida* tends to diminish over subsequent crosses as the various QTLs involved in the resistance become separated in the progeny. However, recently varieties with resistance from both of these sources have been produced and these now provide parental material for the breeders.

Resistance to PCN is a high priority in potato breeding programs. At James Hutton Limited, the ~10 companies that invest in the potato breeding program have *G. pallida* resistance as a top priority with dual resistance to both species as the eventual goal. Combining PCN and Spraing resistance is also underway due to the threat on nematicides. In the JHL breeding program varieties with different levels of *G. pallida* resistance including Innovator, Vales Everest (H3), Royal, Ambassador, Performer, Gladiator, Crisps-for-all and Arsenal are being used as parents, some for nearly 10 years. Processing, table and salad markets are all priorities. Advanced lines suited for the table sector, which is of particular interest for Scotland, are expected to progress to national list testing in the next couple of years. Tests in 2019 of a range of advanced lines from JHL breeding programs with good agronomic characters with more virulent G. pallida populations identified at least 10 clones with high levels of resistance.

Table varieties from various breeding programs with high levels of *G. pallida* resistance already available include Camel, Eurostar, and Elland. There is also potential for using moderately resistant varieties in a control program to suppress multiplication of *G. pallida* when used with nematicides as can be demonstrated in the AHDB PCN calculator. Varieties currently available with moderate resistance, suitable for the table sector, include Lady Balfour (organic), Tyson, Kestrel, Harmony, Tribute and Diva. A serious consideration should be made to use more of the available varieties with moderate or high levels of resistance to *G. pallida* that are suitable for the table and salad sectors in Scotland as part of a strategy to protect seed land.

The efficiency of breeding programs can be improved with the use of molecular markers to deploy marker assisted selection. Undertaking phenotyping assays to determine the susceptibility of progeny is time-consuming and utilises significant resources and it is difficult to distinguish between individuals that have more than one resistance loci. Screening of progeny at the seedling stage for the presence of a character of interest, such as PCN resistance, using molecular markers can greatly increase the size and number of progeny that can be examined and decrease the cost relative to phenotyping. Recent developments in potato genomics is having a significant impact on the speed with which resistance loci are being identified and in providing opportunities for molecular marker development. There is an urgent need to develop reliable markers for PCN resistances in a cost efficient and high throughput format.

To achieve high levels of resistance to *G. pallida* that are durable (i.e. not overcome due to the reliance of a single resistance source) an approach being used by breeders is to combine, or pyramid, more than one resistance source. Used in conjunction with marker assisted selection, this is now feasible within breeding programs. Combining *Solanum vernei* and *S. tuberosum* ssp. *andigena* CPC2802 resistances is well advanced in the JHL breeding program. Other sources of resistance to PCN from various wild species such as *S. multidissectum*, *S. spegazzinii* and *S. tarajense* are also in the pipeline but, as these are wild progenitors, considerable backcrossing may be required to eliminate undesirable characters, so this is a longer-term prospect. A potential complication with breeding for *G. pallida* resistance is that in the UK, field populations of *G. pallida* are genetically more complex than those of *G. rostochiensis*. Whether this will impact the durability and effectiveness of resistance to *G. pallida* remains to be seen, as few varieties with resistance to *G. pallida* have been grown here in a significant hectarage to date. In the Netherlands, which typically have shorter rotations (3-4 years) than in the UK, breakdown of *G. pallida* resistance has been observed in starch production areas where varieties such as Innovator have been grown for several crop cycles (Niere *et al.*, 2014). In Scotland, if ground-keeper control is not efficient, these can act as reservoirs for PCN and can negate the benefits of longer rotations with regard to PCN.

The tolerance of a particular variety to PCN is another aspect in considering variety choice, particularly where PCN infestations tend to be high. Tolerance is genetically distinct from resistance and is thought to be associated with vigorous growth and production of larger root systems as found with varieties such as Cara, Arsenal, Performer, Rock, Royal and recently released Lanorma and Iodea. There is a demand for tolerant varieties, but the determination of tolerance requires the undertaking of extensive field trials, which has hampered the breeding for this character. Undertaking a genetic analysis of tolerance is needed and, once better understood, could lead to the development of molecular markers for tolerance.

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