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Mapping Infestations of Potato Cyst Nematodes and the Potential for Spatially Varying Application of Nematicides

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Abstract. The most important constraint to potato production in the UK is the damage caused by the potato cyst nematodes (PCN) *Globodera pallida* and *Globodera rostochiensis*. These are serious pests, capable of causing substantial yield loss. Modern management systems depend heavily on nematicides which, at *c*. £360 ha^{-1} for granular and *c*. £550 ha^{-1} for fumigant nematicides, are costly to use. Mapping field infestations of PCN gives growers the option of applying nematicide variably across their fields. We intensively sampled a field, infested with *G. pallida*, before and after potatoes were grown and used the results to consider decisions the grower might have taken and to examine the consequences of various actions. Sampling intensity is important in generating accurate maps. In our results, spatial independence in PCN counts occurred at about 60 m, although there was also evidence of spatial independence at a range of 10–20 m in intensively sampled areas of the field. A strategic requirement to keep PCN population densities small, rather than the more tactical objective of avoiding yield loss, would mean blanket treatment of infested fields with granular nematicide. Maps could then be used to target 'hot spots' of PCN infestation for additional treatment with fumigant. This procedure would avoid blanket treatment with both types of nematicide, thereby diminishing the cost of chemicals applied and reducing possible environmental damage. However, the inverse relationship between pre-planting population density and multiplication rate of PCN makes it difficult to devise safe spatial application procedures, especially when the pre-planting population density is just less than the detection threshold.

Keywords: maps, nematicides, nematode control, potato cyst nematodes, spatial variation

Introduction

The potato cyst nematodes (PCN) *Globodera pallida* and *Globodera rostochiensis* are the most problematic pests faced by potato growers in Britain, being both persistent and capable of causing substantial loss of yield (Trudgill, 1986). A recent survey of potato production in England and Wales revealed that 64% of the fields surveyed were infested with PCN and that, of the infested fields, 67% contained essentially pure *G. pallida*

(Minnis *et al*., 2000). Only 8% appeared to be pure *G. rostochiensis*, and the remaining 25% contained mixtures of the two species. Yield is lost at population densities as small as 5 eggs g^{-1} soil (Trudgill, 1986), which means that nematicides are essential to control PCN if profitable yields are to be maintained. Barker *et al*. (1998) have shown how nematicides influence the yields and gross margins of potato crops grown on PCN-infested land, and that it is common for potato production in such circumstances to be more profitable if two different types of nematicide—a fumigant and a granular nematicide—are used in combination.

Operation over the last 30 years of systems for managing PCN that rely on rotation, resistance and granular nematicides has led to the current dominance of *G. pallida*. Fumigants such as 1,3-dichloropropene (1,3-D) appear to kill the two species of PCN non-selectively and have the additional benefit of releasing plant nutrients through the mineralisation of nitrogen. Granular nematicides are usually more effective than fumigants at killing PCN but act differentially on the two species—they are somewhat less effective against *G. pallida* than against *G. rostochiensis*. This means that each use of granular nematicide selects for *G. pallida*, a fact that is all the more serious because other components of programmes for managing PCN also act selectively in favour of *G. pallida*. When non-host crops are grown, *G. pallida* populations decline more slowly than those of *G. rostochiensis*, and resistant cultivars are much less effective against *G. pallida* than they are against *G. rostochiensis*. In the 1960s, *G. rostochiensis* was the dominant species in Britain (Brown, 1970). The current predominance of *G. pallida* is what has led to the increasing likelihood that growers will use 1,3-D plus a granular nematicide to control PCN, a practice that is in conflict with mounting pressure from environmentalists to use less nematicide.

Potato growing is highly specialised and capital intensive, with certain of the cultivation equipment and all types of planting and harvesting machinery suitable only for the potato crop itself. It is probably the single most profitable arable crop grown in Britain, and simple economics dictate that farmers who are able to produce good potato crops grow them in as short a rotation as can be sustained. This inevitably means the tactical use of nematicides to minimise yield losses due to PCN. Such an approach, which overlooks the more strategic aim of keeping PCN population densities as small as possible, frequently means that growers find that their PCN populations are increasing (Parker, 1998) as *G. pallida* comes to dominate.

Concern to protect the environment and recent narrow gross margins for potato production have stimulated the investigation of variable rate application for nematicides. Such approaches would reduce use of nematicide in Integrated Crop Management (ICM) schemes which growers have to adopt for assured produce schemes (Haydock and Evans, 1998). Of the current inputs on whole fields for potato production, variable application of pre-emergence herbicides or prophylactic blight fungicides would be inappropriate. Of the rest, nematicides are the most expensive inputs to potato production, and therefore the ones that offer the greatest potential savings. Granular nematicides cost *c*. £360 ha^{-1} and fumigants *c*. £550 ha^{-1} (Table 1).

The Global Positioning System (GPS) has made it possible for modulated treatments with nematicides to be accurately targeted (Haydock and Evans, 1995), and commercial packages have followed (e.g. Anon., 1997). These packages are usually based on individual sampling of hectare blocks within a field, followed by application (or not) of

Table 1. Inputs for potato production and their potential for spatial application. Costs are taken from ABC (1999)

Input	Potentially variable?	Cost (£ ha^{-1})	Potential saving (£ ha^{-1})
N, P, K fertiliser	Yes	220	33 (15%)
Lime	Yes	30	6 (20%)
Herbicides			
Pre-emergence	No	60	—
Post-emergence	Yes	60	60 (100%)
Fungicides	No	144	—
Insecticides	Yes	26	26 (100%)
Nematicides			
Granular	Yes	360	360 (100%)
Fumigant	Yes	550	550 (100%)

a nematicide to individual hectare blocks, depending on the presence in or absence from the soil samples of PCN. The costs of processing soil samples to determine PCN densities prohibit intensive mapping of any field. The results of more readily affordable (i.e. sparser) sampling, made without proper understanding of the aggregation characteristics of PCN populations, are not trustworthy, even though maps may look convincing. We sampled intensively in one field, both before and after a commercial potato crop, and counted the *G. pallida* that were present. The data have been used to investigate the potential for patch treatment with nematicide and to generate treatment maps based on various sampling grids. On a second field, we examined the effects of treating a range of PCN population densities with nematicide, in order to generate information on the effects of nematicide use on the management of PCN populations. We report some of our results below.

Materials and methods

The field surveyed, covering *c*. 8 ha, at Ram Farm, Nocton, Lincolnshire, UK (53.157° N, 0.483° W) grew spring barley in 1996. On 1 May 1996, the field was sampled at 20-m intervals, measured by tape along the tramlines, which were 24 m apart and ran parallel to the western boundary of the field. One hundred and seventy-five samples were collected, each consisting of *c*. 1 kg of soil, taken with a trowel to a depth of 150 mm. The PCN population density was estimated by standard methodology (Southey, 1986) in 200-g subsamples of the air-dried soil. Potatoes, cultivar Cara, were grown in 1997, without nematicide treatment, in 1.83-m-wide beds. The crop was planted on 22 March and harvested on 1 October. All cultivation operations were parallel to the western field boundary.

On 26 November 1997, the field was re-sampled using three strategies. First, the field was sampled on a regular 20 m × 20 m grid at 177 sample stations. The position of each station was determined using a differential GPS receiver mounted on an all-terrain vehicle. The sampling grid was aligned north–south. Twenty GPS computations were averaged over a 1-min interval at each sample point. Second, a sampling point at a

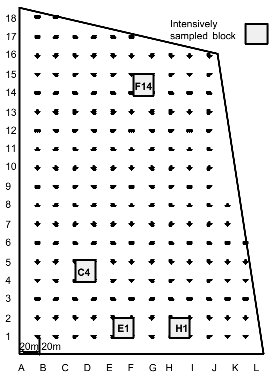

Figure 1. Plan of the field at Ram Farm showing the positions of the intensively sampled squares.

randomly determined position within a 20 m × 20 m square centred on the sampling station was selected. Third, samples were taken at 2-m spacing in four randomly chosen 20 m × 20 m squares (C4, E1, F14, H1 in Figure 1) formed by the main sampling grid, giving a total of 121 samples for each square. All samples were extracted and processed as previously described.

To examine more closely the influence of PCN population density on multiplication rates, the data were divided into 1-ha blocks. The average initial population density (P_i), final population density (P_f) and multiplication rate (P_f/P_i) for PCN were computed for each of the resulting 10 blocks or part blocks.

Sample variograms were computed using the standard formula (Webster and Oliver, 2001) and, where feasible, models were fitted to them by weighted least squares minimisation using GenStat (Payne, 2000). The post-cropping data lent themselves to local estimation by kriging, and ordinary punctual kriging was used at intervals of 5.5 m, using moving neighbourhoods of $n = 20$ sampling points from the original grid. This produced a dense figure-field from which the kriged estimates and their variances could be mapped.

The mapping software Surfer® (Golden Software Inc., Golden, Colorado, USA) was used to display the kriged estimates as maps from both the pre- and post-cropping data. The same software was also used to produce treatment maps for threshold levels of 5, 10 and 20 eggs g^{-1} soil based on the PCN distributions before and after cropping. Distribution maps derived from reduced sets of data to show the effects of wider spaced sampling were also produced. These data were obtained by using the south-westernmost sampling position as the starting point and ignoring the next one, two, three or four data values to create the 40, 60, 80 or 100 m spaced datasets.

To provide data on the effects of nematicides on a range of population densities, an area of a field infested with *G. rostochiensis* (Horsepool Field, Woburn Experimental Farm, Bedfordshire, UK, 52.009° N, 0.608° W) was divided into 64 plots (each 6 m × 3 m). Soil samples were taken (40 cores 200 mm deep by 25 mm diameter) in a rectangular grid pattern from each plot to determine PCN densities. Twenty-four of the plots were selected for study, eight in each of three classes, corresponding to densities expected to cause no, little or moderate crop damage:

>12.0 eggs g^{-1} soil	moderate infestation
5.0–12.0 eggs g^{-1} soil	light infestation
0.1–5.0 eggs g^{-1} soil	very light infestation

Four plots in each class were treated with oxamyl (as Vydate® 10% granules, Du Pont) at 4.5 kg active ingredient per hectare. The field was then planted with potato cv. Estima, which was left to mature before post-harvest samples were taken to estimate final PCN population densities. Potato yields were also recorded from each plot and the effects analysed by two-way analysis of variance.

Results

The data for the pre- and post-cropping Ram Farm samples are summarised in Table 2. After harvesting, the average density of the PCN population over the whole field was found to have increased more than eight-fold, from 8 to 66 eggs g^{-1} soil, and the number of zero counts fell from 48 samples to just one. The variance also increased ten-fold, and both distributions were strongly positively skewed.

The relationship between PCN multiplication rate and initial density in hectare blocks is shown in Figure 2. The specific values used in Table 5 were read from this curve.

The sample variograms for the pre- and post-cropping data are shown as the plotted points in Figure 3. The pre-cropping data showed a scatter of semi-variances about a horizontal line, approximately the variance of the data, with no evidence of spatial correlation above the sampling distance of 20 m. However, the semi-variance for the post-cropping data increased with increasing lag distance up to *c*. 55 m, and we fitted a spherical model as follows:

$$\gamma(h) = \begin{cases} c_0 + c\left\{\frac{3h}{2a} - \frac{1}{2}\left(\frac{h}{a}\right)^3\right\} & \text{for } 0 < h \leq a \\ c_0 + c & \text{for } h > a \\ 0 & \text{for } h = 0 \end{cases} \quad (1)$$

Table 2. Summary of the statistical data for the two samplings

	Before planting	After harvest
Number of points	175	354
Minimum (eggs g^{-1} soil)	0	0
Maximum (eggs g^{-1} soil)	160.2	495.6
Mean (eggs g^{-1} soil)	8.4	65.6
Median (eggs g^{-1} soil)	2.5	45.3
Variance	522.3	5042.4
Standard deviation	22.8	71.0
Skewness	4.95	2.08

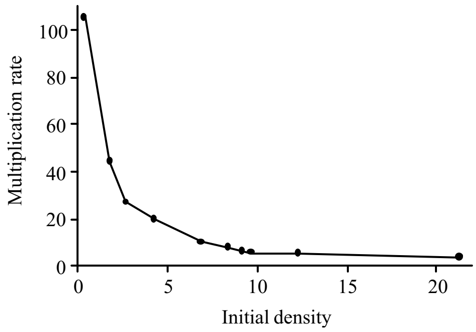

Figure 2. Relationship between initial population density (P_i) and multiplication rate (P_f/P_i) from hectare blocks at Ram Farm.

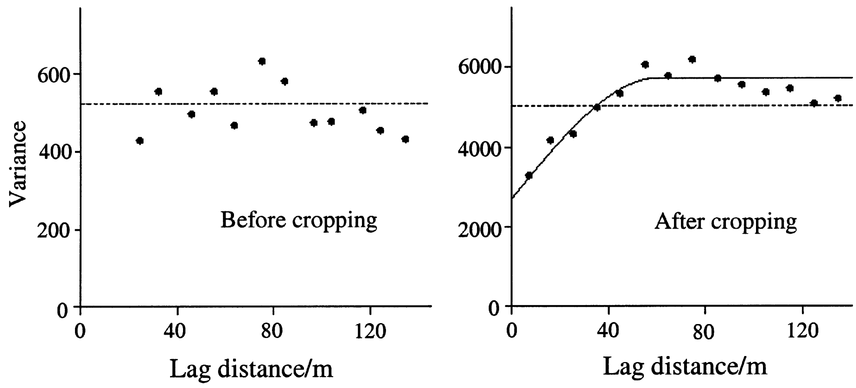

Figure 3. Variograms of nematode density before and after cropping with spherical model $\gamma(h) = 2753 + 2658$ sph(53.5m) fitted to the post-cropping data. In this equation, h is in m, and the quantity 53.5 m is the range of the model. The dashed horizontal lines show sample variances.

where h is the separating distance, c_0 is the so-called nugget variance, c is the spatially correlated component of variance, and a is a distance parameter, the correlation range. We can shorten this equation to $c_0 + c\,\mathrm{sph}(a)$.

Mapping the pre-cropping data (Figure 4) suggested that there was alignment in the direction of cultivation. When the variogram was computed along and orthogonal to the direction of cultivation, the pre-cropping data showed no correlation across the rows but strong correlation along them (Figure 5). Variograms for the two directions for the post-cropping data were very similar to each other (Figure 6).

The distribution of PCN in the field after cropping is shown in Figure 4.

The data for the squares that were sampled at 2-m spacing are summarised in Table 3 and the models that were fitted and estimates of parameters are in Figure 7. This introduces an additional model, the Gaussian function, with equation:

$$\gamma(h) = c_0 + c\left\{1 - \exp\left(-\frac{h^2}{r^2}\right)\right\} \tag{2}$$

where r is a distance parameter and the other quantities are as in Eq. (1).

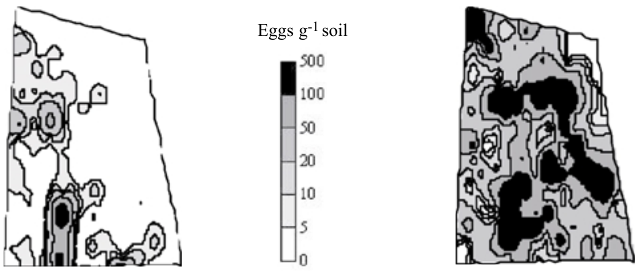

Figure 4. Pre-crop (left) and post-harvest (right) distributions of PCN at Ram Farm.

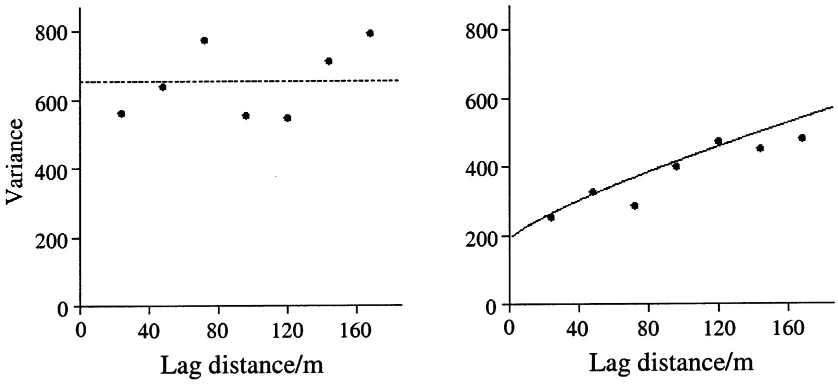

Figure 5. Variograms of nematode density, before cropping, at right angles to cultivation (left) and in the direction of cultivation (right) with fitted model $\gamma(h) = 189.6 + 6.143h^{0.79}$, where h is in metres. The horizontal line (left) is the sample variance.

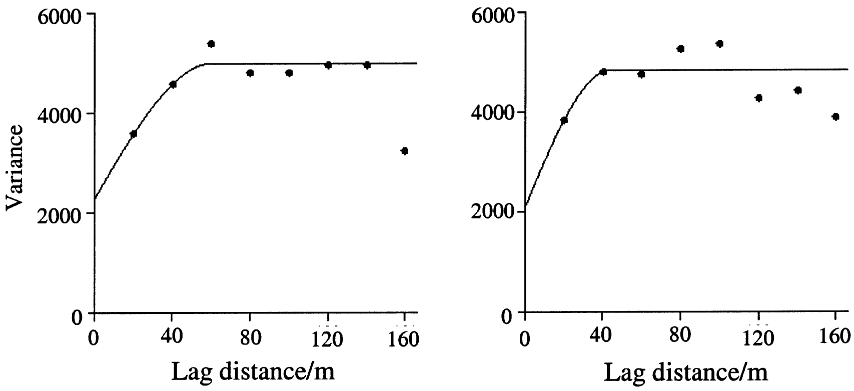

Figure 6. Sample variograms of nematode density, after cropping, at right angles to cultivation (left) and in direction of cultivation (right), with fitted spherical models $\gamma(h) = 2272 + 2726$ sph(60.5m) and $\gamma(h) = 2100 + 2746$ sph(44.2 m). As in Figure 5, h is in metres and the quantities 60.5 and 44.2 m are the ranges of the models.

Table 3. Summary of the statistical data for the four intensively sampled squares

Square	C4	E1	F14	H1
Number of points	121	121	121	121
Minimum (eggs g^{-1} soil)	3.8	0.0	0.5	0.8
Maximum (eggs g^{-1} soil)	477.0	194.5	162.3	329.8
Mean (eggs g^{-1} soil)	126.4	34.2	38.9	54.8
Median (eggs g^{-1} soil)	122.8	21.9	33.8	48.4
Variance	9152.4	1341	845.4	2122.5
Standard deviation	95.7	36.6	29.1	46.1
Skewness	0.78	2.08	1.56	2.37

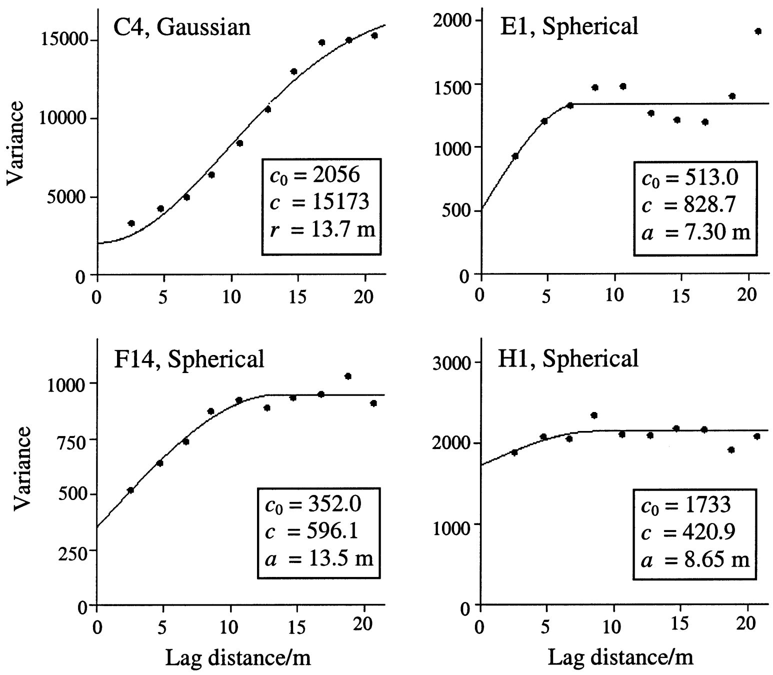

Figure 7. Variograms for the PCN density in the intensively sampled squares. The quantities c_0, c, a and r are as defined in Eqs (1) and (2).

The variograms for the intensively sampled squares are shown in Figure 7, and the distribution maps of the squares are in Figure 8. These variograms are different from those of the whole field (Figure 6). They are of much smaller regions with sides (20 m) less than the range in the field (40–60 m), and therefore encounter less variance, on average. Their ranges, 7–13 m for squares E1, F14 and H1, refer to the denser sampling over shorter distances. Square C4 happens to lie across the boundary between a dense patch and an area of light infestation, and so encounters more variance than average. The trend across the square appears in the sigmoid shape of the variogram.

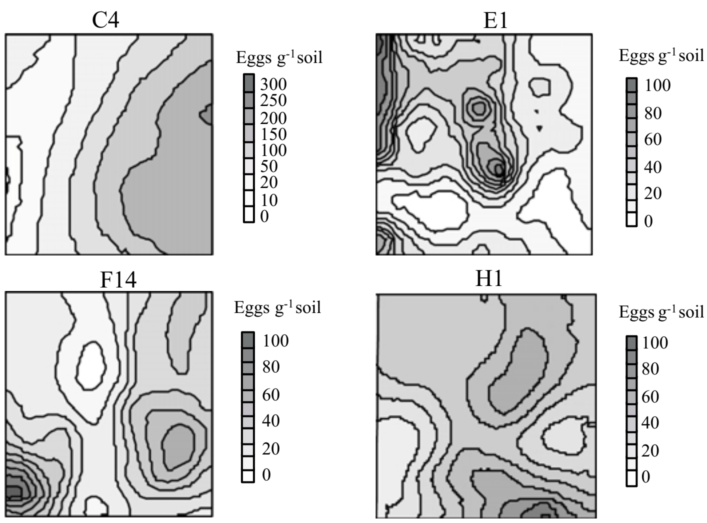

Figure 8. Maps of PCN distribution in the four intensively sampled squares after kriging with the models in Figure 7.

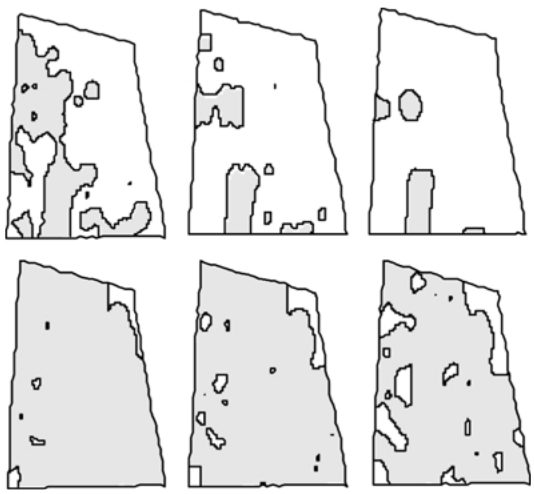

Figure 9. Regions of the field that exceeded thresholds (5, 10 or 20 eggs g^{-1} soil—left, middle, right, respectively) for treatment with nematicide, pre-cropping (top) and post-cropping (bottom).

The mapping software was used to produce maps of regions that exceeded the nematicide treatment thresholds of 5, 10 or 20 eggs g^{-1} soil in the pre- and post-cropping data (Figure 9). These regions represented 34%, 14% and 8% before cropping and 93%, 88% and 72% after cropping, respectively, of the whole field.

Where models could be fitted to the whole-field data taken on the 20-m sampling grid, the variograms (Figures 3 and 6) showed that spatial dependence extends to between 40 and 60 m but no more. To show the effect of sampling on grids coarser than this, maps of

PCN distribution were interpolated from subsets of data from the 20-m sampling grid to simulate sampling grids of 20, 40, 60, 80 and 100 m, and the five resulting maps are shown in Figure 10. The longer range variation in the 20-m map can be seen in the 40-m map but an increasingly different pattern is observed with more widely spaced sampling grids. A treatment map derived from the 100-m sampling grid—a typical value used in commercial sampling—would be a poor reflection of the true PCN distribution.

The experiment in Horsepool field at Woburn was carried out to test the hypothesis of treating small population densities of PCN with nematicide for optimum control. The P_f/P_i ratios in untreated plots ranged from 55 in the very light infestation through 16.5 in the light to 11 in the moderate (Table 4), clearly demonstrating the density dependence of the reproductive rate. With Vydate treatment, the ratios were 0.74, 1.88 and 2.06 in the very light, light and moderate classes, respectively, demonstrating the greater efficacy of nematicide treatment at low densities. Yield differences between plots treated with Vydate in the three infestation classes were not statistically significant, and there was no

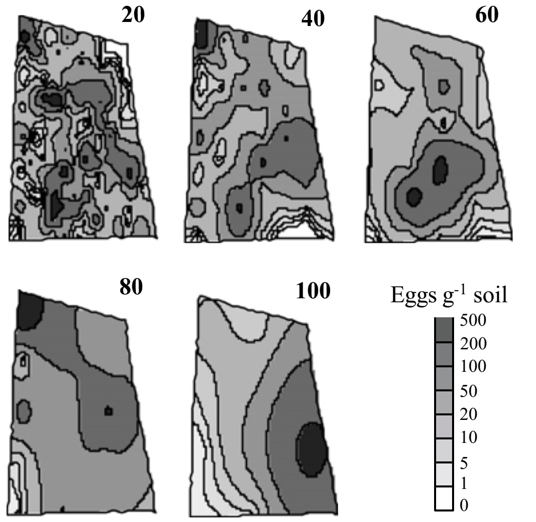

Figure 10. Interpolated maps of the post-cropping distribution of PCN (eggs g^{-1} soil) produced from 20, 40, 60, 80 and 100 m spaced samples.

Table 4. Initial and final population densities, P_f/P_i ratios, and yields of plots treated or untreated with Vydate

P_i range (eggs g^{-1} soil)	Treatment	Mean P_i (eggs g^{-1} soil)	Mean P_f (eggs g^{-1} soil)	Mean P_f/P_i	Mean yield (kg)
0.1–5.0	Vydate treated	2.3	1.9	0.74	21.9
0.1–5.0	Untreated	1.7	101	55.0	21.3
5.0–12.0	Vydate treated	7.9	16.6	1.88	23.8
5.0–12.0	Untreated	7.4	132	16.5	19.2
>12.0	Vydate treated	29.5	61.9	2.06	22.8
>12.0	Untreated	31.6	274	11.0	14.3

yield penalty of not applying Vydate to plots in the very light infestation class. The deleterious effect of PCN on potato yield on this sandy soil is, however, seen in the untreated plots of the light and moderate infestation classes (significant at $P < 0.001$ in both instances). For long-term nematode control, it may thus be wise to use a nematicide even at very small population densities of PCN, even though there will not necessarily be yield benefit in the current crop.

Discussion

PCN, in common with other species of plant parasitic nematodes, are fairly immobile and are spread mainly by operations that move the soil. Apparently discrete patches that are surrounded by uninfested areas are often actually surrounded by areas where the PCN density is simply below the detection threshold. There are *c*. 2.5×10^9 g of soil to a depth of 20 cm ha^{-1}, which means that, if the detection threshold for PCN is 1 egg g^{-1} soil, there can be up to 2.5×10^9 PCN ha^{-1} even though none is detected. With just one susceptible potato crop, this could become *c*. 2.5×10^{11}, or 100 eggs g^{-1} soil. This appears to have happened in parts of the Ram Farm field, where zero PCN was recorded at 48 stations before cropping but post-harvest densities reached more than 50 eggs g^{-1} soil (see Figure 4). This implies that the pre-cropping density was just below the threshold for detection. There would be no yield penalty for not treating such an infestation with nematicide or even one as large as 5 or more eggs g^{-1} soil, but such failure would leave the legacy of a large PCN infestation with which to contend in the future. Thus, the wisdom of using simple spatial applications of nematicide is questionable.

The risks associated with spatially varying application of nematicide would be lessened if the characteristics of patches that are found within fields could be related to the age of infestation and, therefore, the degree to which any one field has been colonised by PCN. Been and Schomaker (2000) observed PCN distribution patterns at large, medium and small scales, corresponding to comparisons at scales of whole field, single patch and local development on individual plants, respectively. However, Schomaker and Been (1999) could not demonstrate correlations between the density gradient of the population of individual patches and variables such as nematode species, time from last potato crop, soil type, cropping frequency and population density in the centre of the focus. The variograms in Figure 7 correspond to the fine-scale distribution of Been and Schomaker (2000), whilst those in Figures 3, 5 and 6 correspond to the medium and coarse-scale distributions. The relationships are complex and variable, and it may be that a more subtle combination of patch characteristics will permit the estimation of the age of an infestation and the likelihood that zero counts surrounding patches of PCN represent true absence of PCN.

Knowledge of whether zero PCN counts represent absence of PCN (rather than simply population densities below the detection threshold) would facilitate decisions on nematicide use if long-term PCN management were the objective, i.e. ‘strategic management’ aiming to reduce PCN populations as opposed to ‘tactical management’ aiming simply to prevent yield loss (Parker, 1998). We can see the effects of choosing to treat PCN infestations of different densities with nematicide by taking the observed initial population densities and the resultant multiplication rates for *G. pallida* found at Ram Farm (Figure 2), and by assuming a mortality independent kill from nematicide of 80% (a value recognised as achievable under good application conditions). In this way, we could compute the effects on nematode multiplication rate of treating smaller and larger infestations with nematicide. The P_i values chosen were 1 and 22 eggs g^{-1} soil because it would normally be a clear-cut choice for a grower not to treat the former with nematicide but to treat the latter. The results are in Table 5 and show that, whereas the potential P_f values with no nematicide are 60 and 77 eggs g^{-1} soil, the effective P_i values with a nematicide are 0.2 and 4.4 eggs g^{-1} soil. These would give P_f values of 20 and 88 eggs g^{-1} soil. The relative effectiveness of nematicide for population control is given by dividing the P_f with nematicide by the P_f value with no nematicide in each case. Treating a small P_i (1 egg g^{-1} soil) with nematicide gives a ratio of 0.33, whereas treating a larger P_i (22 eggs g^{-1} soil) gives a ratio of 1.14. The degree of population control is much greater at the small P_i. This effect is clearly demonstrated by the results from Woburn in Table 4, the first practical demonstration of this effect.

Even without the knowledge that zero counts represent true absence of PCN, spatial sampling for PCN would still permit the economic decision of not treating areas where no PCN were found in order to save nematicide use and therefore money, that is, a tactical rather than a strategic decision. The only proviso would be that it would still be possible for patches of damage smaller than the sampling interval to appear. Such a possibility could never be avoided—even with a 10-m sampling grid, a patch of damage of up to 14 m diameter could appear when PCN was believed to be absent if the patch were midway between sample points.

Multiplication of PCN depends on density. Treating populations with nematicide only when they are likely to cause loss of yield merely kills surplus nematodes such that the survivors multiply greatly, perhaps even to greater densities than if no treatment were applied. This is because the protected crop grows better and provides more roots for nematode invasion, and was clearly demonstrated by the results from Woburn (Table 4). In terms of crop gross margins, a combination of blanket fumigation and blanket granular nematicide treatment has been shown to be more profitable than treatment with either nematicide alone (Barker *et al*., 1998). Patch fumigation should enable growers to increase those profits by using less fumigant. Table 6 shows the potential benefit:cost ratios of mapping the Ram Farm field at spacings from 20 to 100 m, based on a cost of £6 to process each sample and costs of fumigation or application of granular nematicide of

Table 5. Effects on final population densities (P_f) of nematicide treatment at different initial nematode population densities (P_i)

	Population density at time of treatment	
	1 egg g^{-1} soil	22 eggs g^{-1} soil
Potential multiplication rate	60	3.5
Potential P_f (eggs g^{-1} soil), B	60	77
Effective P_i with nematicide (80% kill)	0.2	4.4
Multiplication rate with nematicide	100	20
P_f with nematicide, A	20	88
A/B	0.33	1.14

Table 6. Potential benefit : cost ratios of mapping PCN at different intensities, based on potential savings from non-use of nematicide and a £6 per sample processing cost

Sample spacing (m)	Samples per ha	Cost per ha (£)	Non-use of fumigant	Non-use of granular	Non-use of both
20	25	150	3.7	2.4	6.1
40	6.3	38	14	9.5	24
60	2.8	17	32	21	54
80	1.5	9	61	40	101
100	1	6	92	60	152

£550 and £360 ha^{-1}, respectively. The benefits accrue from decisions not to treat with either or both nematicides and the costs are those incurred by sampling at the various spacings.

Although the potential benefit:cost ratios are, of course, much greater with sparser sampling, the accuracy of the information on which any decision is based is less, and the wisdom of basing decisions on such sparse sampling is open to question, as shown by the maps in Figure 10. Thus, the most sensible option with the current state of knowledge is probably to apply the more expensive fumigation treatment in a spatial manner but to combine this with a blanket treatment with the granular nematicide. Such a combination would maximise profits with few risks. Full spatial application of both nematicides would be possible if growers were to accept the possibilities of PCN patches being missed by the sampling procedure and of areas of zero count simply being below detection threshold and likely to increase dramatically if not treated.

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