Ann. appl. Biol. (2003), **143**:73-80
Printed in UK

The white potato cyst nematode (*Globodera pallida*) – a critical analysis of the threat in Britain

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(*Accepted 18 February 2003; Revised version received 7 January 2003*)

Summary

Over the last 30 years, there has been an epidemic of the white potato cyst nematode (wPCN, *Globodera pallida*). It has progressively replaced the yellow species (yPCN, *G. rostochiensis*) throughout most of England and Wales and is now a widespread problem. As damaging populations of wPCN are enormous (>10^9 eggs ha^{-1}), several crops of potato cultivars resistant only to yPCN were required to produce this change. The threat it poses is reflected in an increase in the numbers of soil samples being tested and in nematicide use, which has increased to > 25 000 ha of potatoes being treated annually. Computer modelling shows that current management of wPCN is mostly ineffective and populations will continue to increase. The multiplication rate of wPCN is inversely related to its population density at planting and, because of this, modelling shows that sufficient eggs are likely to survive to enable large populations of wPCN to "rebound" following nematicide treatment. This is supported by recent trial results showing that wPCN population increase was almost as great in nematicides-treated plots as in the untreated. Modelling also showed that current rotations (typically potatoes once every 5 or 6 years) are too short to prevent wPCN populations from progressively increasing, even when used in conjunction with a nematicide. Similarly, except with avirulent populations, the partially resistant cultivars currently available will not prevent wPCN from increasing. However, as the effectiveness of partially resistant cultivars is independent of population density, they can be very effective when integrated with a nematicide. Unfortunately, only *c.* 8% of the potato area is planted with partially resistant cultivars, and much of that is in land not known to be infested with wPCN. Consequently, the current epidemic of wPCN is likely to become progressively more serious. However, many farmers are failing to recognise and respond to this threat until it is too late because of the slow rate of increase of wPCN, the difficulties of detecting small populations and the costs of nematicides. To respond to the current epidemic of wPCN, the greatest priority is to have available an increased number of commercially-attractive partially resistant cultivars.

Key words: Computer modelling, integrated control, sustainable management, epidemiology, population dynamics, nematicides, damage

Introduction

In a recent survey (Minnis *et al.*, 2002), potato cyst nematodes were detected in 64% of 484 fields in England and Wales that had grown potatoes the previous year. Of these infestations, 66% were wholly the white species of potato cyst nematode (wPCN; *Globodera pallida*) and 25% were a mixture of the white and the yellow species (yPCN; *G. rostochiensis*). Compared with earlier survey results (Hancock, 1986, 1996), this represents a decrease in the occurrence of yPCN and an increase in that of wPCN, especially in East Anglia. In Scotland, PCN is less abundant and was mostly yPCN. However, the proportion of wPCN is now increasing.

Trends in the occurrence of wPCN have to be considered in the context of the trends in potato production. The number of producers and the area of ware potatoes in England and Wales have decreased from *c.* 80 000 and 224 000 ha in 1960 to less than 10 000 and 118 000 ha in 2001 (G Gagen, personal communication; Walker, 1998). Over the same period, mean yields have doubled from 22 t ha^{-1} to 44 t ha^{-1}. Maris Piper, the first commercially successful cultivar with resistance to yPCN, was introduced in 1966 and by 1971 it occupied 6% of the potato area. By 1981, Maris Piper occupied 17.6% of the potato area, and two more recently introduced cultivars with the same resistance, Cara and Pentland Javelin, occupied 1.0% and 3.3% respectively. By 2001, 52% of the potato area was planted with yPCN-resistant cultivars (G Gagen, personal communication).

Whilst the survey by Minnis *et al.* (2002) provides the best available indication of current levels of infestation with PCN, it does not indicate future

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trends. This analysis seeks to use current information and computer modelling as the basis for predicting future trends.

Past and Present

Epidemiology of PCN and sampling for detection

Both species of PCN are introduced pathogens dependent for their spread on the movement of infested planting material and of soil moved by machinery, wind, water and animals. Introductions are typically patchily distributed and, because they comprise few cysts, cause no damage and are almost impossible to detect (Been & Schomaker, 2000). Once introduced, the rates of increase of PCN are influenced by several factors, including the length of the rotation and the initial level of infestation. Currently, *c.* 60% of potatoes are grown on rotations of 5 to 7 yr, *c.* 20% are grown on shorter, and *c.* 20% on longer rotations (Minnis *et al.*, 2002). With the repeated cropping of susceptible potato cultivars, populations of PCN, and the probability of their detection, progressively increase. But, with current sampling strategies that typically involve processing only 100 g soil from 4 ha, it is only after several potato crops, when populations have become very large and widely distributed, that detection becomes likely (Trudgill *et al.*, 2001). This is demonstrated by a simple calculation of the PCN population density that might be represented by one cyst in a 200 g soil sample, as used by Minnis *et al.* (2002).

Minnis *et al.* (2002) took 50 cores of soil from 4 ha (equivalent to one core 800 m^{-2}) to give a total sample of *c.* 2 kg of soil. However, cysts were extracted from a mixed 200 g sub-sample (one tenth). Assuming a soil bulk density of 1.25 and a 25 cm plough depth, it can be calculated that one cyst (the minimum that can be detected) in such a sub-sample is equivalent to a population density of *c.* 62 million viable cysts in one 800 m^2 block. To generate such a population would require five to seven potato crops, assuming that initially 10 cysts of wPCN were introduced and there was a 10- to 20-fold increase in cyst numbers with each potato crop. On a 1 in 5 rotation, this would take between 25 and 35 yr. Consequently, many recently infested fields will still be below the threshold for detection, especially as this simple analysis ignores complicating factors such as a patchy distribution (see Been & Schomaker (2000) for a detailed analysis).

Incidence of PCN

PCN is indigenous to the Andean regions of South America, but has been present in the UK for at least 90 years (Massee, 1913). By the early 1970s it was distributed throughout most of the UK potato growing area with yPCN predominating in East Anglia and wPCN in northern England. Levels of infestation were uncertain prior to the survey by Minnis *et al.* (2002) because of a lack of unbiased survey data. In the 5 yr up to 1986, 62% of samples submitted to ADAS laboratories in Cambridge, Leeds and Newcastle were PCN infested (Hancock, 1986), but this value is probably biased because sampling would tend to have been concentrated on known infested farms. A subjective survey by the Potato Marketing Board in 1992 estimated that 42% of potato fields were infested (Hancock, 1996). However, analysis of a sub-set of soil samples taken only from ware potato fields in 1994/5 indicated that *c.* 67% were PCN infested (Hancock, 1996).

Changes in the incidence of the two species of PCN

Prior to the growing of cv. Maris Piper, yPCN predominated in Scotland and Northern Ireland and in the major potato producing areas in south Lincolnshire and East Anglia, whereas wPCN was more frequent in the East Midlands and northern England (see Minnis *et al.* (2002) for more details). Growing a crop of Maris Piper, or similar cultivar with the same gene for resistance, decreases the population density of yPCN by up to 80%, and it provides very effective control of yPCN when combined with several years of rotation that cause further decline (by *c.* 20 - 40% per annum; Turner, 1996). However, Maris Piper is fully susceptible to wPCN and, from its introduction, nematologists warned against repeated cropping with Maris Piper, arguing that any wPCN present would increase free of competition from the yPCN. Cowton (1983) confirmed these predictions by showing that, at a site where the detectable infestation was initially yPCN, wPCN become dominant and damaging after only four crops of Maris Piper in 12 yr. Up to 1986, yPCN was still the dominant species in East Anglia, but there were already indications of an increase in wPCN (Hancock, 1986). By 1996, wPCN had become the dominant species in East Anglia (Hancock, 1996) and it is now the dominant species throughout most of England and Wales (Minnis *et al.*, 2002).

Sampling and nematicide use

Prior to planting potato, farmers frequently sample fields to determine the need for a nematicide. In 1996, a total of 18 300 samples were processed by the eight main laboratories in England. By 2002 this had increased to 30 300 such samples, indicating that farmer awareness of PCN has greatly increased. As samples are generally taken from blocks of land of 1-4 ha, the total area that is sampled is uncertain, but it must be a substantial proportion of the area planted with potatoes.

Nematicide use provides another indication of the importance of PCN to farmers. In 1983, a total of 81 450 kg a.i. of granular nematicides/insecticides were applied to 33 720 ha of potatoes in Great Britain. In

1996 80 500 kg were applied to 32 170 ha, but in 1999 (the last year of complete figures) it had increased to 120 270 kg applied to 36 550 ha (Table 1). Interpretation of these figures is complicated by variations in recommended rates of application of nematicide for early and main crop potatoes, different soil types, and by their use for the control of other pathogens (e.g. lower rates of aldicarb are used for control of TRV-spraing transmitted by trichodorid nematodes and aphids). Consequently, in 1998 only 56% of the area treated with aldicarb received the rate appropriate for control of PCN in main crop potatoes (D Garthwaite, personal communication). However, the rate of application (ha^{-1}) of active ingredients increased by 50% between 1996 and 1999, suggesting an increase in that applied for control of PCN to between 25 000 and 30 000 ha in 1999.

The Future

wPCN has been increasing, but future trends will depend on many factors, including the effectiveness of control. Most farmers already integrate nematicides with rotation, and a few also grow partially resistant cultivars, but analysing the future impact of such strategies requires an ability to model the interactions between control methods.

Modelling wPCN Population Dynamics and Effects on Yield

The two species of PCN are biologically similar and, whilst most of what follows applies equally to both species, this review concentrates on wPCN as this now poses the greater threat.

Environmental influences on damage and wPCN multiplication

The ability to predict wPCN population dynamics and associated yield losses is a prerequisite for making management decisions. Yield loss and wPCN multiplication are both directly related to population density at planting (P_i); crop damage increases and the wPCN multiplication rates decrease with increasing P_i. Seinhorst (1965, 1967) and Seinhorst & den Ouden (1971) developed equations, based on results from pot experiments, that described these relationships. These equations were not predictive as damage and wPCN multiplication are influenced by environmental factors, especially soil type, husbandry and cultivar (Elston *et al.*, 1991; Trudgill, 1987). In a series of field trials (Phillips *et al.*, 1998*b*) damage was less in a loam soil than in a sandy (Fig. 1a) or in an organic soil, and with a tolerant cultivar (e.g. Cara) rather than with an intolerant cultivar (e.g. Pentland Dell; Trudgill, 1987). In contrast, the multiplication rate of wPCN was greatest with a tolerant cultivar and in a sandy rather than a loamy soil (Fig. 1b).

Modelling wPCN damage in the field

Elston *et al.* (1991) showed that there was a simple inverse linear relationship between P_i and yield, but that the slope of this relationship was influenced by site (s) and cultivar (g) (Phillips *et al.*, 1998*b*). Damage was greater in light than heavy soils and some cultivars were more tolerant of wPCN damage (i.e. their yield was proportionally less affected). Allowing for these effects enabled the predictive potential of the damage equation to be increased (Eqn 1).

$$Y = Y_{max}(1/(1 + P_i/s*g)) \qquad (1)$$

where Y equals the yield in PCN infested soil expressed as a proportion of the nematodes-free yield (Y_{max}), and P_i is the wPCN population density at planting.

Modelling wPCN population dynamics

The basic equation for the relation between the population density (eggs g^{-1} soil) of wPCN before (P_i) and after (P_f) a potato crop is given by Eqn 2.

$$P_f = M[1 - \exp(-aP_i/M)]Y/Y_{max} \qquad (2)$$

In addition to P_i, this equation is driven by three parameters:-

1. The maximum multiplication rate (a) that is achieved only at low P_i when there is no competition or damage. The value of a is primarily determined by the proportion of the inoculum that successfully invades the potato roots and becomes female. Invasion rates are influenced by soil factors that

Table 1. *Use in Great Britain of nematicidal chemicals, as estimated by the Pesticide Usage Survey Group. Results for 1999 are provisional, and probably slight underestimates*

	1983		1996		1999	
	ha	a.i (kg)	ha	a.i (kg)	ha	a.i (kg)
Aldicarb*	17280	19400	21660	37900	16470	35270
Ethoprophos*	0	0	3510	15500	4140	21900
Fosthiazate*	0	0	0	0	3380	9680
Oxamyl**	16440	62000	7000	27150	12560	53400
Dichloropropene***	1140	234950	1250	317900	-	-

*Granular nematicide/insecticide; **Granular nematicide; ***Liquid, fumigant determine the ease with which juveniles can migrate to the potato roots, and tend to be least in heavy soils. They are also influenced by the root density as this influences hatch rate and the length of the migration from cyst to root.

2. The potential maximum population density (M) is that which could be supported, at a high P_i, by an undamaged root system. It is a theoretical value that reflects the size of the undamaged root system – the greater the size, the greater the numbers of female wPCN that it can theoretically support, and the greater the value of M. Root system size increases with the vigour of the crop, and the progressive increases in potato yields in recent years have undoubtedly increased M, thereby benefiting wPCN. Because of their larger root system and their tolerance, vigorous, tolerant cultivars (e.g. Cara) support larger population densities of wPCN than more weakly growing, intolerant cultivars (e.g. Pentland Dell and Maris Peer) (Fig. 2).

3. In practice, M is never achieved because of wPCN damage that decreases the actual maximum population density (Fig. 2). This damage is modelled in Eqn 2 by adding the function Y/Y_{max} derived from Eqn 1.

Further functions (not shown) are included that decrease the proportion of eggs that hatch as P_i increases (to allow for decreased root-diffusate production), that allow for the effects of applying a nematicide, and for growing a partially resistant cultivar.

Density-dependent and density-independent control measures

The effects on P_f of control measures are dependent on whether they decrease a and/or M, or whether they decrease P_i. The effectiveness of the former is independent of P_i. The latter become less effective as P_i increases because the multiplication rate of the surviving nematodes is P_i dependent, i.e. it increases as P_i is decreased, leading to a 'rebound' in P_f.

P_i *sensitive control measures*

These include crop rotation, fumigant nematicides, some biological control agents and trap cropping. Granular nematicides that reduce/delay invasion could affect both P_i and a, but we assume that their main effect is to reduce P_i. Such control measures tend to be P_i sensitive because they also decrease crop damage (Fig. 3a), thereby increasing the multiplication rate of the surviving wPCN (Fig. 3b). Hence, as is shown in Table 2, where a nematicide is used in a heavily infested field, the P_f can be greater in the treated than the untreated plots, depending on the effectiveness of the nematicide. However, at low P_i when the multiplication rate is at maximum, the P_f is decreased in direct proportion to the reduction in P_i (Table 2). This leads to two important conclusions in relation to the long-term management of wPCN. Firstly, the effectiveness of nematicides,

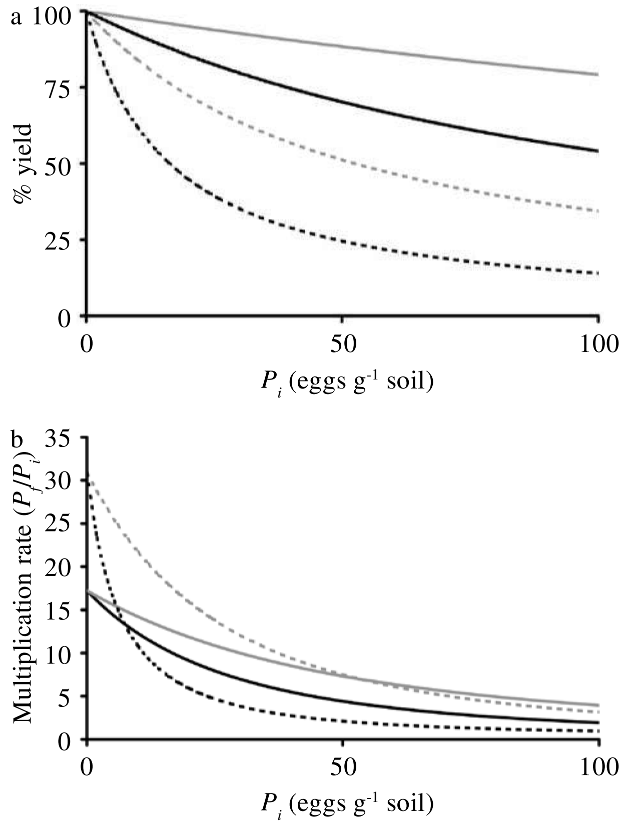

Fig. 1. Effect of increasing wPCN population density (P_i) on (a) the relative yields of an intolerant (Pentland Dell (black lines)) and a tolerant (Cara (grey lines)) cultivar in a loamy (—) or a sandy (– – –) soil, and (b) wPCN multiplication rates on the same soils. Yield is expressed as a percentage of the nematode-free yield.

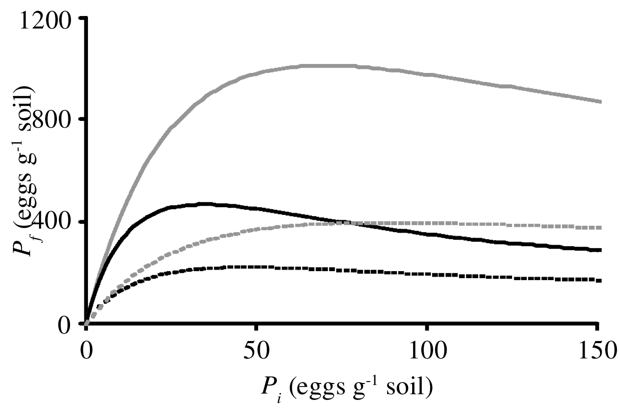

Fig. 2. Effect of increasing wPCN population density (P_i) on the population at harvest (P_f) in a loam (– – –) or an organic soil (—) with a tolerant (e.g. Cara (grey lines)) and an intolerant (e.g. Maris Peer (black lines)) cultivar.

and of other measures that reduce the P_i, tends to decrease as the P_i increases. Secondly, whatever the P_i, it is important to maximise nematicide effectiveness.

P_i *insensitive control measures*

Similar numbers of PCN juveniles typically invade resistant and susceptible cultivars; resistance affects

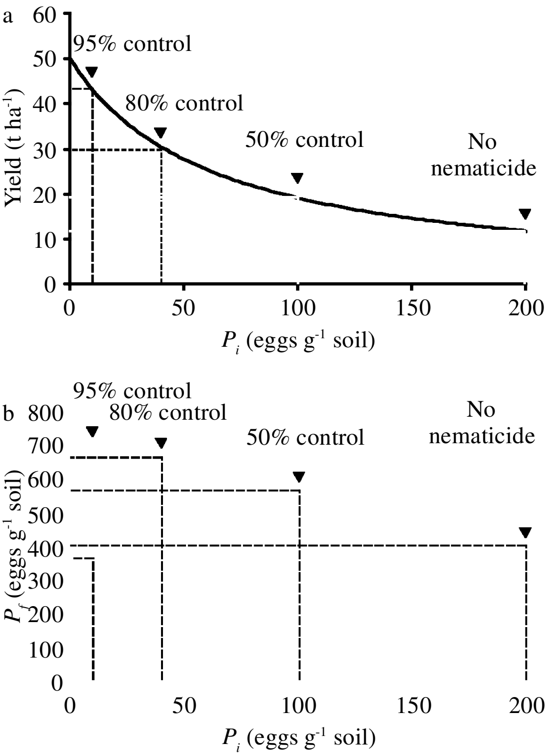

Fig. 3. Effect of a nematicide with different levels of effectiveness (50%, 80% and 95% control) on (a) the yield and (b) the population at harvest (P_f) for Maris Piper in a heavily infested organic soil (P_i = 200 eggs g^{-1} soil).

Table 2. *Influence of the population density at planting* (P_i) *on the population at harvest* (P_f) *when nematicides giving different percentage control are applied to an organic soil growing cv. Maris Piper. Results are computer modelled*

P_i (eggs g^{-1} soil)	P_f (eggs g^{-1} soil) No nematicide	50% control	80% control	95% control
0.2	10	5	2	> 1
2.0	96	50	20	5
20	553	370	180	50
200	402	567	668	370

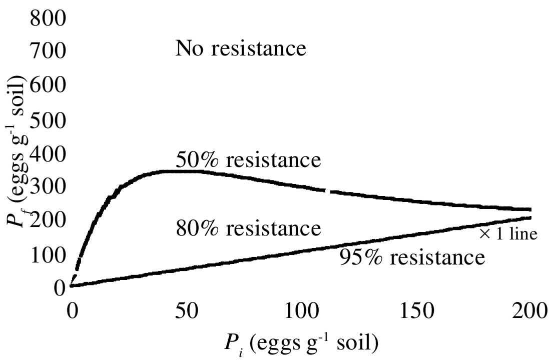

Fig. 4. Effects of increasing resistance on the wPCN population at harvest (P_f) in an organic soil for a cultivar similar in tolerance to Maris Piper.

juvenile development only after invasion. Partially resistant cultivars decrease the proportion able to become female, and this is largely independent of P_i. Consequently, the decrease in P_f across a wide P_i range is directly proportional to the level of resistance (Fig. 4) and, unlike with nematicides, there is no 'rebound' in the post-harvest population at high P_is. However, the effectiveness with which the P_f is decreased is affected by the proportion of eggs that remain unhatched, and this tends to increase as P_i, and damage increase.

Resistance is independent of tolerance, but damage is decreased in some resistant cultivars because PCN females do not develop. For example, Maris Piper is comparatively more tolerant of yPCN (to which it is fully resistant) than of wPCN (to which it is susceptible). Conversely, some resistant cultivars are comparatively intolerant, presumably because of their sensitivity to the damage associated with PCN invasion and/or the resistant response to invasion (Trudgill & Cotes, 1983).

Integration of control measures

Rotation, trap cropping, a fumigant nematicide and a granular nematicide applied at planting all decrease P_i and can be integrated to decrease a high P_i, and hence crop damage. However, they do not necessarily decrease P_f and the population may 'rebound' depending upon the surviving P_i (see Fig. 3b). In contrast, partially resistant cultivars prevent the P_f from 'rebounding' and the integration of rotation and a nematicide with the growing of a partially resistant cultivar provides a powerful means of controlling heavy wPCN infestations (e.g. 100 eggs g^{-1}; Table 3).

With full resistance the P_f largely comprises the unhatched eggs that are 'carried over' to the next potato crop. This ranges from *c.* 10-60%, depending on several factors including the vigour of the potato crop, soil type, and amount of PCN damage. Consequently, granular nematicides do not help further decrease the P_f.

Modelling Future Trends in wPCN

The model was used to explore the effect of various control strategies on wPCN population densities and crop damage over six rotations. A parameter was added to account for wPCN decline between potato crops and the program allowed for changes in tolerance to damage, partial resistance, the decline rate in the rotational years when potatoes are not grown, and the effectiveness of granular nematicides. The values of the core parameters used here to describing crop damage and wPCN multiplication were those derived from the field trial results for susceptible, moderately intolerant cv. Maris Piper.

Susceptible potato – effects of rates of decline and rotation length

Decline rates of wPCN in the field are uncertain and variable (Turner, 1996), but are probably closer to 20% than 30% per annum. Assuming a 20% decline in wPCN each and every year that susceptible potatoes are not grown, rotations of 15 yr and 18 yr respectively were required to maintain the P_i below 5 eggs g^{-1} soil in a sandy and an organic soil respectively. In a loamy soil, the P_i could be maintained below 5 eggs g^{-1} soil in a 13 yr rotation. If the decline rate is increased to 30% per annum, in a sandy soil growing Maris Piper, the P_i can be maintained below 5 eggs g^{-1} by a 10 yr rotation. On a 5 yr rotation in a sandy soil, with a 20% decline rate the P_i stabilised at *c.* 70 eggs g^{-1} (Fig. 5) and tuber yields were decreased by *c.* 80%. The P_i stabilised at *c.* 120 eggs g^{-1} (Fig. 5) when a more tolerant cultivar was grown (e.g. Cara).

Susceptible potato plus rotation and a granular nematicide

The effectiveness of granular nematicides in farmers' fields is also uncertain and variable. Assuming a 20% decline rate and an 80% effective granular nematicide, modelling indicates that rotation lengths can be decreased to 7, 9 and 12 yr in a loamy, sandy and an organic soil respectively if each and every potato crop is treated. On a 5 yr rotation in a sandy soil, P_i progressively increased to 68 eggs g^{-1} (Fig. 5) and yield was eventually decreased by *c.* 45%, even if each and every potato crop was nematicide treated. To maintain the P_i below 5 eggs g^{-1} required a 92% effective nematicide.

Partially resistant cultivars

Currently, only partially resistant cultivars are available to control wPCN. These provide from 10% to > 90% control, depending on their level of resistance and the virulence of the wPCN. Assuming 75% control and a 20% decline rate between potato crops, modelling indicates that a 9 yr rotation is required in a sandy soil to maintain the population below 5 eggs g^{-1}. On a 5 yr rotation, the P_i stabilises at *c.* 20 eggs g^{-1} and yield is decreased by 75%. However, control of wPCN is sustainable, even on a 3 yr rotation, if every partially resistant potato crop is treated with an 80% effective granular nematicide.

Discussion and Conclusions

We are in the middle of a wPCN epidemic that, because of the long time scale, is difficult to recognise. Unlike aerial pathogens where an epidemic can develop in a few days or weeks, it may take 30 yr or more after first introduction for wPCN infestations to increase to a detectable level and cause damage. Already, *c.* 60% of potato fields in England and Wales are detectably infested (Minnis *et al.*, 2002), and it is probable that a substantial proportion of the remainder are "incubating" infestations too small to detect. This wPCN epidemic was initially driven by the widespread growing of resistant (to yPCN only) cv. Maris Piper that enabled wPCN to compete with and eventually replace yPCN. However, now that it is the dominant species, the epidemic is being sustained by current management practices that ensure wPCN is spread between fields

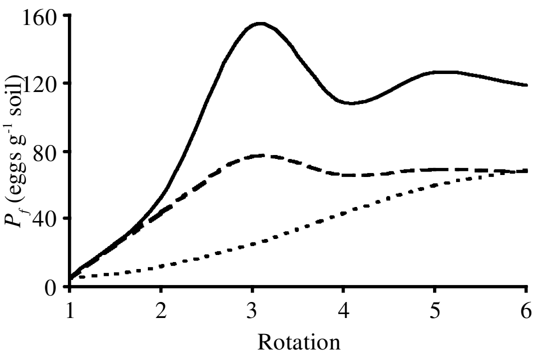

Fig. 5. Effect of an 80% effective nematicide on P_i when cv. Maris Piper is grown in a 5 yr rotation with and without a nematicide. Cara - solid line; Maris Piper untreated - dashed line; Maris Piper treated - dotted line.

Table 3. *Effects on the population at harvest* (P_f) *and on yield (percentage decrease) of integrating different control measures, each of which is assumed to be 80% effective. Results are for cv. Maris Piper (or partially resistant equivalent) modelled for an organic soil,* P_i = *100 eggs* g^{-1} *soil. Between potato crops the population is assumed to decline by 20% per annum*

	Susceptible untreated	Partially resistant untreated	Suseptible + granular nematicide	Susceptible + granular nematicide + fumigant	Partially resististant + granular nematicide + fumigant
Effective P_I (eggs g^{-1} soil)	100	100	20	4	4
Yield (% of PCN free)	38%	38%	76%	94%	94%
P_f (eggs g^{-1})	567	136	553	180	36
P_i (eggs g^{-1}) 5 yr later	189	45	181	59	12

and that provide the conditions for populations to increase. These changes have also led to wPCN becoming a greater problem in those parts where it has always been the dominant species (e.g. northern England).

The future rate of increase of wPCN can only be deduced by what has gone before, or by modelling. There is persuasive evidence based on both approaches to suggest that wPCN is not being controlled and is progressively increasing. If 64% of the 118,000 ha planted with ware potatoes in 2001 in England and Wales were infested with PCN (Minnis *et al.*, 2002), this equates to about 75 000 ha being grown on detectably infested land. However, in 1999, less than half of this (*c.* 25 000 to 30 000 ha) was nematicide treated for control of PCN. Median levels of infestation in the survey by Minnis *et al.* (2002) were 10 eggs g^{-1} soil for soils infested with wPCN. Potatoes planted in such fields are likely to suffer some damage and damaging populations are, once created, difficult to manage because of their ability to persist between potato crops and to "rebound" following density-sensitive control measures.

Control of wPCN is proving more difficult than that of yPCN. Its heterogeneity, evident from molecular studies (Armstrong *et al.,* 2000*b*; Blok *et al.,* 1997, 1998; Burrows *et al.,* 1996), has frustrated attempts to breed fully resistant cultivars. This heterogeneity is evident in the range of virulence (from 4% to > 90%) of UK populations on standard clones with partial resistance derived from *Solanum vernei* (Blok *et al.,* 1997; Phillips & Trudgill, 1998). Although there has been more than one introduction of wPCN into the UK (Armstrong *et al.*, 2000*a*), much of this variation appears to be due to fragmentation (genetic drift) of the most widespread of the introduced gene pools during its subsequent spread within the UK (Phillips *et al.*, 1998a). This heterogeneity also allows for progressive selection for increased virulence when populations of wPCN are repeatedly multiplied on the same resistant clone (Turner, 1990; Schouten & Berniers, 1997; Blok *et al.*, 2000).

Modelling is used here as a means of anticipating future trends in wPCN. Our model is based on the results of field trials but its predictions regarding future trends depend on assumptions about the effectiveness of current control strategies for which we have insufficient data. This particularly applies to the effectiveness of nematicides in reducing wPCN multiplication. Nematicides are applied primarily to protect wPCN-infested crops from damage, but it is increasingly important that they also control wPCN multiplication. Modelling suggests that they do the former more effectively than the latter, especially at high population densities because of population "rebound". It also shows that wPCN multiplication is decreased most effectively when nematicides are applied to low rather than high populations.

Nematicides are currently applied to less than 40% of the wPCN-infested area, and are typically concentrated on the most heavily infested fields. Where no nematicide is applied, both modelling and experience indicate that wPCN will increase greatly. Even where a nematicide is applied, unless it is > 90% effective, modelling indicates that the population of wPCN will probably still increase, though more slowly than if no nematicide had been used. There are, however, few data on the effectiveness of commercially applied nematicides, but recent field results indicate only poor control of PCN multiplication. In three replicated field trials (Grove, 1999), compared with the untreated, the nematicide oxamyl decreased P_f in one (from 448 eggs g^{-1} to 124 eggs g^{-1}) but had no effect in two (means 209 eggs g^{-1} and 207 eggs g^{-1} for untreated and treated respectively). Similarly, in four fields in 2001 planted with susceptible cultivars (mean P_i = 15 eggs g^{-1}), farmer-applied nematicides were only partially effective. The mean population at harvest (P_f) was decreased from 272 (mean of 10 untreated plots per field) to 171 eggs g^{-1} soil (mean of 10 treated plots per field). Consequently, an increased understanding of the factors that determine the effectiveness of farmer-applied nematicides is required.

The effectiveness of rotation as a means of controlling wPCN is determined by the length of the rotation and the annual rate at which the population declines. Decline rates are difficult to determine but current information indicates are they are low (< 30% per annum) and independent of P_i. In the farmer trials described above, for the post-harvest wPCN infestations of 272 eggs g^{-1} and 171 eggs g^{-1} to decline to the initial P_i of 15 eggs g^{-1} soil would take 9 and 8 yr respectively for untreated and treated assuming a 30% annual decline rate, and 14 and 12 yr assuming a 20% decline rate. Consequently, wPCN increase is unlikely to be controlled by current management involving 5-7 yr rotations, even where nematicides are used.

Growing partially resistant cultivars provides the third main option for wPCN control. Their effectiveness varies with their level of resistance and the corresponding virulence of the wPCN, but only with very avirulent populations will they give > 80% decrease in wPCN multiplication rate compared with a susceptible cultivar. With current rotations and assuming a 20% annual decline between potato crops, this is insufficient to prevent wPCN from increasing and causing damage. However, the effect of partial resistance on wPCN multiplication is insensitive of P_i and this makes it particularly effective when combined with rotation and a granular nematicide. Unfortunately, in 2001 only 8% of the potato area was planted with partially resistant cultivars (G Gagen, personal communication), and much of this (*c.* 40%) was on land not known to be wPCN infested (Minnis *et al*., 2002).

If the analysis above is realistic, then action is required now to prevent the wPCN problem from progressively increasing. Uninfested land needs to be managed to minimise the opportunities for the introduction of wPCN, and soil sampling and cyst extraction procedures need to be appropriate to the purpose (Trudgill *et al*., 2001). In infested land, greater use of integrated control strategies based on partially resistant cultivars is a priority. Despite the difficulties associated with resistance to wPCN being quantitatively inherited, the breeding of more resistant, commercially attractive cultivars is highly important. Rotations need to be lengthened and alternative control measures, including trap cropping with cultivars bred for the purpose, need to be developed to the point where they are commercially attractive. In addition, those buying potatoes, whose choice of cultivar determines what producers grow, need to recognise the increasing threat posed by wPCN, and the need to favour partially resistant cultivars.

Acknowledgements

The British Potato Council, the Scottish Executive Environment and Rural Affairs Department, the Biotechnology and Biological Sciences Research Council, and the Department of Environment, Farming and Rural Affairs supported this work. David Garthwaite of the Pesticide Usage Survey Group is thanked for providing information on nematicide use and Guy Gagen for the data on the areas and yields of potatoes in 2001.

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