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Improving a pest management tool for scenario analysis of economic populations of *Globodera pallida*

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Summary – *Globodera pallida* is the most damaging pest of potato in the UK. This work underpins enhancement of a well-established, web-based scenario analysis tool for its management by recommending additions and modifications of its required inputs and a change in the basis of yield loss estimates. The required annual decline rate of the dormant egg population is determined at the individual field sample level to help define the required rotation length by comparing the viable egg content of recovered cysts to that of newly formed cysts for the same projected area. The mean annual decline was 20.4 ± 1.4% but ranged from 4.0 to 39.7% annum^{-1} at the field level. Further changes were based on meta-analysis of previous field trials. Spring rainfall in the region where a field is located and cultivar tolerance influence yield loss. Tolerance has proved difficult to define for many UK potato cultivars in field trials but uncertainty can be avoided without detriment by replacing it with determinacy integers. They are already determined to support optimisation of nitrogen application rates. Multiple linear regression estimates that loss caused by pre-plant populations of up to 20 viable eggs (g soil)$^{-1}$ varies from *ca* 0.2 to 2.0% (viable egg)$^{-1}$ (g soil)$^{-1}$ depending on cultivar determinacy and spring rainfall. Reliability of the outcomes from scenario analysis requires validation in field trials with population densities over which planting is advisable.

Keywords – decline rate, improved yield loss model, pest management, potato cyst nematode, *Solanum tuberosum*, tolerance, yield.

The two potato cyst nematodes (PCN) *Globodera pallida* Stone and *G. rostochiensis* (Wollenweber) Behrens are the most damaging crop pests of potato in the UK (Agriculture and Horticulture Development Board; AHDB, 2021a). The overall cost to the UK potato industry is estimated to be about £50 million year^{-1} (Bhattarai *et al.*, 2009). That figure is considerably higher across Europe with widespread damage in many other potato-growing countries (CABI, 2019). In 2016, PCN was detected in 48% of potato fields in England and Wales with just *G. pallida* present in 89% of infested fields and occurring in a further 6% where both species were present (AHDB, 2018). *Globodera pallida* normally completes only a single substantial generation on a potato crop with a life cycle duration of 9-11 weeks depending on environmental conditions (Ebrahimi *et al.*, 2014; Jones *et al.*, 2017; Kaczmarek *et al.*, 2019). Several cultivars favoured by UK growers provide qualitative resistance to *G. rostochiensis* by reducing population densities to challenge future potato crops. This effective resistance has probably reduced the prevalence of that species in the UK (Trudgill *et al.*, 2014; AHDB, 2015). By contrast, among the ten most planted cultivars in the UK only 'Innovator' provides effective resistance to *G. pallida* (ranked 8 on an increasing resistance scale from 1 to 9; AHDB, 2020a). It contributed only 3.05% to the area planted with potato in Great Britain in 2020 (AHDB, 2020b) and is grown for the French-fry market (AHDB, 2011). A second desirable but complex genotypic trait is tolerance. It is divided into two main categories of tolerance and intolerance (Evans &

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Haydock, 1990; Trudgill, 1991) often with sub-categories (AHDB, 2015). These values indicate the relative yield loss under challenge by a given population of PCN. A tolerant cultivar offers the important benefit of reducing yield loss of a potato crop infected with PCN but, unless it is also resistant, it is likely to enhance multiplication of the nematode (Trudgill *et al*., 2003) that might damage future potato crops.

The pest management of an established field infestation of *G. pallida* is best achieved using integrated control. PCN eggs remain dormant within the cyst (tanned body wall of the former female) but there is an annual decline in their density when potato plants are not present due to spontaneous hatch and some mortality imposed by natural enemies (Hockland *et al*., 2016). Consequently, rotation with crops other than potato results in a gradual, density-independent decline in the dormant population available to challenge the next potato crop (Trudgill *et al*., 2003).

The relationship between yield and density of PCN at planting has been described by several different mathematical relationships. A curve has been proposed that both accommodates plant compensation for a limited nematode challenge and competition effects between the parasites at high densities (Seinhorst, 1965). Other curved and linear fits have been proposed (Elston *et al*., 1991) with the latter considered appropriate when a moderate infestation causes slight damage (Trudgill *et al*., 2014), as prevails for the field work analysed in the current work.

A personal computer-based decision support system for the control of plant-parasitic nematodes has been developed in The Netherlands (NemaDecide; Been *et al*., 2006), dealing with PCN control on seed, starch and ware potato crops in use in that country since 2006.

A parallel UK effort introduced a computer-based model for population growth and damage of PCN for UK potato growers and other stakeholders. It is not intended as a decision support system but is an educational tool for scenario analysis. It was developed (Ehwaeti *et al*., 2000) and made widely available by The British Potato Council, the predecessor of AHDB, initially as a freely available compact disc-based programme. This was subsequently replaced in 2015 by the current web version with presentation improvements as a 'PCN calculator' with emphasis on *G. pallida* (AHDB, 2021b). The inputs required of the user are: *i*) soil type; *ii*) viable eggs (g soil)$^{-1}$ prior to planting ($P_{\rm i}$); *iii*) length of rotation; *iv*) estimated maximum yield in the absence of PCN; *v*) tolerance and resistance values of the cultivar entered manually or selectable for 19 cultivars; *vi*) percentage control achieved by any application of a granular or fumigant chemical control; and *vii*) the annual decline rate of the population. One or more of these values can be altered for a 'what if' analysis. The relevance of these factors for control of PCN have been reviewed with regard to the recent tool (AHDB, 2018). The key outputs from the model are the expected loss of yield and the expected post-harvest population of *G. pallida*. It estimates the longer term consequences of repeated planting of the same or different cultivar with a changed or unchanging duration of rotation on both future projected yield and PCN population density.

The current work reports effort to enhance the calculator. Utility of tolerance is limited by the relatively few UK cultivars for which this factor has been determined. This often involves replicated field trials using a factorial approach of yields with and without chemical control (Evans & Haydock, 1990). Unfortunately, considerable variability sometimes limits the reliable assignment of tolerance categories to a cultivar (Keer, 2013) without several field trials. This questions the cost effectiveness of the approach given the large number of cultivars grown in the UK for which tolerance values are required. Various mechanisms have been suggested to contribute to tolerance, including size of the root system, compensatory root growth, delayed plant senescence, and enhanced water and nutrient uptake (Trudgill, 1991). For instance, the tolerance of 'Cara' is considered to be related to its large haulm and late maturity (Lane & Trudgill, 1999). It is considered, therefore, that vigorous and late-maturing varieties with strong top growth are often tolerant because they are able to compensate for loss in leaf area caused by nematode damage (AHDB, 2019). Thus, the current work considers whether or not determinacy provides a proxy for tolerance. The determinacy of a cultivar is a measure of the extent of leaf appearance after the first flowers occur (Allen & Scott, 1992) and, physiologically, the extent to which the canopy retains priority for carbon after tuber initiation (Dathe *et al*., 2014). It has relevance in determining appropriate nitrogen fertiliser regimes with values currently assigned to 91 cultivars grown in the UK (AHDB, 2021c). Like tolerance, determinacy is assigned to one of four categories.

This work investigates establishing spring rainfall as an environmental factor that influences the tool's predictions. Determinacy is proposed as a widely available proxy integer for tolerance. A simple method (Atkinson *et al*., 2001) for routine determination of the annual rate of decline of *Globodera* populations is applied to provide an estimate of the likely annual decline rate of any population of *G. pallida* between potato crops. The overall aim of the work is to enhance the precision and utility of a future UK tool for scenario analysis to underpin management of *G. pallida* by various stakeholders.

Materials and methods

Decline rate estimates

The approach is based on the shape of a cyst of *G. pallida* approximating to a sphere, which has a defined relationship between its projected area (πr^2) and its volume ($4/3\pi r^3$). Each egg it contains has a defined volume and so a calibration can be achieved between the projected area and the maximum possible egg content of newly formed full cysts of known projected areas (Urwin *et al*., 1995). The actual egg content provides an estimate of the loss of viable eggs from that cyst.

Samples of 27 field populations of *Globodera* collected for pre-plant population estimates in other work were kindly donated for the current study. For each sample, the projected area of 30 randomly selected individual cysts representing *ca* 40% of the cysts recovered was measured before the egg content for three groups of ten of the same cysts was determined. The samples were taken from four of the six meteorological areas of England (Met Office, 2021) as follows: 15 from east and northeast England, eight from the Midlands, two from East Anglia and two from the southeast and central south England. The samples were collected as pre-plant populations 1-12 years post the last potato harvest.

Cysts were extracted from dried soil samples using standard methods (Shepherd, 1972). A Fenwick can was used to collect floating debris with cysts from air-dried soil onto a 250 μm sieve for transfer in water to filter paper and their collection from a strand line. The cysts were picked from the sample under a stereo microscope. All populations were analysed using PCR with species-specific primers to determine the species present in each sample. Ten cysts from each sample were mechanically disrupted with a micropestle in 50 μl worm lysis buffer (50 mM KCl, 10 mM Tris pH 8.2, 2.5 mM $MgCl_2$, 60 μg ml^{-1} proteinase K, 0.45% NP40, 0.45% Tween 20 and 0.01% gelatine; Castagnone-Sereno *et al*., 1995). Samples were frozen at -80°C for 10 min and incubated at 60°C for 60 min, followed by 95°C for 15 min to deactivate the proteinase K (Castagnone-Sereno *et al*., 1995). PCR was carried out on 1 μl of this template DNA with *G. pallida* and *G. rostochiensis* specific primer sets, ITS5/PITSp4 and ITS5/PITSr3, respectively (Bulman & Marshall, 1997). MyTaq polymerase (Bioline) was used according to the manufacturer's instructions and under the following conditions: 94°C for 60 s and 40 cycles of 94°C for 10 s, 55°C for 30 s, 72°C for 30 s and 72°C for 5 min. Presence of a PCR product with primer set ITS5/PITSp4 (265 bp) or ITS5/PITSr3 (434 bp) confirmed the presence of *G. pallida* or *G. rostochiensis*, respectively.

Individual cysts were imaged initially as previously described (Jones *et al*., 2017) using a Leica MZ16 stereo microscope and a MicroPublisher 3.3 RTV colour camera (Qimaging). The projected surface area of each cyst was measured in mm^2 using Image-Pro Analyser 7.0 (Media Cybernetics) standardised with a calibration slide with a linear scale and a 0.6 mm diam. circle. Subsequently, it was found that acceptable accuracy (data not shown) could be achieved using a simple digital microscope (Dino-lite Model AM4113T (R4); AnMo Electronics) attached to a personal computer (PC). These captured images were analysed on the PC using a public domain image processing and analysis programme (ImageJ; developed by NIH, USA https://imagej.nih.gov/ij/). The egg content of groups of *ca* ten cysts was obtained after the area of each had been measured individually. Egg counts were made by standard methods involving a brass plate with a glass rod to open cysts before releasing their egg content into 10 ml of water by shaking in a tube. An aliquot of 1 ml was transferred to a counting slide observed under a stereo microscope (Shepherd, 1972) and viable eggs assessed visually. A linear regression between viable egg content and the projected area of a wide size range of newly formed cysts has been established and used previously (Urwin *et al*., 1995; Jones *et al*., 2017). The regression equation used was used in this work of the number of viable eggs cyst^{-1} $= (1333.2\times$ cyst area in mm$^2 - 52.829$; $R^2 = 0.918$) was determined for previous work (Jones *et al*., 2017).

Yield loss estimates

Meta-analysis of six extensive field trials for yield loss with a range of cultivars to determine tolerance values was analysed. The trials involved 12-14 cultivars each in 2005, 2006 (Keer, 2007), 2010, 2011 and 2012 (Keer, 2013) with some changes in cultivars grown between years. Six of the trials were planted in April and one in early May. A total of 21 susceptible cultivars challenged by *G. pallida* (see Supplementary Table S1) with determinacy were analysed from 75 trial plots in the seven trials over

5 years. Only 16 cultivars planted in 50 plots had known tolerance values.

The design for the trials was to compare yield in the presence and apparent absence of *G. pallida*. This takes no account of any residual population after chemical control (Pi_c). A previously defined relationship (Model D; Phillips *et al.*, 1991) determines the fecundity and establishment factor (*f'*) of *G. pallida*, which is cultivar-specific for a given site. It can be determined when the pre-plant (P_i) and post-harvest (P_f) values are known. If the P_f is also known for the chemical control treatment, back calculation allows the $P_{i,c}$ to be estimated for any *f'*. This allows minor adjustment for yield losses egg^{-1} (g soil)$^{-1}$ to be made based on the likely difference in P_i of the two treatments.

Cultivar related factors were included in the analysis when known for determinacy, drought tolerance, resistance to *G. pallida* and to *G. rostochiensis*. Environmental factors were the proportion of sand contributing to soil texture, day degrees above a threshold taken to be 7.2°C (Wohleb *et al.*, 2014) during potato crop growth, spring rainfall (in March, April and May), rainfall both during the crop overall and sub-divided into 30 day periods post-planting, and sunshine hours during the cropping season. The lapsed years since the last potato crop added new eggs to the population and viable eggs cyst^{-1} were also factors. Rainfall, temperature and sunshine hour values from the closest weather stations to the field trials were obtained from the national weather service of the UK (Met Office, 2012). They were 4-16 miles (6.4-25.7 km) from the trial sites. Regional spring rainfall values for the past 30 years were also obtained from this source as they are freely available in contrast to individual weather station data.

Statistical analyses

All data were analysed using a standard statistical package (SPSS v26; IBM). Analysis of linear regression followed recommended approaches (Field, 2017) with retention of variables that contributed significantly ($P < 0.05$) to the regression fit. The variance-inflation factors, collinearity diagnostics based on Eigen values and Akaike information criteria were used to verify the retention of certain variables.

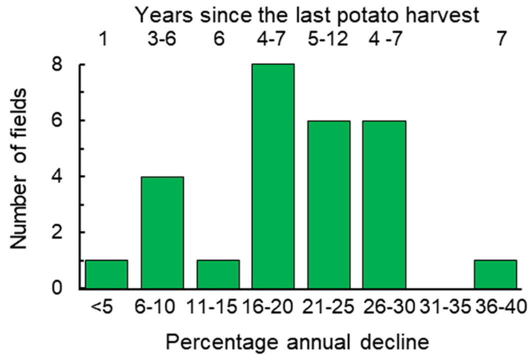

Fig. 1. The estimated percentage annual decline rate for dormant populations of *Globodera pallida* sampled from 27 fields in England with the range in years between 1 and 12 since the last potato crop given above each bar. The decline rates are estimated from measurement of projected surface area of 30 cysts and the egg content measured for three sub-groups of ten of these cysts.

Results

Annual decline rate of *G. pallida* in the absence of potato

Only *G. pallida* was detected by PCR analysis as present for all the populations used to measure decline rates. The decline rates ranged for the 27 fields analysed from 4.0 to 37.0% annum^{-1} with a mean decline rate of 20.4 ± 1.4% (Fig. 1) and a normal distribution (Skewness = −0.946, Kurtosis, 0.311, Shapiro-Wilk normality test, $W = 0.977$, $P = 0.662$).

Cultivar characteristics

Field data (Keer, 2007, 2013) was used to compare the effects on yield of *G. pallida* population density (ranging from 11.7 to 21.0 viable eggs (g soil)$^{-1}$) for 47 plots with 14 cultivars for which both determinacy and tolerance integers (1-4) are known (see Supplementary Table S1 for their names). One way ANOVA established significant differences in loss egg^{-1} g^{-1} in comparisons of both sets of integers (Fig. 2). Multiple linear regression provided a significant relationship between yield loss viable eggs^{-1} (g soil)$^{-1}$ and determinacy ($P < 0.001$; adjusted $R^2 = 0.381$). The procedure selected determinacy over tolerance, which also did not enhance the fit when added as an additional independent variable. The data indicate that tolerance is not a better predictor than determinacy of the impact on harvested yield of *G. pallida*.

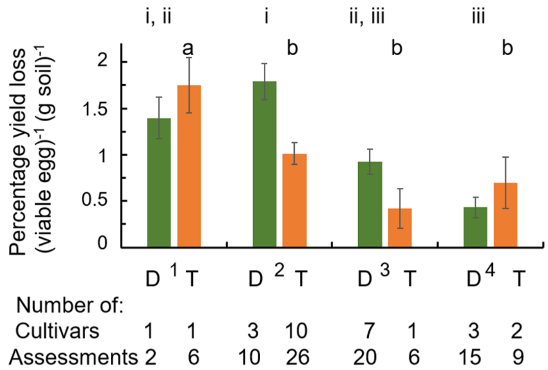

Fig. 2. The percentage yield losses (viable egg of *Globodera pallida*)$^{-1}$ (g soil)$^{-1}$ for cultivars in the field trials for which determinacy (D) and tolerance (T) values are known (see Supplementary Table S1 for a list of the cultivars). Tolerance values are: 1: very intolerant; 2: intolerant; 3: tolerant: 4: very tolerant. Determinacy values 1-4 are for an increasing longevity of haulms. The number of cultivars and assessments made in the trials for each category is given. Values are means ± standard error. Significant differences ($P < 0.05$; SNK test, one way ANOVA) are indicated for both determinacy (three SNK subsets i ii and iii) and tolerance (two SNK subsets, a and b). Fourteen cultivars included have known determinacy and tolerance integers but often different values on the two scales (see Supplementary Table S1 for details).

Improving the predictive value of yield loss caused by *G. pallida*

The recent AHDB calculator did not provide close agreement with yield loss (viable eggs)$^{-1}$ (g soil)$^{-1}$ by soil texture in a set of field trials. The categories given in the results for the field data (Keer, 2007, 2013) and the equivalent model values (in parenthesis) were a fine sandy loam (loamy sand), fine sandy silt (light silt), sandy loam (loamy sand) and silt loam (light silt). The model predictions severely overestimated losses for both light silt for which there were many assessments and sandy loam (Fig. 3A). The model also overestimated losses for all four categories for all 14 cultivars trialled for which tolerance values are available in the model (Fig. 3B). This outcome resulted in our effort to improve the prediction of yield loss.

A range of cultivar-related factors was considered for the field data (Keer, 2007, 2013). They were determinacy (values known for 21 cultivars in the trials), drought tolerance (values known for 20 cultivars) and resistance to *G. pallida* and to *G. rostochiensis*. A range of environmental factors was also considered. These were: accumulated sun hours during cropping, whether or not irrigation was used,

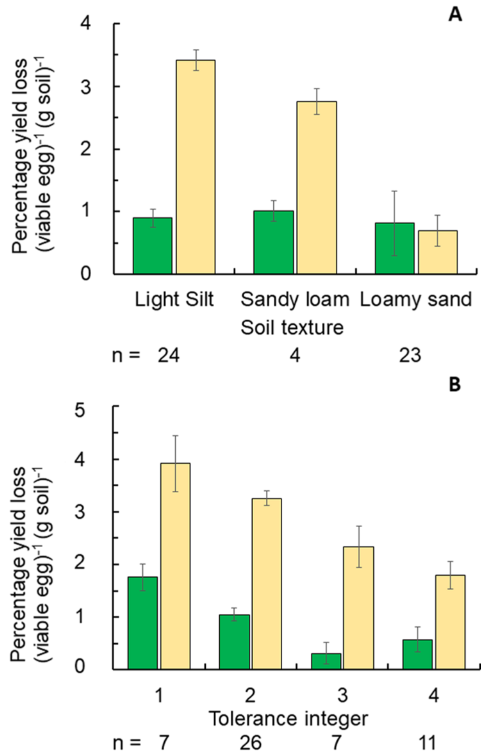

Fig. 3. Paired comparisons of values for yield loss (viable egg of *Globodera pallida*)$^{-1}$ (g soil)$^{-1}$ (left bar) in the analysed field trials, and losses predicted by the AHDB model (right bar) for A: Six trials for different soil textures; B: Five trials for *G. pallida* with the cultivar tolerance integers as given by the current model. Values are means ± standard error. The number of assessments made in the trials for each category is given (n).

day degrees above 7.2°C during crop growth, accumulated rainfall for the following days after planting: 1-30, 31-60, 61-90, 91-120 (Met Office, 2012), and the proportion of sand from the soil texture given for the site. The nematode population factor was the lapsed years since the previous potato crop. Only factors that made a significant contribution to the multiple linear regression ($P < 0.05$) were retained.

The revised relationship provides an estimate of the losses (viable egg)$^{-1}$ (g soil)$^{-1}$ based on the field trial data for the range of spring rainfall values across the six trials involving *G. pallida* (Keer, 2007, 2013; Fig. 4A). Estimating likely rainfall with either long-term values for the weather station closest to a field trial site or those for the corresponding UK meteorological region (Met Office, 2012) provided similar model outcomes. Both determinacy and spring rainfall contributed significantly to the multiple linear regression ($P < 0.001$ and $P <$

0.01, respectively). The predicted loss (viable egg)$^{-1}$ (g soil)$^{-1}$ at planting is provided for determinacy values and the spring rainfall range recorded in the field trials (Fig. 4B). Together they explained 35% of the variation (adjusted $R^2 = 0.352$) in the data set with determinacy making a larger contribution (R^2 change $= 0.301$) than spring rainfall (R^2 change $= 0.069$). A similar analysis substituting tolerance for determinacy did not achieve statistical significance presumably as a smaller data set with fewer cultivars was available. The predicted losses ranged from 0.1% (viable egg)$^{-1}$ (g soil)$^{-1}$ for a cultivar with a determinacy of 4 in a season with the highest recorded spring rainfall of 220.8 mm to about 20× that value (2.1% (viable egg)$^{-1}$ (g soil)$^{-1}$) when the cultivar had a determinacy of 1 and the spring rainfall was just 79.4 mm.

Discussion

This work considered revision of required inputs into the recent PCN calculator of AHDB. Change would require two new inputs from the user *i.e.*, determinacy as proxy for tolerance and the region in England or Wales of interest from which the approximate latitude and mean historic spring rainfall could be derived from imbedded values in any future revised model. The main findings from the current work are discussed in the following sections.

Decline rates

Determining the outline area of individual cysts using an inexpensive digital microscope before they are opened for a viable egg count allows the apparent decline rate of a field population to be determined after years without a potato crop by a single measurement. This information could be gained during pre-plant population estimates of the nematode. Occasionally, more than a minority of cysts in the soil sample may originate from earlier potato crops than the most recent. Often a useful sign of some relatively empty cysts is a greater translucence under transmitted light than the remainder. A second indicator would be an apparently high decline rate because not all cysts in the sample contributed substantially to the egg count. Any history of use of fumigation that kills unhatched juveniles, trap crops that induce unproductive hatch or a high frequency of potato cropping would be pertinent. In those cases, each cyst for which an outline area is measured should be opened individually for a viable egg count and

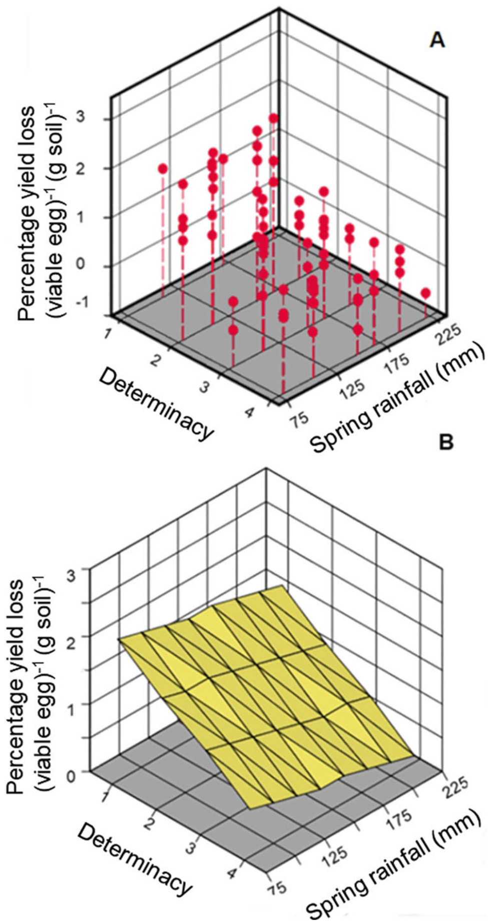

Fig. 4. Meta-analysis for the relationship of percentage yield loss of a potato cultivar (viable egg of *Globodera pallida*)$^{-1}$ (g soil)$^{-1}$ at planting with both the determinacy of the cultivar grown and spring rainfall (see the supplementary file for a list of the 21 cultivars included in the analysis). A: The data points for each cultivar from six field trials; B: A surface plot based on linear regression of the same data back-transformed from a logarithmic transformation. Details of the linear regression equation are:

$$\% \text{ yield loss (viable egg)}^{-1} \text{ (g soil)}^{-1} = b_0 + (b_1 \times \text{ determinacy value}) + (b_2 \times \text{ rainfall in mm})$$

Coefficients	Estimate (± SE)
Intercept (b_0)	0.02894 ± 0.00322***
Determinacy (b_1)	−0.00465 ± 0.000795***
Spring Rainfall (b_2)	−0.00004237 ± 0.00001492**

Probability (based on t value): ***, $P < 0.001$ and **, $P < 0.01$.
Residual standard error: 0.006005 with 74 degrees of freedom.
Multiple R^2: 0.3694, Adjusted R^2: 0.3523.
F-statistic: 21.67 with 2, 74 df, P value: 3.9e−08.

only included if the content is not substantially less than most others in that sample. The decline of the dormant egg population of *Globodera* spp. in the field in the absence of additional control measures is normally exponential (Whitehead & Turner, 1998; Atkinson *et al*., 2001; Trudgill *et al*., 2003). The mean apparent decline rate of *G. pallida* was 20.4 ± 1.4% (viable eggs)$^{-1}$ year^{-1}. This compares closely with a previous estimate of 19.5 ± 1.5% for populations in microplots (Stone *et al*., 1993) and about 20% in fields (Lane & Trudgill, 1999). Values varied considerably among the sites ranged from 4.0 to 39.7% annum^{-1} (Fig. 1). Previous work has also detected differences ranging from 14.5-33.5% for four sites assessed over 2-4 years (Trudgill *et al*., 2014). Detection of decline rates that deviate considerably from 20% annum^{-1} is of value. High decline rates might arise from an adventitious benefit from crop protection activities. These include the use of fosthiazate to control wireworms (Lewis *et al*., 2016) or agronomic practices not directed at PCN control, such as the non-host crops selected for the rotation (CABI, 2019). The results indicate young unhatched juveniles may show a dormancy in the field as reported before for PCN (Gonzalez & Phillips, 1996). The frequency of this effect in UK requires further study. Populations with low decline rates over several years raise considerable issues for rotational control and so their detection by a single measurement before a decision to plant potatoes is advantageous. Adding an estimate of the annual decline rate to a pre-plant population estimate would add little to the cost of extension services. Values for decline rates at the individual field level have not been routinely available before as they have required a series of viable egg counts for each population over several years (Turner, 1996; Trudgill *et al*., 2014). Assuming fields with persistent populations are retained for potato cropping, advice may include application of a pre-plant nematicide or deferring potato crop planting until a second population estimate is made in a subsequent year, possibly after growing a biofumigant crop. The frequency of low decline rates in the UK needs further study. This may identify contributing environmental factors but the possibility that this is due in part to genomic variation among populations of *G. pallida* also requires investigation.

Yield losses

The yield losses, (viable egg)$^{-1}$ (g soil)$^{-1}$, were linear over the limited range of pre-plant nematode densities analysed in this study. Previous work has suggested an empirical approach to defining losses is sufficient for field data given its variability (Ferris, 1978; Brown & Sykes, 1983; Evans & Haydock, 1990). Further work is required to define the full range over which this simple, practical approach applies. The risk of substantial variation in yield loss having impact on the profitability of the potato crop increases with the pre-plant population (P_i). For this reason, predictions of yield losses and population change of *Globodera* over several rotation courses may be inappropriate although this is provided by both the recent PCN calculator of ADHB and NemaDecide. Any population estimate has a variance that defines its precision (Binns & Nyrop, 1992) so errors in the P_i influence the predicted post-harvest population, which will also be affected in the field by environmental factors. The errors introduced are compounded when estimates are made over several rotation courses. This also applies to yield losses over several rotations. The accumulated error is likely to be considerable given that predictions by the recent calculator did not provide a high concordance with yield losses in the field for a single potato crop. Scenario analysis over more than a single crop prediction is likely to mislead the user with false precision.

Tolerance and determinacy as its proxy value

Work in The Netherlands concluded that the tolerance value of a cultivar can be obtained reliably from pot experiments in a glasshouse plus one field experiment for all varieties under the same conditions (Been *et al*., 2006). A different view is that tolerance evaluation is best performed in the field at several uniformly infested sites so that environmental effects can be considered (Hockland *et al*., 2016). Considerable effort to date has not enabled many UK cultivars to be assigned reliably to tolerance classes. Attempts to define the tolerance of cultivars in such field trials by comparing yields with and without chemical control have provided equivocal results (Keer, 2013). One cause is the assumption that a nematicide application prevents all yield loss, whereas this may not be achieved even with populations of the order analysed in this work of 11.2-20.0 eggs (g soil)$^{-1}$. Soil type or other differences between sites may also influence tolerance estimates (Trudgill *et al*., 2014). Consequently, several field trials may be required to define the likely tolerance of a cultivar for a range of soil types. As a result, considerable effort and cost is required to define tolerance values for the many cultivars on the UK market. We suggest that determinacy can be used as a proxy for tolerance without detriment until the latter can be reliably determined in UK fields. Like tolerance, determinacy provides a 1-4 integer scale and is defined as the ability of a cultivar to maintain yield when challenged by *G. pallida* with a similar reliability to tolerance (Fig. 4). It has agronomic value in optimising application rates of nitrogen fertilisers and as a consequence is already defined for 91 of the cultivars grown in the UK (AHDB, 2021c). The determinacy value relates to the growth period after first flower formation and it is likely to influence the duration of root growth (Allen & Scott, 1992). Damage by the invading juveniles of *Globodera* is considered to impair the function of the root system so reducing top growth of the potato plant (Trudgill, 1987). The increased growth period of potato plants associated with increasing determinacy provides more opportunity for the plant to compensate for damage of *G. pallida* to its root function given this nematode normally has only one generation per crop. Also some high determinacy value cultivars, *e.g.*, 'Cara', are vigorous (Evans & Haydock, 1990) and produce a large root system. This is likely to reduce the pathological impact by reducing the relative density of infective juveniles on a unit root biomass basis. Earlier work concluded that there is a relationship between maturity date (determinacy) and tolerance (Evans & Franco, 1979) and that early cultivars are generally less tolerant than those that are main crops but exceptions were considered to occur (Trudgill & Cotes, 1983).

Modification of yield loss estimates

Neither soil texture nor tolerance reliably predicted actual losses recorded in field trials using the recent AHDB model (Fig. 3). Yield losses were reduced significantly by increasing determinacy and historic spring rainfall but not by any others of the wide range of environmental and genotype factors available to be considered in this work. The spring rainfall period in this work preceded first irrigation of the trials, which would moderate any plant stress from lack of rain. Water uptake in early stages of potato plant growth is reduced by *Globodera* (Haverhort *et al*., 1991). This is likely to impair the high transpiration rate that prevails at this growth stage (Nelson & Hang, 1975) suppressing yield (Haverkort *et al*., 1990) by delaying the progress of canopy growth (Aliche *et al*., 2018). The multiple regression of yield with determinacy and spring rainfall defined 35% of the variation in the data set (Fig. 4B). It would be of value for future work to identify other factors that contribute to the recorded variation. This would require collection of a range of abiotic data for analysis. For instance, soil temperatures above *ca* 17.5°C reduce the reproductive success of *G. pallida* (Jones *et al*., 2017). Future increases in soil temperatures with climate change may impact on the predicted reproductive success of this nematode and possibly yield loss. In addition, biotic factors need to be considered. They include the normally patchy distribution of PCN in fields (Hockland *et al*., 2016) and both pathogens and pests that interact with PCN on potato, including *Rhizoctonia solani* and *Myzus persicae* (Back *et al*., 2006; Hoysted *et al*., 2017, 2018).

The cultivars grown were not the same for the six trials with *G. pallida* (Keer, 2007, 2013) but the mean loss (viable egg)$^{-1}$ (g soil)$^{-1}$ for all cultivars that were planted did not differ significantly among sites (*a priori* contrast, one way ANOVA). The grand mean losses for all cultivars grown was 1.18 ± 0.26% (viable egg)$^{-1}$ (g soil)$^{-1}$ after correction for incomplete control by the nematicide. Figures provided for yield and pre-plant density of *G. pallida* for eight previous trials in the absence of chemical control (Trudgill *et al*., 2014) indicate that the relationship was approximately linear over a P_i range 21-83 and 21-214 viable eggs (g soil)$^{-1}$ for six and seven of these trials respectively. The mean yield losses in these trials are in accordance with the current results at approximately 1% viable egg^{-1} (g soil)$^{-1}$ without correction for partial chemical control compared with 0.9 ± 0.21% in the current work. Further field trials are required to verify the precision of the yield losses estimated by the revised regression equation. Precision of extension advice may be enhanced in future by considering historic rainfall data for a UK weather station close to a particular field. This would rely on a charged-for service replacing the free approach based on regions used in this work. The benefit / cost of that option would need to be established.

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Author contributions

HJA and PEU conceived and designed the research. A-KK developed the data base and completed the statistical analyses with HJA. CAB identified the species of *Globodera* spp. in the field samples. MB provided cyst samples and advice as the work progressed. HJA drafted the manuscript and all authors edited it and approved the submitted manuscript.

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Supplementary Table S1. Determinacy and tolerance values for cultivars used in the field trials analysed in the manuscript.

Cultivars analysed in the six field trails with their determinacy integers and those for tolerance when known	Determinacy integer[1]	Tolerance integer in PCN calculator[2]
'Estima'	1	2
'Lady Rosetta'	2	2
'Marfona'	2	2
'Maris Peer'	2	1
'Harmony'	2	-
'Lady Claire'	2	-
'Melody'	2	-
'Saxon'	2	-
'Vivaldi'	2	-
'Hermes'	3	2
'Desiree'	3	2
'King Edward'	3	2
'Maris Piper'	3	2
'Pentland Dell'	3	2
'Sante'	3	2
'Saturna'	3	4
'Cabaret'	3	-
'Cara'	4	4
'Vales Everest'	4	3
'Vales Sovereign'	4	2
'Markies'	4	-
All additional cultivars with tolerance values in the PCN calculator that were not planted in the trials analysed		
'Kerrs Pink'	3	3
'Nadine'	2	1
'Pentland Crown'	-	2
'Pentland Squire'	-	2
'Valor'	3	3

These cultivars are those represented in both Figures 2 and 4. Other cultivars for which tolerance values are known are also listed with their determinacy integers. Determinacy is currently defined for 91 cultivars. PCN = potato cyst nematodes.
[1] https://ahdb.org.uk/knowledge-library/potato-nitrogen-groups.
[2] https://pcncalculator.ahdb.org.uk/.

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