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"Modelling the within-field spread of the potato cyst-nematode, *Globodera rostochiensis* Woll."

By F. G. W. Jones
Formerly of Rothamsted Experimental Station, UK

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Foreword

This significant unpublished manuscript was written by our late father Dr Frederick G.W. Jones in the mid 1980s but remained unfinished after his work on it ceased in 1987. We found it among his belongings following his death in 2003, after he emigrated to Australia in 1991 at the age of 77. It was written in the period 1985-1987 while he was Honorary Scientist in the Computer Department at Rothamsted Experimental Station. It constitutes a very substantial document which includes 17 tables and three figures. We believe it to be complete apart from missing a summary, conclusion/discussion and, probably, one or two figures. It describes two models of the within-field spread of the potato cyst nematode *(Globodera rostochiensis)* and their validation against very extensive historical data sets. The first model, which simulates the production of nematode eggs and cysts from an initial infestation, is derived from the model of Jones & Perry (1978). It supplies information to the second, two-dimensional model which simulates the area occupied in successive years when susceptible potato and crops other than potatoes are grown. Case histories provided by long-term experiments at Woburn Experimental Farm, Rothamsted, UK, are used to validate the models.

His first job (1937-1947) was in the Agricultural Advisory Service based at the School of Agriculture at Cambridge University, UK[1,2]. This included the 2nd World War period when he was in a 'reserved' profession dedicated to ensuring 'self-sufficiency' in food. From 1947 to 1955 he was first Demonstrator, then Senior Lecturer in Agriculture at Cambridge University. In his time at Cambridge, his research focussed mostly on nematode pests of crops. He then moved to Rothamsted Experimental Station, Harpenden, UK, where he worked from 1956 to 1979. He was Head of the Nematology Department throughout his time at Rothamsted, taking on the additional role as Deputy Director of Rothamsted in 1971. Following his retirement in 1979, he worked as an Honorary Scientist in the Computer Department at

[1] Obituary: F.G.W. Jones MA, ScD, Cbiol, FIBiol, 1914 - 2003. *Journal of the Royal Society of Western Australia* **86**, 143-144 (2003).
[2] Obituary: F.G.W. Jones 1914-2003. *Annals of Applied Biology*, **43** (2003).

Rothamsted until 1987. During this period, among other things such as producing a third edition of the book *Pests of Field Crops* and acting as Managing Director and Secretary of the International Trust for Zoological Nomenclature (1980-1987), he continued his research on models for cyst nematodes. This manuscript constitutes a component of his research during that period.

The manuscript represents a valuable, carefully-considered study of considerable benefit to other researchers. We therefore decided to produce it as the fourth in a series of historical bulletins containing unpublished manuscripts by members of our family. It is published in its entirety without any attempt to bring it up to date by reference to more recent scientific publications since 1987 on this subject. It should, therefore, be viewed as a historical document published posthumously.

Roger Jones
Susan MacDougall
May 2008

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This article is available on the family web site,
www.geocities.com/macdougalljones/
and by e-mail from Susan MacDougall at smacdougall@actewagl.net.au

Modelling the within-field spread of the potato cyst-nematode, *Globodera rostochiensis* Woll.

By F. G. W. Jones
Formerly of Rothamsted Experimental Station
Harpenden, Hertfordshire, AL5 2JQ, UK
1987

Introduction

The colonisation of infested fields by alien plant parasitic nematodes has sometimes been documented and the spread from field to field and farm to farm mapped (e.g. Petherbridge & Jones, 1942; Chitwood, 1951), but on-one seems to have been able to record the origin, early spread and progress of within-field infestations. Indeed, even for cyst-nematodes of which the cyst-envelope is rather persistent, detection of the origin and early spread by soil sampling is virtually impossible. Only after the progeny of the first arrival or arrivals within a previously uninfested field have multiplied and spread appreciable does crop damage appear. When attention has been alerted by losses in neighbouring fields, early infestations are sometimes observed but by then these are well-established.

This paper describes two models. The first, which simulates the production of eggs and cysts from an initial infestation, is derived from the model of Jones & Perry (1978). It supplies information to the second, two-dimensional model which simulates the area occupied in successive years when susceptible potato and crops other than potatoes are grown. This model does not simulate the pattern of spread. An attempt is made to fit the models to case histories provided by long-term experiments at Woburn Experimental Farm, Rothamsted, UK.

Definitions, assumptions and explanations

Definitions

Self-spread is that arising from the migration of second-stage juveniles that later become females and eventually cysts containing eggs. Although males are mobile and essential for reproduction, they play no part in spread.

The area colonised by the progeny of a single gravid female (i.e. the contents of a single cyst) or from several arriving together in a small lump of soil is defined as the *domain* (Jones, 1980) with superficial area πr^2 where r is the domain radius. Theoretically the *domain volume* is a sphere or part sphere of radius r but is better conceived as a cylinder of volume $\pi r^2 h$ where h is the plough depth. This is because, rather than migrating equally in all directions, juveniles probably tend to move downwards with the predominantly downward growth of potato roots and the percolation of rain water. The *domain weight* in terms of air-dried soil is the domain volume multiplied by the bulk density of the soil after removing stones and soil water.

The superficial area colonised at the end of successive host-crop years is: -

$$\pi r^2\left[(1g)^2,(2g)^2,(3g)^2,\ldots,(yg)^y\right] \qquad \ldots(1)$$

where g is the number of generations a year on the susceptible host crop and y the number of host crop years. As πr^2 is the domain area, successive terms represent the area occupied in domains.

Artificial spread arises when cysts are transported with soil by agricultural operations or other means. It is greatest during the harvesting of root and tuber crops, which are lifted physically and separated from soil. It is far less when cereal crops are grown and least under direct-drilled cereals, clover, lucerne or grass. Spread is especially marked when potatoes are harvested as the soil immediately around the plants contains many newly formed cysts filled with eggs. When a susceptible potato crop is grown in a rotation or sequence, the rate of spread is the sum of that due to all farming operations during each cycle and is greater when the rotation or sequence contains

additional root crops (e.g. sugar beet or carrots). Ploughing is not thought to cause much spread as the furrow is usually inverted or turned on its side. Rotavation is also mainly a local mixing operation but nevertheless may scatter some soil.

The cyst has evolved as an efficient dispersal and survival stage in non-agricultural environments. Unlike the multitudes of fungal spores or the plentiful dispersal stages of some animals, it seems 'designed' to succeed and is part of the *K*-adapted strategy of cyst nematodes (Jones, 1980). It is also worth noting that the cyst-nematodes spend most of their time as eggs within cysts or as stages within roots. Only the migratory infective stage (i.e. the second stage juvenile) spends a relatively brief period exposed in the soil environment and usually at a time when conditions, especially moisture, are favourable.

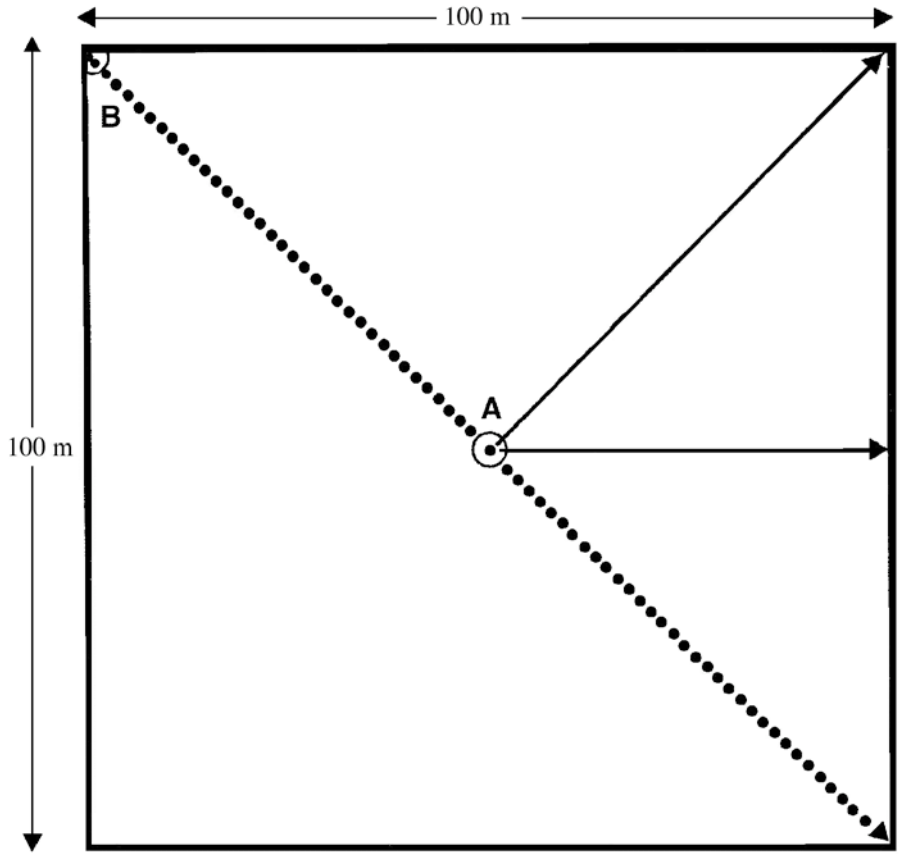
To compare the relative importance of *self-* and *artificial spread,* consider a square field with 100 m sides (1 ha) and diagonal 141.4 m (Fig. 1). Placed in the centre, the most favourable position, the progeny of a single female with one generation a year whose juvenile spread with a domain radius of 0.1 m would, by self-spread alone, take 500 host crop years or cycles to reach the sides of the field and 707 to reach the corners. From a female placed in one corner, the least favourable position, its progeny would take 1414 years/cycles to reach the diagonally opposite corner. It is well-known that fields of 1 ha are colonised in fewer than 20 years/cycles. Hence within-field spread plays an overwhelming role in within-field dispersal.

Spread can be defined in two ways. Either as the number of propagules (cysts) disseminated *(dissemination)* or as the colonisation of territory *(occupation of territory),* the difference being that the first is unlimited and the second limited by competition between propagules for unoccupied territory within a given area (e.g. a field or plot).

Assumptions

Domain radius. There is little information about the distances second-stage

Fig. 1. *Self-dispersal of the potato cyst nematode*



100 m

Legend to Fig. 1:

The inadequacy of spread by 2nd-stage juveniles. The square with 100 m-long sides represents a field of 1 ha. From a cyst landing at A in the centre, spread in concentric circles at a distance of 0.1 m per host crop year would take 500 years to reach the centre of any side and 707 years to reach all four corners. From a cyst landing in corner B, spread would take 1,414 host crop years to reach the opposite corner.

Figure also in Jones (1993, publ. 2007)

juveniles travel in soil between hatching from the egg and establishing themselves in potato roots. Personal experience and such information as can be gathered from the publications (e.g. Wallace, 1963) suggest a domain radius of approximately 0.1 m (diameter 0.2 m). This implies an ability to cover distances greater than 0.1 because nematode tracks are convoluted. A domain radius of 0.1 m is assumed in all following calculations giving a domain area of 0.01 π (0.03 m^2) or 3.1831 x 10^6 domains per hectare. *Plough depth* is assumed to be 0.3 m giving a domain volume of 9425 ml. Soil samples from Woburn Experimental Farm indicate an average field density for air-dried soil less stones and water of 1.25 and hence a domain weight of 1178 g. This conversion from domain volume to domain weight is essential because estimates of population density are expressed as eggs/g and cysts/100 g of air-dried soil without stones.

Generations. The potato cyst-nematode passes through one generation a year on susceptible potato plants. A small partial second generation is possible for, when yellow females are taken from potato roots and potted in 'sterile' loam with potato plants, new females are produced in small numbers (Jones 1950). Working with soil samples from fields at Woburn Experimental Farm Evans (1968) found suggestions of a small second generation in August-September which had little effect on final population densities. Sheppard & Cox (1967) found that the hatch of eggs immediately after extraction from field soils decreased sharply during late July, August and September to almost zero in November and December, suggesting some kind of diapause. In my models, one generation a year is assumed and the effects of any partial second generation confounded with domain area and the apparent rate of population increase.

Eggs per new cyst. Hesling (1961) working with *Solanum demissum* in pots found that neither size grade of cyst used to inoculate the pots nor inoculum density affected the egg content of new cysts. The overall egg content of new cysts produced on eight potato cultivars grown in 60 microplots on Long Mead Woburn Experimental Farm in 1960 gave an average value of 205 eggs/new cyst (Table 1). A value of 200 was assumed in the models.

Table 1. *New cysts and eggs/new cyst. Microplot experiment, Long Mead, Woburn 1960.*

Estimates based on soil samples from four or more replicate plots after the 1960 potato crop.

Cysts	Cultivar							Plant breeders' hybrid†	Mean
	Great Scott	Golden Wonder	King Edward	Magestic	Arran Banner	Epicure	Ulster Chieftain		
New cysts/100 g	257	208	176	168	166	109	78	52	
Eggs/new cyst	198	199	230	188	200	167	228	227	205
									S.E. ± 7.9

† With resistance gene H1.

Decrease in egg and cyst densities under non-host crops. Evidence has been presented in support of the assumption that egg densities in field soils usually decrease by a more or less constant fraction each year when non-host crops are grown (Huijsmann, 1961; Jones & Perry, 1978; Jones & Kempton, 1978) but there is little information in the literature about the decrease in cyst numbers. This is because they are the dead envelopes of females that contribute nothing to crop damage. Nevertheless, they may throw light on the history of the population and, when they contain viable eggs, play an important role in population dispersal. Work in pots at Rothamsted suggests incidentally that cyst decay is in the region of 15% (i.e. $1 - D = 0.85$) per annum but the data are very variable.

Latency. Initially, an infestation arising from one or a few cysts arriving in a small lump of soil produces too few new cysts at the end of one generation to ensure that any soil dispersed from the resultant domain will initiate new ones. This suggests a period of *latency.* But when the concept was explored further using the first model (which simulates the production of new eggs and new cysts derived from an initial infestation), it became clear that any idea of a period of absolute latency was untenable. Rather, after each year/cycle in the crop sequence the chances of new infestations being established increase, fluctuate and tend towards a fraction that varies with crop sequence.

The chance of starting new domains from one already infested is related to the total cyst density within the old domain and the average egg content of the cysts. Further, a full cyst containing on average some 200 eggs will be almost certain to succeed ($p = 1$ where p is the chance of success) and an empty cyst will have no chance ($p = 0$). So, we may write

$$p = k \times \frac{\text{total cysts / g soil} \times \text{average number of eggs per cyst}}{\text{average number of eggs per new cyst}} \qquad \ldots(2)$$

where k is the coefficient of proportionality. As there is no information about k it was assumed to be 1.

Model 1

The first model simulates the development of a potato cyst-nematode population within a domain after successful establishment following the arrival of an inoculum of one or more cysts containing a given number of viable eggs.

The model is derived from equation 10 p. 352 of Jones & Perry (1978) which calculates the change in population density when a susceptible potato crop is grown.

$$Pf = (1 - Cp)Pi \times \frac{a}{1 + \frac{(a-1)Pi}{c(E/e)^{Pi/E}}} + Cp\,Pi \qquad \ldots(3)$$

Where Pf is the population density after harvesting the host crop, Pi that before planting, a the multiplication rate, Cp the proportion of the egg population remaining unhatched, c the rate of compensation for root damage inflicted and E the observed equilibrium density of the population. Pf, Pi and E are all expressed as a proportion of $\overline{E}l$, the equilibrium population density (eggs/g soil) in the absence of root damage. E so expressed is a measure of root damage at the observed equilibrium density.

The first term on the right hand side of the equation represents the number of eggs that hatch and participate in reproduction, the second, complex term is the rate of increase moderated by the initial population density and the damage inflicted to the root system. Multiplied together they compute the number of new eggs produced. Dividing the product by the average number of eggs per new cyst gives the estimated number of new cysts produced. The last term on the right hand side represents the number of unhatched eggs carried over to the next year.

When non-host crops are grown, egg densities decrease by a constant fraction each, i.e. $Pf - CoPi$, where Co is the fraction of unhatched eggs remaining. Similarly old cysts decrease by a constant fraction i.e. cysts at end of season

immediately before planting – (new cysts from previous year if any + old cysts from previous and earlier years) x *D* where *D* is the fraction remaining.

Inputs and outputs: Model 1

Inputs. The crop sequence to be studied is input as a character string composed of S (= susceptible potato crop) and O (= other, non-host crop) in any desired order. Thus, 'SSSSSSSSS' would represent ten potato crops grown continuously, 'SOOSOOSOOSOOSOO' five cycles of a regular 3-course rotation and 'SOOSOSSOSSSSSS' an irregular sequence containing ten potato crops. Other inputs are the parameters of equation (3) and of the equations for the decrease in egg densities *(Co)* and cyst densities *(D)* when non-host crops are grown. Also needed is the inoculum of eggs and cysts that founded the infestation (the 'seed') and the domain weight in g of air-dried soil.

Output. A typical example of output is in Table 2.

Model 2

The two dimensional model simulating the area colonised over a period of host-crop years or cycles is based on the lower triangular halves of three matrices. The first simulates the propagation of new foci (domains) from old ones in the simplest situation, i.e. one old focus generates one new one *(N* = 1), and follows their growth with each year/cycle. It is concerned with dissemination and self-spread only and not with the occupation of territory. The second matrix simulates the chances that cysts disseminated will be successful in establishing new foci. The third is the product of the first and second, multiplied element by element, which is further manipulated to take into account values of $N > 1$. The sums of the rows then give the area potentially able to be colonised at the end of each year/cycle. Next, a competition function is used which attempts to moderate the sums of rows so that occupation of a limited area of territory (expressed in domains) is completed in a given time (expressed as host-crop cycles).

Table 2. *Model 1. Typical inputs and outputs; rearranged for presentation.* (Page i of ii)

For details see text.

Crop sequence *SO*SOO*SO*SOO*SO*SOO*SO*SOOSOSOO

Values input: -

Eggs = 242 Cysts = 1 Domain wt = 11781 g Eggs/new cyst = 200

$D = 0.85$ $Cp = 0.34$ $a = 50$ $E = 0.17$ $\overline{E} = 85.6$ eggs /g soil $c = 1.05$ $Co = 0.66$

Values output: -

$\overline{E}l = 505.53$ eggs/g soil Length of rotation string = 26

Crop sequence	Year	Cycle	Population density at end of year	Eggs/

Table 2 continued. (Page ii of ii)

Crop sequence	Year	Cycle	Population density at end of year				Eggs/cyst	Chance of establishing an infestation *p* (equation 2)
			Eggs/g	Cysts/100 g	New eggs/g	New cysts/g		
S	11		153.73	118.12	140.77	70.40	130.1	
O	12	5	101.46	100.40	0.00	0.00	101.1	0.50724
S	13		75.14	105.66	40.65	20.32	71.1	
O	14		49.59	89.81	0.00	0.00	55.2	
O	15	6	32.73	76.34	0.00	0.00	42.9	0.16367
S	16		163.57	141.11	152.43	76.22	115.9	
O	17	7	107.96	119.95	0.00	0.00	90.0	0.53977
S	18		72.18	119.69	35.47	17.74	60.3	
O	19		47.64	101.74	0.00	0.00	46.8	
O	20	8	31.44	86.48	0.00	0.00	36.4	0.15721
S	21		165.84	151.08	155.14	77.57	109.8	
O	22	9	109.45	128.42	0.00	0.00	85.2	0.54726
S	23		71.59	126.34	34.37	17.19	56.7	
O	24		47.25	107.39	0.00	0.00	44.0	
O	25	10	31.19	91.28	0.00	0.00	34.2	0.15593

Note: In crop sequence, test crops are in italics.

First matrix: dissemination and self-spread

The primary infestation expands as the square of the year giving successively 1, 4, 9, 16, …, y^2 domains (equation 1, $g = 1$). These self-spread values are placed in column 1. In the second and subsequent years, the self-spread values are transferred to the second and subsequent columns but stepped down one year (Table 3). As before, assuming the simplest situation, i.e. one old domain generates one new one and there is no competition for space, the columns in the array of secondary infestations contain the self-spread values multiplied by the number of domains from which they were derived. Thus, the first column of the secondary array (the second of the matrix) is multiplied by 1, the second by 4, the third by 9 and the nth by $(n - 1)^2$. The array of secondaries is then summed row by row to column 2 of the matrix and all subsequent columns reset to zero. The sums of the secondary array now become the self-spread values of the tertiary infestation and the process is repeated giving the results in Table 4.

Second matrix: chances of establishing new infestations

So far it has been assumed that one old domain generates one new one. As already explained, however, the chances of transported cysts being successful depend on cyst numbers and their 'fullness' (equation (2)). For a given crop sequence, Model 1 outputs the appropriate values of p and these are used to set up the second matrix similar to the first (Table 5). Because the initial or primary infestation was successful all the values of p in the first column are 1. The values of p output from Model 1 are fed into subsequent columns stepped down by one year/cycle. The multipliers for the successive columns in the first matrix were the self-spread values of the arrays (1, 4, 9, …, y^2 for the primary infestation, Table 3). For the probability matrix the multipliers are the differences between successive self-spread values of the array from which they were generated. For example, in Table 5A the multipliers for the columns in the secondary array are $1 - 0 = 1$, $4 - 1 = 3$, $9 - 4 = 5$ and so on. This is because in the 2nd year/cycle there is one domain that is 1 year old with probability p_1. In the 3rd year/cycle there are 4 domains, one 2 years old (p_2) and three 1 year old (p_1). Similarly, in the 4th year/cycle there are 9 domains, one

Table 3. *Components of Model 2. Derivation of arrays of secondary infestations from the primary infestation.*
Numbers are domains. They assume one domain generates only one new domain in the following year.

Host-crop years/cycles	Primary infestations	Array of secondary infestations								Total of secondary units
1	1									
2	4	1								1
3	9	4	4							8
4	16	9	16	9						34
5	25	16	36	36	16					104
6	36	25	64	81	64	25				259
7	49	36	100	144	144	100	36			560
8	64	49	144	225	256	225	144	49		1092
9	81	64	196	324	400	400	324	196	64	1968
10	100	81	256	441	576	626	576	441	256	3333

Note: The dotted lines and arrows indicate how the successive stages of the secondary infestation develop in a step-down manner.

Table 4. *Matrix containing the primary infestation and the sums of secondary and subsequent orders of infestation derived from it.*

Numbers of domains. One domain generates only one new domain in the following year and there is no competition for space.

Host-crop	**Orders of infestation**										**Totals**
years/cycles	1º	2º	3º	4º	5º	6º	7º	8º	9º	10º	
1	1										1
2	4	1									5
3	9	8	1								18
4	16	34	16	1							67
5	25	104	132	32	1						294
6	36	259	752	520	64	1					1632
7	49	560	3338	5728	2067	128	1				11868
8	64	1092	12336	48164	44736	8224	256	1			114873
9	81	1968	39572	3310016	733320	353664	32832	512	1		1491966
10	100	3333	113360	1920632	9699648	11452944	2812672	131200	1024	1	26134916

Table 5. *Construction of the chance matrix*

A. Development of probabilities for secondary array

Host-crop years	Self-spread values primary infestation	Probabilities							Mean probability secondary array
		Primary infestation	Secondary infestation						
1	1	1							1
2	4	1	p_1						$p_{1,2}$
3	9	1	p_2	$3p_1$					$p_{2,2}$
4	16	1	p_3	$3p_2$	$5p_1$				$p_{3,2}$
5	25	1	p_4	$3p_3$	$5p_2$	$7p_1$			$p_{4,2}$
6	36	1	p_5	$3p_4$	$5p_3$	$7p_2$	$9p_1$		$p_{5,2}$
7	49	1	p_6	$3p_5$	$5p_4$	$7p_3$	$9p_2$	$11p_1$	$p_{6,2}$

B. Final probability matrix

	Mean values of p for arrays						
	1º	2º	3º	4º	5º	6º	7º
1	1						
2	1	$p_{1,2}$					
3	1	$p_{2,2}$	$p_{1,3}$				
4	1	$p_{3,2}$	$p_{2,3}$	$p_{1,4}$			
5	1	$p_{4,2}$	$p_{3,3}$	$p_{2,4}$	$p_{1,5}$		
6	1	$p_{5,2}$	$p_{4,3}$	$p_{3,4}$	$p_{2,5}$	$p_{1,6}$	
7	1	$p_{6,2}$	$p_{5,3}$	$p_{4,4}$	$p_{3,5}$	$p_{2,6}$	$p_{1,7}$

3 years old (p_3), three 2 years old (p_2) and five 1 year old (p_1), and so on. To get the mean probability for the array of secondary infestations, the rows are totalled (omitting the primary infestation) and divided by the self-spread value for the year/cycle which is the sum of the multipliers. The mean probabilities for the secondary infestation is transferred to its column (col. 2) and the right-hand columns re-set to zero to be used for the calculation of the mean probabilities of the tertiary and subsequent arrays.

Third matrix: colonisation matrix

This matrix is the product of matrices 1 and 2 which require further manipulation. In the field, established foci generate many new ones especially during the harvesting of potatoes. If N is the number of new foci produced, then the second column of the third matrix must be multiplied by N, the third by N^2 and so on to produce the third matrix in its final form. Summing the rows now produces the best estimate of the combined effects of self-spread and dissemination.

Occupation of territory

To simulate the occupation of territory, the sums of rows must now be multiplied by a fraction representing the effects of competition for space because some cysts disseminated fall on domains already occupied. If sufficient information were available, it would be desirable to set up a fourth competition matrix in which competition would increase stepwise with every year/cycle and the initiation of each new order of infestation (secondary, tertiary, etc.). Instead, the problem was approached empirically using the negative logistic law defined by: -

$$f = 1 - [1 + \exp(-b(t-T))]^{-1} \qquad \ldots (4)$$

where f is the fraction of the territory unoccupied, b is the slope parameter, t is the time when half the territory remains unoccupied (i.e. 0.5 when the time required for complete colonisation is 1) and T (also a fraction) the time of the current estimate of f. Note that f is inversely proportional to competition for

space: when T is small $f \rightarrow 1$ and when large $f \rightarrow 0$. Competition is increased when the slope b is increased. At the point of inflection of the curve t, T and $f = 0.5$, i.e. $t - T = 0$. Because competition intensifies with time, such a symmetrical curve does not portray the competition for space in the field. However, this can be simulated by raising f to a power x. For example, when $x = 1$ the point of inflection has the value 0.5, when $x = 2$, $f = 0.25$; and when $x = 3$, $f = 0.125$. Thus, the degree of competition can be manipulated by varying b and x.

Inputs for Model 2

The inputs required for Model 2 are: -

1. The crop sequence under study and probabilities that any cyst spread will initiate new infestations – from Model 1, equation (2).
2. Number of generations a year.
3. Inoculum, number of eggs and cysts introduced initially, the 'seed'.
4. Domain weight in g of air-dried soil for calculation of population densities.
5. The time *(Tf)* in years/cycles needed for all available territory to be occupied – equation (2).
6. Area of territory available for occupation in domains.
7. The number of new foci *(N)* produced by each old one.
8. The slope parameter *(b)* of the competition curve – equation (4).
9. The power *(x)* to which *f*, the fraction of territory occupied, is to be raised – equation (4) *et seq.*

Inputs and outputs: Model 2

A typical example of inputs to and outputs from Model 2 are in Table 6. The crop sequence and the chances of starting new infestations are derived from Model 1 and are for the first seven cycles. The sequence and the values input are for the continuous arable (AAA) rotation of the Ley-arable Experiment in Stackyard, Woburn Experimental Station, to be considered later.

Table 6. *Model 2. Typical input and output rearranged for presentation. Ley-arable experiment, Stackyard Series D, continuous arable (AAA).*

Input from Model 1 (see Table 2)

Crop sequence: *SO*SOO*SO*SOO*SO*SOO*SO**

Chances of a single cyst from a domain starting a new infestation at the end of each cycle.

Values input	
Number of generations	1
Area to be colonised, domains	5323
Time for colonisation, cycles, *Tf*	7
Number of new domains generated, *N*	128
Slope parameter of competition curve, *b*	3.075
Power to which fraction of territory occupied is raised, *x*	1.660

Output A Dissemination of 'successful' cysts measured as the area in log domains they might occupy were there no competition.

Cycles, end of	**Order of infestation**						
	1º	2º	3º	4º	5º	6º	7º
1	0.00						
2	0.60	-0.54					
3	0.95	0.99	1.57				
4	1.20	2.40	3.19	3.68			
5	1.40	3.13	4.65	5.44	5.78		
6	1.56	3.66	5.69	6.98	7.74	7.89	
7	1.69	4.07	6.51	8.26	9.42	10.08	10.00

Output B Summary of projections from Model 2

	†Log. area of dissemination	**Competition f^x**	**Log. area occupied**	**Percentage occupied**
1	0.00	0.99984	-0.00007	0.002
2	0.63	0.99647	0.63085	0.08
3	1.75	0.92778	1.71420	0.97
4	3.82	0.31644	3.31705	38.98
5	5.97	0.00563	3.71742	98.01
6	8.15	0.00004	3.71753	98.03
7	10.39	<0.00001	3.74299	103.95

Log. area to be colonised 3.72616

* Test crops in italics

† Log. arithmetic totals

Output A gives the area potentially able to be occupied in log domains when there is no competition for available space (derived from Matrix 3). Output B summarises the predictions from Model 2, the most important of which is the percentage of area colonised at the end of each cycle.

Case histories

Five long-term field experiments at Woburn Experimental Farm provided case histories in which the Models could be applied. It is essential to know when potatoes were first planted in the two fields where the experiments were sited and how they were harvested.

Long Mead is a small field situated close to the farm buildings. It was first ploughed from grass in 1945 and first planted with potatoes in 1947. The crop sequence from 1947 to 1965 may be represented as 'SOOSOOSOSOSSOSSSSSS'. From 1960 to 1965, potatoes were grown continuously in the Microplot Experiment (Jones & Parrott, 1969) which provided population data for Model 1. Previously, six susceptible potato crops had been grown in 13 yrs. The non-host crops were winter wheat (1948, 1949, 1951, 1952, 1954) and sugar beet (1949, 1956, 1959). Until 1960, potato crops were harvested using a 'spinner'. Thereafter, the microplots were harvested with hand forks.

Stackyard is a large, rectangular field isolated from the rest of the Experimental Farm by a distance of 2 km. No potatoes were planted anywhere in the field between 1877 and 1928 and before that it was said to have been in grass for 50 years (Voelker, 1897). In 1877, the field was divided into six large strips. The first two were the sites of the classical experiments on continuous wheat and continuous barley. The four other strips (Rotation I, II, III and IV, subsequently Series A, B, C and D) carried a long-term rotation experiment without potatoes until it was discontinued.

Series A. This series was assigned to the 'Green manuring Experiment' in 1936. The first scheme ended in 1953: no potatoes were grown from 1936 to 1953. The second scheme was launched in 1954 and treatments began in 1955. The upper half of the site was planted with early potatoes cv. Ulster Chieftain

in the even years commencing in 1954. The fifth crop in 1962 'showed signs of damage from potato cyst-nematode'. The lower half grew four potato crops between 1955 and 1961: no signs of cyst-nematode damage were observed. Soil samples from the 80 plots of the experiment were collected in the winter of 1955-56 by the late D.W. Fenwick which revealed that the site was heavily infested with lemon-shaped cysts, presumably *Heterodera avenae* Woll. A few cysts were classified as 'round' but it is doubtful whether they were *G. rostochiensis:* no egg counts were obtained from them.

From 1963 to 1966 no potatoes were planted on Series A. The lower half was then assigned to an experiment on 'Nematicides in a 3-course rotation' (Whitehead *et al.,* 1980). Although the lower half may have harboured a covert infestation with *G. rostochiensis,* five preparatory crops of potatoes were needed before experimentation could begin despite the inoculation of the third crop in June with 60 cysts applied to alternate plants in every other row (see Table 17 on page 44).

During the second scheme of the green manuring experiment potatoes were harvested with a 'spinner'. During the experiment on 'Nematicides in a 3-course rotation' harvesting was by elevator-lifter.

Series B. The '6-course rotation experiment' on Series B began in 1930 after two preparatory years (Anon., 1930, 1932). Potatoes were planted in 1928 (cvs Ally and Majestic) over the whole area of the experiment. In 1930, potatoes were planted in block II and not on block V as indicated in Anon (1930), when the block order was inadvertently reversed. Subsequently, each block was planted with potatoes (cv. Ally until 1941, Majestic thereafter) every 6 years, the policy of the experiment being to complete five rotations on each block by 1960. The late D.W. Fenwick sampled all plots in the winter of 1955-56. All potato plots were harvested using a 'spinner'.

Series C. No potatoes were grown on Series C until after 1939, and possibly not for several years later. Hence, Series C exerted no influence on Series A, B or D.

Series D. No potatoes were grown on Series D until the commencement of the Ley-arable Experiment in 1938. Yields of potatoes varied with the previous rotational treatments and especially with effects attributable to season, but were otherwise satisfactory until 1955 (Fig. 2). Then all yields were depressed by adverse growing conditions but those from plots subjected to continuous arable treatments were a failure averaging no more than 4.3 t/ha total tubers and only 1.0 t/ha of saleable tubers passing the 4.13 riddle (23.1%). These plots had previously been planted with potatoes cv. Majestic 7 times in 7 years. The late D.W. Fenwick confirmed that these plots were heavily infested with *G. rostochiensis* and took soil samples from all 80 sub-plots of the experiment during the winter of 1955-56, from which the density of cyst and egg populations were estimated. During the period 1938-1955, potatoes were harvested using a 'spinner'.

Fitting the models to case histories

The Microplot Experiment, Long Mead data

Jones & Perry (1968) fitted their model to population data (eggs/g soil) from the microplot experiment made by Jones & Parrott (1969). The data were the pre-plant means from seven microplots planted with different susceptible potato cultivars during the years 1960 to 1965. The plots were replicated in four randomised blocks. The sampling area in each plot was 1.95 m^2 (six planting stations) or 62 domains ($r = 0.1$).

Model 1 was fitted to the data (Tables 7, 8 and 9), including the mean values for cyst/100 g soil obtained from unpublished records, using a range of values for cyst decay *(D),* a 'seed' of 1 cyst containing 242 eggs, the best fitting parameters from Jones & Perry (1978, Fig. 7, p. 359) and other parameters discussed earlier. Details are in Table 7: hereafter these are 'standard' inputs for Model 1.

Estimates of cyst density are subject to greater errors than estimates of egg density because old cysts are difficult to define and standards in routine

Fig. 2 *Potato yields 1938 to 1955. Ley-arable experiment, Stackyard Series D.*

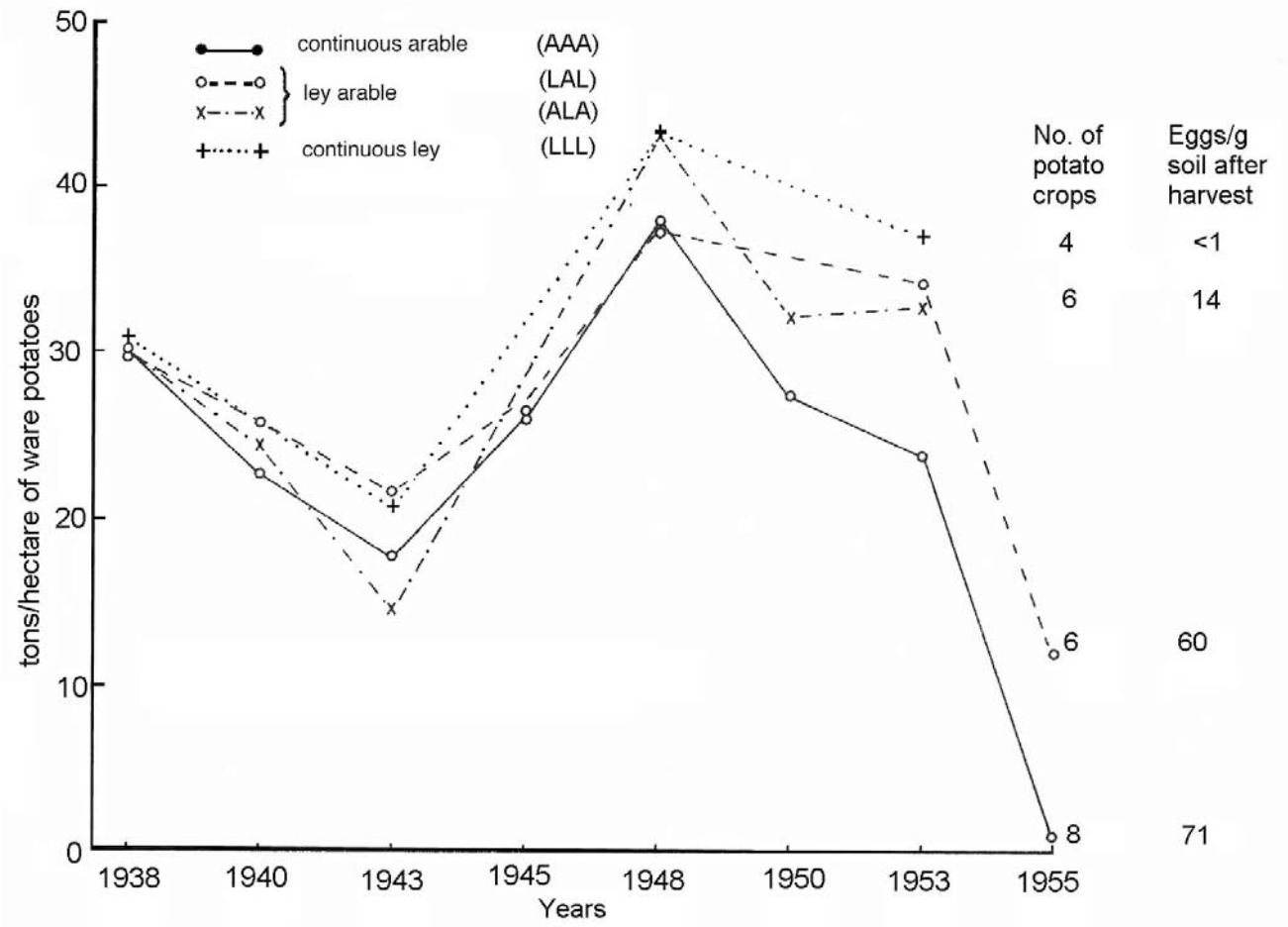


Table 8. *Model 1 applied to the Long Mead data (cycles 6-12)*

Inputs as in Table 7, except that the multiplication rate *(a)* was varied and 1-cyst decay *(D)* was 0.85.

Years	Observed	Calculated						
		a = 25	26.6	50	75	100	112.6	150
				Eggs/g soil				
1959	59	53	57	50	43	43	65	43
1960	140	121	116	131	147	149	108	151
1961	64	68	70	66	65	65	72	65
1962	112	102	101	106	108	108	100	108
1963	75	75	76	73	72	72	76	72
1964	86	95	94	99	99	100	95	100
1965	61	79	79	76	76	76	79	76
Means	†*67*	*85*	*85*	*86*	*87*	*88*	*85*	*88*
				Cysts/100 g				
1959	70	78	82	87	96	102	110	102
1960	139	118	118	131	148	154	137	155
1961	109	114	115	122	137	138	134	139
1962	135	136	137	146	156	160	151	161
1963	166	136	137	142	151	154	150	154
1964	170	150	151	158	165	168	162	169
1965	134	151	152	158	162	164	161	164
Means	*132*	*126*	*127*	*135*	*145*	*149*	*144*	*149*
				Eggs/cysts				
1959	84	68	70	57	45	42	65	42
1960	101	103	99	100	99	97	113	97
1961	59	60	60	54	49	47	58	47
1962	83	75	71	73	69	67	77	67
1963	45	55	55	51	48	47	53	47
1964	51	63	63	62	60	59	65	59
1965	46	52	52	49	47	46	51	46
Means	*67*	*55*	*67*	*64*	*60*	*58*	*69*	*58*
				Chances of a single cyst initiating an infestation				
1959	††0.29	0.27	0.29	0.25	0.22	0.22	0.33	0.22
1960	0.70	0.61	0.58	0.66	0.74	0.74	0.50	0.75
1961	0.32	0.34	0.35	0.33	0.33	0.33	0.36	0.33
1962	0.56	0.51	0.50	0.53	0.54	0.54	0.50	0.54
1963	0.37	0.38	0.38	0.37	0.36	0.36	0.38	0.36
1964	0.43	0.47	0.47	0.50	0.50	0.50	0.48	0.50
1965	0.31	0.40	0.40	0.39	0.38	0.38	0.40	0.38
Means	*0.43*	*0.43*	*0.42*	*0.42*	*0.44*	*0.44*	*0.42*	*0.44*

† Best fitting equilibrium density ($\overline{E}$) = 85.6.

†† Calculated from observed data.

Table 9. *Model 1 applied to Long Mead data (cycles 6-12)*

Inputs as in Table 7, except that the multiplication rate was held at 50 and the 'seed' of eggs and cysts was varied.

Eggs added:-	10	50	250	1250	6250	31250
Cysts added:-	1	1	1	5	25	125
Eggs/g:-	0.0008	0.004	0.02	0.11	0.53	2.65
Cysts/100 g:-	0.008	0.008	0.008	0.004	0.21	1.06
			Eggs/g soil			
1959	46	69	50	43	47	50
1960	138	104	132	144	137	131
1961	66	74	66	66	66	66
1962	107	97	106	107	107	106
1963	73	78	73	73	73	73
1964	98	93	98	98	98	98
1965	77	90	77	77	77	77
Means	*86*	*86*	*86*	*87*	*86*	*86*
			Cysts/100 g			
1959	72	94	87	98	99	105
1960	122	121	132	148	145	146
1961	113	122	123	134	133	135
1962	139	140	146	156	155	157
1963	136	141	143	151	150	151
1964	152	153	158	165	164	165
1965	151	154	156	162	161	162
Means	*126*	*132*	*135*	*145*	*145*	*146*
			Eggs/cysts			
1959	65	72	57	44	47	48
1960	113	86	100	97	95	90
1961	58	61	54	49	50	49
1962	77	69	73	69	69	68
1963	53	55	51	48	48	48
1964	65	61	62	60	60	59
1965	51	62	49	47	48	47
Means	*69*	*58*	*64*	*59*	*60*	*58*
			Chances of a single cyst initiating an infestation			
1959	0.23	0.34	0.25	0.22	0.23	0.25
1960	0.69	0.52	0.66	0.72	0.69	0.67
1961	0.33	0.37	0.33	0.33	0.33	0.33
1962	0.53	0.48	0.53	0.54	0.53	0.53
1963	0.36	0.39	0.36	0.36	0.36	0.36
1964	0.49	0.46	0.49	0.49	0.49	0.49
1965	0.38	0.40	0.38	0.38	0.38	0.38
Means	*0.43*	*0.42*	*0.43*	*0.43*	*0.43*	*0.43*

population estimation vary from year to year and observer to observer (Jones, 1950, 1980). Nevertheless, a cyst decay rate of 15% ($1 - D = 0.85$) gives a reasonable loose fit to the observed cyst densities.

A puzzling feature of the data from the microplots on Long Mead is that they illustrate classical population oscillations whereas estimates from large field plots do not. Presumably in large plots the many domains of which they are composed are out of phase with each other so that the means drift upwards and downwards according to circumstances. However, the classical oscillations shown by the estimates for plots averaged over cultivars and replicates obscure much variability in the individual plot estimates but the cultivar means vary less and tend to oscillate together. The conclusion drawn is that the populations in most of the domains within plots were in phase.

Two peculiarities of the Long Mead rotation stand out. Firstly, the sugar beet crop grown at the end of the first phase in 1949 which would have greatly increased the number of new foci generated by the secondary infestation. Secondly, the planting of two potato crops in succession in the years 1957 and 1958. To study the effect of this juxtaposition, the Long Mead crop sequence was altered (a) by the insertion of a non-host crop between the two potato crops and (b) by the deletion of one of the potato crops. Both sequences then began with two cycles of 'SOO', followed (a) by four of 'SO' and (b) by three 'SO', and both ended with potatoes grown continuously. The effects of modified rotations were compared with that of the Long Mead crop sequence over a range of multiplication rates (Table 10).

Unfortunately, the second and higher orders of infestation cannot be related to starting cycles in any simple way because of the step-down effect (Table 3) in the manner in which arrays are generated. Discounting the slight contribution that the primary infestation makes to the occupation of territory (Table 4), because it is based on self-spread alone, Table 10 suggests that the unmodified sequence and modified sequence (a) starting with cycles 2, 3 and 4 would favour in-phase oscillations in 1960 to 1965 more than modified sequence (b). Otherwise no firm conclusions can be drawn.

Table 10. *Long Mead data. Effects of varying the initial crop sequence on population densities and oscillations in the years 1960 to 1965 when potatoes were grown continuously.*

Multiplication rate (a) varied, otherwise inputs as in Table 7.

Initial crop sequence			Starting cycle	No. of potato crops	Values of 25	50	75	100	150	*Mean effect*
Long Mead sequence										
2(SOO)	2(SO)	SSO	1	6	†125	131	147	149	151	*140*
SOO	2(SO)	SSO	2	5	135	121	102	101	116	*115*
	2(SO)	SSO	3	4	(80)	143	139	149	143	*131*
	SO	SSO	4	3	144	(70)	(70)	(84)	96	*93*
Modification (a)										
2(SOO)	4(SO)		1	6	97	101	129	133	133	*119*
SOO	4(SO)		2	5	121	92	(78)	(77)	(85)	*91*
	4(SO)		3	4	(77)	132	145	142	110	*121*
	3(SO)		4	3	144	(75)	(67)	(70)	106	*92*
Modification (b)										
2(SOO)	3(SO)		1	5	111	106	(79)	(77)	(76)	*90*
SOO	3(SO)		2	4	(81)	119	149	147	131	*125*
	3(SO)		3	3	149	(75)	(67)	(70)	98	*92*
	2(SO)		4	2	(38)	154	194	172	(70)	*126*

† Eggs/g soil after the first of the continuous potato crops grown in 1960: parenthesis indicates a value less than $\overline{E} = 85.6$ and out of phase.

The Ley-arable Experiment, Stackyard Series D

Plot area was 167 m^2 (5323 domains). A plan of the experiment is in Anon (1938) and the layout of a typical block, of which there were five, is in Fig. 3. Records of yields are summarised in Anon (1939-1955) and changes in crops grown are in Anon (1962.)

The experiment compared the effect on soil fertility of three-year-leys with three years of arable crops grown continuously and alternately. Effects were measured by test crops of potatoes and a cereal, usually wheat, planted between ley or arable rotations. For our purposes the crop sequences begin with the first potato crop grown, whether a rotation or test crop, and may be represented as in Table 11 where test crops are in italics.

In the various replicates, not all sequences began in the first year of the experiment and not all ended with potato crops in the last year under consideration (1955). Foreshortening the sequences to allow for the infestation with *G. rostochiensis* arriving after the first potato crop has no effect on the LLL sequence but switches the AAA sequences from (1) to (2) or *vice versa* as successive cycles are deleted. [Similarly foreshortening of the LAL and ALA sequences switches them from (1) to (2), (2) to (3) and from (3) to (1) successively.] The alternating sequences LAL and ALA were considered but added little information not provided by AAA and LLL.

Fitting Model 1 to the Ley-arable sequence

AAA. Table 12 compares the predicted and observed population densities of the AAA sequences in the five blocks of the experiment. The predictions show the anticipated population densities of a single domain (i.e. the primary infestation) initiated by one cyst containing 242 eggs using the input parameters found best fitting for the Long Mead data. The predictions are for an experience of three to eight potato crops. After one crop, all egg and cyst densities are <1 per g or 100 g respectively. After two crops the maximum egg density predicted was 14 eggs/g and the cyst density 7/100 g, below the threshold that stunts plants visibly. Only in block IV were the expected and

Fig. 3. *Typical block layout with infestation, 1938[?], Ley-arable Experiment, Stackyard Series D*

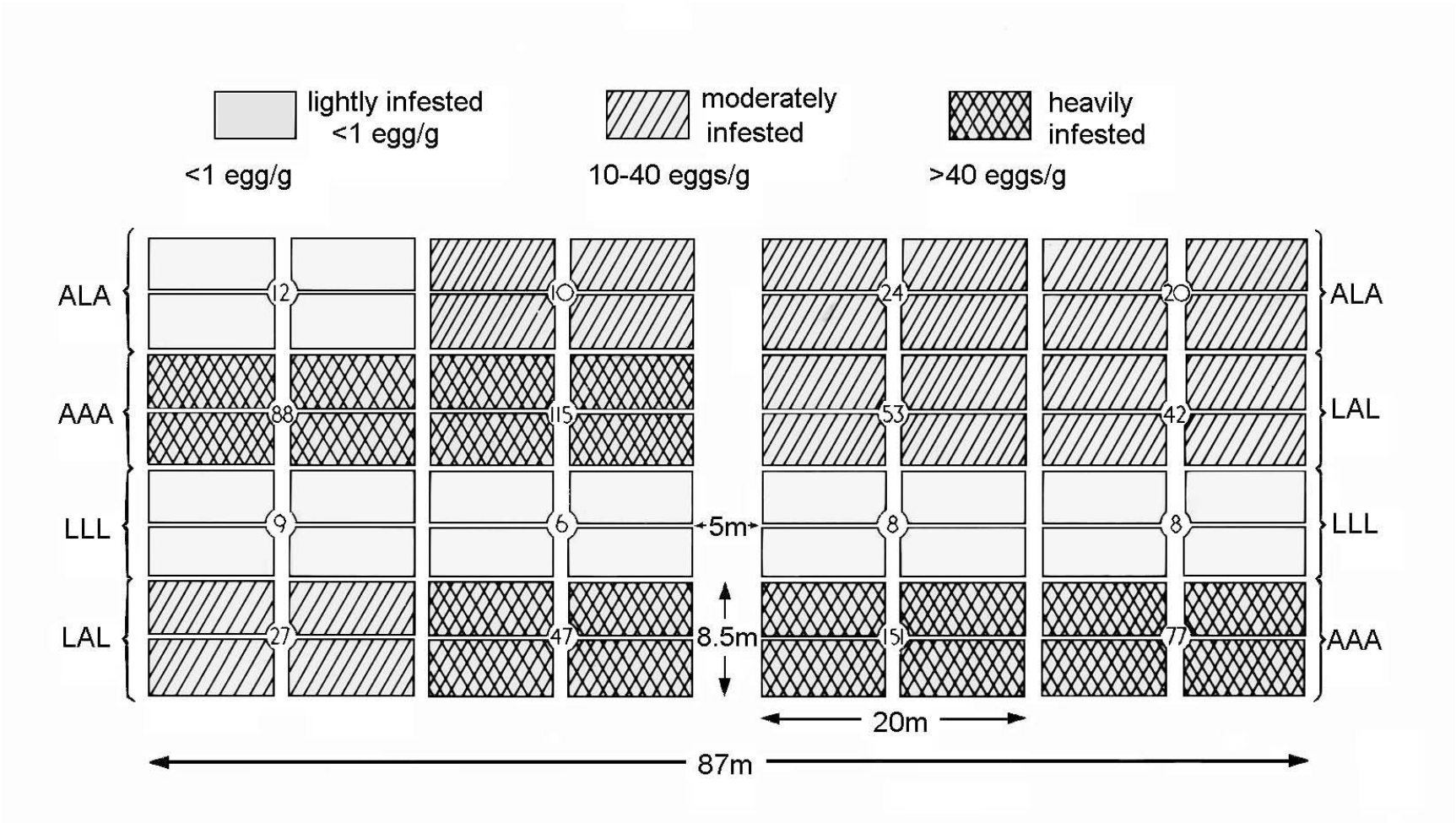


Table 11. *Crop sequences in the Ley-arable experiment, Stackyard Series D*

Symbol	Description	Sequence	Rotation	Maximum no. of potato crops
LLL	Continuous ley	†*SO*OOO	5-course	3 or 4
AAA	Continuous arable	(1) *SO*SOO (2) SOO*SO*	5-course	7 or 8
LAL and ALA	Alternate ley and arable	(1) *SO*SOO*SO*OOO (2) SOO*SO*OOOOO*SO* (3) *SO*OOO*SO*SOO	10-course	5 or 6

† Test crops in italics

Table 12. *Model 1. Woburn Ley-arable experiment, Stackyard Series D. Predicted and observed egg and cyst densities after the 1955 crop.*

Multiplication rate, $a = 50$, 1-cyst decay = 0.85, other inputs as in Table 7. (Page i of iii)

Sequence	No. of potato crops experienced	BLOCKS I eggs/g	I cysts/100 g	II eggs/g	II cysts/100 g	IV eggs/g	IV cysts/100g	V eggs/g	V cysts/100 g	III eggs/g	III cysts/100 g
						PREDICTED					
AAA	Cycle ending:-	*O*SOO*S*† (1)		SOO*SO* (1)		OO*SO*S (2)		O*SO*SO (2)		*SO*SOO (2)	
	8	-	-	-	-	72	120	-	-	-	-
	7	164	141	108	120	76	114	50	97	33	82
	6	151	129	100	110	75	106	50	90	33	76
	5	154	118	101	100	90	98	59	83	39	71
	4	122	92	60	78	87	78	58	66	38	56
	3	127	68	64	58	128	66	84	56	56	48
						OBSERVED					
	Sub-plot estimates	5	6	1	9	56	72	36	33	4	20
		<1	9	0	9	60	**179**	5	22	<1	29
		5	15	0	11	91	**124**	2	22	16	23
		<1	15	<1	11	56	**109**	<1	29	45	29
	Means	*3*	*12*	*<1*	*10*	*6*	*121*	*11*	*27*	*16*	*25*

Table 12 continued. (Page ii of iii)

Sequence	No. of potato crops experienced	BLOCKS I eggs/g	I cysts/100 g	II eggs/g	II cysts/100 g	IV eggs/g	IV cysts/100g	V eggs/g	V cysts/100 g	III eggs/g	III cysts/100 g
						PREDICTED					
LLL	Cycle ending:-	*O*OOO*S*		OOO*SO*		OO*SO*O		O*SO*OO		*SO*OOO (2)	
	4	107	59	71	50	47	42	-	-	-	-
	3	25	13	17	11	11	10	7	8	5	7
	2	4	2	3	2	2	2	1	1	<1	<1
	1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
						OBSERVED					
	Sub-plot estimates	4	9	<1	17	2	15	6	13	0	33
		1	2	<1	18	<1	19	<1	8	0	19
		0	17	<1	13	1	22	0	24	3	9
		<1	8	0	24	0	13	0	13	<1	17
	Means	*1*	*9*	*<1*	*18*	*<1*	*17*	*2*	*15*	*<1*	*20*

Table 12 continued. (Page iii of iii)

Sequence	No. of potato crops experienced	BLOCKS I eggs/g	I cysts/100 g	II eggs/g	II cysts/100 g	IV eggs/g	IV cysts/100g	V eggs/g	V cysts/100 g	III eggs/g	III cysts/100 g
						PREDICTED					
LAL/ALA	Cycle ending:-	I (LAL) *O*OOO*S* (3)		IV (LAL) OO*SO*S (3)		IV (ALA) OO*SO*O (1)		III (LAL) *SO*SOO (1)		All others (24 sub-plots)	
	6	-	-	72	105	73	100	-	-	19-168 eggs/g	
	5	162	122	69	97	44	70	30	70	30-138 cysts/	
	4	176	114	161	95	72	72	70	68	100 g	
	3	52	28	74	38	55	48	32	27		
						OBSERVED					
	Sub-plot estimates	0	18	36	43	4	23	<1	16	0-2 eggs/g	
		16	21	246	**127**	8	27	<1	14	11-40 cysts/	
		<1	10	50	47	26	24	2	22	100 g	
		0	14	56	67	19	21	12	25		
	Means	*4*	*16*	*97*	*71*	*14*	*24*	*4*	*19*	*<1*	*18*

† No. of the sequence starting with the first potato crop planted. Number changes as the sequence is foreshortened, see text. Sequence always ends as shown. In crop sequences, test crops are in italics.
Bold print signifies the most heavily infested sub-plots (IV AAA, IV LAL).

observed estimates comparable tending to suggest that all domains were infested and that most had experienced from four to eight potato crops. However, cyst densities were more in line with the notion that most domains had experienced from six to eight potato crops. In the other blocks, all of which had grown seven potato crops, most domains in the sub-plots were either uninfested or, if infested, had experienced few potato crops. The maximum egg and cyst densities observed in these plots were 26/g and 28/100 g respectively.

LLL. The observed egg densities on all sub-plots (Table 12) indicated that many domains in them were un-colonised or that, after colonisation, few had experienced more than two potato crops. The cyst densities, however, were greater than this conclusion would suggest, implying that infestations were of longer standing. A possible explanation of the discrepancy is that many cysts, arriving in domains well before the next potato crop was grown, had lost most of their eggs by then and were unsuccessful in founding colonies.

LAL/ALA. After six potato crops, all four LAL sub-plots in block IV were heavily infested, one especially so (246 egg/g, 127 cysts/100g). When allowance was made for the years since the last potato crop, the ALA sub-plots in this block were also appreciably infested (means 33 eggs/g, 33 cysts/100 g). These sub-plots had also experienced six potato crops. After five potato crops, one LAL sub-plot in block I (16 eggs/gm 21 cysts/100 g) and one in block (?)* (28 eggs/g, 35 cysts/100 g, after allowing for 2 years without potatoes) were also appreciably infested.

All sequences. The most heavily infested sub-plots (Table 12, IV AAA, IV LAL, figures in bold print) were after eight or six potato crops, one was appreciably infested after six (IV ALA) and two after five years (I LAL, III LAL). Many plots were only sparsely or slightly infested after seven, six, or five potato crops (e.g. II AAA after seven crops). The LLL sequences after four or three crops were without exception only slightly infested. The term 'slightly' is relative for its absolute terms 1 egg/g air-dried soil represents 1171 per domain as here defined and 63 millions per sub-plot.

* Block number omitted from manuscript.

Besides the frequency of potato crops, position in the experiment seems to play a part in colonisation. Judging from cyst densities, which are more indicative of the age of an infestation than fluctuating egg densities, the original infestation seems to have been on the AAA sub-plots of block IV, notably sub-plots 54, 63 and 64 (Fig. 3, Table 12 cyst densities in bold print). Sub-plots nos 53 (AAA), 55 (LAL) and 56 (LAL) also had large cyst densities (especially no. 56) and were in the same row as no. 54 (AAA). Similarly sub-plots nos 61 and 62 (LAL), also with large cyst densities, were in the same row as nos 63 and 64 (AAA). Potato planting, harvesting and cultivations were lengthwise along the rows or plots.

Observed cyst densities of AAA, ALA and LAL sub-plots in blocks III and IV tended to relate to their proximity to heavily infested sub-plots in block IV. All sub-plots in block IV were planted with 'test crop' potatoes in 1938 and the infestation may have originated in soil adhering to the seed potato stock planted in that year. The only other plots planted with the same stock in 1938 were in block III ALA nos 35, 36, 47 and 48 which experienced five potato crops. All had <1 eggs/g and an average of 22 cysts/100 g. After allowing for the decrease in egg and cyst densities during the last 4 years of crops other than potatoes, the infestation in these plots was slight (means <1 egg/g, 42 cysts/100 g). The yield of potatoes in 1955 from sub-plots 1, 2, 5 and 6 in block I (ALA), which experienced seven potato crops, was decreased to about half, suggesting an infestation greater than the estimates of population density after harvest. A second sample in the winter of 1956, after allowing for the decrease in egg density under a non-host crop, gave larger egg densities in plots 1, 2 and 5 (11-23 eggs/g) suggesting that these plots were heavily infested in patches. This infestation and that in one other sub-plot of block I appear to be somewhat isolated from those in blocks II, IV and V.

Fitting Model 2 to the AAA sequences

Assuming that infestations in the sub-plots of block IV were initiated by single cysts in 1938, 1940 or 1943, they would subsequently experience seven, six or five potato crops respectively leaving populations in some plots that

resulted in the harvest of the final potato crop planted in 1955 being a failure. Evidently for this to happen almost all the domains in the affected sub-plots were infested. Table 12 suggests that two or three potato crops would have been required to develop such populations. Using the standard inputs from Model 1 derived as in Table 2, for sequences A and C (the chances of single cysts initiating infestations were slightly different for sequence B) and the inputs for Model 2 (additional inputs) as in Table 7, Model 2 gave estimates of the number of new domains generated and the percentages of the sub-plot area occupied at the end of successive host crop cycles as shown in Table 13.

The most realistic fit to the model was obtained for $T = 7$ and $N = 128$. The greater part of the sub-plot (98%) was occupied at the end of the fifth cycle, allowing two more years for those domains last infested to develop damaging population densities. Those members would also be enhanced by 'recruitment', i.e. the acquisition of these domains of cysts that contributed nothing to the occupation of territory because it was already occupied.

Possible but perhaps slightly less realistic was the fit to $T = 6$ and $N = 411$. Even so, with 79 per cent of territory occupied at the end of cycle 4, there were still 2 years for damaging population densities to develop. The fit for $T = 5$ and $N = 1732$ is unrealistic.

It seems reasonable to conclude that infestations began in 1938 in the first potato crop planted.

The 6-course Rotation Experiment, Stackyard Series B

Plot size was 0.010765 ha or 3427 domains ($r = 0.1$ m), and there were fifteen plots per block in six blocks. In the winter of 1955/56, the late D.W. Fenwick sampled all plots to estimate egg and cyst densities.

Table 14 compares observed egg and cyst densities with those predicted by Model 1. Blocks I and II carried six potato crops between 1930 and 1955 inclusive, the remaining blocks III to VI carried five. Dr Fenwick detected no

Table 13. *Model 2. Ley-arable experiment, Stackyard Series D, AAA sequences. Estimates of the number of new domains generated* (N) *and the percentages of the sub-plot area occupied at the end of successive host-crop cycles.*

	Sequences	**No. of potato crops experienced**
A	*SO*SOO*SO*SOO*SO*SOO*SO*	7
B	SOO*SO*SOO*SO*SOO*SO*	6
C	*SO*SOO*SO*SOO*SO*	5

Sequence	A	B	C
T, time for colonisation, cycles	7	6	5
N, number of new domains generated	128	411	1732
b, slope parameter of competition curve	3.075	3.465	3.80
x, power to which *f* is raised	1.66	1.76	1.95

Cycles	% area of sub-plot occupied		
1	0.02	0.02	0.02
2	0.08	0.09	0.12
3	1.0	4.1	22.14
4	39.0	79.1	87.1
5	98.0	99.9	96.0
6	98.0	100.0	102.8
7	104.0	103.0	

In crop sequences, test crops are in italics.

Table 14. *Model 1. Woburn 6-course rotation 1928-55, Stackyard Series B. Predicted and observed egg and cyst densities after the 1955 crop.*

Multiplication rate *(a)* = 50, 1-cyst decay *(D)* = 0.85, other inputs as in Table 7.

	Blocks					
	I		**II**		**III-IV**	
	Sequences					
	SOO+ 4(SOOOOO)+ S		SO+ 4(SOOOOO)+ SO		SOOO-SOOOOOO+ 3(SOOOOO)+ SOO-SOOOOO	
Number of potato crops experienced	**eggs/g**	**cysts/100 g**	**eggs/g**	**cysts/100 g**	**eggs/g**	**cysts/100 g**
			PREDICTED			
*6	178	125	117	109	-	-
5	114	65	75	55	20-39	36-42
4	42	23	28	20	2-18	2-18
3	11	6	8	5	1-5	1-5
2	3	2	2	1	<1-1	<1-1
1	<1	<1	<1	<1	<1	<1
			OBSERVED			
Population estimates after 1955 crop			2	6		
			9	5		
			22	8		
			0	2		
			8	3		
			10	4		
			10	3		
			10	4		
			40	15		
			23	9	(1) 2	<1
	**(15) 0	0	(5) 0	0	(59) 0	0

* Sequences foreshortened by deleting successive cycles to give 5 to 1 potato crops.
** Number of plots, 15 plots per block.

measurable infestation in any plot on blocks I, III, V and VI but there were substantial infestations in some plots of block II and an incipient infestation in one plot in the middle of block IV.

As all plots grew potatoes in 1928, it seems probable that the infestation was by cysts adhering to seed potatoes. As only block II was found appreciably infested, suspicion falls on those used to plant block II in 1930. If so, the nematode population would have experienced up to five potato crops by 1955 whereas those in blocks III to VI would have experienced a maximum of four. The layout of block II (Table 15) shows that plots with measurable infestations were contiguous, the most heavily infested being No. 29 where the infestation may have originated. This plot had an estimated 40 eggs/g and 15 cysts/100 g compared with 75 and 55 respectively predicted by Model I after five potato crops and 117 and 109 after six. There was too little information for Model 2 to be applied.

The Green Manuring Experiment, Stackyard Series A upper half

The progress of the infestation in the upper half of the experiment, which led to the appearance of symptoms in one or two plots after five crops of early potatoes in alternate years, can be simulated using Model 1 to predict egg densities and the first matrix of Model 2 to indicate the area occupied. It is reasonable to assume that there is little or no competition and that each old focus generates 100 more. Table 16 shows the combination of the matrix which, in five cycles, is limited to the primary infestation and the first and second arrays of the secondary infestation. The number of arrays in which population densities exceed the threshold for crop injury (20 eggs/g) are shown in bold print and these are summed at the bottom of the table to give the maximum area likely to be affected. The simulation predicts that no crop symptoms would be discernable until the 5^{th} or 6^{th} crops. Because Model 1 calculates population at the *end of each* cycle, it is the crop *following* that suffers when the threshold is exceeded. The standard multiplication rate of 50 times was used in the calculations as the early potatoes were lifted late, usually after 15^{th} July. Early lifting may not allow a full complement of eggs to develop in

Table 15. *Woburn 6-course rotation, Stackyard Series B. Layout of Block II showing the estimated population densities of eggs and cysts in the plots.*

Plot No.					
eggs/g	*16* 0	*17* 0	*18* 9	*19* 22	*20* 0
cysts/100 g	0	0	5	8	2
	21 0	*22* 0	*23* 8	*24* 10	*25* 10
	0	0	3	4	3
	26 0	*27* 0	*28* 10	*29* 40	*30* 23
	0	0	4	15	9

Table 16. *Simulated progress of the infestation in the Green Manuring Experiment, Stackyard, Series A. Early potatoes cv. Ulster Chieftain grown in alternate years.*

Assumes that $a = 50$, there is no competition and that the rate of generation of new foci *(N)* is 100. Eggs/g and those predicted by Model 1 at the end of each cycle.

(Page i of ii)

Crop sequence SOSOSOSOSO

Cycle	**Area infested domains**	**Domains**	**Eggs/g**	**Domains**	**Eggs/g**	**Domains**	**Eggs/g**	**Domains**	**Eggs/g**	**Domains**	**Eggs/g**
		Primary infestation									
1	1	1	0.5								
2	4	1	9.5	3	0.5						
3	9	1	**101.8**	3	9.5	5	0.5				
4	16	1	**49.5**	3	**101.8**	5	9.5	7	0.5		
5	25	1	**87.4**	3	**49.5**	5	**101.8**	7	9.5	9	0.5
		Secondary infestation, 1st array									
1	-										
2	100	100	0.5								
3	400	100	9.5	300	0.5						
4	900	100	**101.8**	300	9.5	500	0.5				
5	1600	100	**49.5**	300	**101.8**	500	9.5	700	0.5		

Table 16 continued. **(**Page ii of ii)

Crop sequence SOSOSOSOSO

Cycle	Area infested domains	Domains	Eggs/g	Domains	Eggs/g	Domains	Eggs/g	Domains	Eggs/g	Domains	Eggs/g
		Secondary infestation, 2nd array									
1	-										
2	-										
3	400	400	0.5								
4	1600	400	9.5	1200	0.5						
5	3600	400	**101.8**	1200	9.5	2000	0.5				

	Domains	*Area significantly affected, maximum* m^2 ($r = 0.1\ m$)	
4	1	0.03	would not be seen
5	104	3.27	small patch of stunted plants
6	809	25.42	large patch of stunted plants

Note: Upper half of experiment found infested, had 5 potato crops (5 cycles) but lower half apparently uninfested, had 4 potato crops (4 cycles)

Bold print signifies the arrays in which population densities exceeded the threshold for crop injury (20 eggs/g). These are summed up at the bottom of the table to give the maximum area likely to be affected.

all females. A decreased rate of multiplication, e.g. 30 times, would give lesser population densities and result in crop symptoms being less intense but leave the area affected unchanged. Competition for space would diminish the area but might sharpen symptoms somewhat because of recruitment. Increasing *N* would leave population densities unchanged but increase the area affected and intensify competition for space.

Experiment on Nematicides in a 3-course Rotation, Stackyard Series A lower half

No signs of crop damage by *G. rostochiensis* were observed in any of the four early potato crops planted in the green manuring experiment on the lower half of Series A. Five years (1962-1966 inclusive) followed without potatoes and then five crops of main crop potatoes were planted in preparation for an experiment with nematicides (Table 17). Egg population densities were trivial after the second crop in 1968 and attempts in inoculate the third crop in all sections of the experiment had little influence. This is not surprising: the numbers of cysts added may seem large but they are trivial compared with the bulk of the soil. Only dispersal and reproduction can result in the vast numbers needed to produce appreciable crop damage in the field.

Table 17 compares the observed egg/densities with those calculated for the primary infestation (1 domain) using Model 1, first on the assumption that the infestation began in 1967 and second that it began in 1955 in the first crop of early potatoes planted in the field. The comparison suggests that the first assumption is most likely to be true. It also tends to confirm that at least five host/crop cycles are needed to infest substantially areas of land equal in size to the Sections (0.23 ha, 7.32×10^4 domains). The actual plots were no more than 0.0032 ha (1017 domains) of which there were 72 to each Section.

Note: Unfortunately, text remains unfinished beyond this paragraph.

Table 17. *Nematicides in a 3-course rotation, Stackyard Series A, lower half. Preparatory phase.*

Sections are called Series in Whitehead *et al. (1980)*
Eggs/g soil after harvest.

	Sections											
	I				II				III			
	Crop	Eggs/g soil			Crop	Eggs/g soil			Crop	Eggs/g soil		
		Observed	Calculated			Observed	Calculated			Observed	Calculated	
			†(1)	(2)			(1)	(2)			(1)	(2)
1967	S_1		<1	15.3	S_1		<1	15.3	S_1		<1	15.3
1968	S_2		21	66	S_2		21	66	S_2		21	66
1969	S_3*	1	178	10	O	0	14	43	O	3	14	43
				7								
1970	S_4	17	68	73	S_3*	4	173	144	O		9	29
1971	S_5	42	103	98	S_4		68	66	S_3*	1	153	170
1972					S_5	56	104	107	S_4		67	67
1973									S_5	48	107	104

† (1) calculated using Model 1 on the assumption that the infestation was initiated in 1967, 5 cycles; (2) on the assumption that it started in 1955 with the first early potato crop of the Green manuring experiment, 9 cycles, last 5 shown.

* To accelerate infestation, alternate plants in every other row were inoculated with 60 cysts.

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