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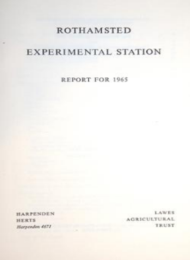

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the Population Dynamics and Population Genetics of the Potato Cyst-nematode Heterodera Rostochiensis Woll. On Susceptible and Re-sistant Potatoes

F. G. W. Jones

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THE POPULATION DYNAMICS AND POPULATION GENETICS OF THE POTATO CYST-NEMATODE *HETERODERA ROSTOCHIENSIS* WOLL. ON SUSCEPTIBLE AND RESISTANT POTATOES

F. G. W. JONES

Of the many kinds of work done at Rothamsted on the potato cyst-nematode, potato root-eelworm or golden nematode (Peters, 1951; Fenwick, 1956; Shepherd, 1962), this article deals with that on the general principles of population changes, many of which apply not only to other cyst-nematodes but also to other nematodes and to animal populations in general. The changes in behaviour of populations when resistant potato varieties are grown have led to hypotheses of the manner in which ability to develop and multiply on these varieties is inherited. A computer programme, combining knowledge of population changes with two alternative hypotheses of inheritance, makes it possible to predict the ways in which populations may behave when the new resistant potato varieties now coming on to the market (Ulster Glade, Maris Piper) are grown. It also shows which factors affecting populations are important and helps to formulate a policy to make the best use of the resistant varieties, so that their useful life will be prolonged by minimising genetic changes in the field populations of the nematode.

World distribution. The potato cyst-nematode was probably introduced into the United Kingdom shortly after 1851, along with potato tubers imported from the Andes plateau, South America (Jones, 1951). There were few imported earlier but many later following the outbreaks of potato blight that caused the Irish famines, with the object of breeding varieties resistant to blight (Jones & Jones, 1964; Salaman, 1926). Symptoms of nematode attack (potato-sickness) seem first to have been observed near Hull about 1900, and the causal organism, *Heterodera rostochiensis*, was first found in Scotland in 1913 and in Yorkshire in 1917 (Southey, 1965). Spread at first was slow, then faster; it was accelerated by overfrequent potato cropping during two world wars, and has now slowed again. It probably followed the S-shaped curve usual with introduced organisms invading new territory (Jones & Jones, 1964), and, as a rough estimate, some 80% or more of potato-growing land in fields and gardens is now infested. This wide distribution has taken about 100 years, and was greatly assisted by farming practices, especially the traffic in seed tubers. The organism, already adapted to a near-European climate in the Andes, found an unoccupied ecological niche in potato roots in the United Kingdom, where it seems to have few enemies or competitors.

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Field population sizes. The weight of soil per acre down to 8 in. is approximately 1,000 tons or 10^9 g. When susceptible potatoes are grown frequently or continuously nematode eggs reach 100–500/g soil, so that terminal field populations are of the order of 10^{11}/acre. Periods of five to six years without susceptible crops decrease populations to about 10^{10} eggs/acre, at which potato crops grow well and yield loss is slight or nil. When potatoes are grown in rotation or continuously, numbers fluctuate within these limits, and the pest rarely multiplies to its maximum capacity. The amount of its food, determined by the amount of potato-root tissue during the 6–8 weeks after the seed tubers are planted, is fairly constant when the same variety is grown on the same land, at the same spacing and with the same amount of fertiliser. Also, temperature and moisture in the soil at 6 in. deep are reasonably constant over the effective period (mid-April – mid-June). Such a potato field when divided into plots is comparable to some of the classical population experiments of Nicholson (1954) with blowflies and meat, in which initial numbers differed but the food supply remained constant. As in Nicholson's experiments, potato cyst-nematode numbers fluctuate in a series of damped oscillations about an equilibrium population (Fig. 1).

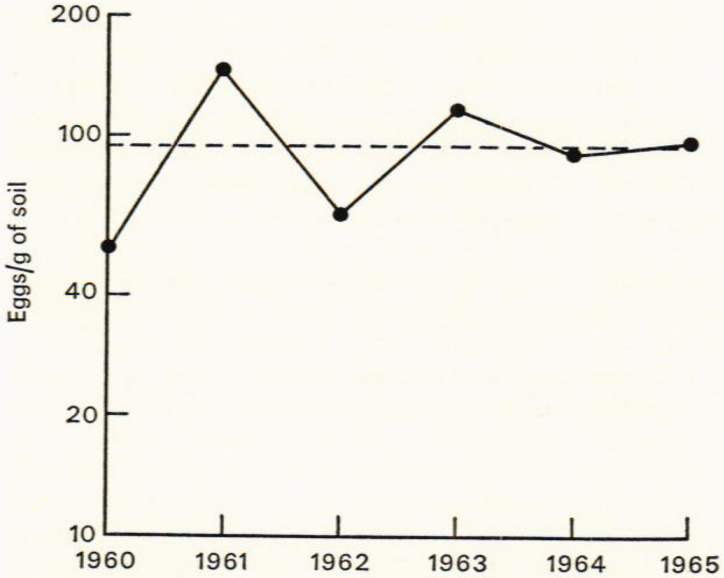

FIG. 1. Population fluctuations of the potato cyst-nematode when susceptible potatoes are grown continuously on the same land. Numbers exhibit classical damped oscillations about an equilibrium level (dotted line). Means of 28 plots.

The relationship between numbers and yield. Fig. 2 shows the relationship between the number of cyst-nematode eggs in soil and the yield of tubers. When they are few, yield is unaffected because the plants compensate fully for the trivial injury to their root systems; indeed, a few sometimes increase yields of plants in pots (Jones, 1957a). As numbers increase, a point is reached where yield begins to decline, at first slowly but then faster, and finally, with large infestations, reaches a minimum below which further increase in numbers has no effect on yield. This is the general curve

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relating yield to numbers, which applies to many pests and probably to some diseases. It can be deduced theoretically (Justesen & Tammes, 1960) and shows in the results of experiments with potato cyst-nematode (Williams, 1958; Peters, 1961) and pea cyst-nematode (Jones, Meaton, Parrott, Shepherd & King, 1965). The number of nematodes (or other pests) is plotted on a logarithmetic scale partly because individuals compete with one another and proportionally more are needed to cause the same yield loss with large than with small populations. Seinhorst (1965) showed that the central part of the yield/numbers curve fits the equation derived from Nicholson's (1933) competition curve:

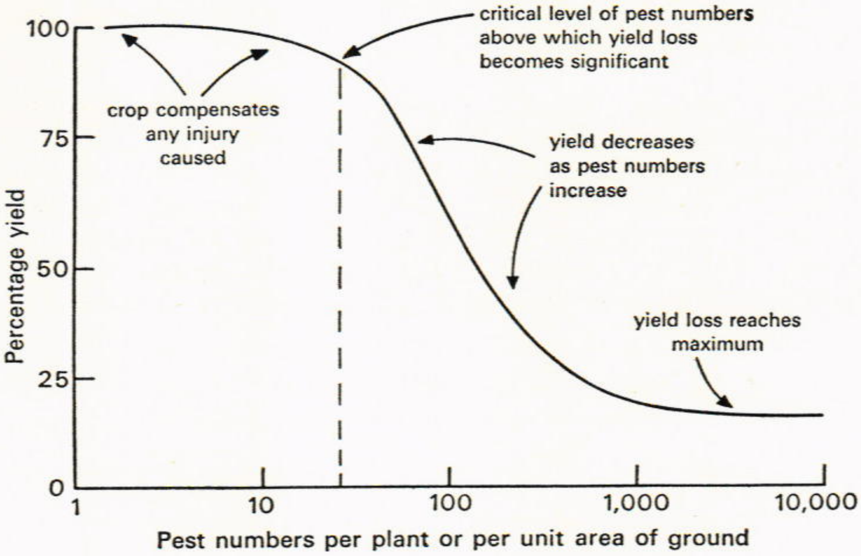

FIG. 2. The general curve relating yield loss to pest numbers.

$$y = \frac{\text{Actual yield} - \text{Minimum yield}}{\text{Maximum yield} - \text{Minimum yield}} = k\ (1 - d)^{Py - Pt}$$

where d is a measure of the injury caused by a single nematode, k is a constant, Py is the population associated with the actual yield and Pt the population threshold at which yield begins to be affected.

The concept of a population threshold at which yield loss begins is often used in connection with crop pests (Jones & Jones, 1964) and is valuable when giving advice on cropping. Estimates of thresholds often differ widely, and must obviously differ in different fields and different seasons. Advisers prefer to relate yield loss to a linear population scale, and an approximate straight-line fit is often adequate to describe the relationship between yield over the relatively narrow range in which field populations fluctuate. Such a fit is descriptive only and is not related to the competition between nematodes for root space (Brown, 1961).

The yield loss from an injured plant, especially when injury affects the root system early in the season, must depend on the climatic stress (insolation, temperature and water deficiency) the impaired plant has to endure before harvest. Experience suggests that, on sandy loam soils, such as at Woburn, yield losses in potatoes begin at approximately 10 eggs/g soil. Measurements on black fen soil (Williams, 1958) suggest a threshold of 10–20 eggs/g, and the National Agricultural Advisory Service uses thresholds ranging from 10 to 50 eggs/g according to circumstances. These compare with 10 eggs/g for beet cyst-nematode (*H. schachtii*) in fenland skirt soil (Jones, 1945) and fewer than 10 eggs/g soil for cereal cyst-nematode (*H. avenae*) at Woburn.

Population decrease. In the absence of a host crop, cyst-nematode numbers seem to decrease at a steady rate regardless of the density of the population per unit of soil (Jones, 1956): evidence to the contrary is slight (Moriarty, 1963a), although when a field population consists mainly of one age group it may behave differently from one of mixed age groups (Moriarty, 1963b). Cooper (1954) followed potato cyst-nematode changes in 389 fields in Eastern England, and Fig. 3 shows his results plotted as log population density against the number of years from the last potato crop grown in 1940. The average rate of decline is the same (32%) for heavily and lightly infested fields, and 68% is carried over every year. This suggests that encysted nematode eggs, containing the dormant second-stage larva, lack effective enemies, for any such would increase and be more active with larger than with small populations. In silt soils, black fen soils (Cole & Howard, 1962a) and sandy soils with an appreciable clay fraction (e.g., Woburn), the annual rate of decrease probably departs little

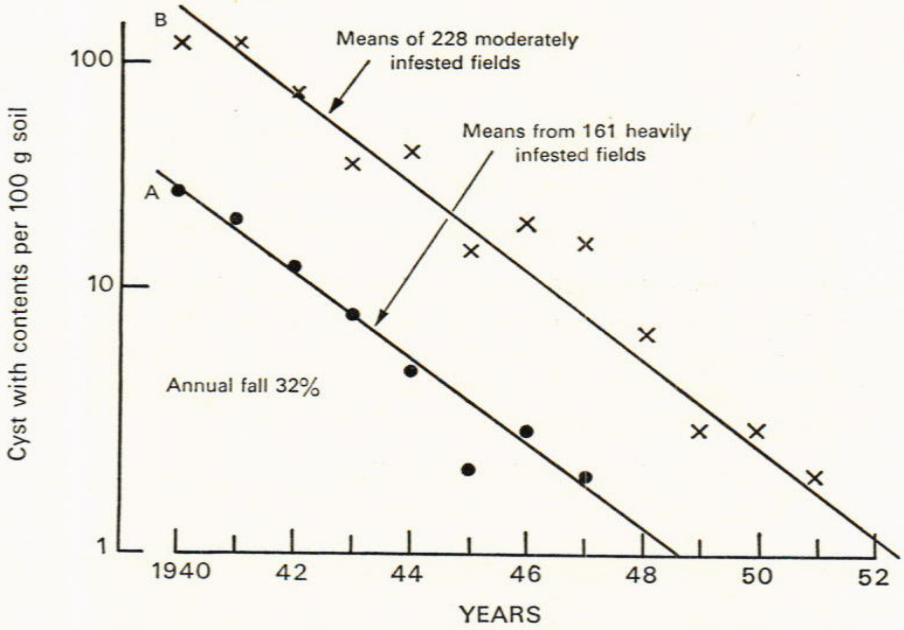

FIG. 3. The rate of decrease of potato cyst-nematode populations when crops other than potatoes are grown. The average rate, 32% per annum, is the same for heavily and moderately infested fields and seems independent of population density. Plotted from data in Cooper (1954).

from Cooper's average of 32%. In sand soils without clay the population apparently decreases much faster, as much as 80% per annum (Cole and Howard, 1962b; Stelter, 1964). This agrees with the much enhanced hatch of cyst-nematodes in coarse sand (Wallace, 1956), and with the fact that the nematode persists longer in cold, wet Scottish soils than in the warm, light, sandy soils of the Channel Islands (Dunn *in litt.*).

When potatoes are not grown the decrease in population size seems to relate to the spontaneous hatch of eggs that takes place in April–May. When potatoes are grown the hatching factor produced by their roots increases the proportion that hatch, so fewer are carried over to the next year. The only estimates of the proportion carried over in these conditions come from experiments in which resistant potatoes were grown continuously for several years in fields where the population contained few individuals able to multiply on the resistant plants. Huijsman's (1961) results indicate an average annual rate of decline of 62%, those of Cole & Howard (1962a), 60–67% and an experiment in progress at Woburn about 40%. The size of the population carried over is important for several reasons. It affects the length of the rotation necessary to control crop losses, determines how fast those remaining multiply when susceptible potatoes are grown and influences the speed of genetic change when resistant potatoes are grown. A large carry over decreases multiplication and provides a store of genetically unchanged larvae which swamps new larvae with different genetics.

Population increase. In contrast to population decrease, which is independent of numbers of nematodes per unit of soil (density), increase when susceptible potatoes are grown is greatly influenced by the density of the initial population. Curves linking log initial and log final population density (Fig. 4) fit a model which can be derived from the logistic population curve (Andrewartha & Birch, 1954; Seinhorst, 1965).

$$P_f = \frac{a(1 - C_P)P_i}{1 + (a - 1)P_i} + C_P P_i$$

where P_i = the initial density, P_f = the final density after a crop of susceptible potatoes, a = the maximum possible rate of increase and C_P the fraction of the population carried over (i.e., taking no part in reproduction).

Increase is the fastest possible only with very small initial population densities. As the density increases, the multiplication rate slows, becomes unity when the initial and final populations are the same and decreases to a fraction when the maintenance (× 1) line is crossed. The flat central parts of the three curves in Fig. 4 are ceiling levels (Jones, 1956), and at excessive initial densities, when multiplication ceases, only the eggs carried over are left. Population changes induced by self-set potato plants growing in other crops fit the same model. Nematodes increase only when their initial density is small, and then not by very much. The self-sets do not increase the hatch above that which occurs spontaneously, and so, at greater initial densities, populations behave in the same way as in crops other than potatoes (den Ouden, 1965).

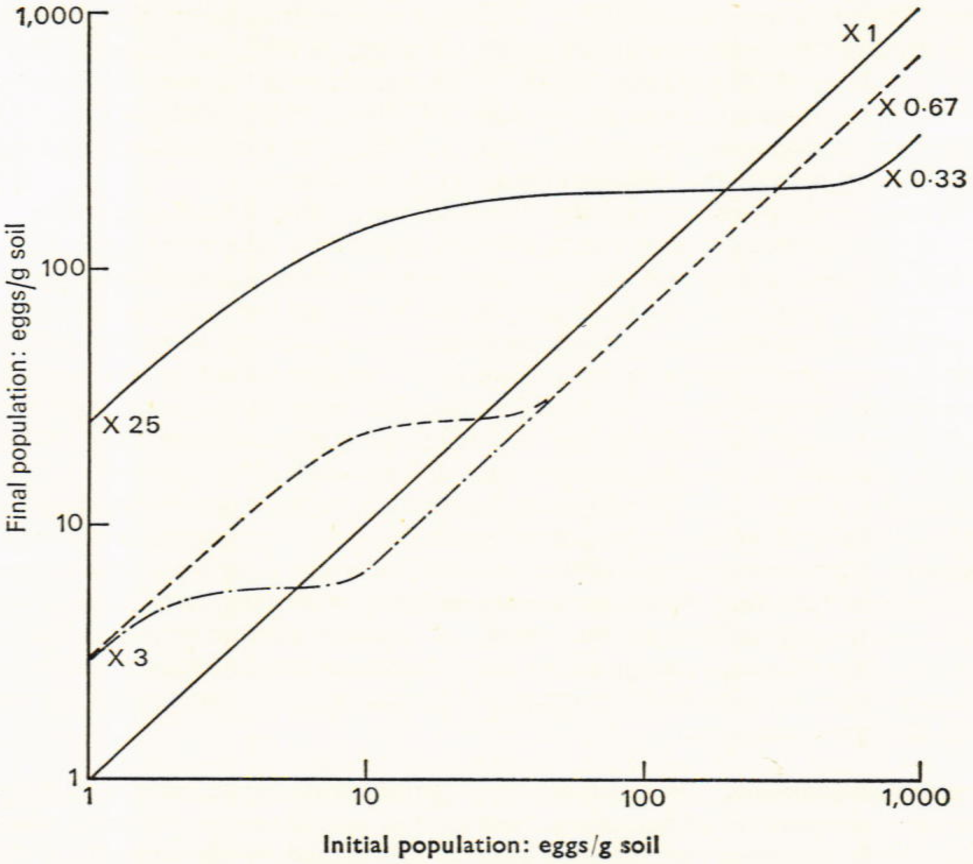

FIG. 4. Curves linking initial and final populations. Main-crop potatoes ———— maximum reproductive rate 25 times, carryover 0·33 (33%) of the initial population. Self-set potatoes in a cereal crop – – – – – 64,000/acre, ·—·—·—·—, 16,000/acre, maximum reproductive rate 3 times, carryover 0·67 (67%). The self-set potatoes have not hatched appreciably more eggs than those hatching spontaneously, whereas the maincrop potatoes have decreased the carryover from 0·67 to 0·33 (67 to 33%). The maintenance line (×1) is the locus of points when the initial and final populations are equal. Partly after den Ouden, 1965; see also Jones, 1956.

Kort (1962) showed that at small densities in pots encounters between the sexes are too few for all females to be mated, the increase then is less than the maximum possible. The fact that the potato cyst-nematode has its eggs in packets (cysts) in a field soil probably ensures that the local density is rarely so small that mating fails.

Components in population increase. We have already seen that only a part of the soil population hatches when potatoes are grown. Only a fraction of this part succeed in invading the potato roots and begins developing. Rao and Peachey (1965) found that only 11% or less of larvae added to soil in pots growing potatoes were recovered from the roots 6 weeks later and only 15% or less were recovered as cysts (new females) 15 weeks later. (Fig. 5). As is common among animals, the success rate became less as the number of larvae added was increased, presumably because larvae compete with each other in the roots. A curious feature of the biology of

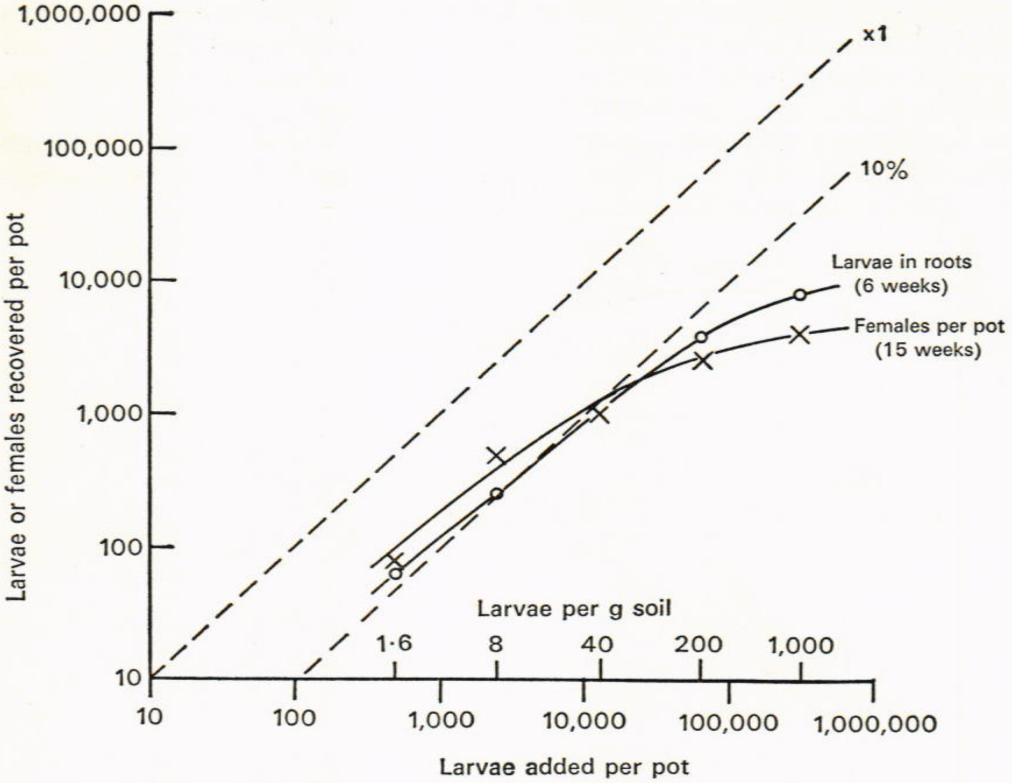

FIG. 5. The proportion of larvae that succeed in invading potato roots and becoming females at different initial populations densities. Success decreases as numbers increase, and ranges from a little more than 10 to 2% or less. Plotted from data in Rao & Peachey (1965).

cyst-nematodes and some others is that the second-stage larvae have the potentiality of becoming males or females according to circumstances. Ellenby (1954b) first suggested this for potato cyst-nematode, and Trudgill confirmed (see p. 146 this *Report*) that competition between larvae for root space is an important determinant. When few larvae invade the roots more females develop than males; when many invade, only about seven females per cm of root successfully complete their development and the surplus larvae become males or die.

Results from pea cyst-nematode in microplots (Jones *et al.*, 1965) suggested that, once a larvae had successfully established itself and become female, intraspecific competition was over, food was adequate and the average number of eggs produced per female (new cyst) was constant over a wide range of initial population densities. Re-examination of earlier results (Peters, 1961; Hesling, 1961) showed that this holds also for potato cyst-nematode (Fig. 6), and beet cyst-nematode (Jones, 1957a), except possibly when the numbers of invading larvae are excessive and the roots are destroyed. Successful female cyst-nematodes may be said to acquire a breeding territory analogous to that established by birds and some other higher animals. This being so, the destruction of larvae by enemies, e.g. fungi (Duddingston, Jones & Williams, 1956) or by nematicides before they invade host roots, tends to remove only those surplus to the carrying capacity of the potato roots. Although nematicides can greatly increase crop yields when nematode densities are large, the final population at the end of the season is little affected and may be enhanced. From this it may be concluded that effective population control is likely to be achieved only when some means has been found of preventing the females developing in the roots, preventing them from mating successfully or killing them before they produce eggs.

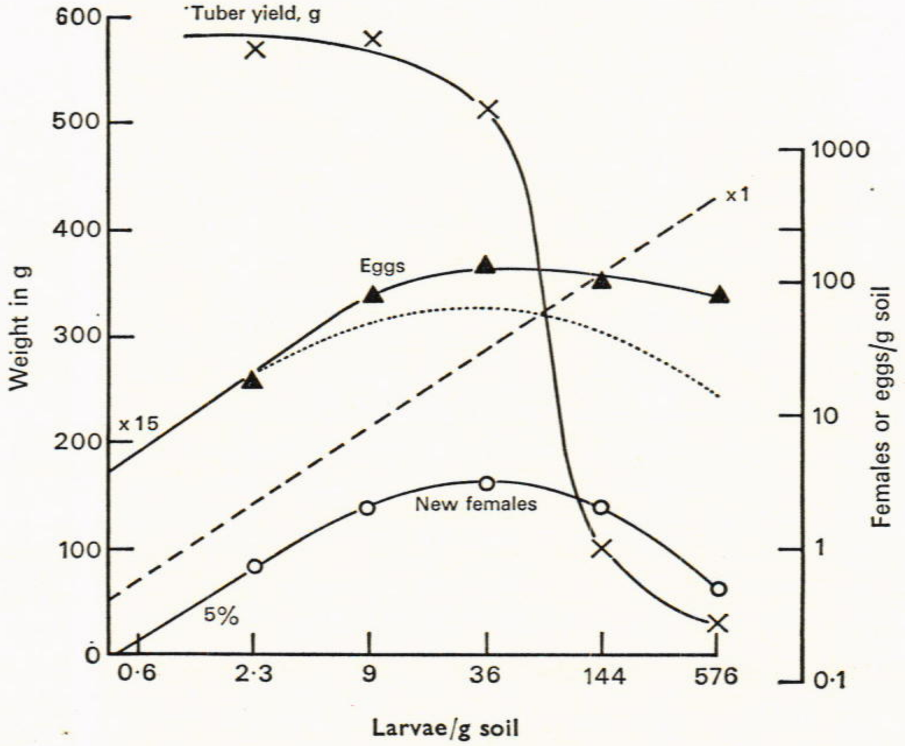

FIG. 6. The relationship between numbers of larvae initially, new females and the final number of eggs. The curves for new females and eggs run parallel at first, indicating that, on average, females contain the same number of eggs. The egg curve departs from expectation (dotted line) at greater initial larval densities, probably because of the fraction of larvae that fail to hatch from the encysted eggs added to the pots initially. Eggs carried over to the end of the year cannot be distinguished from new eggs. The yield/initial density curve is added. Yield loss begins as larval competition in the root systems decreases the success rate (5%) and the maximum reproductive rate (×15).

Differences between field populations from different localities. Before Ellenby (1954a) showed that some species of potato are resistant (i.e., do not support nematode reproduction), and plant breeders had begun to incorporate resistance into cultivated varieties, there was no reason to think that populations of potato cyst-nematode differed genetically from place to place. Dunnett (1957) first showed such differences and that some populations could multiply on the resistant plants. Jones (1957b, 1958), in collaboration with the National Agricultural Advisory Service, produced a map showing the distribution of populations able and unable to multiply well on resistant potatoes bred from *Solanum tuberosum* ssp. *andigena*. (Jones & Pawelska 1963) tested the ability of the field populations to multiply on a range of resistant plants and studied the effects of selecting them by growing resistant varieties in infested pots for several years. Field populations differ less in their ability to multiply on plants derived from *Solanum multidissectum* than from *S. tuberosum* ssp. *andigena*, but most reproduced to a moderate extent. Ex *andigena* and ex *multidissectum* plants carry single dominant genes for resistance. Combining these genes greatly increases the number of populations the plant can resist, and resistance can be further increased by including a third factor, as in the seedling D40 bred by Dr. J. M. Dunnett. Then resistance is equivalent to the polygenic resistance of plants bred from *Solanum vernei* (*ballsii*).

On allotments at Rothamsted and in the fields at Woburn the potato cyst-nematode populations resemble those common in East Anglia and S.E. England generally, in reproducing poorly on resistant potatoes ex *andigena*, better on those ex *multidissectum* and scarcely at all on plants combining the resistance of both. All fields at Woburn are infested, some heavily, but potato cyst-nematodes are relatively few at Rothamsted. This may be partly because potatoes are grown more often at Woburn and partly because the sandy loam there favours nematode activity more than the clays at Rothamsted (*Rothamsted Report* for 1964, p. 150).

Different pathotypes of the potato cyst-nematode can be distinguished by their different abilities to develop on potatoes with known differences in genetic constitutions and on other solanaceous plants, such as the weed black nightshade (*Solanum nigrum*). Pot tests with over forty populations of nematodes from widely scattered localities in England and Wales show that there are many pathotypes, and a start has been made in unravelling their genetic inter-relationships (Howard, 1959; Jones, & Pawelska, 1963; Jones & Parrott, 1965). Ability to reproduce depends on the ability of larvae to inject saliva which stimulates the host rootlet to produce proper giant cells on which they feed. When this happens the larvae may become females and, after mating, produce eggs: when it does not, larvae either become males or die. All pathotypes in British populations appear to have the ability to reproduce on fully susceptible potato plants, but not on all those containing genes for resistance (Table 1).

TABLE 1

Designation of pathotypes occurring on ab, Ab, aB and AB plants

	Plant constitutions			
	Susceptible	Resistant		
Pathotypes	Arran Banner *ab*	ex *andigena* *Ab*	ex *multidissectum* *aB*	ex both *AB*
0	+	−	−	−
1	+	+	−	−
2	+	−	+	−
1,2	+	+	+	+

+ indicates ability of larvae to become female, i.e., to reproduce

Table 1 designates pathotypes found on susceptible potatoes lacking genes for resistance (ab plants), potatoes with one gene for resistance bred ex *andigena* (*Ab* plants), another bred ex *multidissectum* (*aB* plants), or combining both (*AB* plants). All four pathotypes can multiply on plants lacking genes for resistance, pathotype 1 can also multiply on plants with gene *A*, pathotype 2 on plant with gene *B* and pathotype 1,2 on plants with gene *A*, gene *B* or both.

The nematodes that can develop into females and multiply on potatoes resistant to the bulk of the population must differ genetically from the bulk of the population. For each gene in the potato that confers resistance against some but not all potato cyst-nematodes, it is necessary to postulate a matching gene in the nematodes that enables them to evoke the response (giant cell formation) that allows them to multiply (become female) despite the gene in the plant. The nematode gene matching the gene in the plant may be dominant or recessive in action. When the plants have two or more genes for resistance the matching nematode genes may occupy independent sites on the nematode chromosomes or be alleles, that is, occupy the same site. This leads to four possible hypotheses of inheritance of ability to multiply on resistant plants (Table 2).

TABLE 2

Genetic hypotheses to explain pathotypes

Genetic constitutions of nematode larvae able to become females. Males have any constitution.

		Independent pairs of genes		Alleles	
Hypothesis Matching genes		1 Recessive	2 Dominant	3 Recessive	4 Dominant
Pathotypes	0	*AABB* *AABb* *AaBB* *AaBb*	*aabb*	G_AG_B	*gg*
	1	*aaBB* *aaBb*	*AAbb* *Aabb*	G_BG_B G_Bg	G_AG_A G_Ag
	2	*AAbb* *Aabb*	*aaBB* *aaBb*	G_AG_A G_Ag	G_BG_B G_Bg
	1,2	*aabb*	*AABB* *AABb* *AaBB* *AaBb*	*gg*	G_AG_B
Fit to expected frequencies		Good	Good	Bad	Near

If only one of the pairs of nematode genes is considered (e.g., *A*, *a*) hypothesis 3 becomes identical with 1, and 4 with 2. The frequency of occurence of females on *ab*, *Ab*, *aB* and *AB* plants has been measured in pot tests (Jones and Parrott, 1965), and the observed frequencies after correction (Table 3) fit hypotheses 1 and 2 well, are a near fit to hypothesis 4 and a bad fit to hypothesis 3 which is eliminated.

Three additional pieces of information agree with the idea that successful females are double recessives (*aa*) and favour hypothesis 1. (1) When field populations that breed only poorly on *Ab* plants are placed in pots planted with *Ab* tubers the frequency of females (cysts) able to develop increases only slightly at the end of the first generation (females *aa*, males mainly *AA*, progeny mainly *Aa*, which become males), and to about 0·5 (50%) at the end of the second (females *aa*, males mainly *Aa*, half the progeny

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aa which can become females). On hypothesis 2 the frequency should be 0·5 (50%) at the end of the first generation (females mainly *Aa*, males mainly aa, half the progeny *Aa* which can become females). (2) Cysts from similar populations raised on *Ab* plants should contain progeny mainly *Aa* on hypothesis 1 and, when tested singly on ex *andigena* plants, their progeny should be predominantly males. On hypothesis 2, all should contain 50% *Aa* progeny and, when tested singly, should give rise to females. In fact, nearly all cysts produce males, and females are rare (Trudgill, see p. 147 this Report). (3) In the field when resistant ex *andigena* (*Ab*) plants are grown every year on the same land the number of years (generations) for nematodes able to overcome resistance to develop and for population increases to begin is longer than expected from hypothesis 2. However, none of this evidence is decisive, and proof of the genetic inheritance of ability to overcome resistance depends on the making and testing of controlled crosses after pure lines of pathotypes have been isolated. Some crosses have already been made but not tested (Webster, 1965), and more are being attempted.

TABLE 3

Comparison of observed and expected frequencies

		Pathotype frequencies			
Source		0	1	2	1,2
*Observed values		0·48	0·28	0·16	0·08
Expected values derived by the method of maximum likelihood	Hypothesis 1	0·48	0·27	0·16	0·09
	Hypothesis 2	0·48	0·27	0·16	0·09
	Hypothesis 3	0·33	0·38	0·26	0·03
	Hypothesis 4	0·46	0·31	0·19	0·05

* See Jones & Parrott (1965), based on the means of 40 populations and 700 pot tests.

All four hypotheses postulate the existence of a pathotype 0 (Table 1). The existence of pathotype 1, pathotype 2 and pathotype 1,2 is based on the occurrence of cysts on *Ab*, *aB* and *AB* plants, but the absence of expected cysts on *ab* plants is based on the fact that the frequencies of 1, 2 and 1,2 do not add up to 1·0, i.e., not on positive evidence. All four hypotheses also assume that there is one generation of potato cyst-nematode per year, sexual reproduction is obligatory, mating is random and there are no fitness differences between gametes. These assumptions are reasonable, except that there is sometimes a partial second generation limited by the onset of dormancy after July (Shepherd, *in litt.*). Another assumption is that test plants produce equal amounts of root when grown in pots and that larvae of different constitutions have equal chances of developing. The last assumptions are only approximately true, and Jones and Parrott (1965) applied an arbitrary correction to allow for the excess of females that develop on resistant plants. All four hypotheses require that pathotype 1,2 should increase when selection with resistant potatoes increases pathotypes 1 or 2: there is some evidence that this occurs (Howard, *in litt.*).

Computer models to simulate population changes. The Orion computer was programmed by G. J. S. Ross to do the arithmetic for population changes that can be expected to occur when resistant potatoes (R), susceptible potatoes (S) and other crops (O) are grown, or for any sequence of crops such as continuous resistant potatoes (RRRR, etc.), alternate resistant and susceptible potatoes (RSRSRS, etc.) or rotations (e.g., ROOSOO, etc., or OOO followed by ROOSOO, etc.). The computer is supplied with values for: (1) the frequency of larvae able to become female (resistance breaking pathotypes); (2) C_P, the fraction of the population carried over when potatoes are grown and, C_O, when other crops are grown or the land is fallowed; (3) a multiplication law derived from the logistic curve; (4) the maximum reproductive rate, m; (5) two mathematical models, one of which fits the first and third hypotheses of inheritance (females are *aa*) and the other the second and fourth hypotheses (females are *AA* and *Aa*). The computer works out the results of the sequences for as many years (generations) as is necessary and prints out the expected frequencies of *AA*, *Aa* and *aa* nematodes according to the two models, as well as the accompanying changes in population size in terms of the maximum population level, which is taken as unity.

Because the computer does arithmetic with great speed, a range of

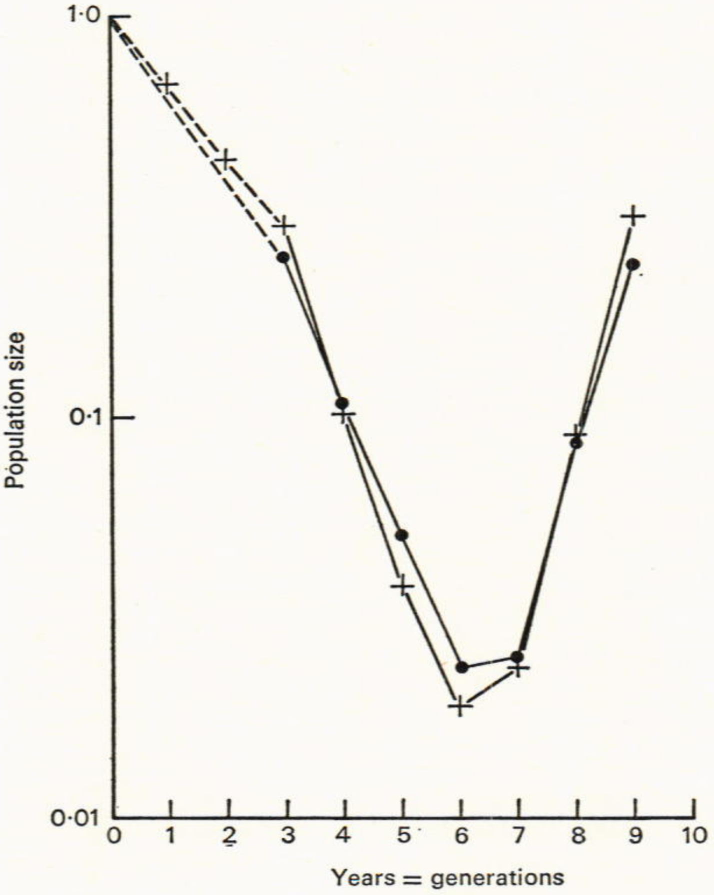

FIG. 7. A computer model fitting the results in Cole & Howard (1962a); observed values ●, computer values +, three years under crops other than susceptible potatoes – – – –, six years under resistant ex *andigena* potatoes ————. Frequency of resistance breakers initially, 0·005; C_O, 0·667; C_P, 0·333; a, ×50.

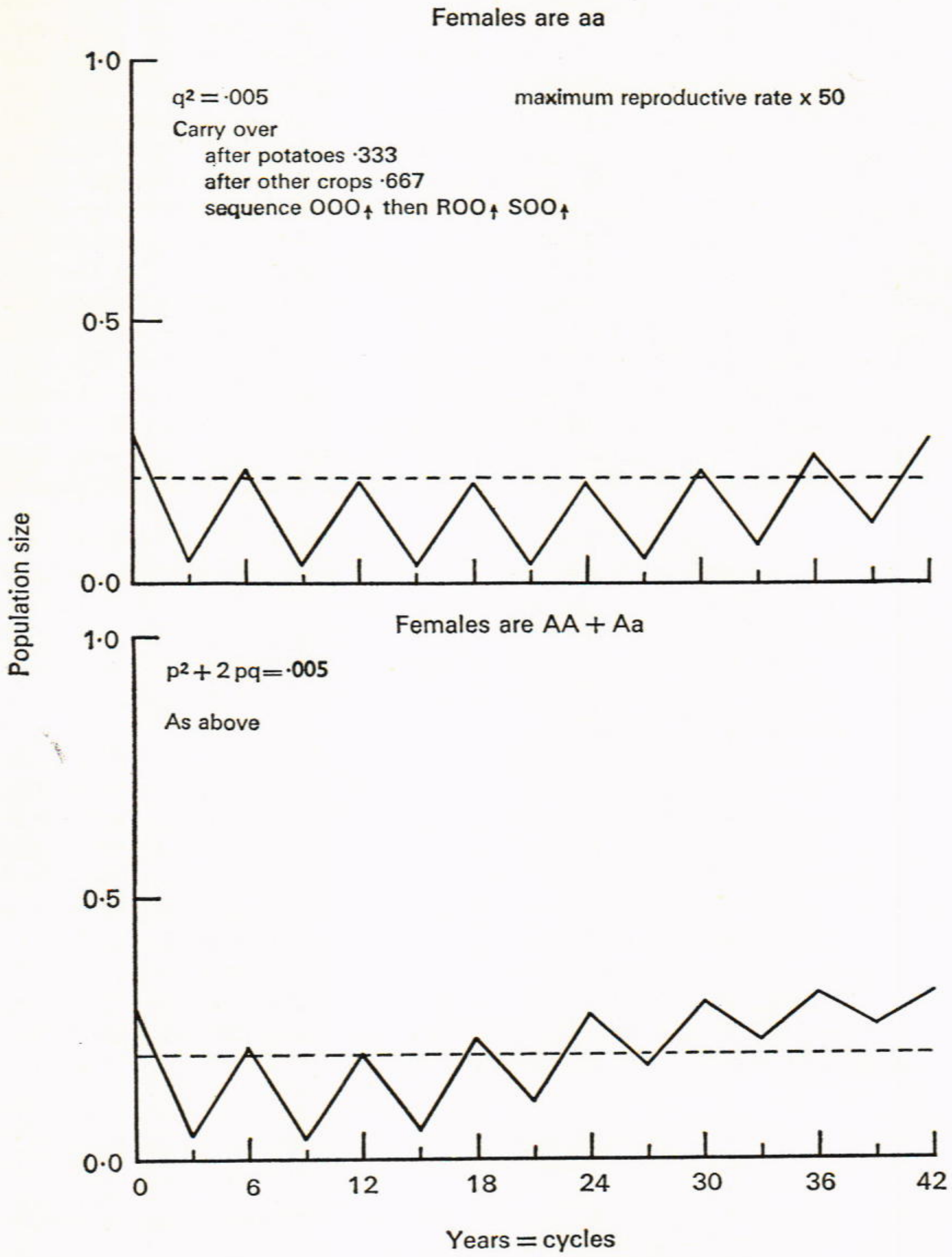

FIG. 8. A computer model showing predicted changes in population size when resistant and susceptible potatoes are grown alternately in rotation after 3 years rest from a susceptible potato crop. Numbers immediately before potatoes are grown fluctuate below the level (dotted line) at which serious yield loss would occur. On the hypothesis that females able to develop are double recessives (*aa*), it would take 30 years before appreciable genetic change caused numbers to rise above the tolerance level. On the alternative hypothesis (females are *AA* or *Aa*), increase would begin after 18 years.

values can be supplied for each of the important variables C_O, C_P, m and the initial frequency of resistant-breaking pathotypes which include estimated values from our own and other workers' experiments. The predictions of the computer of expected changes in the frequency of resistance-breaking pathotypes and in population size can be compared with those observed in field experiments. Few experiments have run long enough, have been done with sufficient accuracy or supply estimates of all the variables. Nevertheless, computer models based on the first genetic hypothesis fit the results of Cole and Howard (1962a) (Fig. 7) and Huijsman (1961). Making a computer programme has brought out the importance of the variables listed above and the need to estimate them more accurately; it also suggested that "genetic" control of the population level may be possible with crop sequences such as OOO, ROOSOO, etc. (Fig. 8), and prompted suggestions for the best use of resistant varieties (Jones & Jones, 1964). It has also shown that long rotation and nematicides, by decreasing the size of the initial population when resistant potatoes are grown, would speed genetic change and shorten their useful life.

To date it has not proved possible to include in the computer programme a law to correct for the effect of seasonal differences on nematode numbers and potato yields. The results referred to above (p. 302), when susceptible potatoes are grown continuously, suggest that such a law may be unnecessary. The yield of tubers is related to what happens climatically after the final population levels have been decided by events in the potato-root systems in April and May.

Another outcome of the work is the realisation that the population dynamics of these simple animals follows simple rules amenable to expression in mathematical form. Not only are the animals simple but the field soil and the crops in which they live provide a relatively stable environment and a food supply that is fairly constant at the time when numbers are determined. The rules and their mathematical counterparts will, no doubt, need refining as more information becomes available.

I acknowledge with gratitude the help of Diana Parrott and G. J. S. Ross, Rothamsted; and of Dr. H. W. Howard, Plant Breeding Institute, Cambridge, and Dr. J. M. Dunnett, Scottish Plant Breeding Institute, Pentlandfield, Midlothian, in the work reviewed.

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