COMPUTER SIMULATION AND POPULATION MODELS FOR CYST-NEMATODES (HETERODERIDAE: NEMATODA) [SIMULACION CON COMPUTADORA Y MODELOS DE POBLACION PARA NEMATODOS ENQUISTADORES].

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SUMMARY

Populations of plant-feeding soil nematodes are relatively immobile, slow to establish, much inbred and difficult to eradicate. *Heterodera* and *Globodera* spp, most of which lack effective enemies, increase fewer than 100-fold during a season and the number of generations passed can be limited by the short vegetative life of host crops. The problems of sampling field populations have been much studied and population structure is similar to that of other animals. Immigration and emigration are negligible so that population fluctuations can be investigated in pots or small field plots.

The relationship between initial and final population densities during one growing season is described by an equation derived from the logistic equation which takes into account the damage caused to the root system by nematode attack and the fact that not all eggs hatch.

Population oscillations are considered theoretically in relation to the modified logistic curve. Those of *Globodera rostochiensis* (Woll.) are damped largely because of the carryover of unhatched eggs. While the increase rate is important in determining the position and rate of approach to equilibrium it has little effect on the nature of the equilibrium when the observed increase is greater than 10-fold.

Egg hatch of *G. rostochiensis* and of *Heterodera* spp. is independent of population density. So also is the rate of invasion of potato roots. The main density regulating process for *G. rostochiensis* and for other cyst-nematode species appears to be competition for root space which determines the sex ratio.

The procedure for building a computer model to simulate the effects of crop rotation on population density is outlined for *Globodera* and *Heterodera* spp. The model incorporates the effect of a preplant nematicide and allows for the selection of pathotypes (sub-species) with dominant or recessive genes that enable nematodes possessing them to circumvent resistance derived from major genes in resistant host plants. The model also includes interspecific competition between *Globodera* and *Heterodera* species for root space.

INTRODUCTION

Nematodes are relatively immobile and their mobility is further curtailed by constraints of the soil-pore system. Nematode populations large enough to inflict economic injury on crops are usually slow to build up, much inbred and difficult to eradicate. The life strategies of plant-feeding nematodes vary greatly. Some with several generations a year have a large potential for increase and may multiply

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more than a thousand-fold within a season; a far smaller potential than that of viral, bacterial or fungal pathogens and of some Hemipterous and other insects. Populations of this kind fluctuate greatly, e.g. *Aphelenchoides ritzemabosi* (Schwarz), some Trichodorid species, the races of *Ditylenchus dipsaci* (Kühn) and many soil species feeding on bacteria and fungi. Plant-feeding 'exploiters' tend to survive the interval between population outbursts upon weeds and other marginal hosts but some species seem able to survive in soil for long periods in the absence of hosts.

Other nematode species, e.g. cyst-nematodes in Northern Europe, pass only one or two generations a year and are often limited to one generation by the short vegetative life of their host crops from planting to harvest (Jones 1950). The maximum observed multiplication rate is usually much less than 100-fold and population fluctuations are limited largely because not all eggs hatch when a host crop is grown and even fewer hatch when it is withheld. Yet other nematode species are thought to lay relatively few eggs, e.g. *Xiphinema, Longidorus* (Flegg, 1968, Weischer, 1975), and have effective multiplication rates of less than ten times a year, as have species of *Trichodorus* and *Paratrichodorus* common in British sandy soils.

POPULATION STRUCTURE

The population densities of nematodes are often large ranging from less than 1 to more than 100 eggs/g soil (from 2.5×10^9 to 2.5×10^{11} eggs/ha) down to plough depth (30 cm). When plants are growing nematodes aggregate around roots and densities there are much greater than the average per unit weight or volume of soil in bulk soil samples. After harvesting, nematodes are densest beneath the rows or, when the crop is lifted and the soil about their roots scattered, in the surface layer. Soil should be sampled after ploughing and cultivation have re-distributed the nematodes otherwise sampling methods and sample sizes must be adopted which eliminate bias. The smallest sampling error obtainable in population work, assuming the organisms do not repel each other is the Poisson error which applies only if nematodes are randomly distributed in top soil. Nematodes are not randomly distributed and methods of sampling, extracting and counting them are imperfect. These factors all increase the errors above those predicted from the Poisson distribution so that it is difficult to obtain accurate assessments of population change without much labour and many replications (Fisher, 1938, Anscombe, 1950, Jones, 1955, Fenwick, 1961, Church *et al.*, 1959 and Southey, 1974).

A stable hypothetical population composed equally of males and females reproducing sexually would have a pyramidal age structure with an excess of juveniles. Mortality of the pre-adult stages would total 98%, leaving two adults, one male, one female, to reproduce for every 100 eggs laid. This structure is often obscured because all stages may not be present at any one time (Jones & Jones, 1974).

POPULATION DEVELOPMENT

Meaningful population studies with nematodes are possible in pots and small field plots. Large plots are inappropriate because populations are usually patchy and the multiplication rate decreases as the population density increases. The average rate for a field gives no indication what is happening in its parts. If, for example, the infestation overall is slight, but made up of a few patches of high density, the average may suggest misleadingly that the multiplication rate is small (Jones, 1945, 1956).

P_i is the population density at planting and P_f that after harvest expressed as eggs/g soil, preferably measured at planting time in the following year. For many species one year is equivalent to one generation but the general form of the population curve is unaltered when there are more (Fig. 1). The curves are uncomplicated by emigration, immigration or the persistence of individuals not participating in reproduction. Effective enemies or competitors are absent. The scales for P_f and P_i are the same so that a line drawn at 45^0 through the origin is the locus of points at which there is neither population increase nor decrease (x 1 line). When P_i is very small, the surviving adults in the population may be so scattered that the males and females of obligate bisexual species fail to meet and the multiplication rate is less than X 1. Asexual species avoid the perils of under-population. In sexual species the production of egg masses tends to ensure locally dense populations although under-population can occur (Kort, 1962, Seinhorst, 1968b). As P_i increases the multiplication rate increases to its maximum and then decreases to X 1 or less, largely because of increasing competition between individuals and decreasing food supply (Jones, 1966).

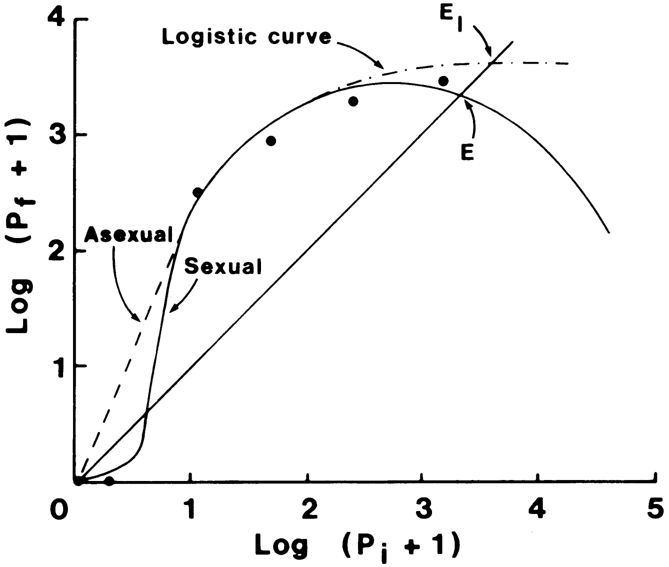

Fig. 1. Hypothetical relationship between preplanting (P_i) and post-harvest population densities (P_f) of asexual and sexual species without effective enemies. The upper, logistic curve would hold if the food supply remained constant. E_l, logistic equilibrium; E, observed equilibrium data for *H. avenae* in pots is from Mukhopadhaya *et al.* (1973).

The observed multiplication rate per generation or per year is usually far less than the reproductive potential of the species. Eggs fail to hatch, larvae fail to find their hosts and enemies, parasites and competitors take their toll at each stage. Enemies that kill juvenile stages remove individuals surplus to the carrying capacity of their host. In contrast, enemies and competitors that kill the few surviving females or seriously decrease the number of eggs they produce have a greater impact on P_f (Kerry & Crump, 1977).

Population densities usually change in a multiplicative rather than an additive manner and P_i and P_f are therefore plotted on logarithmic scales (Fig. 2). Lines representing X 10 multiplication or a population decrease of X 0.33 do not pass through the origin but are parallel to the X 1 line. A constant annual rate of population decrease shows up as a straight line when plotted on a log-scale, whereas on a linear scale it forms an exponential curve from which the constant rate is not immediately apparent. Logarithms may falsely exaggerate differences between small densities but this may be avoided by using log (x + 1) which also provides a (0,0) origin in graphs.

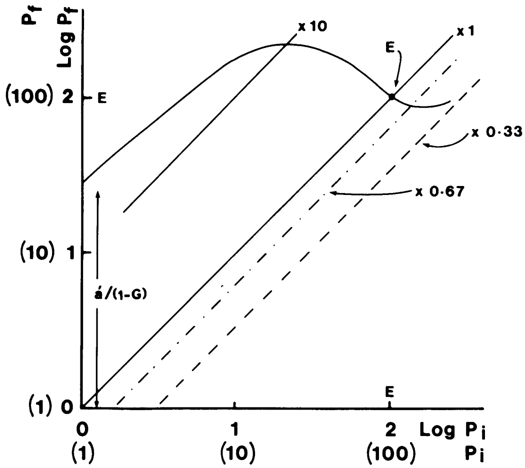

Fig. 2. Population curves for potato cyst-nematodes. P_i and P_f, log eggs/g soil; _______ , old plus new eggs: ---- , eggs unhatched by resistant or susceptible potato cultivars; -·-·-·-, unhatched eggs when crops other than potatoes are grown; a', observed maximum multiplication rate. E, observed equilibrium density.

LOGISTIC EQUATION FOR POPULATION GROWTH. If a female nematode produces a surviving offspring $P_f = aP_i$ and the population will increase exponentially without limit. However, multiplication at large densities is restricted by the limited food supply. Density dependent regulation is given by the equation relating final to initial egg densities,

$$P_f = \frac{aP_i}{1 + (a-1)P_i/El} = amP_i \qquad \ldots (1)$$

derived from the logistic law (Jones, Parrott & Ross, 1967, Seinhorst, 1966) where $m = 1/ [1 + (a-1)P_i/E_1]$ and E_1 is the equilibrium population density. The maximum reproduction rate a is deminished by m which varies with P_i. When P_i is small, m approaches the value 1 and the maximum rate a operates. When $P_i = E_1$, $m = a^{-1}$ and the effective multiplication rate am = 1. When P_i is greater than E_1, am is less than 1. The food supply, which in a growing plant is an expanding one, diminishes as P_i increases, and that corresponding to the observed equilibrium density E may be as small as a half to a fifth of that found when there is no nematode damage (Evans, Trudgill & Brown, 1977).

RELATIONSHIP BETWEEN POPULATION DENSITY AND YIELD. Most nematodes decrease the size of the root systems and the yield of leaf tissue, grain or tubers is affected indirectly as the result of climatic and other stresses, operating after root size is determined. Only in crops like sugar beet is yield related directly to root size. The yield of plants is unaffected when nematode density at planting or sowing was below a certain threshold T, but above this threshold decreases exponentially with egg density (Seinhorst, 1965):

$$\frac{Y - Ymin}{Ymax - Ymin} = e^{-k(P-T)} = z^{P-T} \quad \text{.... (2)}$$

where Y is the expected yield, Ymax and Ymin the maximum and minimum yields and $P > T$ the initial egg density. k = - log z where z is a constant slightly less than 1 and is notionally the expected yield when nematode density exceeds the threshold by unity. z will vary with the nematode species and the plant attacked. $z^{-T} = c$ is a constant usually ranging from 1.05 to 1.15 and can be regarded as the tendency of the plant to compensate for damage done to the extent of 5 to 15%.

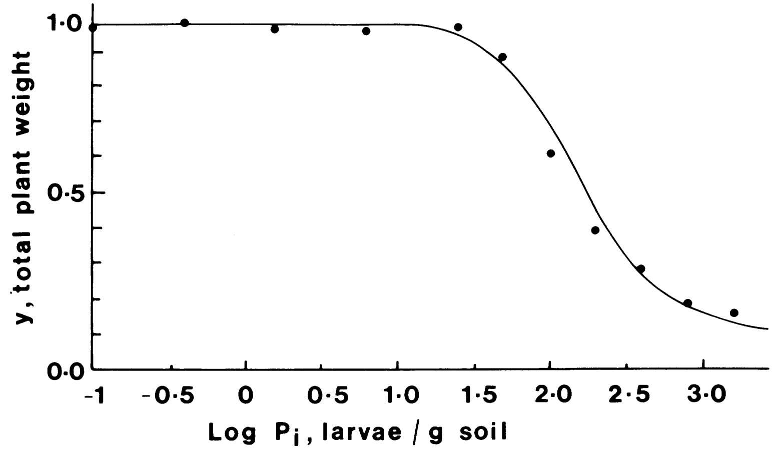

Fig. 3. Relationship between P_i and total plant weight (expressed as a proportion of weight when $P_i = 0$) for the potato cv. Libertas supplied with extra nitrogen. (Redrawn from Seinhorst & den Ouden, 1971).

The yield approaches its maximum asymptotically as nematode density decreases to its threshold (Fig. 3). Whether this threshold always exists and whether there is always a minimum yield is debatable (Oostenbrink, 1966). Sometimes the yield curve in pot experiments suggests that small numbers of nematodes actually cause an increase. In models which concern roots the minimum usable root size is zero.

POPULATION EQUATIONS FOR CYST-NEMATODES. Of the larvae contained in eggs in the soil a proportion H establish themselves in the roots. H appears to be independent of density (Fig. 4). Some larvae then become females and the number of eggs they produce also appears to be independent of density (Hesling, 1961, Jones, 1966, Seinhorst, 1968b). In the absence of effective predators or parasites, the main density dependent mechanism seems to act by regulating the sex-ratio, as the proportion of larvae becoming female decreases markedly with density (Trudgill, 1967) i.e. with P_r, the numbers of larvae per cm of root. Thus

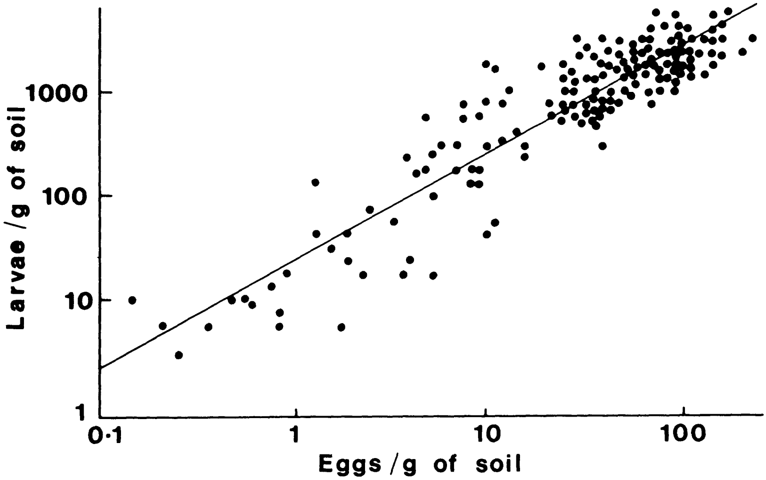

Fig. 4. Relationship between population density (eggs/g soil) and larvae density in roots (larvae/g root).

$$^{M}/_{F} = bP_r \qquad \text{.... (3)}$$

where M is the number of males and F the number of females/cm of root. Hence P_r = M + F and

$$F = \frac{P_r}{1 + bP_r} \qquad \text{.... (4)}$$

Assuming h cm of root/g of soil, $P_r = HP_i/h$, and thus if each female produces an average of a eggs, then

$$P_f = \frac{aHP_i}{1 + \frac{bHP_i}{h}} \qquad \text{.... (5)}$$

The equilibrium density

$$E_1 = \frac{h}{bH} \; (a'-1) \qquad \text{.... (6)}$$

where $a' = aH$ is the maximum increase rate achieved at low nematode densities. Note that H is defined as the number of larvae which succeed in invading the roots as a proportion of the total number of eggs in the soil rather than as a proportion of the eggs that hatch in that year, as this is directly estimable from Fig. 4. Equation (5) is now identical with the logistic equation (1). This assumes that food h, is unaffected by nematode attack, i.e. P_i is smaller than the threshold density T. For values of P_i greater than T, h in equation (5) must be replaced by hz^{P_i-T}. This follows from equation (2) where h represents the greatest length of roots/g, i.e. that produced in soil without nematodes, and assumes that the minimal length of useable root at very high densities is zero. Equation (5) for P_i greater than T becomes:

$$P_f = \frac{aHP_i}{1 + \dfrac{bHP_i}{hz^{P_i-T}}}, \qquad \ldots. \ (7)$$

that is

$$P_f = \frac{a'\ P_i}{1 + (a'-1)\dfrac{P_i z^{-P_i}}{cE_1}}$$

which is the logistic equation when $z = 1$. The density equilibrium E is given by

$$Ez^{-E} = cE_1\ , \qquad \ldots; \ (8)$$

and the size of roots at this density is:

$$Y/Ymax = cz^{E} = E/E_1.$$

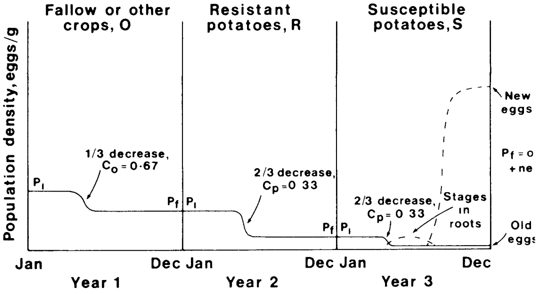

Fig. 5. Population input-output diagram for *Globodera rostochiensis* over three years in which successively, (1) fallow and other crops, (2) a resistant potato cultivar and (3) a susceptible potato cultivar were grown. (Redrawn from Jones & Jones, 1974).

THE RESIDUAL EFFECT. The reasons why cyst-nematodes persist is that the eggs can remain dormant for many years. This carry-over varies with the crop grown (Fig. 5). In the example given, approximately 0.33 of the eggs hatch during April - May of year 1. Thus, $P_f = C_o\ P_i$, where C_o or 0.67 is the fraction of the population carried over to become P_i for the second year. If the soil were left uncultivated or planted with crops other than potatoes for n years, $P_f = C_o{}^{n}P_i$ where P_f would be the population density at the end of n years. In the second year two-thirds of the population hatches under the influence of the resistant potato crop. Hence $P_f = C_p P_i$ where C_p or 0.33 is the fraction of the population carried over to the next year, and if resistant potatoes were grown for n years $P_f = C_p^n P_i$.

In the third year under susceptible potatoes, a proportion H of the eggs hatch and the larvae establish themselves in the roots to produce a new generation of eggs for the next year.

$$\text{Hence} \quad P_f = \frac{a'(1 - C_p)P_i}{1 + (a'-1)\frac{P_i z^{-P_i}}{cE_1}} + C_p P_i \qquad \ldots . \ (9)$$

where

$$a' = \frac{aH}{1-C_p}$$

is now the maximum multiplication rate for those eggs which hatch.

FLUCTUATIONS AND POPULATION EQUILIBRIA. The way in which populations behave in the neighborhood of the equilibrium (E in Figs. 1 and 2) depends on the rate of population increase and the degree to which the host is damaged. If increase is moderate and little or no damage is done, the logistic situation exists and, in successive years of continuous cultivation of the same host, the equilibrium population density is approached gradually (Fig. 6A). However, when increase is excessive and damage to the root system great, the population tends to overshoot the equilibrium and large oscillations occur (Fig. 6C). Cyst-nematodes provide examples of an intermediate type. Fluctuations about the equilibrium are small and sometimes damped (Fig. 6B, see also Jones & Parrott, 1969, Jones, 1974). An important factor restricting oscillations for cyst-nematode populations is the fraction of the population which fails to hatch even when the host crop is grown.

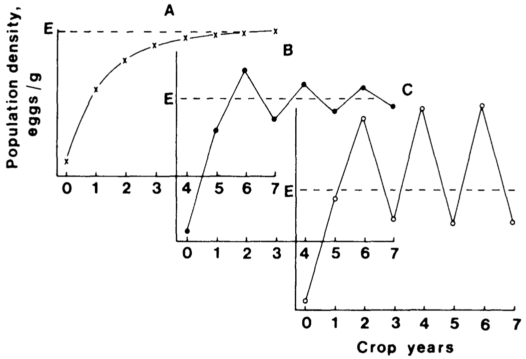

Fig. 6. Population oscillations when a host crop is grown in consecutive years. A, gradual approach to equilibrium (logistic); B, approach by damped oscillations; C, large undamped fluctuations about the equilibrium.

The behavior of the population at the equilibrium may be investigated for the population equation (9). Differentiating with respect to P_i, the slope at the equilibrium:

$$\left[\frac{d(P_f - P_i)}{dP_i}\right]_{P_i = E} = (1 - C_p)\left(\frac{a' - 1}{a'}\right)(E \log z - 1) \qquad \ldots.\ (10)$$

and the nature of the equilibrium depends on whether the right hand side of the equation is greater than -1 (a steady approach to E, no oscillations), less than -1 but greater than -2 (damped oscillations about E) or less than -2 (unstable equilibrium). The three regions are plotted in Fig. 7 for different values of C_p and the equilibrium ratio E/cE_1. Whereas a' is important in determining the rate of approach to the equilibrium, it has little effect on the oscillations for values of a greater than 10 observed in practice since then $(a' - 1)/a' \rightarrow 1$.

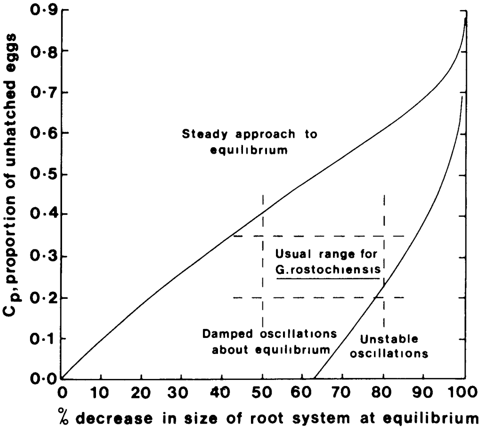

Fig. 7. Influence of the size of the unhatched portion of the population, C_p and the extent to which the root system is stunted at the equilibrium point (E expressed as a percentage of E_l) on the manner in which the population density fluctuates about the equilibrium point, E. At 0% decrease in root size $E = E_l$ and the unmodified logistic equation applies.

COMPUTER SIMULATION OF CYST-NEMATODE POPULATIONS. Jones *et al.* (1967) developed a model for *G. rostochiensis* Ro1 to predict population changes under different rotations when susceptible potatoes, resistant potatoes or crops other than potatoes are grown. They were also interested in simulating the increase in frequency of a resistance-breaking gene in a nematode population when resistant potato varieties are grown. The model did not allow for the effect of root damage on nematode density and used an alternative function for the sex ratio which was separate from the main specification of the model.

Table 1. Parameters, linking equations and hypotheses in the population model.

i) Parameters

Symbol	Usual values for *G. rostochiensis*		
C_o	Mineral soils	0.67	Proportion of eggs remaining unhatched when crops other than potatoes are grown.
	Peat Soils	0.75	
C_p		0.33	Proportion of eggs remaining unhatched when potatoes are grown.
c		1.05	Representing a root compensation rate of 5%, i.e. a threshold egg density of 0.05 E_l.
E		0.25	The observed equilibrium population density as a fraction of the logistic equilibrium, E_l.
a'	from 25 to 75		The maximum multiplication rate at very small population densities. These have not been determined experimentally so trial values were used within this range.
P_o			Starting population density as a fraction of the equilibrium density.
q_o			The initial frequency of the recessive gene for hypotheses b) and c) in iii) below.

ii) Linking equations

Symbol	Equation	
O	$P_f = C_o P_i$	Density independent population change when crops other than potatoes are grown for one year.
R	$P_f = C_p P_i$	The same when resistant potatoes are grown for one year.
S	$P_f = a'm'P_i$	Density dependent population change when susceptible potatoes are grown for one year. The multiplication factor m' is given by equation (11).
N	$P_f = (1-K)P_i$	The effect of a nematicide which kills a specified fraction K of the population

iii) Hypotheses

(a) *G. rostochiensis Ro1* is an interbreeding continuum, there are no fitness differences between gametes, and Hardy-Weinberg equilibrium between genotypes is achieved in one generation of random mating.

(b) On the roots of hybrid potato plants possessing resistance gene H_1 (e.g. Maris Piper), males may have any genetic constitution (*AA*, *Aa* or *aa*) whereas females are double recessives (*aa*) (Jones, 1975c).

(c) The males are as in (b) but females must possess a dominant gene (*AA* or *Aa*).

Table 2. Print-out from computer model for cyst-nematodes. (See Table 1 for explanation of symbols and hypotheses).

Parameters:- $a' = 25$ $C_o = 0.667$ $C_p = 0.3333$

Hypothesis (b) $q_o^2 = 0.0010$ Hypothesis (c) $1 - q_o^2 = 0.0010$

Year	Crop	Frequency of *aa*	Population size	Frequency of *AA+Aa*	Population size
0		0.0010	1.000	0.0010	1.000
1	R	0.0011	0.334	0.0020	0.334
2	R	0.0012	0.112	0.0074	0.113
3	R	0.0018	0.038	0.0526	0.041
4	R	0.0036	0.013	0.3120	0.032
5	R	0.0108	0.005	0.5295	0.105
6	R	0.0449	0.002	0.6290	0.298
7	R	0.1783	0.003	0.6988	0.483
8	R	0.4132	0.008	0.7492	0.608
9	R	0.5922	0.049	0.7875	0.689
10	R	0.7122	0.239	0.8178	0.746
11	R	0.7948	0.501	0.8421	0.786
12	R	0.8490	0.677	0.8621	0.818
0		0.0010	1.000	0.0010	1.000
1	R	0.0011	0.334	0.0020	0.334
2	0	0.0011	0.223	0.0020	0.223
3	0	0.0011	0.148	0.0020	0.148
4	S	0.0011	0.592	0.0020	0.592
5	0	0.0011	0.395	0.0020	0.395
6	0	0.0011	0.263	0.0020	0.263
7	R	0.0013	0.088	0.0087	0.089
8	0	0.0013	0.059	0.0087	0.059
9	0	0.0013	0.039	0.0087	0.039
10	S	0.0013	0.350	0.0087	0.351
11	0	0.0013	0.233	0.0087	0.234
12	0	0.0013	0.156	0.0087	0.156

METHOD

The model (Jones *et al.*, 1967) was revised to include the effect of crop damage, using equation (9) rather than the logistic equation (1). All nematode densities are expressed as fractions of the logistic equilibrium density, E_1. Equation (9) becomes

$$P_f = \frac{a'(1-C_p)P_i}{1 + (a-1)\frac{P_i}{c} z_1^{-P_i}} + C_p P_i \qquad \text{.... (11)}$$

where $z_1 = z^{E_1} = (^{E}/c)^{1/E}$ (from equation 8), and the equilibrium density E is now expressed as a fraction of E_1, i.e. the root size at equilibrium expressed as a fraction of the maximum root size. If for example, $E = {}^{1}/4$, then $z_1 = {}^{1}/256$. The model contains seven parameters, four linking equations and three hypotheses concerning ability to circumvent host resistance (Table 1). Crop rotations are specified by arranging the crop symbols in order e.g. OOROOOS, RRRRR or NSOOONROOO, where N indicates a nematicide applied before the susceptible and the resistant potato crop. The values of the model parameters and the rotations are input to the computer where the crop symbols are used in turn to specify the appropriate linking equation which predicts final egg density after harvest. This final density then becomes the initial density for the next year, to be operated on by the appropriate linking equation for the next crop symbol in the rotation.

RESULTS

FITTING THE MODEL TO OBSERVATIONS. The model parameters were estimated by comparing observational data on changes in nematode density under a given rotation policy with those predicted. Examples of computer output are in Tables 2 and 3. The model was validated using data from small plots where susceptible potatoes were grown continuously (Jones & Parrott, 1969). The model parameters were adjusted until the best fit between predicted and observed values was achieved. The fitted values mimicked well the damped oscillations about an equilibrium observed in practice (Fig. 8). The actual equilibrium value, E, was estimated as 85.6 eggs/g soil. Information on the proportion of eggs unhatched, C_p, and root damage, E/E_1, was confounded, similar patterns of oscillations being achieved by reducing C_p or E/E_1. The best estimates were $C_p = 0.34$ and $E/E_1 = 0.17$ respectively, with $a' = 50$ and $c = 1.05$. All these values are in reasonable agreement with those normally observed. The model, developed for *G. rostochiensis* which is without effective enemies, also applies to *G. pallida* (Stone) and to some other cyst-nematodes.

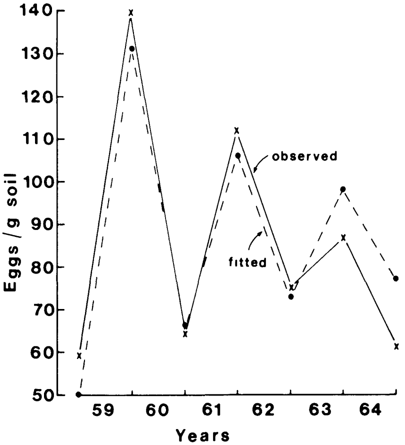

Fig. 8. Observed, X, and fitted values, ●, of the oscillations in population density, eggs/g soil of potato cyst-nematodes, when susceptible potatoes were grown every year for 5 years (Data from Jones & Parrott, 1969).

INTERSPECIFIC COMPETITION. Many fields have two or more nematode species from the same genus. Members of the same genus are similar in habits and often feed almost identically on the same host plants. Sometimes, one or more species may be relicts from previous crops that especially favoured them, and are in the process of being replaced by species favoured by the current crop. Sometimes, two nearly identical species may be competing for the same host.

Competition between the two *Globodera* species is likely to be strongest between females which require more than 100 times as much food as males to develop

Table 3. Printout from computer model of *G. rostochiensis* and *G. pallida* assuming they do not compete. See Table 1 for explanation of symbols.

			a'		c_p		c_o				
P_i	Proportion of *G. pallida*	Kill by nematicide	*G. rostoch.*	*G. pall*	*G. rostoch.*	*G. pall.*	*G. rostoch.*	*G. pall.*	E_{lp}/E_{lr}	v_r	v_p
0.10	0.01	0.00	40	50	0.33	+ 0.70	0.67	+ 0.80	1.00	0.0	0.0

Root damage:-

c	E_r	E_p
1.05	0.25	0.25

Crop rotation	Proportion of *G. rostochiensis*
-	0.990
R	0.727
R	0.133
R	0.032
R	0.010
R	0.003
R	0.001
R	0.000
R	0.000
R	0.000
R	0.000

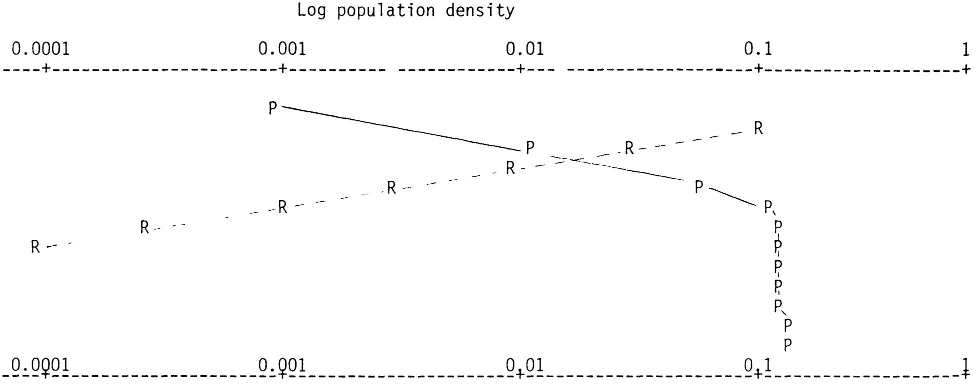

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Table 3. Continued.

P_i	Proportion of *G. pallida*	Kill by nematicide	a' *G. rostoch.*	a' *G. pall.*	c_p *G. rostoch.*	c_p *G. pall.*	c_o *G. rostoch.*	c_o *G. pall.*	E_{lp}/E_{lr}	v_r	v_p
0.10	0.01	0.00	40	50	0.33	+ 0.70	0.67	+ 0.80	1.00	0.0	0.0

Root damage:-	c	E_r	E_p
	1.05	0.25	0.25

Crop rotation	Protection of *G. rostochiensis*
-	0.990
S	0.920
0	0.906
0	0.890
R	0.299
0	0.263
0	0.230
0	0.539
0	0.495
0	0.451
0	0.173
0	0.149
0	0.128
S	0.475
0	0.431
0	0.389
R	0.138
0	0.119
0	0.101

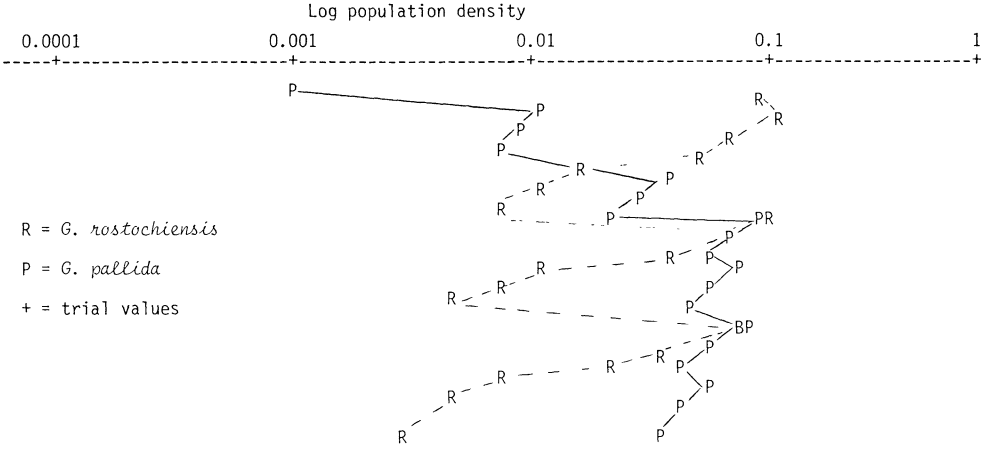

Table 4. Calculated period in years to establishment of a mutant or immigrant form of potato cyst-nematode able to overcome resistance

	Frequency of genotype $(1-q_o^2$ or $q_o^2)$ initially					
	1 in 10000		1 in 100000		1 in 1000000	
Crop sequence	Dominant	Recessive	Dominant	Recessive	Dominant	Recessive
*RRRRRRR	9	> 40	11	> 40	> 40	> 40
ROOROO	34	> 60	> 40	> 60	> 60	> 60
ROOOROOO	53	> 60	> 60	> 60	> 60	> 60
ROOOOROOOO	> 60	> 60	> 60	> 60	> 60	> 60

*R, resistant potato cultivar grown; 0, other crops grown

Table 5. Simulated final population densities, eggs/g soil, after growing a susceptible crop for 6 years in fields with different degrees of patchiness

	Mean of infested part	SE	Overall mean
Uniform	78.0	--	78.0
Fairly uniform	77.6	0.011	77.6
Moderately patchy	77.4	0.012	61.7
Very patchy	88.3	0.055	17.7

and reproduce. The relative proportions of the two species becoming females will depend on relative hatching dates, the minimum necessary size of the female's territory in the roots, and other genetic differences. We extend the equations relating sex ratio to density to two species using densities, P_1, P_2

$$^{M_1}/_{F_1} = b_1 (P_1 + v_1 P_2), \qquad \text{.... (12)}$$

$$^{M_2}/_{F_2} = b_2 (P_2 + v_2 P_1).$$

If the two species exploit totally different parts of the root system, then $v_1 = v_2 = 0$ and in the absence of root damage they will coexist independently. If their exploitation is identical then $v_1 = {}^1/v_2$, the species share the same ecological niche and coexistence is impossible.

Assuming densities are below the threshold at which root damage occurs, the difference equations relating final egg densities P_{f1}, P_{f2} to initial egg densities, P_{i1}, P_{i2} when a susceptible crop is grown are of the form:

$$P_{f1} = \frac{a_1' (1 - C_{p1}) P_{i1}}{1 + (a_1' - 1)(P_{i1} + v_1 P_{i2})/E_{11}} + C_{p1} P_{i1} \qquad \text{.... (13)}$$

$$P_{f2} = \frac{a_1' (1 - C_{p1}) P_{i1}}{1 + (a_2' - 1)(P_{i2} + v_2 P_{i1})/E_{12}} + C_{p2} P_{i2}$$

where $\acute{a}_1$, $\acute{a}_2$ are the maximum multiplication rates; C_{p1}, C_{p2} the proportions of eggs carried over unhatched each year; and E_{11}, E_{12}, the egg densities at the logistic equilibrium when there is no competition.

There are four possible outcomes for the system depending on the relative magnitudes of E_{11}, E_{11}, v_1 and v_2 (Williamson, 1972). (1) $E_{11} > E_{12}/v_2$ and $E_{12} < E_{11}/v_1$ species 2 eventually becomes extinct, (2) $E_{11} < E_{12}/v_2$ and $E_{12} > E_{11}/v_1$ the situation is the reverse and species 1 becomes extinct, (3) $E_{12}/v_1v_2 > E_{11}/v_1 > E_{12}$ a stable equilibrium mixture is established with both species coexisting and (4) $E_{12}/v_1v_2 < E_{11}/v_1 < E_{12}$ the equilibrium is unstable and either species may become extinct, depending on the initial population densities. In the last, stochastic variation may have an important effect on the outcome. The respective proportions or unhatched eggs C_{p1} and C_{p2} have no effect on the eventual outcome when stochastic effects are ignored although they may affect the rate of extinction of either species. Note that when a stable equilibrium exists each species suppresses its own numbers more than those of its competitor, i.e. intraspecific competition is greater than interspecific, but the joint equilibrium population is greater than either population alone.

For nematode densities above the threshold where root damage occurs, we may express the relative root size as a function of the densities of the two individual species by

$$Y/Ymax - ce^{-(k_1N_1 + K_2N_2)} = cz_1^{N_1}z_2^{N_2} \qquad \ldots. \ (14)$$

When this factor is incorporated into the model the loci of equilibria for the individual species become curved. The criteria for determining the eventual outcome of the system are more complex, but one interesting possibility is that the joint equilibrium population and hence the crop damage for the two species system may be smaller than when either species occurs separately. This requires further investigation.

Investigating the effects of competition experimentally requires a great range and variety of combinations of species population densities. These can be limited to manageable proportions only when there is some previous knowledge of likely equilibrium mixtures (Seinhorst, 1970). In the field the study of mixed populations is of more than academic importance especially when resistant varieties are available and the attacking nematodes are related species, as are *G. rostochiensis* and *G. pallida*. For races within species there may be competition between genotypes, as in hypotheses (b) and (c) of Jones *et al.'s* model. Then, a large value of C_pP_i representing unhatched eggs composed of unselected genotypes may greatly delay the spread of superior genes within the population (Table 4).

The competition element in the model was validated using data in Cole & Howard (1962). Figure 9 compares the observed sum of the egg densities of *G. rostochiensis* and *G. pallida* assuming (a) that they compete for root space and (b) that they do not. The best fitting parameters are shown in the Figure. Values for V_1 and v_2 (equations (12) and 13)) were 0.91 and 1.10 respectively when it was assumed the species were competing and $v_1 = v_2 = 0$ when they were not.

EFFECTS OF PATCHINESS

The computer model is based on small plots within which variations in population density can be neglected, but large variations occur in fields. Estimates of field populations are usually based on *circa* 50 soil cores which are bulked, thoroughly mixed and subsampled. The subsample gives average densities for cysts and eggs but no indication of variability. Fields can be classified into three types: (1) recently infested with a few heavily infested patches and the rest virtually uninfested, (2) more heavily infested fields with a pattern of heavily and lightly infested patches and (3) totally infested fields with fluctuating densities from place to place arising from past events, topography, soil variations and so on.

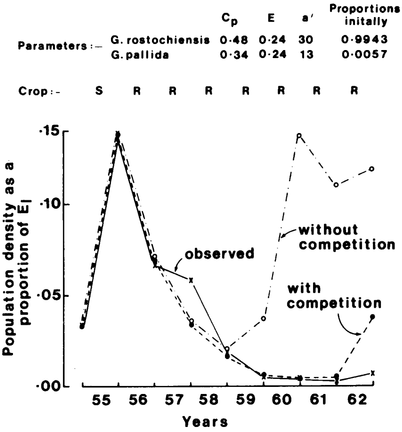

Fig. 9. Delay in the selection of *G. pallida* by a resistant potato variety with gene H_1 due to competition with *G. rostochiensis Ro1* initially more abundant. Other data sets show similar trends. Both species can multiply on susceptible (S) potatoes but only *G. pallida* can multiply on the resistant potato (R). Competition is mainly between larvae of both species which invade the potato roots of resistant and susceptible alike.

Suppose P_i has a distribution with mean μ_{P_i} and C_o a distribution with mean μ_{C_o}. It can be shown that after n years under non-susceptible crops the expected population density will be

$$E\,[P_f,\ \text{after n years}] = \mu^n_{C_o}\,\mu_{P_i}$$

so the equation $P_f = C_o{}^n P_i$ may adequately represent the decline in the field population, so long as the variance of P_f is not too large.

When a host crop is grown continuously the situation is more complex. Of the parameters governing the model the most variable are likely to be P_i and C_p. We therefore investigated the effect of varying degrees of patchiness by simulation from three hypothetical populations of P_i (1) very patchy - 40 zero values and 10 from a log-normal distribution with mean 100 eggs/g and variance 2900; (2) moderately patchy - 10 zero values and 40 from a long-normal distribution with mean 25 eggs/g and variance 120; (3) fairly uniform - 50 values from a normal distribution with a mean of 20 eggs/g and variance 1. The overall means for all three were 20 eggs/g soil. For each 'field' the 50 values of P_i were randomly paired with values of C_p obtained by random sampling from a normal distribution with mean 0.34 and standard deviation 0.017. The model was run for 6 years under a susceptible crop using the values for potatoes which were the best fit to Jones & Parrott's data in Fig 8, viz E = 85.6 eggs/g, E/E_1 = 0.17, a' = 50 and c = 1.05. The final populations output by the computer were compared with each other and with those of a field assumed to be uniformly infested, P_i = 20 eggs/g and Cp = 0.34 (Table 5).

The larger mean for the infested parts of the very patchy field occurs because the oscillations about the equilibrium E are out of phase. The damping of the oscillations leads to similar final densities in the infested parts of all types of fields as they approach equilibrium and so to a smaller overall mean in patchy fields when zero values are included. This method of studying patchiness is limited because no account is taken of spread, i.e. a decrease in the proportion of patches (soil cores) containing zero nematodes with time. Unfortunately little is known about the rate of spread of cysts within fields once they become infested. However, the simulation suggests that only in very patchy fields is the mean population density likely to be a misleading indicator of the current level of infestation or of the infestation likely to be generated after growing one or more susceptible crops.

DISCUSSION

Too much should not be expected of population models. They may provide qualitative information which is valuable in understanding the population dynamics of a species, but cannot be used for serious prediction, particularly for individual fields, where crop variety, local farm practices and other factors affect population development. Fortunately, soil climatic factors other than rainfall are relatively stable within an area as small as Great Britian. Farming practices for particular crops tend also to be stereotyped. Consequently generalizations for root endoparasitic nematodes have a wider validity than would otherwise be the

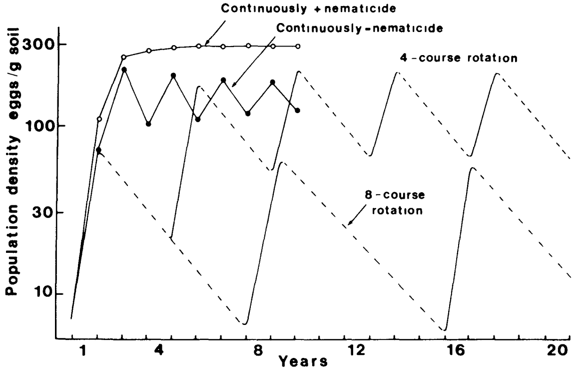

Fig. 10. Stylized population graphs drawn from the output of computer models: ———, susceptible potatoes grown; - - - - , other crops grown. Nematicide depicted is a soil fumigant killing 70-80% of encysted eggs.

case, but those for root ectoparasitic nematodes are more difficult (Jones, 1975a, 1975b). Models may be used to observe the character of populations fluctuating under different cropping regimes (Fig. 10). They also suggest that nematicides which kill some 70-90% of cyst-nematode eggs would, after harvest, tend to leave nematode numbers near the maximum of the population curve. This is confirmed by old field experiments (Peters & Fenwick, 1949) and by more recent ones which also suggest that such nematicides, rather than preventing the selection of a race or species able to reproduce on a resistant cultivar, would make selection more rapid. As yet in fields in Long Island, New York and in Britian, there is no evidence that growing resistant potatoes with gene H_1 from *Solanum tuberosum* spp *andigena* Juz. & Buk. has selected from *G. rostochiensis* Rol (genetic constitution AA) types equivalent to populations of race Ro2 such as occur in the Netherlands and Bolivia (constitution aa: Jones,1975c). This fits predictions from the model shown in Table 4. Selection in the U.K. and in the Netherlands has usually resulted in the replacement of *G. rostochiensis* Rol by *G. pallida* Pa3 after growing up to five successive crops of a resistant potato cultivar bearing gene H_1. The observed data of Cole & Howard (1962), and those of Huijsman (1961) to which Jones, Parrott & Ross's model was fitted, were inappropriate because it is now known that *G. pallida,* which does not interbreed with *G. rostochiensis,* was being selected, i.e. an interspecific competition model was required not an intraspecific one. Table 2 shows the printout from a preliminary model based on interspecific competition. The relationship between P_i and P_f for *G. pallida* on potatoes susceptible to it differs in the values of a′ (maximum multiplication rate), C_p (fraction that hatches when other crops are grown). No terms were included to allow for the differential effect of *G. pallida* on *G. rostochiensis* and *vice versa,* i.e. $v_1 = v_2 = 0$, and the equilibria E_{11} and E_{12} were the same. Such a model suggests that rotations with frequent crops of potatoes bearing gene H_1 would eliminate *G. rostochiensis* whereas others containing potatoes with and without H_1 would establish an equilibrium mixture. However, the current distribution pattern of these two species in Britain suggests they are mutually exclusive. Either one species is displacing the other (competitive displacement, outcome 2 or 3, page 000) or whether a field is now dominated by one or other may have been decided by which arrived first or in greatest numbers (outcome 4).

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