Modelling Populations of Cyst-Nematodes (Nematoda: Heteroderidae)

Author(s): F. G. W. Jones and J. N. Perry

Source: *Journal of Applied Ecology* , Aug., 1978, Vol. 15, No. 2 (Aug., 1978), pp. 349–371

Published by: British Ecological Society

Stable URL: https://www.jstor.org/stable/2402596

MODELLING POPULATIONS OF CYST-NEMATODES (NEMATODA: HETERODERIDAE)

By F. G. W. JONES and J. N. PERRY

Rothamsted Experimental Station, Harpenden, Herts.

SUMMARY

(1) Because cyst-nematode populations are relatively static, immigration and emigration are negligible and population fluctuations under different crops can be studied in small field plots. A modification of the logistic equation (see eqn (10)) for population growth adequately describes the relationship between initial and final population densities during one growing season on a susceptible host crop. This equation allows for eggs that persist unhatched and for damage to the host root system. Population oscillations are considered both theoretically and in relation to field data.

(2) Equations are proposed for the effects on populations of non-host and resistant crops, fumigant or oxime carbonate nematicides, selection of pathotypes within species, competition between sibling species, and the effects of ground-keepers (weed hosts).

(3) A computer program has been developed which simplifies the fitting of the population equations to field data and enables the effects of crop rotations on population densities to be simulated. Some samples of computer output are given illustrating the predicted effects of rotations on population density and population genetics. The equations developed for *Globodera* spp. also apply to related *Heterodera* spp., especially those with one main generation a year.

(4) The difficulties of fitting the model to field data, the limitations of modelling, unsolved problems in extending the models to species with more than one generation and the need to take account of variable environmental factors are discussed.

INTRODUCTION

Compared with mammals, birds and insects, nematodes are relatively immobile and their mobility is further constrained by the soil pore system. The life strategies of plant-feeding nematodes vary greatly. Some, which complete several generations a year, are able to increase more than a thousand-fold within a growing season. This is a far smaller potential than that of viral, bacterial or fungal pathogens and of some hemipterous and other insects. Populations of this kind of nematode, which may be described as exploiters, 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 without hosts. Cyst-nematodes in northern Europe pass only one or two generations a year and are often limited to one 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. Populations large enough to inflict economic injury are slow to build up and difficult to

eradicate. Yet other nematode species have generation times which may exceed 12 months. These lay few eggs, e.g. *Xiphinema, Longidorus* (Flegg 1968; Weischer 1975), and increase less than ten-fold during a year, as also do species of *Trichodorus* and *Paratrichodorus* common in British sandy soils.

POPULATION CHARACTERISTICS

When plants are growing, nematodes aggregate around roots or stem bases, and densities there exceed the average obtained from soil samples. After harvesting, nematodes are densest beneath crop 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. Sampling methods 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 when nematodes are randomly distributed. If n is the total number of a given nematode counted in a single sample or a series of samples, the standard error of the total is $\pm \sqrt{n}$ and the 95% confidence limits are approximately $\pm 2\sqrt{n}$ about n. Thus for $n=25$, $\sqrt{n}=5$, S.E.% $=20$, and the 95% confidence limits are 15–35 approximately and for $n=100$; 10, 10 and 80–120 respectively. Nematodes are not randomly distributed and methods of sampling, extracting and counting them are imperfect. These factors all increase the errors to more than those predicted from the Poisson distribution (Fisher 1938; Anscombe 1950; Jones 1955; Fenwick 1961; Church, Gough & Southey 1959; Southey 1974).

Field experiments on mobile pests are complicated by emigration and immigration or by sampling problems associated with small population densities and great variations from season to season. Their population dynamics can be studied only in cages or very large plots. Meaningful population studies are possible with nematodes in small field plots. Large plots or fields are inappropriate because populations are patchy and multiplication decreases as density increases. The average rate for large areas gives no indication of 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 that the multiplication rate is small, which could be misleading (Jones 1945, 1956).

Agriculturally, the most convenient time scale for measuring population densities is 1 year. When numbers are very small, surviving adults may be so scattered that the males and females of obligate bisexual species fail to mate. Asexual species avoid under-population and, in sexual species, the production of egg masses or cysts containing many eggs tends to ensure locally dense populations although under-population may still occur (Kort 1962; Seinhorst 1968b; Mukhopadhaya *et al.* 1973). We have not attempted to model this situation.

The observed multiplication rate per year is usually far less than the reproductive potential of the species. Eggs may fail to hatch, juveniles may fail to find their hosts or fail to develop into females, and competitors may exacerbate these effects. Enemies that eliminate a proportion of juvenile stages remove individuals surplus to the carrying capacity of host roots. In contrast, enemies and competitors that kill the few surviving females or decrease the number of eggs they produce have a much greater impact on post-harvest populations.

THE BASIC POPULATION MODEL

Figure 1 shows chronologically those events in the cyst-nematode life cycle which we have modelled, and Table 1 gives estimated values for parameters used. The basic model was derived by Jones & Kempton (1978) from a previous model proposed by Jones, Parrott & Ross (1967). It includes events shown in upper case in Fig. 1, the alternative paths are determined by crop type.
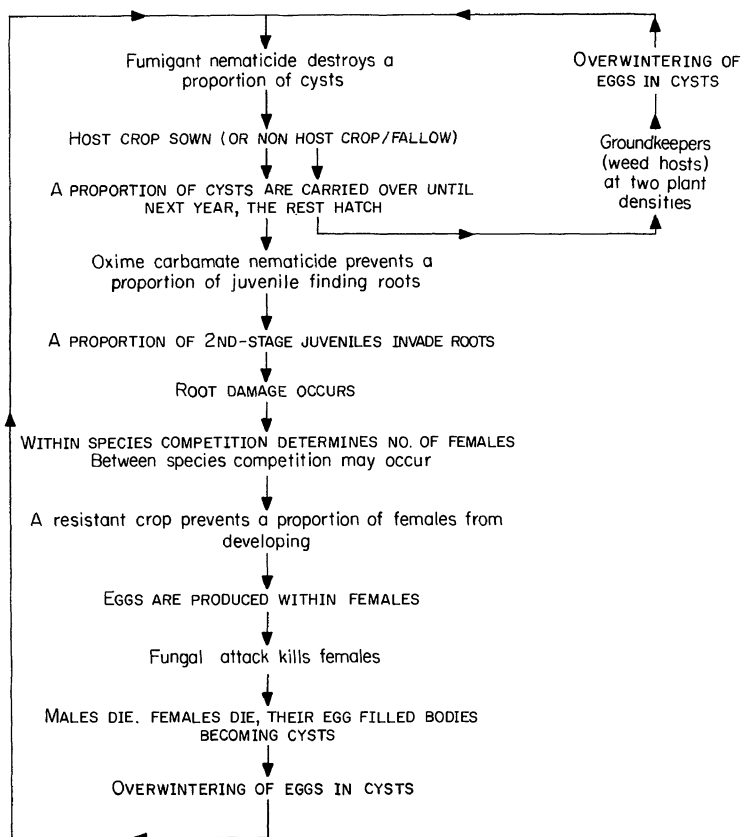

Fig. 1. Cyst nematode life-cycle. Events in upper case are included in the basic model which is extended to cover those in lower case.

Non-host crop grown

Suppose P_f = population density at end of year in eggs/g of soil, and
$\quad\quad$ P_i = population density initially, in eggs/g of soil, overwintering in cysts.

A major reason for the persistence of cyst-nematodes is the ability of eggs to remain dormant in the soil for several years. The carry-over proportion of unhatched eggs depends on the crop, being larger for non-host crops (Table 1) the roots of which do not produce appropriate hatching factors. The carry over proportion is density-independent and remains virtually constant from year to year (Fig. 2).

TABLE 1. Some parameter values obtained from literature or estimated by the model; those considered most reliable are in bold type

C_p	C_o	E	a	c	z	Source
*Globodera rostochiensis**						
0·18 (1957)	0·36					
0·18 (1958)	0·85					Cole & Howard (1962b),
0·44 (1959)	0·92					sandy loam, microplots
0·48 (1960)	0·92					
0·32	**0·65**					Huijsman (1961), mineral soil, plots
0·48	**0·74**	0·24				Cole & Howard (1962a, 1966), black fen soil, plots
0·34		0·17	50			Estimated from data of Jones & Parrott (1969), sandy loam, small plots
			$\dot{a}=318$			Hesling 1961, *Solanum demissum,* in pots.
			10–30			Seinhorst (1967)
				1·02	0·995	Estimated from Seinhorst & den Ouden (1971), in pots
		0·40				Data in Fig. 8, sandy loam, plots.
			41			Peat ⎤ Field plots, underestimates
			15			Silt ⎬ (Whitehead 1975)
			13			Sand ⎦
Globodera pallida						
0·33		0·24	13			Estimated from Cole & Howard (1962a)
0·63		0·40	20			Data in Fig. 8, sandy loam, plots.
	0·72					Cooper (1954), 228 heavily infested fields over 10 years,
	0·70					161 lightly infested fields over 8 years, mostly mineral (silt) soils
Heterodera schachtii						
			20–50			Seinhorst (1967)
	0·49					Jones (1945), 18 fields, 6 years, 53 replicates, silty peaty loam
0·18	0·50 ⎫					Jones (1956), microplots
0·30	0·66 ⎭					
			40–84			Jones (1957), plots
H. avenae						
	0·67					Jakobsen (1974), 9 plots, 6 years, 2 sites
0·20	0·50	0·20	30			Andersen and Andersen (1970), 81 trials, several years, mineral soils, sparse populations
	0·40					Hesling (1958), in pots
0·35		0·30	30	1·05		Estimated from Gair, Mathias & Harvey (1969)
H. bifenestra						
	0·28					Andersson (1976), 2 fields, 4 years mineral soils
H. goettingiana						
			a′ = 129		0·990	Estimated from Jones *et al.* (1965), fine sandy loam, microplots, cv. Big Ben.

* For maincrop varieties in sandy soil at Woburn Experimental Farm $\bar{E}$ is approx. 100 and E_1 about 300 eggs/g soil.
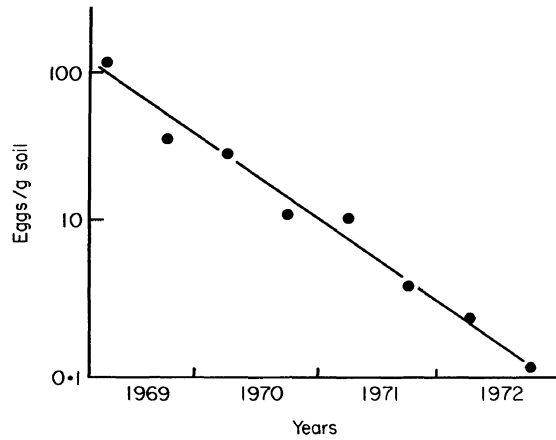
Fig. 2. Example of density independent population decrease when non-host crops are grown. *Heterodera bifenestra* Andersson, data from Andersson (1976).

Suppose C_0 = non-host carry-over proportion. Then $\overline{P}_f = C_0 \overline{P}_i$.

Host crop grown

Suppose C_p is the carry-over proportion for host crops, $(1 - C_p)\overline{P}_i$ eggs/g hatch.

Of the eggs that hatch releasing second-stage juveniles, a proportion H successfully invade the roots of the host crop and this proportion appears to be independent of density up to the equilibrium density and possibly beyond (Fig. 3).
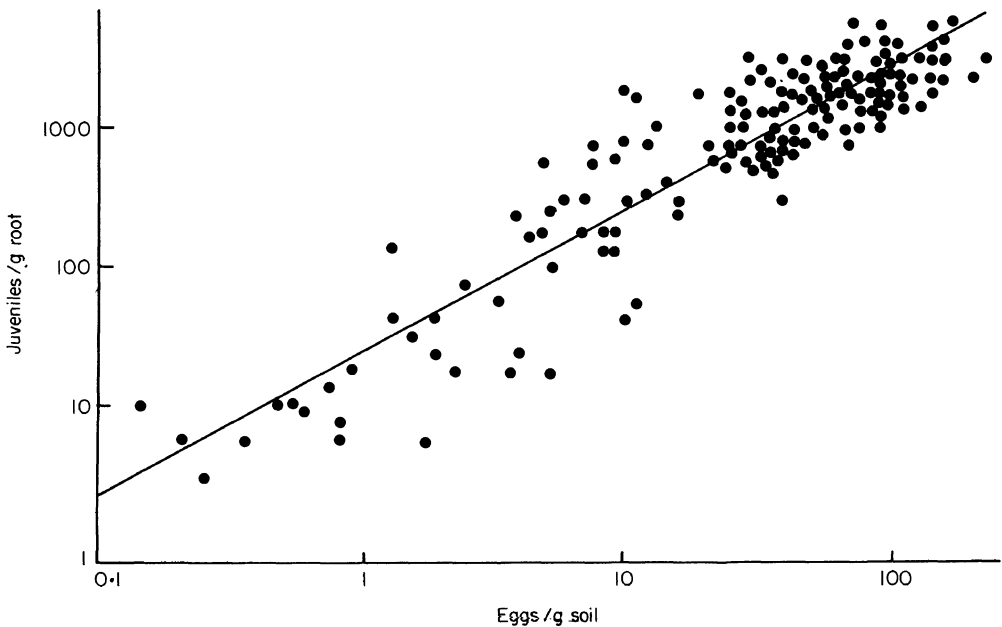

Fig. 3. *Globodera rostochiensis*, relationship between juveniles that establish themselves in roots and preplanting egg densities in soil. The relationship is linear up to and beyond $\overline{E}$ at approximately 100 eggs/g soil. From Jones & Kempton (1978).

$H(1 - C_p)\bar{P}_i$ juveniles/g invade roots so there are

$$\bar{P}_r = \frac{H(1 - C_p)\bar{P}_i}{h} \text{ larvae/cm root,} \qquad (1)$$

where $h = $ cm root/g soil.

Most nematodes attack roots and their main effect is to decrease the size of root systems but they also suppress nodulation of leguminous crops. Only in crops like sugar beet where roots are harvested is yield related directly to root size. In other crops the yield of leaf tissue, grain or tubers is affected indirectly or is the result of climatic and other stresses, mostly operating after root growth has been stunted by nematode attack. Seinhorst (1965) argued that the yield of plants was unaffected when nematode density at planting or sowing was below a certain threshold T. Above this threshold yield decreased exponentially with egg density, i.e.

$$\frac{Y}{Y_{max}} = \frac{Y_{min}}{Y_{max}} + \left(1 - \frac{Y_{min}}{Y_{max}}\right) z^{\bar{P}_i - T} \qquad \text{for } P_i > T \qquad (2)$$

where Y is the expected yield, Y_{max} the yield in the absence of nematodes, Y_{min} the yield given a very large initial nematode density and z a constant slightly less than one (Fig. 4).
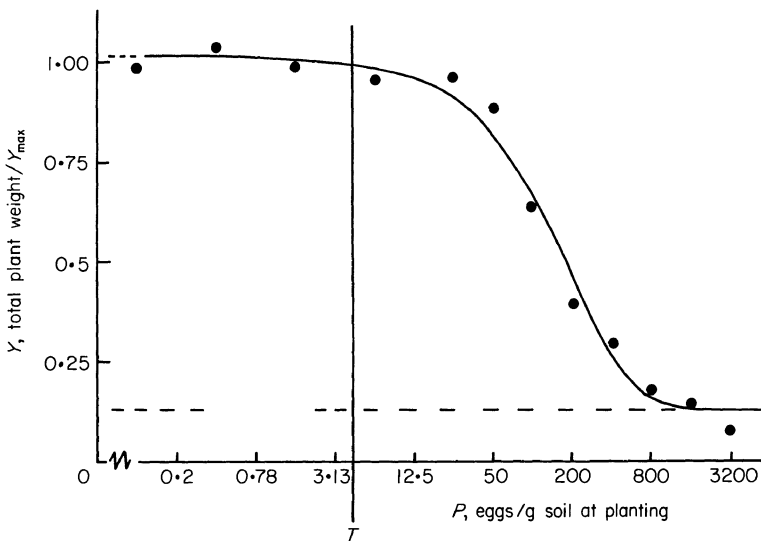

FIG. 4. *Globodera rostochiensis*, relationship between total plant weight and preplanting nematode numbers. Potato cv. Libertas in pots (Seinhorst & den Ouden 1971). $Y_{min} = 0.134$, $T = 4.2$, $c = 1.02$ and $z = 0.995$. $Y = 0.134 + (0.866 \times 1.02 \times 0.995^P)$.

There is evidence (Lownsbery & Peters 1955; Jones 1957; Peters 1961) that yields at very small nematode densities slightly exceed those in uninfested soil. We therefore assume eqn (2) holds for all values of P_i. Then $z^{-T}, = c$ say, is a constant slightly larger than one which measures the tendency of the plant to compensate for root damage. Data from Seinhorst (1965) fitted by the method of maximum likelihood gave $c = 1.02$, $z = 0.995$, $T = 4.2$ and $Y_{min} = 0.134$ (Fig. 4). Unfortunately in fields the yield in the absence of nematodes is rarely known, and the threshold for economic damage is greater than T. Furthermore in our

modelling, which concerns roots, we have taken Y_{min} to be zero. Hence eqn (2) becomes

$$Y = Y_{max}cz^{\bar{P}_i} \qquad \bar{P}_i > 00$$

Root damage decreases h to $hcz^{\bar{P}_i}$ cm root/g soil and eqn (1) becomes

$$\bar{P}_r = \frac{H(1 - C_p)\bar{P}_i}{hcz^{\bar{P}_i}} \text{ juveniles/cm root.} \qquad (3)$$

The main density-dependent population regulatory mechanism of cyst-nematodes appears to be intra-specific competition which limits the space to develop syncytial transfer-cells (Jones & Northcote 1972); these are necessary for development of females and are comparable with a feeding territory (Jones 1966; Ross & Trudgill 1969). Trudgill (1967) found that the ratio of males to females increased proportionately with numbers of juveniles per cm root, $\bar{P}_r$.

Hence

$$\frac{M}{F} = b\bar{P}_r \qquad (4)$$

where M = male juveniles/cm root, F = female juveniles/cm root and

$$M + F = \bar{P}_r. \qquad (5)$$

Equations (3), (4) and (5) give

$$F = \left[\frac{H(1 - C_p)\bar{P}_i}{hcz^{\bar{P}_i}}\right] \bigg/ \left[1 + \frac{bH(1 - C_p)\bar{P}_i}{hcz^{\bar{P}_i}}\right] \text{ female juveniles/cm root}$$

$$= \frac{H(1 - C_p)P_i}{1 + \left[\dfrac{bH(1 - C_p)\bar{P}_i}{hcz^{\bar{P}_i}}\right]} \text{ female juveniles/g soil.} \qquad (6)$$

It is equation (4) that models population regulation and generates a logistic-type equation for population growth. In the absence of root damage eqn (6) leads to a simplified equation (Jones & Kempton 1978) with stable (logistic) equilibrium density E_l eggs/g, where

$$a'F = (1 - C_p)E_l \text{ and } a' = \text{average number of eggs laid/female.} \qquad (7)$$

Equations (6) (without root damage, at $\bar{P}_f = \bar{P}_i = E_l$) and (7) give

$$\frac{bH(1 - C_p)}{h} = \frac{a'H - 1}{E_l}.$$

Hence eqn (6) may be simplified to

$$F = \frac{H(1 - C_p)\bar{P}_i}{1 + \dfrac{(a'H - 1)\bar{P}_i}{cz^{\bar{P}_i}E_l}} \text{ female juveniles/g soil, after root damage.}$$

The number of eggs produced by females (cysts) a', appears to be density-independent (Fig. 5) (Jones *et al.* 1965; Hesling 1961; Jones 1966; Seinhorst 1968a).
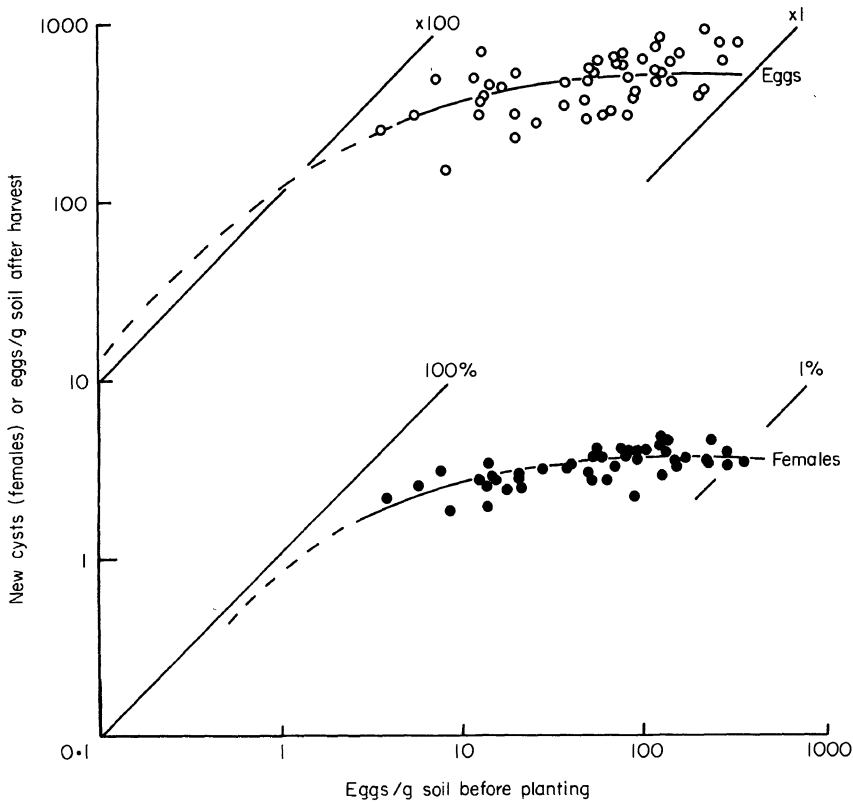

Fig. 5. *Heterodera goettingiana*, females and eggs/g soil after harvest plotted against eggs/g soil before planting. The curves (drawn by eye) are roughly parallel and indicate an average of 129 eggs/female (a') over the population densities observed (Jones *et al.* 1965).

New eggs produced/g soil $= a'F$

$$= \frac{a'H(1 - C_p)\bar{P}_i}{1 + \dfrac{(a'H - 1)\bar{P}_i}{cz^{\bar{P}_i}E_1}}.$$

Replacing $a'H$ by a and adding the $C_p\bar{P}_i$ eggs/g carried over we obtain $\bar{P}_f$ the final density

$$\bar{P}_f = \frac{a(1 - C_p)\bar{P}_i}{1 + \dfrac{(a - 1)\bar{P}_i}{cz^{\bar{P}_i}E_1}} + C_p\bar{P}_i \text{ eggs/g.} \qquad (8)$$

Equation (8) has an equilibrium value given by $\bar{P}_f = \bar{P}_i = \bar{E}$ say, which we would intuitively expect to be smaller than E_1 because of root damage. By inspection of eqn (8) we can confirm that

$$cz^{\bar{E}} = \bar{E}/E_1 \text{ at equilibrium.} \qquad (9)$$

Recall that $cz^{\bar{E}}$ measures the damage to roots, y/y_{max}, at this equilibrium and that $\bar{E}E_l$ denotes the reduction in population density, so that eqn (9) shows the relationship between damage and density at equilibrium. Generally cz^E lies between 0·2 and 0·5 (Evans, Trudgill & Brown 1977).

It is often convenient to express densities not as eggs/g but as proportions of the logistic equilibrium, E_l.

Now

$$z^{\bar{P_l}} = \left(\frac{\bar{E}}{cE_l}\right)^{\bar{P_l}/\bar{E}} \qquad \text{from eqn (9)}$$

$$= \left(\frac{E}{c}\right)^{\bar{P_l}/E} \qquad \text{where } P_i = \bar{P}_i/E_l,\ E = \bar{E}/E_l,\ \text{etc.}$$

Hence eqn (8) may be rewritten in the form

$$P_f = \frac{a(1-C_p)P_i}{1 + \dfrac{(a-1)P_i}{c\left(\dfrac{E}{c}\right)^{\bar{P_l}/\bar{E}}}} + C_p P_i \text{ eggs as a proportion of } E_l. \qquad (10)$$

Equation (10) is the standard formulation of the basic model

POPULATION OSCILLATIONS AND POPULATION EQUILIBRIA

The way in which populations behave in the neighbourhood of the equilibrium, E, 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. However, when increase is excessive and damage to the root system great, the population tends to overshoot the equilibrium and large oscillations occur. Seinhorst (1967) gives examples of the first kind for *Tylenchorhynchus dubius* (Bütschli), *Pratylenchus crenatus* Loof and *Rotylenchus uniformis* Goodey & Seinhorst). The large population fluctuations of races of *Ditylenchus dipsaci* on onions and narcissus and of *Aphelenchoides ritzemabosi* on chrysanthemums are examples of the second. Cyst-nematodes provide examples of an intermediate type in which fluctuations about the equilibrium are small and sometimes damped (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.

The behaviour of the population at the equilibrium may be investigated theoretically for the population equation (10). May (1973) gives conditions that enable us to determine the type of equilibrium to be expected.

Suppose

$$\Delta = \left[\frac{d(P_f - P_i)}{dP_i}\right]_{P_i = E}$$

$$= (1 - C_p)\left(\frac{a-1}{a}\right)\left[\log_e\left(\frac{E}{c}\right) - 1\right] \qquad \text{from (10).} \qquad (11)$$

May showed that $-1 < \Delta$ implies a steady approach to E, no oscillations, $-2 < \Delta < -1$ damped oscillations about E and $\Delta < -2$ unstable equilibrium.

Equation (11) shows that for values observed in practice (in excess of thirty) the 'multiplication rate', a, has little effect on the type of equilibrium reached. Large values of C_p have a stabilizing effect on the oscillations as do large values of E, indicating small root damage. The effect of a is most marked at small initial nematode densities. Then

$$P_f \simeq [a(1 - C_p) + C_p]P_i \qquad \text{from eqn (10)}$$

when population growth is rapid.

Figure 6 shows a population curve generated by the model with parameter values giving $\Delta = -1 \cdot 24$. As P_i becomes large few new eggs are produced due to effects of root damage and competition and
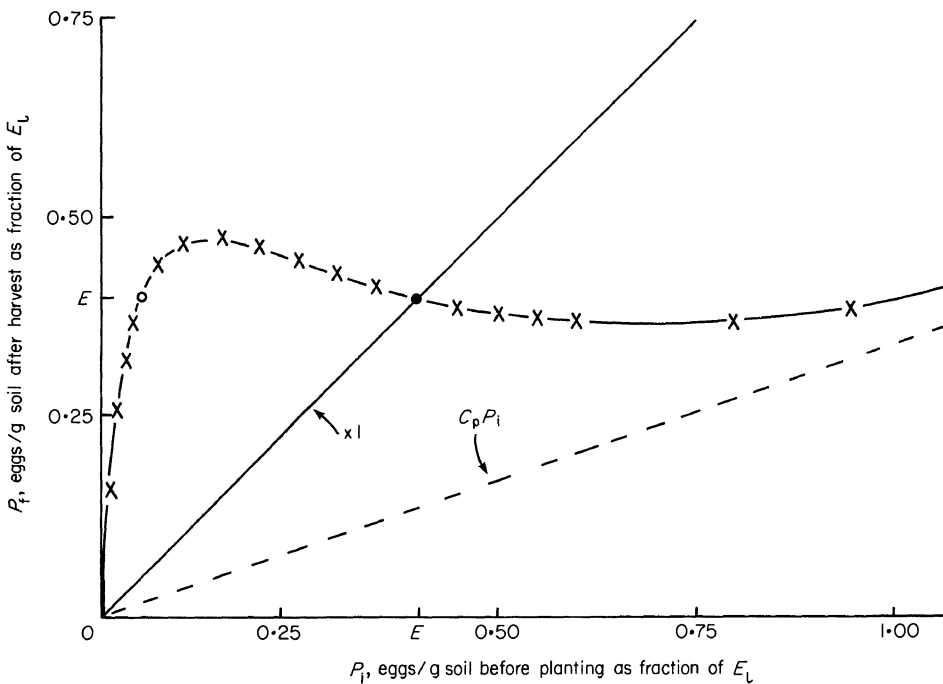
$$P_f \simeq C_p P_i.$$

FIG. 6. Population curve generated by the basic model, susceptible crop grown. When values of P_i are smaller than that represented by o root damage is slight and increase approaches $a(1 - C_p)$. At values of P_i between o and ●, populations overshoot, beyond ● they undershoot and approach $P_f = C_p P_i$.

FITTING THE BASIC MODEL TO OBSERVATIONS

We may compare observational data on changes in nematode density under a given rotation policy and thus arrive at rough estimates of the model parameters. This requires good field data; indeed the modelling process is often useful in highlighting areas of work where new or better information is required. Often qualitative information predicted by the model is of more use than quantitative parameter estimates.

The model was fitted to data from small plots where susceptible potatoes were grown

continuously for 7 years (Jones & Parrot 1969). The data consists of geometric means of eggs/g of *Globodera rostochiensis* replicated four times on seven varieties. We assumed $c = 1.05$ and $\bar{E} = 85.6$ eggs/g, and varied E, a and C_p over ranges suggested by previous data, using the computer program. This program, which is based on the extended population model requires as input model parameters, crop rotation policies and lengths of rotations and uses the appropriate model equation to predict final egg density from initial density. This final density then becomes the initial density for the next year.

The parameter values which minimized the residual sum of squares were $a = 50$, $E = 0.17$, $C_p = 0.34$ (for which $\Delta = -1.79$), (Fig. 7). No estimates of the standard errors of these parameters are available. The data provided little information on the multiplication rate a, due to lack of observations at small nematode densities. A formal sensitivity analysis was not considered worthwhile.
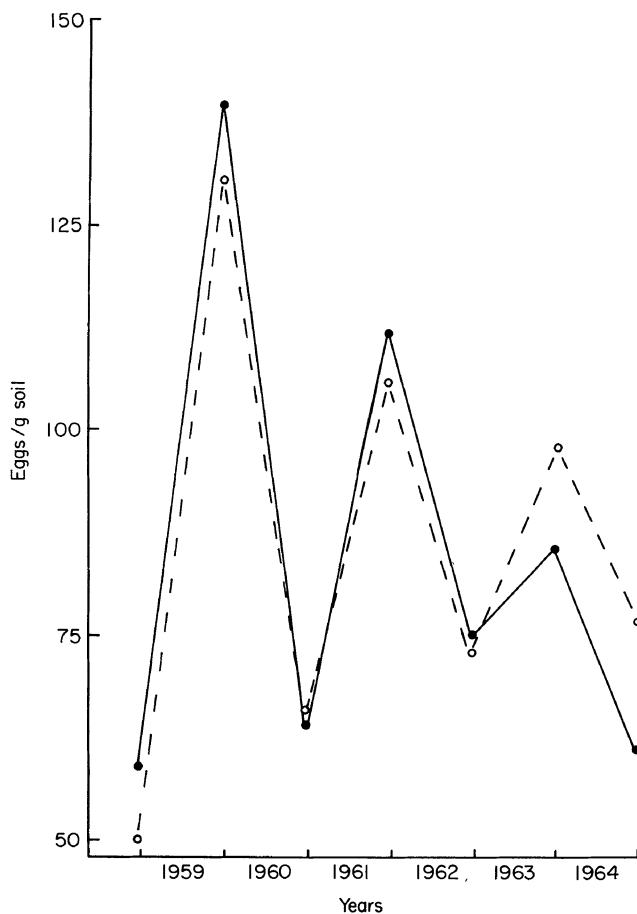

FIG. 7. Population oscillations of *Globodera rostochiensis* in small plots planted with potatoes every year. ● observed densities, ○ fitted densities. For parameters see text, data in Jones & Parrott (1969).

EXTENSIONS TO THE BASIC MODEL

Resistant crops grown

Jones, Parrott & Ross (1967) attempted a model for *Globodera rostochiensis* Ro1.

Besides trying to predict population changes under different rotations when susceptible potatoes, resistant potatoes (with gene H_1) or crops other than potatoes are grown, they simulated the increase in frequency of a resistance-breaking gene in a nematode population when resistant potato varieties are grown. Their model did not allow for the effect of root damage on nematode density and used an alternative function for the sex ratio separate from the main model.

Jones & Kempton (1978) updated their model to include the effect of crop damage, using equation (10) rather than the logistic equation, but did not include the effects of resistant crops. We have developed and used the model further, the genetic aspects of which are reiterated below. The few juveniles that develop into adult females in the roots of resistant plants are able to evoke the formation of long-lasting syncytial transfer-cells (Jones & Northcote 1972). The remainder that fail to induce proper transfer-cells are destined to become males or die. These differences are genetically linked and two simple alternative hypotheses can be advanced to explain them:

(1) females are double recessives (aa),
(2) females are double dominants and heterozygotes (AA and aa).

Hypothesis (1) applies to races of *G. rostochiensis* that develop on potato cultivars with resistance gene H_1 (Jones 1975c, 1976) and probably to genes conferring resistance to some pathotypes of *G. pallida* and *Heterodera avenae* Woll., but hypothesis (2) may apply to some pathotypes able to circumvent resistance. On both hypotheses it is assumed that males can be AA, Aa or aa. Suppose U_i, V_i, W_i are the initial frequencies of genotypes AA, Aa and aa in the population, and $U_i + V_i + W_i = 1$.

For non-host or susceptible crops the basic equation (10) is unaltered but for resistant crops it is modified to

$$P_f = \frac{ga(1-C_p)P_i}{1 + \dfrac{(a-1)P_i}{c\left(\dfrac{E}{c}\right)^{P_{i/E}}}} + C_p P_i$$

where $g = W_i$ under hypothesis (1) and $g = 1 - W_i$ under hypothesis (2)

For the model it is necessary to know U_f, V_f, W_f the genotype frequencies of the progeny. For a non-host crop these are unaltered, and for a susceptible or resistant crop may be easily calculated (e.g. if $f = F/\bar{P}_f$ = proportion of female juveniles (see eqn (4)), then for a resistant crop under hypothesis (1) it can be shown for example that

$$W_f = \left[\frac{V_i\left[W_i + \dfrac{V_i}{2}(1-f)\right]P_f}{2(1-f+fW_i)(1-W_i)} + C_p W_i P_i\right]\Bigg/ P_f.$$

We shall not however give further such derivations here).

When a susceptible variety is grown continuously the genotype frequencies can be shown to approach Hardy-Weinberg equilibrium. When a resistant variety is grown continuously the model confirms that selection takes place. Over a wide range of initial genotype frequencies, as long as the species starts with some non-zero proportion of genes able to circumvent resistance, these genes are eventually selected. This process takes far longer for hypothesis (2) than for (1), (Table 2). Additionally the population density,

initially depressed below E by the resistant crop, approaches E as selection continues negating the initial decrease in root damage.

Selection is impeded when a resistant crop is sown in conjunction with an agent that depresses initial densities greatly, e.g. an oxime carbamate nematicide. This is because absence of competition allows many juveniles with appropriate genotypes to become females which are then mated by the excess of males of inappropriate genotype. Hence the 'poor' genes are transmitted by the males to the progeny and kept in the population. It can then be shown that the equilibrium genotype frequencies under either hypothesis are $U = 0$, $V = W = \frac{1}{2}$, i.e. selection cannot operate fully and the population density remains suppressed and can fall to zero. We have been unable to establish whether this effect occurs in practice.

TABLE 2. Period in years until mutant or immigrant gene (a for recessive model. A for dominant) has frequency of 0·99; in parentheses, the same but to a frequency of 0·50

Initial frequency: dominant model, $1 - W$; recessive model, W

| Crop sequence | 0·000010 | | 0·000001 | |
	Dominant	Recessive	Dominant	Recessive
RRR	321 (6)	35 (23)	322 (7)	70 (50)
R0R0R0	569 (11)	75 (49)	574 (13)	161 (135)
R00 R00	823 (16)	133 (88)	829 (19)	295 (160)
R000 R000	1137 (25)	229 (121)	1145 (29)	521 (237)
R0000 R0000	1641 (31)	426 (136)	1656 (36)	986 (246)

Nematodes in Hardy-Weinberg equilibrium initially.
Parameters: $C_0 = 0.67$, $C_p = 0.33$, $a = 30$, P_i initially $= E = 0.25$.

Interspecific competition

In many fields it is usual to find mixtures of species from the same genus of nematodes, e.g. of *Trichodorus*, *Tylenchorhynchus*, *Pratylenchus* and *Meloidogyne*. 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: *Globodera rostochiensis* and *G. pallida* in the roots of a mutually susceptible potato crop are a good example of this. Jones & Kempton (1978) extended the basic model to include the effects of competition.

Competition between sibling species such as *G. rostochiensis* and *G. pallida* is likely to be strongest in the search for root space to enable the juveniles to become female and reproduce. The relative proportions of the two species becoming females will depend on relative hatching rates, the minimum necessary size of the female's territory in the rootlets, as well as other genetic differences.

To incorporate interspecific competition into the basic model we amend equation (4), $M_x/E_x = b\bar{P}_{rx}$, for intraspecific competition within species X to $M_x/F_x = b\bar{P}_{rx} + v_x\bar{P}_{ry}$ where $\bar{P}_{ry}$ = juveniles/cm root, species Y and v_x = effect of one nematode of species Y on one nematode of species X.

Root damage is modified from $cz_x^{\bar{P}_{ix}}$ for species X to $cz_x^{\bar{P}_{ix}}z_y^{P_{iy}}$ for both species together. Equation (8) is thus modified to

$$\bar{P}_{f_x} = \frac{a_x(1-C_{px})\bar{P}_{ix}}{1+\dfrac{(a_x-1)(\bar{P}_{ix}+v_x\bar{P}_{iy})}{c(z_x)^{\bar{P}_{ix}}(z_y)^{\bar{P}_{iy}}E_{l_x}}} + C_{px}\bar{P}_{ix} \text{ eggs/g.} \tag{12}$$

Equation (10) can be modified in a similar manner and there is a similar equation to eqn (12), including parameter v_y, for species Y.

If the two species exploit totally different parts of the root system $v_x = v_y = 0$, and the species will coexist. If their exploitation is identical then $v_1 = 1/v_2$, the species share the same ecological niche and coexistence is impossible. In practice some competing species, e.g. *G. rostochiensis* and *G. pallida*, occupy almost coincident niches.

In the absence of root damage the joint equilibrium densities, $\bar{X}$ and $\bar{Y}$ say, of the species can be calculated and conditions on these found for different values of v_x, v_y, E_{l_x}, E_{l_y}. With root damage, equations for $\bar{X}$ and $\bar{Y}$ become intractible. However it appears from intuition and test runs of the model that the conditions are identical. These are:

$v_x < E_{l_x}/E_{l_y} < 1/v_y$	Species coexist in stable equilibrium.
$E_{l_x}/E_{l_y} < v_x < 1/v_y$	Species Y outcompetes species X which becomes extinct.
$v_x < 1/v_y < E_{l_x}/E_{l_y}$	Species Y becomes extinct.
$1/v_y < E_{l_x}/E_{l_y} < v_x$	Unstable equilibrium. Whichever species becomes extinct depends on initial densities, generally the species with larger initial density dominates. In field conditions stochastic variation may have a large effect on the outcome.

Neither C_{px}, C_{py}, E_x or E_y have any effect on the eventual outcome although they may affect the rate of extinction of either species. 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. It has been suggested that the joint equilibrium population could be less than when either species occurs separately. It can be shown that this is not so when $z_x = z_y$ (i.e. when both species damage roots equally) and it is also thought not to be so when $z_x \neq z_y$.

Fitting field data on competition

Investigating the effects of competition experimentally requires a great range and variety of combinations of species and 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 *Globodera rostochiensis* and *G. pallida*.

However the number of parameters we now have to deal with has become large, since we are dealing with two species, and may even be larger than the number of data points, causing problems in fitting. We now consider data from Plot 87 of Experiment CS/16 at Woburn Experimental Farm, Bedfordshire. Potatoes resistant to *G. rostochiensis* Ro1, which lacks genes to circumvent resistance, were planted every year from 1965 until 1971.

After a year, observed egg totals began to rise due to the colonization of the plot by *G. pallida*, a species which suffers no resistance from this crop. Both species invade the roots and interspecific competition takes place, but as no new *G. rostochiensis* eggs are produced this species declines exponentially by a constant factor C_p each year. The data consisted of total egg numbers from both species, since it was only later that *G. pallida* was identified as a separate species. It was decided to fit the model to the data by holding certain parameters constant at sensible values and varying others.

We set:

$\bar{E}_r = 200$, $\bar{E}_p = 220$, $E_{lp}/E_{lr} = 1.1$, $v_p = E_{lp}/E_{lr} = 1/v_r$ (unstable equilibrium), $a_r = 30$, $C_{pr} = 0.33$, $c = 1.05$, $E_r = E_p$ and the initial densities in 1965 in the ratio $P_{lr}/P_{ip} = 100$.

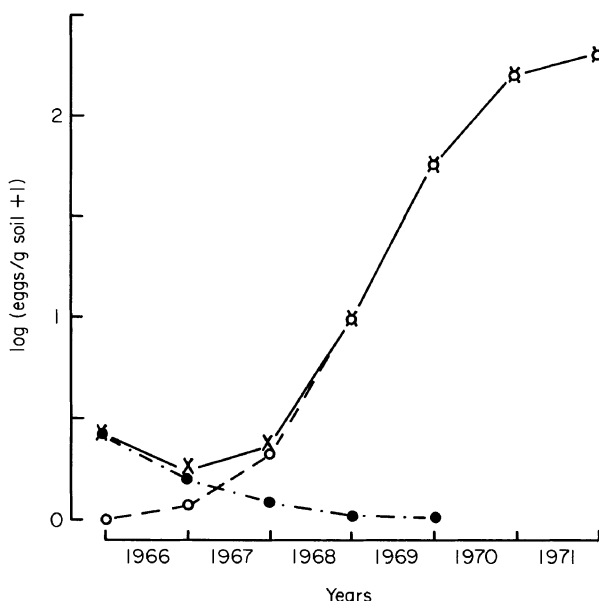We varied a_p, C_{pp} and E_p whose values were estimated as 20, 0.63 and 0.4 (Fig. 8).

Fig. 8. Competition model fitted to data from plot No. 87 Woburn Experimental Farm. For parameters see text. × total eggs, ● eggs of *Globodera rostochiensis*, ○ eggs of *G. pallida*.

In datasets where initial densities are high we often observe a characteristic delay in the rise of the *G. pallida* population from initially small densities. To explain this and to test the robustness of parameter estimates to changes in data, we examined the data of Cole & Howard (1962a). Six sets of data were presented for the following crop rotations on plots on a black fen soil in Norfolk.

(a) 1955–1960   Fallow
(b) 1955–1960   Continuous resistant potatoes
(c) 1955   Fallow
      1956–1960   Resistant potatoes
(d) 1955   Resistant, *Solanum nigrum* 1.
      1956–1960   Resistant potatoes
(e) 1955   Susceptible potatoes (Ulster Chieftain)
      1956–1960   Resistant potatoes

TABLE 3. Parameters estimated from data of Cole & Howard (1962a)

| Dataset	Parameters estimated and values	Used subsequently in:
(a)	$C_{0_r} = 0.74$	(c)
(b)	$E_p (= E_r) = 0.24$	(c)　(d)　(e)　(f)
	$C_{pp} = 0.33$	(c)　(d)　(e)　(f)
	$a_p = 13$	(c)　(d)　(e)　(f)
	Initial density of *Globodera pallida* $= 0.00005 E_{l_p}$	–
(c)	Initial density *G. pallida* $= 0.000103 \ E_{l_p}$	–
(d)	Initial density *G. pallida* $= 0.000321 \ E_{l_p}$	–
	Initial density *G. rostochiensis* $= 0.35 E_{l_r}$	–
(e)	Initial density *G. pallida* $= 0.000039 E_{l_p}$	–
	Initial density *G. rostochiensis* $= 0.198 E_{l_r}$	–
(f)	Initial density *G. pallida* $= 0.000001 E_{l_p}$	–
	Initial density *G. rostochiensis* $= 0.0696 \ E_{l_r}$	–
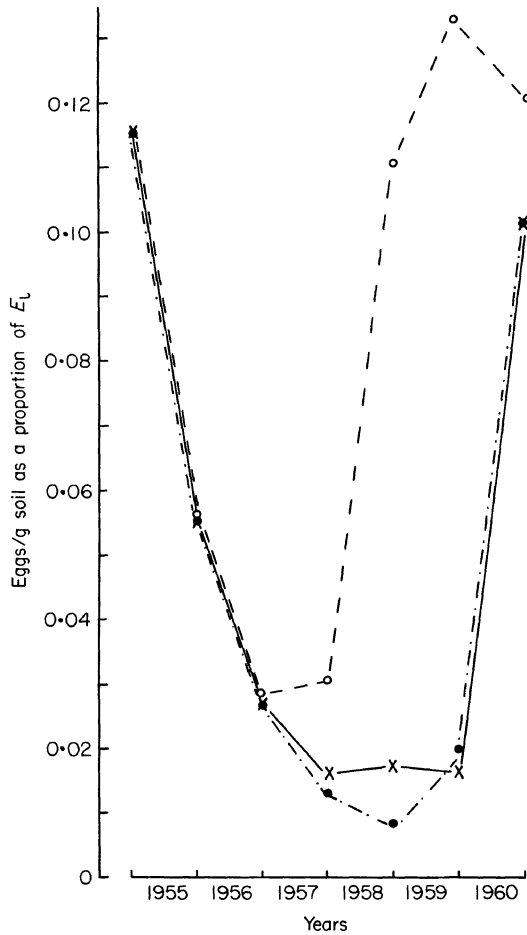
FIG. 9. Competition model fitted to dataset (b), Cole & Howard (1962a). For parameters see text. ×, observed eggs densities, ● fitted density with competition, ○ fitted without competition. Up to 1956 eggs mostly *Globodera rostochiensis,* after 1959 mostly *G. pallida.*

(f) 1955   Susceptible potatoes (Majestic)
     1956–1960   Resistant potatoes.

We estimated parameters for dataset (b) and used them for datasets (c)–(f) to check whether reasonable fits were still obtained. E_{1p}/E_{1r}, v_p, v_r, a_r and c were set as for data from Plot 87. Additionally $E_r = E_p$ by assumption and $C_{pr} = 0\cdot48$ by estimation over datasets (b)–(f). In (b) and (c) initial density $= E_r$ by assumption after noting the crop rotation prior to 1955. The parameters estimated, their values and the datasets in which they were subsequently used are summarized in Table 3. Fits to datasets (c)–(f) were good which suggests that our estimated parameters were robust. We realize the drawbacks of this procedure but are restricted by lack of more extensive data.

The observed and fitted values are plotted, (together with fitted values without competition, i.e. with $v_p = v_r = 0$), for dataset (b) (Fig. 9). We now see that the characteristic delay in the increase of *Globodera pallida* densities is caused by competition with *G. rostochiensis* which, until it has fallen to a low level, suppresses the *G. pallida* population. This phenomenon is observable in datasets (c), d), (e) and (f) and also in data of Huijsman (1961).

EFFECT OF GROUND-KEEPERS

Ground-keepers are 'volunteer' potato plants that may occur in fields which carried potatoes the previous year, especially after a mild winter (den Ouden 1967). Although sometimes numerous these plants receive less fertilizer than do maincrop potatoes, are in competition with the current crop, are often checked by herbicides and may be attacked by the potato cyst-nematode. Den Ouden presented data for two densities of volunteer plants (16 and 4 plants per m²) on which *Globodera rostochiensis* could multiply. He showed that C_p for ground-keepers was $0\cdot65$, about the same as C_O for the normal crop. This is possibly due to the much decreased size of the root system resulting in a reduction in the output of the root exudate that stimulates hatching. He also showed that a, the effective multiplication rate, was about 7, well below that for a normal crop. This is probably due to a reduction in H, the proportion of hatched eggs successfully invading the reduced root system. Given these values of C_p and a, we set $c = 1\cdot0$ and estimated the values of $\bar{E}$ and E at both ground-keeper densities by the method of maximum likelihood. $\bar{E} \simeq 16\cdot5$ and $4\cdot42$ eggs/g at 16 and 4 ground-keepers/m² respectively, both much smaller than for normal potato crop (E for both densities was about $0\cdot78$). Since nematode densities from the previous potato crop will usually be far above E_1 for ground-keepers, we would expect few new eggs to be produced, due to competition and root damage, and the population to be reduced by a factor $1 - C_p (= 1 - C_O)$. That is, effectively the same as when a non-host crop is grown, and we conclude that ground-keepers will normally have little effect on population densities. Table 4 shows some simulations of realistic crop rotations involving ground-keepers and indicates that their genetic effect is also similar to that of a non-host crop.

Extending the model to nematicides

Two types of nematicide may be included in the model.

A fumigant nematicide is assumed to leave a specified proportion N of viable eggs after application and equation (10) is modified to

$$P_f = \frac{Na(1 - C_p)P_i}{1 + \dfrac{(a-1)NP_i}{c\left(\dfrac{E}{c}\right)^{NP_i/E}}} + N\,C_p P_i. \tag{13}$$

No explicit equilibrium solution is possible. In fields N ranges from $0\cdot1$ to c. $0\cdot3$. At these values using fumigants every year can produce equilibria above E, i.e. increased densities after harvest. This arises from better root growth and decreased competition, due to smaller juvenile densities after fumigation. This is confirmed by old field experiments (Peters & Fenwick 1949) and by recent ones which also suggest that such nemati-rather than preventing the selection of a race or species able to reproduce on a resistant cultivar, would make selection more rapid.

In glasshouse tomatoes attacked by *Globodera pallida*, N may be as small as $0\cdot01$ (Whitehead *et al.* 1975) and root damage is generally slight so $c(E/c)^{NP_i/E} \simeq 1$ and equilibrium P is achieved at

$$P \simeq \frac{aN(1 - C_p) - (1 - NC_p)}{(1 - NC_p)N(a - 1)} \qquad \text{from (13)}$$

TABLE 4. Simulated effect of ground-keepers

Crop	Population density	Crop	Population density	Crop	Population density
–	0·3700	–	0·3700	–	0·3700
S	0·5171	S	0·5171	S	0·5171
S	0·4982	O	0·3361	SG16	0·3415
S	0·5002	O	0·2185	SG4	0·2225
S	0·5000	O	0·1420	SG4	0·1451

Crop	Population density	Genotype frequencies AA	Aa	aa
–	0·3700	0·81	0·18	0·01
R	0·1260	0·78	0·21	0·01
R	0·0477	0·68	0·29	0·03
R	0·0257	0·42	0·50	0·08
R	0·0316	0·11	0·65	0·24
–	0·3700	0·81	0·18	0·01
R	0·1260	0·78	0·21	0·01
O	0·0819	0·78	0·21	0·01
O	0·0533	0·78	0·21	0·01
O	0·0346	0·78	0·21	0·01
–	0·3700	0·81	0·18	0·01
R	0·1260	0·78	0·21	0·01
RG16	0·0820	0·78	0·21	0·01
RG4	0·0534	0·78	0·21	0·01
RG4	0·0346	0·78	0·21	0·01

All densities are proportions of E_l for potato crop.
S = Susceptible potato crop, O = Non-host crop, R = Resistant potato crop.
G16 = Ground-keepers at 16/m², G4 = Ground-keepers at 4/m².
$E_l(G4)/E_l(\text{potato}) = 0\cdot02375$, $E_l(G16)/E_l(\text{potato}) = 0\cdot0883$.
Parameters for potatoes: $C_O = 0\cdot65$, $C_p = 0\cdot33$, $a = 30$, $E = 0\cdot50$, $c = 1\cdot02$.
Parameters for G16 and G4: $C_O = 0\cdot65$, $C_p = 0\cdot65$, $a = 7$, $E = 0\cdot78$, $c = 1\cdot00$.

with extinction occurring if $N < [a(1 - C_p) + C_p]^{-1}$.

Oxime carbamate or organophosphate nematicides operate on the nervous system of newly hatched juveniles and prevent them from invading roots. We suppose a proportion X are left after application and eqn (10) is modified to

$$P_f = \frac{Xa(1 - C_p)P_i}{1 + \dfrac{(a - 1)XP_i}{c\left(\dfrac{E}{c}\right)^{P_i/E}}} + C_p P_i.$$

Again no explicit equilibrium solution is possible. However field values of X are generally as small as $0{\cdot}01$ and excellent population control is often possible (Whitehead 1975). When root damage is slight, equilibrium P is achieved at

$$P \simeq \frac{aX - 1}{(a - 1)X} \text{ with extinction occurring if } aX < 1.$$

Oxime carbamates thus provide a very efficient way of controlling nematode populations.

Attack by the Entomophthora-like fungus†

Population densities of *Heterodera avenae* Woll. are strongly controlled in most British cereal fields by an *Entomophthora*-like fungus that attacks young females (Kerry & Crump 1977). This fungus is known to have a density-dependent effect causing mortality in two stages. A model has been attempted for this effect (Perry 1978), which has the form:

$$P_i = \frac{f(P_i)\, a(1 - C_p)P_i}{1 + \dfrac{(a - 1)P_i}{c\left(\dfrac{E}{c}\right)^{P_i/\bar{E}}}} + C_p P_i$$

where $f(P_i)$ is the density dependent proportion of females (and hence of eggs) that survive attack.

PREDICTIONS FROM THE MODELS

Population models provide qualitative information which is valuable in understanding the population dynamics of a species, but cannot be used to predict numbers in individual fields without additional information on within-field variability, local farm practices and other factors affecting population development. Soil-climatic factors other than rainfall are relatively stable within an area as small as Great Britain (Jones 1974) and farming practices for particular crops tend also to be stereotyped, so generalizations for root endoparasitic nematodes are possible but those for root ectoparasitic nematodes are greatly influenced by rainfall which can be erratic (Jones 1975a, 1975b). Models may be used to observe the character of populations fluctuating under different cropping regimes (Table 5). Some predictions in accord with experience are illustrated in Table 2. For example, in fields in Long Island, New York and in Britain, there is as yet no evidence that growing resistant potatoes with gene H_1 from *Solanum tuberosum* ssp. *andigena* Juz. & Buk. has selected from *Globodera rostochiensis* Ro1 (genetic constitution AA) types equivalent to populations of race Ro2 such as occur in the Netherlands and Bolivia

† Now known to be an Oomycete with motile zoospores (Kerry & Crump 1977).

(constitution aa; Jones 1975c). Selection in the U.K. and in the Netherlands has usually resulted in the replacement of *G. rostochiensis* Ro1 by *G. pallida* after growing up to six successive crops of a resistant potato cultivar bearing gene H_1.

TABLE 5. Two examples of computer printout

Parameters: $C_0 = 0.70$ $C_p = 0.33$, $a = 20$, $E = 0.40$, $U = 0.25$, $V = 0.50$, $W = 0.25$. Starting population density $E_1 = 0.55$. % surviving fumigant nematicide $(N) = 30$. % surviving oxime carbamate nematicide $(X) = 3$

Example 1		Example 2				
Crop sequence	Population density	Crop sequence	Population density	Genotype frequencies		
				AA	Aa	aa
—	0·5500	—	0·5500	0·25	0·50	0·25
S	0·3728	NR	0·1560	0·09	0·52	0·40
S	0·4071	O	0·1092	0·09	0·52	0·40
XS	0·2677	O	0·0764	0·09	0·52	0·40
S	0·4386	XS	0·0547	0·10	0·48	0·41
S	0·3910	NR	0·0750	0·01	0·50	0·49
XS	0·2580	O	0·0525	0·01	0·50	0·49
S	0·4415	O	0·0368	0·01	0·50	0·49
S	0·3904	XS	0·0266	0·04	0·44	0·52
XS	0·2577					

S = susceptible host-crop, R = resistant host-crop, O = non host-crop.
All population densities given as proportions of logistic equilibrium, E_1.

DISCUSSION

The models described apply to population changes in small field plots. They need to be made stochastic for a number of reasons, the most important of which are variation in both parameter values and initial densities. The overall solution from a stochastic model may not be equal to the deterministic solution. Additionally, difficulties occur with very low densities in deterministic models which may be overcome by allowing extinction locally. In advisory work, mean population densities are obtained by collecting representative soil samples and estimating the number of cysts and eggs/cyst after pooling and mixing. This obscures the population distribution within the field. However, fields can be classified as very patchy (e.g. recently infested), patchy (e.g. infested for some years) and generally infested (e.g. infested for many years). Using criteria from Fenwick (1961), it would be possible to generate, from a pooled mean, estimates of egg densities at fifty or more points within a field. Suitable standard errors could also be applied to parameters and their effects estimated to show which have the most influence on population dynamics. The models could also be extended to give yield projections using Seinhorst's relationship between yield and pre-planting population densities.

The models apply best to cyst-nematodes having one generation during a crop year (*Globodera* spp. on potatoes, *Heterodera avenae* on cereals, *H. goettingiana* on peas and field and broad beans, *H. schachtii* and *H. cruciferae* on some brassicas and other Cruciferae). They have still to be tested and perhaps modified to fit data from *H. schachtii* on sugar beet, *H. carotae* on carrots and *H. humuli* on hops: all species that complete two or more generations on these hosts which have long vegetative periods. To fit the models to *H. cruciferae* and *H. carotae*, it would be necessary to estimate the many eggs laid in egg sacs outside the cysts (Jones 1950).

Volunteer potatoes are weeds. If the parameters were known, even approximately, the model simulating their effects could be applied to grass weeds in fields infested with *H. avenae,* to wild beet, cruciferous and other host weeds in fields infested with *H. schachtii* and to cruciferous weeds in fields infested with *H. cruciferae.* Few field weeds support *H. goettingiana.*

The race of *Solanum nigrum* common in British potato fields appears resistant to most populations of *Globodera rostochiensis* and *G. pallida.* Since its roots produce the hatching factor it behaves rather like resistant potatoes but, like volunteer potatoes, it presumably affects numbers of these species very little.

It is hoped that these models will stimulate work designed to estimate more accurately the values of important parameters such as a, E_1, E, C_0 and C_p, and their variation. More work is also needed to assess mortality. That of juveniles within roots is probably slight, largely accounted for by competition for feeding sites and implicit in the modified logistic equation (eqn 10) and its derivatives. Mortality of various kinds, in the egg and juvenile stages before they enter the roots, is confounded within the values of a, C_0 and C_p.

In extending the model to include genetic changes within species when resistant cultivars are grown we have adopted the hypothesis that second-stage juveniles can become either male or female according to circumstances, i.e. that sex is environmentally determined (Trudgill 1967). This leads to the conclusion that selection is impeded at trivial population densities (p. 361). If this hypothesis is disproved and the sex ratio is determined genetically at 1, the model can easily be modified. However, the change would have little effect except at trivial densities.

REFERENCES

Andersen, K. & Andersen, S. (1970). Population changes of the cereal root eelworm under grass species and resistant barley varieties. *Tidsskrift. for Planteavl,* **74,** 559–65.

Andersson, S. (1976). Occurrence and behaviour of *Heterodera hordecalis* Andersson and *H. bifenestra* Cooper in Swedes, with some references to *H. avenae* Wollenweber and a similar *Heterodera* sp. *Statens Växskyddsanstalt Meddelanden,* **16** No. 170, 245–87.

Anscombe, F. J. (1950). Soil sampling for potato root eelworm cysts. A report presented to the Conference of Advisory Entomologists. *Annals of applied Biology,* **37,** 286–395.

Church, B. M., Gough, H. C. & Southey, J. F. (1959). Soil sampling procedures for potato root eelworm cysts. *Plant Pathology,* **8,** 146–51.

Cole, C. S. & Howard, H. W. (1962a). Further results of growing resistant potatoes on a potato-root eelworm (*Heterodera rostochiensis*) population. *Nematologica,* **7,** 57–61.

Cole, C. S. & Howard, H. W. (1962b). The effect of growing resistant potatoes on a potato-root eelworm population–a microplot experiment. *Annals of applied Biology,* **50,** 121–7.

Cole, C. S. & Howard, H. W. (1966). The effects on a population of potato-root eelworm (*Heterodera rostochiensis*) of growing potatoes resistant to pathotype B. *Annals of applied Biology,* **58,** 487–95.

Cooper, B. A. (1954). Eelworm problems in north Fenland with special reference to crop rotation. *Report of the horticultural Educational Association* 1953, 106–15.

Evans, K., Trudgill, D. L. & Brown, N. J. (1977). Effects of potato cyst-nematodes on potato plants. V. Root system development in lightly and heavily infested susceptible and resistant varieties and its importance in water and nutrient uptake. *Nematologica,* **23,** 153–64.

Fenwick, D. W. (1961). Estimation of field populations of cyst-forming nematodes of the genus *Heterodera.* *Journal of Helminthology, R. T. Leiper, 80th birthday vol.,* 63–76.

Fisher, R. A. (1938). *Statistical Methods for Research Workers.* Oliver & Boyd, London.

Flegg, J. J. M. (1968). Life-cycle studies of some *Xiphinema* and *Longidorus* species in south eastern England. *Nematologica,* **14,** 197–210.

Gair, R., Mathias, P. L. & Harvey, P. N. (1969). Studies of cereal nematode populations under continuous or intensive culture. *Annals of applied Biology,* **63,** 503–12.

Hesling, J. J. (1958). *Heterodera major*–population changes in the field and in pots of fallow soil. *Nematologica,* **3,** 274–82.

Hesling, J. J. (1961). *Heterodera rostochiensis* Woll. 1923 on *Solanum demissum*–a population study. *Annals of applied Biology*, **49**, 350–9.

Huijsman, C. A. (1961). The influence of resistant potato varieties on the soil population of *Heterodera rostochiensis* Woll. *Nematologica*, **6**, 177–80.

Jakobsen, J. (1974). The importance of monocultures of various host plants for the population density of *Heterodera avenae*. *Beretning fra Statens Forsøgksvirksamhed i Plantekultur* No. **1190**, pp. 697–700.

Jones, F. G. W. (1945). Soil population of beet eelworm (*Heterodera schachtii* Schm.) in relation to cropping. *Annals of applied Biology*, **32**, 351–80.

Jones, F. G. W. (1950). Observations on the beet eelworm and other cyst-forming species of Heterodera. *Annals of applied Biology*, **37**, 407–40.

Jones, F. G. W. (1955). Quantitative methods in nematology. *Annals of applied Biology*, **42**, 372–81.

Jones, F. G. W. (1956). Soil populations of beet eelworm (*Heterodera schachtii* Schm.) in relation to cropping. II. Microplot and field plot results. *Annals of applied Biology*, **44**, 25–56.

Jones, F. G. W. (1957). Soil populations of beet eelworm (*Heterodera schachtii*) in relation to cropping III. Further experiments with microplots and with pots. *Nematologica*, **2**, 257–72.

Jones, F. G. W. (1966). The population dynamics and population genetics of the potato cyst-nematode *Heterodera rostochiensis* Woll. on susceptible and resistant potatoes. *Report of the Rothamsted Experimental Station for 1965*, 301–16.

Jones, F. G. W. (1974). Control of nematode pests, background and outlook for biological control. *Biology in Pest and Disease Control*. (Ed. by D. Price Jones and M. E. Soloman), pp. 249–68. Blackwell Scientific Publications, Oxford.

Jones, F. G. W. (1975a). Accumulated temperature and rainfall as measures of nematode development and activity. *Nematologica*, **21**, 62–70.

Jones, F. G. W. (1975b). The soil as an environment for plant parasitic nematodes. *Annals of applied Biology*, **79**, 113–39.

Jones, F. G. W. (1975c). Host parasite relationships of potato cyst-nematodes; a speculation arising from the gene-for-gene hypothesis. *Nematologica*, **20** (1974), 437–43.

Jones, F. G. W. (1976). Nematology Department. *Report of the Rothamsted Experimental Station for 1975*, Pt. 1, 191–212.

Jones, F. G. W. & Kempton, R. A. (1978). Population dynamics, population models and integrated control. *Plant Nematology* (Ed. by J. F. Southey), pp. 333–61. MAFFA AS Publication GD/1. HMSO, London.

Jones, F. G. W. & Parrott, D. M. (1969). Population fluctuations of *Heterodera rostochiensis* Woll. when susceptible potato varieties are grown continuously. *Annals of applied Biology*, **63**, 175–81.

Jones, F. G. W. & Parrott, D. M. & Ross, G. J. S. (1967). The population genetics of the potato cyst-nematode, *Heterodera rostochiensis*: mathematical models to simulate the effects of growing eelworm-resistant potatoes bred from *Solanum tuberosum* ssp. *andigena*. *Annals of applied Biology*, **60**, 151–71.

Jones, F. G. W., Meaton, V. H., Parrott, D. M., Shepherd, A. M. & King, J. M. (1965). Population studies on pea cyst-nematode. *Annals of applied Biology*, **55**, 13–23.

Jones, M. G. K. & Northcote, D. H. (1972). Nematode induced syncytium—a multinucleate transfer cell. *Journal of Cell Science*, **10**, 789–809.

Kerry, B. R. & Crump, D. H. (1977). Observations on fungal parasites of females and eggs of the cereal cyst-nematode, *Heterodera avenae* Woll., and other cyst-nematodes. *Nematologica*, **23**, 193–201.

Kort, J. (1962). Effect of population density on cyst production in *Heterodera rostochiensis* Woll. *Nematologica*, **7**, 305–8.

Lownsbery, B. F. & Peters, B. G. (1955). The relation of the tobacco cyst nematode to tobacco growth. *Phytopathology*, **45**, 163–7.

May, R. M. (1973). Stability in randomly fluctuating versus deterministic environments. *American Naturalist*, **107**, 621–50.

Mukhopadhyaya, M. C., Dalal, M. R., Saran, S. & Kharub, S. S. (1973). Studies on the 'molya' disease of wheat and barley. *Indian Journal of Nematology*, **2**, (1972), 11–20.

Ouden, H. den (1967). The influence of volunteer potato plants in oats on the population density of *Heterodera rostochiensis*. *Nematologica*, **13**, 325–35.

Perry, J. N. (1978). A population model for the effect of parasitic fungi on numbers of the cereal cyst-nematode, *Heterodera avenae*. *Journal of applied Ecology*, **15**; (in press).

Peters, B. G. (1961). *Heterodera rostochiensis* population density in relation to potato growth. *Journal of Helminthology*, R. T. Leiper, 80th birthday vol., 141–50.

Peters, B. G. & Fenwick, D. W. (1949). Field trials with D-D mixture against potato-root eelworm. *Annals of applied Biology*, **36**, 364–82.

Ross, G. J. S. & Trudgill, D. L. (1969). The effect of population density on the sex ratio of *Heterodera rostochiensis*; a two-dimensional model. *Nematologica*, **15**, 601–7.

Seinhorst, J. W. (1965). The relation between nematode density and damage to plants. *Nematologica*, **11**, 137–54.

Seinhorst, J. W. (1967). The relationship between population increase and population density in plant parasitic nematodes. III. Definition of the terms host, host status and resistance. IV. The influence of external conditions on the regulation of population density. *Nematologica, 13,* 429–42.

Seinhorst, J. W. (1968a). The relationships between population increase and population density in plant parasitic nematodes. V. Influence of damage to the host on multiplication. *Nematologica, 13,* (1967), 481–92.

Seinhorst, J. W. (1968b). Underpopulation in plant parasitic nematodes. *Nematologica, 14,* 549–53.

Seinhorst, J. W. (1970). Dynamics of populations of plant parasitic nematodes. *Annual Review of Phytopathology, 8,* 131–56.

Seinhorst, J. W. & den Ouden, H. (1971). The relation between density of *Heterodera rostochiensis* and growth and yield of two potato varieties. *Nematologica, 17,* 347–69.

Southey, J. F. (1974). Methods for detection of potato cyst nematodes. *EPPO Bulletin, 4,* 463–73.

Trudgill, D. L. (1967). The effect of environment on sex determination in *Heterodera rostochiensis. Nematologica, 13,* 263–72.

Weischer, B. (1975). Ecology of *Xiphinema* and *Longidorus. Nematode Vectors of Plant Viruses* (Ed. by F. Lamberti, C. E. Taylor and J. W. Seinhorst), 291–307. Plenum Press, New York.

Whitehead, A. G. (1975). Chemical control of potato cyst-nematodes. *ARC Research Review, 1,* 17–23.

Whitehead, A. G., Fraser, J. E., French, E. M. & Wright, S. M. (1975). Chemical control of potato cyst-nematode, *Heterodera pallida,* on tomatoes grown under glass. *Annals of applied Biology, 80,* 75–84.