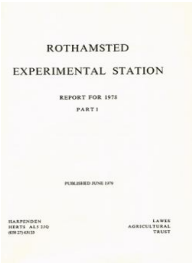
ROTHAMSTED RESEARCH

Report for 1978 - Part 1

Full Table of Content



Nematology Department

F. G. W. Jones

F. G. W. Jones (1979) *Nematology Department ;* Report For 1978 - Part 1, pp 167 - 189 **- DOI: https://doi.org/10.23637/ERADOC-1-135**

NEMATOLOGY DEPARTMENT

F. G. W. JONES

Staff

Head of Department F. G. W. Jones, SC.D.

Principal Scientific Officers

A. J. Clarke, PH.D.
C. C. Doncaster, B.SC.
D. J. Hooper, M.I.BIOL.
M. K. Seymour PH.D.
Audrey M. Shepherd, PH.D.
A. R. Stone, PH.D.
A. G. Whitehead, PH.D.
T. D. Williams, PH.D.

Senior Scientific Officers

R. H. Bromilow, PH.D.
Mrs. Sybil A. Clark, B.SC.
K. Evans, PH.D.
D. N. Greet, B.SC.
B. R. Kerry, PH.D.
Diana M. Parrott, B.SC.
R. N. Perry, PH.D.
D. J. Tite, N.D.A.

Higher Scientific Officers

Alison M. Spaull, PH.D.
R. M. Webb, B.SC.

Scientific Officers

J. Beane
Mrs. Margaret M. Berry
A. J. Callewaert
Mrs. Janet A. Cowland
D. H. Crump, H.N.D.
Mrs. Janet E. Fraser
Mrs. Eileen M. French
Judith A. Hennessy, H.N.C.
P. G. Mewton, B.SC.
Mrs. Janet A. Rowe

Assistant Scientific Officers

S. A. Cham
Geraldine Eyre, H.N.C.
Mrs. Irene A. Farr
Jean E. Firth
Mrs. Carole A. Elsworth
Mrs. Lesley A. Mullen
A. J. Nichols

Visiting Scientists

E. I. Agbakuribe
N. Krishnananda, PH.D.
G. W. Yeates, PH.D.

Students

M. R. Bridgeman, B.SC.
Jennifer W. Cuthbert, M.SC.
Joanna L. Feachnie
Amanda J. Hill, B.SC.
R. A. Plowright
S. J. Pye
W. J. C. Oswald, B.SC.
P. A. Roberts, PH.D.
Susan J. Turner, B.SC.
J. A. Walsh, B.SC.

Personal Secretary

Mrs. Doris M. Daniels

Shorthand Typist

Mrs. E. P. Joy Munnerley

Laboratory Attendants

A. Duffus
Mrs. Phoebe M. Smith.

Introduction

As explained last year (*Rothamsted Report for 1977*, Part 1, 171) we have concentrated on potato cyst-nematodes because they are important pests in the UK, field infestations are widespread and the encysted eggs are able to withstand desiccation making them ideal laboratory animals. Nematologists are few and problems many, so by narrowing our efforts we have been able to push our enquiries more deeply in the hope of establishing principles in nematode biology, in population ecology and in control that hold for other species of cyst-nematodes and more generally. Recently we have worked on cyst-nematodes in crops other than potatoes and paid more attention to cereal crops (p. 172).

Work on population dynamics of cyst-nematodes has culminated in a versatile model that simulates on the computer most of the situations encountered in ordinary fields (p. 173). The model still needs to be made stochastic and has disclosed a gap in our knowledge of the way in which new infestations spread within fields. A more rigorous proof of the existence of a gene-for-gene relationship has been obtained (p. 182) and an additional model built to simulate the effects of the oomycetous fungus that controls

https://doi.org/10.23637/ERADOC-1-135

populations of the cereal cyst-nematode in the field (p. 177). By skilful time-lapse cinematography it has been shown that this fungus and another similar one has motile zoospores (p. 176) which explains why they are less effective in some dry soils (p. 177). The fungi seem unaffected by crop rotations or the application of nematicides other than formalin.

Trials with nematicides

Potato cyst-nematodes

Assessment of potential nematicides. Thirteen pesticides were assessed as nematicides in pots inoculated with 60 *Globodera rostochiensis* (Woll.) eggs g^{-1} soil. Each compound was assessed at 3·5, 7 and 14 mg a.i. per pot of 1500 ml of soil (1·7, 3·4 and 6·8 ppm). In pots of soil treated with terbufos, oxamyl, aldicarb, carbendazim, thiophanate methyl, thiophanate ethyl or ethoprophos at one or more of the three concentrations, the nematode failed to increase on the roots of susceptible Arran Banner potato plants grown for 12 weeks. In untreated pots increase was 25-fold.

Terbufos, thiophanate methyl and bendiocarb were further assessed as nematicides in loamy sand on Great Hill field, Woburn (Table 1). Yields of tubers were small but were

TABLE 1

Effect of three pesticides on yields of Pentland Crown potatoes and control of potato cyst-nematode (G. rostochiensis Ro1), *Great Hill, Woburn, 1978*

Treatment	kg a.i. ha^{-1}	Tubers over 3·8 cm diam. (t ha^{-1})	Nematode increase, times
Untreated	0	11·2	3·5
Thiophanate methyl (50% w/w)	5	15·3	4·1
	10	16·8	3·7
	20	18·3*	1·3**
Terbufos (2% granule)	2·5	20·8**	1·1***
	5	19·9**	0·9***
	10	22·8***	0·5***
Bendiocarb (80% w/w)	5	22·7***	1·5**
	10	24·5***	1·0***
	20	21·6**	0·5***
LSD (5%)		6·2	1·2
(1%)		8·4	1·7
(0·1%)		11·1	2·3

*, **, *** Significantly greater (yields) or smaller (nematode increase) than untreated at $P < 0·05$, 0·01, 0·001, respectively.

doubled by treating the soil with terbufos or bendiocarb, both of which controlled nematode increase better than thiophanate methyl. (Whitehead, Fraser, French and Nichols)

Methods of incorporating granular nematicides in soil. Last year we described a new technique of incorporating granular pesticides in soil by the 'Vertical Band-Roterra' technique (*Rothamsted Report for 1977*, Part 1, 183). Granules are blown into vertical bands in the top 12–15 cm of the soil and mixed laterally by a rotary harrow (Lely 'Roterra'). Compared with the usual method of applying the granules to the soil surface and incorporating them by rotavation, the technique is faster, does not mix weathered with unweathered soil and does not harm soil structure.

The distribution of oxamyl was again assessed in successive 5 cm depth fractions down to 25 cm, following different methods of applying and incorporating 10% granules

https://doi.org/10.23637/ERADOC-1-135

TABLE 2

Control of potato cyst-nematode (G. rostochiensis *Ro1*) *by different methods of applying oxamyl to peaty loam at Mepal*

				Pentland Crown Potatoes			
				Site 1		Site 2	
Treatment	kg a.i. ha^{-1}	Method of application to soil†	Method of incorporation in soil	Tubers over 3·8 cm diam. (t ha^{-1})	Nematode increase, times	Tubers over 3·8 cm diam. (t ha^{-1})	Nematode increase, times
Untreated	0	—	Roterra	49·3	37·2	31·2	6·6
Untreated	0	—	Rotavator	46·8	32·7	—	—
Oxamyl (granules)	5·4	SVB 12·5 cm	Roterra	59·3	3·0	44·3	2·6
	5·4	VB 12·5 cm	Roterra	59·0	9·5	50·1	2·8
	5·4	VB 25 cm	Roterra	64·9	4·2	43·7	2·9
	5·4	S	Rotavator	65·1	5·8	41·7	2·7
Oxamyl (liquid)	5·4	VB 25 cm	Roterra	—	—	50·1	2·6
LSD (5%)				6·5	14·2	8·5	1·1
(1%)				9·1	19·7	11·4	1·4
(0·1%)				12·9	27·4	14·9	1·9

†S = to soil surface; VB 12·5 cm or 25 cm = in vertical bands 12·5 cm or 25 cm apart in top 12–15 cm of the soil; SVB = ⅓ to soil surface, ⅔ in vertical bands 12·5 cm apart in top 12–15 cm of the soil.

TABLE 3

Residual effect of cultivars, formalin and aldicarb H. avenae *pre- and post-crop egg counts 1978, Butt Close, Woburn*

	Nelson (R)								Maris Tabard (S)							
1977 Crop	Aldicarb				Untreated				Aldicarb				Untreated			
1977																
Formalin (76) (77)	†– –	–F	F–	FF	– –	–F	F–	FF	– –	–F	F–	FF	– –	–F	F–	FF
Pre-crop (eggs) 10g^{-1}	16	17	13	26	38	33	26	37	9	34	12	36	101	179	118	173
means		(18)				(34)				(23)				(143)		
Post-crop (eggs) 10g^{-1}	33	43	55	53	68	85	48	68	40	89	20	28	161	235	137	191
means		(46)				(67)				(44)				(181)		

† – –, FF no formalin or formalin in 1976 and 1977; F–, –F formalin 1976, no formalin 1977 and *vice versa*.

https://doi.org/10.23637/ERADOC-1-135

in peaty loam at the Arthur Rickwood Experimental Husbandry Farm, Mepal, Cambs. (AREHF) and in silt loam at Walpole St. Andrew, Norfolk. Oxamyl was equally well distributed in the soil when the granules were blown into vertical bands 12·5 cm apart in the top 12–15 cm of the soil and then incorporated by 'Roterra' as when they were applied to the soil surface and incorporated by a rotavator with L-shaped tines. When the granules were blown into vertical bands 25 cm apart and incorporated by 'Roterra', rather more oxamyl was recovered from 10–15 cm than from 0–5 or 5–10 cm deep in the soil. In peaty loam on site 1 (on average 41 eggs g^{-1} soil) and on site 2 (on average 105 eggs g^{-1} soil), yields of Pentland Crown tubers were increased as much and *Globodera rostochiensis* (Woll.) was controlled as well by the 'Vertical Band-Roterra' technique as by rotavating oxamyl granules into the seedbed. On site 2, oxamyl sprayed into vertical bands 25 cm apart and incorporated by 'Roterra' was equally effective as when applied as granules in the 'Vertical Band-Roterra' technique (Table 2).

From these results and those obtained in 1977 we conclude that applying nematicide granules in vertical bands in the soil and incorporating them with a 'Roterra' mixes them as effectively with the soil as when they are spread on the soil surface and incorporated by rotavation. (Whitehead, Tite, Bromilow with Mr. L. Short, ADAS)

Effect of oxamyl as a foliar spray. Potato cyst-nematodes reproduce sexually. To mate with mature females the males must pass out of the roots and into the soil close to the roots. When oxamyl is applied to leaves, some of it is translocated to the roots and may be exuded from the roots into the soil. Applied in this way, oxamyl might therefore prevent mating and so prevent nematode increase. Oxamyl applied to leaves may also be washed off and into the soil by rain. On Butt Close, Woburn, in sandy loam lightly infested with *G. rostochiensis* Ro1 (on average 9 eggs g^{-1} soil) oxamyl at 1, 2 or 4 kg a.i. ha^{-1} sprayed on the leaves of susceptible Pentland Crown potatoes twice (June and July), four times (June, July, August) or six times (June, July, August, September) lessened nematode increase (Table 4). Following six sprays, each of 1 kg a.i. ha^{-1},

TABLE 4

Effect of oxamyl sprayed on potato haulms on yield of Pentland Crown tubers, oxamyl residues in tubers and numbers of eggs of G. rostochiensis Ro1 *left in the soil after harvest*

Oxamyl in each spray (kg a.i. ha^{-1})	Number of sprays	Tubers over 3·8 cm. diam. (t ha^{-1})	Oxamyl residues ($\mu g\ g^{-1}$)	Nematode eggs g^{-1} soil after harvest
0	0	22·0	—	171
1	2	16·5	—	53**
	4	21·8	—	65*
	6	25·0	0·03	80*
2	2	23·8	—	67*
	4	26·8	0·15	29***
	6	24·6	0·30	98
4	2	21·7	—	39***
	4	17·7	0·82	20***
	6	23·0	1·94	40***

*, **, *** Significantly less than untreated at $P < 0.05$, 0.01, 0.001, respectively.

nematode increase was halved and oxamyl residues in the tubers were acceptable. After more than 6 kg a.i. ha^{-1} had been applied to the potato foliage there were unacceptably large residues of oxamyl in the harvested tubers. In terms of nematode increase the results were variable and not as good as those obtained when oxamyl granules are incorporated in the seedbed. (Whitehead, Tite, Fraser and French)

https://doi.org/10.23637/ERADOC-1-135

Carrot cyst-nematode. At Methwold Hythe, Norfolk, in peaty loam infested with carrot cyst-nematode, *Heterodera carotae* Jones, the effect of 10% aldicarb or oxamyl granules rotavated into the seedbed on carrot yields and nematode increase was assessed. Oxamyl, 5 kg a.i. ha^{-1} was also applied to carrot foliage in three sprays, each of 2 kg a.i. ha^{-1} applied in June, July and 1 September, to plots in which 4 kg oxamyl or aldicarb ha^{-1} had been rotavated into the seedbed.

Although the soil was heavily infested with the nematode (on average 204 eggs g^{-1} soil within cysts) carrots grew and yielded well in untreated soil (Table 5). Yields were increased somewhat by aldicarb, less by oxamyl. Yields of carrots (t ha^{-1}) averaged over all treatments were 24·5 (25 July), 61·9 (31 August) and 74·1 (11 October.) Invasion and development of the nematode in carrot roots was studied by Mr. L. Coppock (ADAS, Cambridge). In untreated soil, increasing numbers of juveniles were found in the roots from 16 May and the first females were observed on the roots on 31 May. In soil treated with aldicarb or oxamyl invasion of the roots by juveniles was delayed. In plots treated with aldicarb or 8 or 16 kg oxamyl ha^{-1}, very few juveniles invaded roots until about 13 July. As a result, numerous females were not found on the roots until about 26 July (oxamyl) or 9 August (aldicarb). After the third and final harvest there were fewer nematode eggs in the cysts than before carrots were sown. We conclude that in this experiment carrot cyst-nematode had little effect on yield and that neither aldicarb nor oxamyl had any lasting effect on nematode numbers. (Whitehead and Tite, with Mr. L. Coppock, ADAS, Cambridge)

TABLE 5

Effect of aldicarb and oxamyl on mean yields of carrots (var. Chantenay stump rooted) and on carrot cyst-nematode, Heterodera carotae

Treatment	kg a.i. ha^{-1}	Carrots (t ha^{-1})†	Nematode increase, times
Untreated	0	48·0	0·6
Aldicarb	4	56·2**	0·6
	8	55·1	0·7
	16	55·6**	0·9**
Oxamyl	4	51·1	0·8*
	8	52·7	0·6
	16	55·1*	0·8*
Aldicarb + Oxamyl (sprays)	4 + 6	53·0	0·7
Oxamyl + Oxamyl (sprays)	4 + 6	54·7*	0·7
LSD (5%)		5·4	0·2
(1%)		7·4	0·3
(0·1%)		9·9	0·4

† Averages of three harvests on 25 July, 31 August and 11 October.
*, ** Significantly different from untreated at $P < 0.05$, 0.01, respectively.

Spiral nematode. In field trials with the spiral nematode *Helicotylenchus vulgaris* Yuen the suitability of winter wheat and sugar beet as hosts was assessed. The two sites used had different soil types and nematode populations and were at Swaffham Prior, Cambridgeshire (c. 6000 $litre^{-1}$) and South Milford, Yorkshire (750 $litre^{-1}$). At both in 1977, damage to sugar-beet roots had been associated with the nematode. Aldicarb was applied at 11·2 kg a.i. ha^{-1} as a split-plot treatment, to determine whether there was any yield loss. The application significantly reduced numbers for only a few weeks at South Milford but gave a more persistent reduction at Swaffham Prior. Although some improvement in the growth of treated crops was visible, at harvest yields from treated

https://doi.org/10.23637/ERADOC-1-135

and untreated plots of both crops were similar. Numbers decreased at both sites this year, indicating the importance of seasonal conditions.

In pot experiments with populations of 0, 30, 300, 3000 and 6000 nematodes litre^{-1} sugar beet grew best at 30 nematodes litre^{-1} during the first weeks after germination. Later, growth decreased as the numbers of nematodes added increased. Similar stimulatory effects of small nematode densities are well substantiated in pot tests with other nematode-crop combinations (see also p. 185). A light nematode attack may cause this effect by stimulating root elongation or proliferation. (Spaull)

Yield variation in cereals. All arable land in Britain is infested with *Pratylenchus* spp. (root-lesion nematodes) and *Tylenchorhynchus* spp. (stunt nematodes, see also p. 185). Their role as plant pathogens in cereals is not well understood and trials were started in 1978 to assess the effect of applying nematicides to infested soils on yields of spring-sown barley.

At Cavenham, W. Suffolk, in sandy loam infested with 1400 *Pratylenchus* litre^{-1} soil and 2700 *Tylenchorhynchus* litre^{-1} soil, barley (var. Jupiter) grew and yielded well and neither 'Telone' injected in the soil in December, 1977, nor aldicarb or oxamyl applied in the seed furrows during sowing in spring, 1978, significantly increased grain yields (Table 6). At Elveden, W. Suffolk, in loamy sand (Lodge Heath) or sand (Landing Ground), yields of barley grain were increased by aldicarb or oxamyl applied in the seed furrows or by 192 kg 'Telone II' (1,3-dichloropropene) ha^{-1}.

At Cavenham and Elveden, the soils were infested with *Pratylenchus crenatus* Loof and

TABLE 6

Effect of 'Telone', aldicarb and oxamyl on yields of spring barley in three sandy soils

		Barley grain at 85% DM (t ha^{-1})		
		Cavenham	Elveden	
Treatment	Target kg a.i. ha^{-1} Variety:	Jupiter	Lodge Heath Tern	Landing Ground Tern
Untreated	0	6·4	2·7	1·0
'Telone II'	47·5	6·6	3·2	1·1
	96	6·2	3·3	1·0
	192	6·2	3·2	1·8***
Aldicarb (NR)†	0·6	6·4	3·2	0·9
	0·9	—	3·4	—
	1·2	6·6	3·5*	1·2
	1·8	—	3·0	—
	2·4	6·3	3·7*	1·4*
	3·6	—	3·8**	—
Oxamyl (NR)	0·6	5·9	2·8	0·9
	0·9	—	2·5	—
	1·2	5·7	3·3	1·2
	1·8	—	3·6*	—
	2·4	6·6	3·7*	1·4*
	3·6	—	4·2***	—
Aldicarb (WR)‡	0·6	6·3	—	1·2
	1·2	6·1	—	1·2
	2·4	6·5	—	1·2
Oxamyl (WR)	0·6	6·8	—	1·2
	1·2	6·5	—	1·4*
	2·4	6·7	—	1·1

† (NR) applied in the seed furrow in a band about 2·5 cm wide.
‡ (WR) applied in the seed furrow in a band about 6 cm wide.
*, **, *** Significantly greater than untreated at $P < 0.05$, 0.01, 0.001, respectively.

https://doi.org/10.23637/ERADOC-1-135

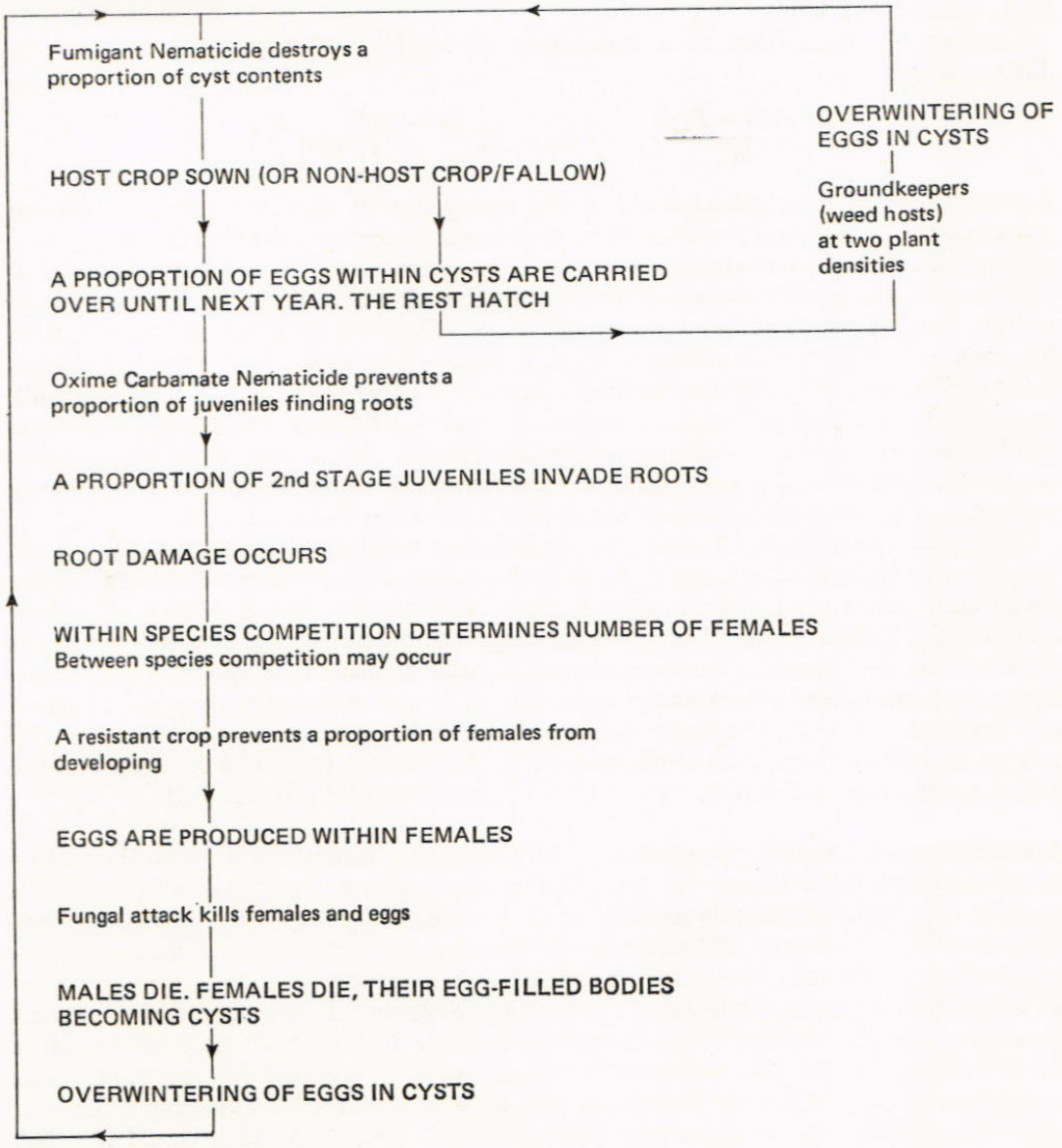
P. neglectus Rensch, *Tylenchorhynchus dubius* (Bütschli) and *Merlinius microdorus* Geraert. Also at Elveden, particularly on Lodge Heath, the soil was infested with *Telotylenchus ventralis*. All these nematodes appeared to feed on or in barley roots. Few *Trichodorus*, *Longidorus*, *Hemicycliophora*, *Heterodera* or *Criconemoides* were recovered from these soils. (Whitehead, Tite, Fraser, French and Nichols)

Population dynamics

Modelling of cyst-nematodes. Work on the modelling of cyst-nematode populations (*Rothamsted Report for 1976*, Part 1, 207–209) has continued and it is now possible to

TABLE 7

Events in the life-cycle of cyst-nematodes included in the model. Those in lower case are optional. For the model simulating fungal attack see p. 177



include the items in Table 7. The standard formulation of the basic model which relates the population density P_i, before planting a susceptible crop to that after harvest, P_f, is

$$P_f = \frac{a(1 - C_p)P_i}{1 + \frac{(a-1)P_i}{c(E/c)^{P_i/E}}}$$

where a is the observed maximum increase rate, C_p the fraction of eggs that do not hatch, E the equilibrium population density and c a constant related to the tendency for the host root system to compensate for damage done by nematode attack. Population densities are expressed in terms of the logistic equilibrium density E_l, i.e. that of an undamaged root system. This equation which is a modified version of the logistic law, was derived from the life cycle of the nematode and relates to the competition between females for feeding sites in host root systems and applies especially to species with one main generation a year.

The expected behaviour of a population at equilibrium may be investigated by differentiating

$$\Delta = \left[\frac{d(P_f - P_i)}{dP_i}\right]_{Pi=E} = (1 - C_p)\left(\frac{a-1}{a}\right)\left[\log_e\left(\frac{E}{c}\right) - 1\right]$$

The first term on the right-hand side is the proportion of eggs that hatch, the second relates to the increase rate and the third to damage to the root system. For values of a greater than 20, $(a - 1)/a$ approaches 1, i.e. large increase rates have no effect and oscillations about the equilibrium are determined by the other two. When there is no damage to the root system and no compensation $\log_e(E/c) = 0$ and the right-hand term becomes -1. Whatever the value of C_p Δ is then -1 or more. May (*American Naturalist* (1973), **107**, 621–650) showed that values of Δ between 0 and -1 imply a steady approach to equilibrium, values between -1 and -2 damped oscillations about the equilibrium and values < -2 an unstable equilibrium. When susceptible potato crops are grown continuously in small plots, the numbers of *G. rostochiensis* oscillate narrowly and seem to be damped indicating values of Δ between -1 and -2.

The models used (Table 7) at present are based on small plots. To be applied to fields they need to be made stochastic to allow for variation in parameter values and for the variation in initial densities from place to place. Applying the models to fields with long-established infestations would be relatively easy. The greatest difficulty arises for newly infested ones as no current model exists to simulate cyst-nematode spread within fields. The model also needs to be extended and explored for cyst-nematodes passing more than one generation a year. For these species suitable field data are scarce. More work is needed to determine the value of parameter a in the equation for the basic model and the relationship between E and E_l. (Jones, with Perry, Statistics Department)

Epidemiology of nematode populations. Fully migratory nematodes disperse themselves in all stages except those in the egg. At the other extreme are types with sedentary females (e.g. root-knot and cyst-nematodes) when the only migratory form is the 2nd stage juvenile. The burrowing nematode, *Radopholus similis* (Cobb), that causes 'spreading decline' of citrus in Florida is largely self-dispersed, being scarce in the top 15 cm of soil in groves that are cultivated little after establishment. Figures quoted by Suit and DuCharme (1957) (*Bulletin State Plant Board Florida* **2**, No. 11, 24 pp.) are a near fit to self-dispersal at the rate of one tree space per year. In contrast cyst-nematodes with one generation a year disperse themselves by a distance of about 0·1 m creating a 'domain' with a superficial area no more than 0·03 m². At this rate of spread it would take 565

https://doi.org/10.23637/ERADOC-1-135

years to colonise a circular area of 1 ha and more than 700 to colonise a square field of the same area, longer if the field were oblong and the initial cyst were not centrally placed. In practice, colonisation of fields is far more rapid when the host crop is grown continuously; obvious infested patches appear within 5–15 years but it is never clear when the infestation was first established. What the 2nd stage juvenile lacks in mobility is compensated for by the ability of cysts to be transported by agricultural operations. Cysts resemble the resting spores of fungi but, whereas these are numerous and expendable, cysts are produced less profligately and are highly adapted to ensure the survival of the population of eggs they contain.

Assuming that increase cyst to cyst is 30-fold, infestation started by a single cyst in clean soil requires two or three generations to occupy the domain around it so that every 1 ml of soil contained one cyst. In effect, from single cyst infestations, there is a 'latent' period of about 2 years before assisted spread commences. Then, it is composed of contiguous spread due to the displacement of soil by implements and a random element which carries soil more distantly. Combining these with self-dispersal into a model has proved difficult. An empirical approach based on rates actually observed in the field is possible but field data are lacking.

Data for the spread of beet and potato cyst-nematodes into uninfested territory indicate that the area of fields detectably infested increases exponentially in the early stages. The rate, however, is far slower than that of airborne fungal leaf pathogens and more akin to that of other soil-borne pathogens. Spread within soil is similar to that of leaf pathogens within a crop and spread above the soil akin to that above a crop.

Competition between species of potato cyst-nematode. Potatoes were grown for 7 years in small field plots originally infested only with *G. rostochiensis* Ro1. *G. pallida* (Stone) Pa3 was introduced into some plots and established by growing the potato cv. Maris Piper which is susceptible to it but resistant to *G. rostochiensis* Ro1. After 6 years the greatest numbers of nematode eggs (mainly *G. rostochiensis*) were in plots not inoculated with *G. pallida* that had grown only the potato cv. Pentland Crown which is susceptible to both species. In plots that grew Maris Piper every year there were few nematode eggs (mainly *G. pallida* plus a few residual *G. rostochiensis*). Numbers were intermediate and of mixed species in plots inoculated with *G. pallida* that grew Pentland Crown every year or alternately with Maris Piper. After the 7th year, 1976, numbers decreased on all plots presumably because of the exceptionally dry summer.

That year *G. rostochiensis* appears to have been favoured, as the percentage of *G. pallida* in inoculated plots growing Pentland Crown decreased and stayed small in 1977. However, in the plots planted alternately with Pentland Crown and Maris Piper, the percentage of *G. pallida* remained at about 70% because Maris Piper was grown in 1976 and therefore *G. rostochiensis* could not develop beyond the early stages, leaving a predominance of *G. pallida* with a small carryover population of *G. rostochiensis*.

Plots which were planted with the cv. Arran Pilot always had fewest nematodes of which only a small percentage were *G. pallida*. This suggests that in this second early variety the life-cycle, and especially that of *G. pallida*, was curtailed by early harvesting of tubers.

In an earlier pot experiment *G. pallida* out-competed *G. rostochiensis* (*Rothamsted Report for 1975*, Part 1, 197) but in a second pot test with greater nematode densities and different ratios of the species, proportionally more *G. rostochiensis* than *G. pallida* females were produced even when the initial combinations of species were similar to those of the 1975 test. This may have resulted from warmer conditions during the second test, as the optimum temperature for *G. rostochiensis* is higher than that for *G. pallida*

https://doi.org/10.23637/ERADOC-1-135

(*Rothamsted Report for 1976*, Part 1, 203). Changing the ratio of *G. rostochiensis* to *G. pallida* did not appreciably alter the total number of new cysts produced. The maximum about 3000 per pot, was obtained when 200 or more cysts of *G. pallida* alone or equal numbers of *G. pallida* and *G. rostochiensis* were added initially. To achieve the maximum, 600 cysts of *G. rostochiensis* alone or other mixtures of both species had to have been added initially. When more than 800 cysts were added the number of new cysts recovered was fewer than the maximum. The mean number of eggs per new cyst was much the same regardless of the numbers added or of the species ratios.

In pots with *G. rostochiensis* only, females took longer to turn yellow the larger the number of cysts added initially. This may be because they were deprived of food or because they were slower in finding feeding sites in the smaller and more slowly extending root system. (Parrott and Berry)

Enemies of cyst-nematodes

Rickettsial parasites. Crosses between the Bolivian population of *G. rostochiensis* infected with intracellular micro-organisms and an uninfected population suggested that the micro-organisms were passed to offspring transovarially and not via the sperm, despite their presence in sperm cells. Since then progeny from uninfected females mated with infected males have been taken to the next generation; no micro-organisms were found in the resulting juveniles. Observations of ultrathin sections of the reproductive tract of infected females have shown that the germinal and growth zones of the ovaries, the oviducts, seminal receptacles (spermathecae) and uteri are all infected. The micro-organisms were also present in developing oocytes within the ovary, mature oocytes in the oviduct and unembryonated eggs. As all the developmental stages of the egg and newly hatched, unfed second-stage juveniles are infected, the rickettsiae must be passed transovarially from generation to generation.

To assess the effect of the micro-organisms on the development and fecundity of *G. rostochiensis*, infected and uninfected populations were treated with penicillin solution (0·02%) or tap water in pots planted with potatoes and kept at 17°C. There were no differences in the number of new cysts produced by the uninfected population in pots receiving penicillin and those receiving water, but the infected population produced ten times as many cysts when treated with penicillin ($P < 0{\cdot}0001$). The antibiotic did not change the egg production of the uninfected females but increased that of the infected ones slightly. Ultra-thin sections of infected juveniles treated with penicillin revealed micro-organisms breaking down and dying. This evidence suggests that the rickettsiae are harmful to their nematode hosts but at what stage was uncertain. Females and eggs seem little affected as untreated females produced almost as many eggs per cyst as treated and mating seems also to be unaffected. Tests on second-stage juveniles showed that infected ones survived less well. As they do not feed from the time they hatch until after they have found and invaded host roots, their lipid food reserves are essential. Both infected and uninfected contained the same total amounts but after 1 week (at 17 and 20°C) the infected population contained significantly less ($P = <0{\cdot}05$) and this difference persisted. Evidently this stage is adversely affected. (Walsh)

Fungi parasitising females

Life-cycles. Two fungi parasitise females of the cereal cyst-nematode, *H. avenae*, Woll. That previously described as *Entomophthora*-like (Crump & Kerry, *Nematologica* (1977), **23**, 398–402) and known to be widespread in cereal fields, produces laterally biflagellate zoospores and is a new species of Oomycete which is being described. Another somewhat similar fungus that parasitises females and eggs of *H. avenae* and *H. schachtii*

https://doi.org/10.23637/ERADOC-1-135

Schm. has been found in two widely separated localities and may be more widespread than this suggests. Like the previous fungus, it disrupts the female cuticle and prevents cyst formation. It also produces biflagellate zoospores but from a vesicle at the tip of discharge tubes and not from the tubes themselves. This fungus, also an Oomycete, belongs to the Lagenidiales but to which genus cannot be determined until sexual structures leading to oospore production have been observed.

The release of zoospores by both fungi was observed and filmed. The production of those of the first fungus takes 2 h at room temperature. Before release the tip of the discharge tube swells and then ruptures. The zoospores swim away immediately, some remaining motile for as long as an hour. Others encyst within a few minutes, lose their flagella and bean-like shape and become spherical. From each nematode female 50 ± 14 sporangia arise each producing 20 to 120 zoospores. The encysted zoospores may give rise to another generation of zoospores (i.e. the fungus is diplanetic) but under the conditions in the laboratory few did so.

During the production of zoospores by the second fungus, cytoplasm is rapidly released (<1 min) into a vesicle formed at the tip of the discharge tube and divides about 5 min later into 20 separate spores which, within a further 4 min, begin to move independently. After about 15 min the spores are released and swim actively for up to an hour before encysting. Germ tubes are produced with no evidence of a second generation of zoospores being formed. (Kerry, Crump and Doncaster)

Modelling fungal attacks. A model was made of attacks by the Oomycetous fungus on females of *H. avenae* based on the following assumptions: (a) the two stages of infection, by resting and infective spores, do not overlap in time, (b) spores are randomly distributed in soil, (c) distances between females are large compared with the distances over which spores can infect, (d) ability of resting spores to infect is independent of that of infective spores, (e) the number of resting spores produced per female is the same whether infection was by resting spores or infective spores and (f) all infected females and their eggs are killed. The number of parameters in the full model was large but they were reduced to six. Then the model produced a good fit to the data of Gair, Mathias and Harvey (*Annals of Applied Biology* (1966), **63**, 503–512). (Kerry, with Perry, Statistics Department)

Soil moisture and the infective process. Juveniles of *H. avenae* were added to pots of soil containing the first of the Oomycetous fungi mentioned above, half of which had previously been drenched with formalin, a chemical strongly fungicidal but only weakly nematicidal. The formalin treatment did not decrease the rate of invasion of the roots of barley seedlings growing in the pots or that of the development of female nematodes. At the stage when females were enlarging and rupturing the root cortex, i.e. were becoming exposed to attack by the fungus, half the pots were watered to field capacity and the other half were kept much drier. Numbers of females were similar at the beginning of this treatment but they decreased in the pots of undrenched soil that were kept at field capacity and continued to increase in all the others. The decrease was associated with increased rates of fungal parasitism. Parasitism was more or less eliminated in soils drenched with formalin whether these were kept wet or dry and was suppressed in undrenched soils kept dry. Presumably, like nematodes, the motile zoospores require soil moisture at small suctions (i.e. matric potentials of no more than about 200–300 cm water suction or 0·2–0·3 bar) before they can move freely and infect females. (Kerry, Crump and Mullen)

Residual effects of cultivars, formalin and nematicides. In 1978 a uniform crop of Manod

https://doi.org/10.23637/ERADOC-1-135

oats, susceptible to *H. avenae* but resistant to *Ditylenchus dipsaci* (Kuhn), was sown in the final year of an experiment in Butt Close, Woburn on the residual effects of formalin sequences, resistant and susceptible varieties and aldicarb.

Formalin applied in 1976 or in 1977 had no significant effect on yields in 1978. Aldicarb applied in 1977 and the variety grown in 1977 both had significant residual effects and there was a highly significant interaction between them. After the resistant variety Nelson in 1977, aldicarb did not further increase yield but after the susceptible variety Maris Tabard it more than doubled yield.

Post-crop *H. avenae* egg numbers (Table 3 page 169) were significantly affected by 1977 varieties and aldicarb 1977. Formalin 1977 was still associated with significantly increased egg numbers, most obviously in the plots following the susceptible variety that did not receive aldicarb.

Numbers of juveniles g^{-1} root were estimated in the ex Maris Tabard plots only. The effects of aldicarb applied in 1977 were still highly significant; 278 g^{-1} in untreated against only 47 g^{-1} in treated. The numbers of females and juveniles g^{-1} root in 1978 were not affected by formalin applied in 1977. The apparent increase in post-crop egg numbers after formalin in 1977 resulted from unhatched eggs that persisted until the next year. The proportion of females attached by parasitic fungi in mid-June 1978 was unaffected by previous formalin treatments. Aldicarb had no discernible effects on the fungus. (Williams and Beane)

In the rotation-fumigation experiment which ran for 9 years at Woburn *H. avenae* had virtually disappeared from the plots and then the experiment ended. Evidently control by the parasitic fungus had not been impeded by the nematicides applied ('D-D', dazomet, aldicarb) or spacing the barley host crop between two others (potatoes and sugar beet) that were not hosts of *H. avenae*. (Williams, Beane, Berry and Webb)

Pathotypes and species of round-cyst nematodes. Pathotypes are physiological races distinguished by the ability or inability to multiply (i.e. to produce females with eggs) in the roots of cultivars with major genes for resistance. They are especially important for plant breeders who need to know whether pathotypes able to multiply on their selections exist in the areas where they are likely to be planted, or are likely to arise by mutation or ingress from other localities at home or abroad. Usually pathotypes within species interbreed freely. In cyst-nematodes, the proportion of the population that does not hatch and is carried over to subsequent years acts as a brake on selection. No such impediment limits the rapid colonisation of a sibling species which does not interbreed freely with its sibs. *G. rostochiensis* and *G. pallida* are a pair of such species and both include within them a number of pathotypes the number of which we can recognise has increased and seems likely to increase further as more major genes for resistance are discovered and exploited.

Pathotypes of *G. pallida* at home and abroad. The presence of Pa2 in England was reported last year (*Rothamsted Report for 1977*, Part 1, 175). It now seems likely that Pa2 is common among populations designated E in the old UK scheme. Of seven E populations used in screening by the Plant Breeding Institute only one, from Mablethorpe, is a mixture of Pa2 and Pa3, the remainder, two from Crowle, Lincs., and one each from Pittingdon, Co. Durham, Little Ouse, Norfolk, Bickerstaff, Lancs., Wainfleet, and Lincs., are Pa2. None reproduced well on potato clone D47/11 and they are thus not the new pathotype reported last year which is differentiated from Pa2 by this clone, although Pittingdon may contain some of the new pathotype. Two of the populations, Bickerstaff and Wainfleet, failed to reproduce well on P55/7 but did so on K6/34, another clone with gene H_2. P55/7 may contain a gene which differentiates between Pa2 populations in yet

https://doi.org/10.23637/ERADOC-1-135

another way. If so the potential number of pathotypes of *G. pallida* would be increased yet again. (Stone, Rowe, Farr and Eyre, with Dr. J. M. Fuller, Plant Breeding Institute)

A population from Newfoundland previously identified as *G. pallida* (*Rothamsted Report for 1976*, Part 1, 202) and thought to be pathotype Pa3 (Stone, Thompson & Hopper, *Plant Disease Reporter* (1977), **61**, 590–591), is now known to be Pa2. (Stone, Rowe, Farr and Eyre)

Five populations from the Nilgiri Hills, India, were tested on all differential potato clones except KTT 60.21.19. One from Mynalai was a mixture of *G. pallida* and *G. rostochiensis*, one from Kathadi Mattam was *G. rostochiensis* Ro1 and others from Thumanatti, Adasholai and Palada were *G. pallida* Pa2. When tested on Plant Breeding Institute clones D47/11 and D42/9, which differentiate *G. pallida* populations of the New Leake type, only Thumanatti produced more females on D47/11 than D42/9. These were few (8% of those on Pentland Crown), perhaps indicating admixture with a small proportion of the unnumbered pathotype. (Krishnananda, Stone and Rowe)

Canto and de Scurrah (*Nematologica* (1977), **23**, 340–349), using European differential potato clones (*Rothamsted Report for 1975*, Part 1, 195) except the ex *vernei* hybrid 65.346/19, reported three pathotypes which were different from any known in Europe (P_1B, P_2A and P_3A in their nomenclature). We tested one population of each of these pathotypes on the full set of differentials except KTT 60.21.19. P_1B, distinguished from Pa3 by Canto and de Scurrah because it reproduced poorly on P55/7, produced large numbers of cysts on this clone in our tests and we regard it as Pa3. We agree that P_3A is a pathotype not detected in Europe as probably is P_2A, although this requires confirmation of Canto and de Scurrah's finding that P_2A is unable to reproduce on KTT 60.21.19. In our tests P_1B produced more cysts on some clones than European populations usually do and P_2A produced very many on P55/7. (Stone, Rowe, Farr and Eyre)

***Globodera* sp. on cultivated tuberous oxalis in Peru.** A species of *Globodera* with white females was found on *Oxalis tuberosa* L. in several localities in the mountains of Southern Peru. The second stage juveniles have short stylets (about 20 μm) with massive hooked knobs. Females have a large Granek's ratio ($3{\cdot}2 \pm 1{\cdot}3$, $n = 20$) and few ridges on the anus-vulva axis ($14{\cdot}5 \pm 4{\cdot}0$, $n = 20$). This combination of characters distinguishes the nematode from *G. rostochiensis* and *G. pallida*, which occur in potato fields in the same area, and also from other described species of *Globodera*; the nematode is evidently a new species. (Stone and Evans, with Dr. P. Jatala and Dr. J. Franco, International Potato Centre, Lima, Peru)

Resistance to potato cyst-nematodes in some ex *vernei* potato hybrid pathotypes. Five hybrid potato clones produced by the Scottish Plant Breeding Station with cyst-nematode resistance derived from *Solanum vernei* Bitt. & Vittm. CPC 2487 and/or CPC 2488 were tested against eight pathotypes of potato cyst-nematodes. On four of the clones there were significant differences ($P \leq 0{\cdot}05$) between numbers of cysts produced. These were greatest among pathotypes of *G. rostochiensis* and two clones were susceptible to Ro5. Differences in susceptibility to *G. pallida* pathotypes also occurred. Two clones were significantly more resistant to Pa1 than to Pa2 and Pa3. These results demonstrate that resistance derived from *S. vernei* is not uniformly effective or entirely race non-specific, a result also found in work on ex *vernei* clones of continental origin (*Rothamsted Report for 1975*, Part 1, 195–196). Only four of the eight pathotypes (*G. rostochiensis* Ro1 and *G. pallida* Pa1, Pa2 and Pa3) are known to occur commonly in the United Kingdom. A fifth, unnamed and scarce (*Rothamsted Report for 1977*, Part 2, 174–175), was not included. It must be presumed that other pathotypes of *G. rostochiensis* (Ro2 to 5) and

https://doi.org/10.23637/ERADOC-1-135

possibly other unknown ones of both species also occur but infrequently. (Turner and Stone)

Host ranges of round-cyst nematodes and their pathotypes. Host range tests of round-cyst nematodes (*Globodera* spp.) on a selection of *Solanum* (subgenus *Leptostemonum*) spp. were continued to see whether some light could be thrown on their coevolution in Latin America. One species *S. prinophyllum* Dun., Australia, was susceptible to all populations of round-cyst nematodes against which it was tried. Two others, *S. torvum* Swartz and *S. viarum* Dun., were resistant to all. Other species had a range of susceptibilities. One interesting contrast was the resistance of spiny solanums to six of the eight European pathotypes of *G. rostochiensis* and *G. pallida* and susceptibility to a *G. rostochiensis* population from Bolivia, to pathotypes Pa1 and Pa3 of *G. pallida* and to *Globodera* species from N. America. Although this might indicate adaptation of European populations to the narrow genetic range of European potato cultivars, populations introduced into Europe may have been drawn from different parts of the S. American cyst-nematode gene pool. The wider host range of the Bolivian population of *G. rostochiensis* may have resulted from long experience of a range of genes for resistance. Conversely the total susceptibility of *S. prinophyllum* suggests that this species has not recently experienced parasitism by round-cyst nematodes (these are not known to occur in Australia). It may never have had genes for resistance or may have lost them as they were linked with a measure of unfitness to other environmental pressures. *S. dulcamara* L., a native European hedgerow plant is likewise generally susceptible and may have evolved latterly in an environment devoid of round-cyst nematodes. (Roberts and Stone)

Invasion and development of species and pathotypes. The extent to which different species and races of round-cyst nematodes (*G. rostochiensis* Ro1 and the Bolivian population, *G. pallida* Pa2 and *G. solanacearum* Miller & Gray, *G. tabacum* Lownsbery & Lownsbery and *G. virginiae* Miller & Gray) invaded and developed on susceptible *S. prinophyllum* and a range of resistant *Solanum* species was studied. All resistant plants were invaded by second stage juveniles. *G. tabacum*, *G. rostochiensis* Bolivia followed by *G. virginiae* and *G. solanacearum* in that order had the greatest invasion rates and developed further into the third or fourth stage. *G. rostochiensis* Ro1 and *G. pallida* Pa2 invaded less numerously and few developed to the third stage. In all combinations of parasite population and host, fourth stage juveniles were mostly males. Only in *G. rostochiensis* Ro1 and *G. pallida* Pa2 did males fail to reach adulthood although these produce abundant males on hybrids with resistance gene H_1 derived from *S. tuberosum* ssp. *andigena* Juz. & Buk. *S. quitoense* Lam. and *S. sisymbriifolium* Lam. were most heavily invaded, allowed most individuals to reach stages three or four and produced most adult males. In highly resistant *S. hirtum* Vahl., *S. torvum* and *S. viarum* development of males and females rarely got beyond the early part of the third juvenile stage. These species appear to possess race non-specific resistance derived from polygenes which operate on processes from invasion onwards. Other less resistant species seem to lack the full range of polygenes and these may include some major genes which confer race-specific resistance. Whether polygenic (horizontal) resistance indicates a longer association of host and parasite than major gene (vertical) resistance is debatable. If the genes blocking development, especially that of the female which remains feeding on one site for a long period, were too numerous the host might remain resistant. If these genes were less numerous, the parasite might adapt and circumvent them. Then long association would lead to susceptibility.

Susceptibility was found in accessions from the Mediterranean, Australia, Africa and Madagascar, where *Globodera* spp. are unknown. Presumably these accessions had never

https://doi.org/10.23637/ERADOC-1-135

been exposed to parasitism. This suggests that susceptibility is the basic condition. In South America, where *Globodera* occurs naturally, resistance is irregularly distributed within species groupings (e.g. sections Acanthophora and Lasiocarpa) and is often effective against only a portion of species and populations, suggesting an association long enough to enable the evolution of resistance genes in the hosts and ability to circumvent them in the parasites. A group of solanums (section Androceras) distributed in Central and North America is uniformly susceptible, suggesting *Globodera* spp. are relatively recent introductions to these areas from S. America. The species of *Globodera* occurring in Central and North America are morphologically similar and can be made to hybridise successfully which also points to a recent origin.

In the range of hosts and round-cyst nematode species studied there was no meaningful correspondence between host status and phylogenetic relationships of the solanums. (Roberts and Stone)

Co-evolution and phylogeny of cyst-nematodes. Cyst-nematodes (*Globodera*, *Punctodera* and *Heterodera*) can be divided into 11 groups on juvenile and adult character combinations. Usually each group has a host-range limited to one botanical order or to closely related orders. By considering the phylogenetic position of the host orders and the distribution of supposedly primitive and advanced characters in the nematode groups, a phylogeny based on the co-evolution of hosts and parasites can be produced.

Cyst-nematode hosts occur in all subclasses of dicotyledons in Cronquist's system except the Magnolidae, regarded as ancestral to the others. Modern Hamamelidae include few hosts and may be the remnants of an early group which proliferated outside the tropics and then declined as other angiosperms adapted to those habitats. The scarce cyst-nematode fauna on Hamamelidae may be due to our ignorance or because their greatest radiation occurred before that of cyst-nematodes. *Heterodera* species parasitising this group, which may be relicts of an early cyst-nematode fauna, are not uniform for each is morphologically close to species parasitising hosts in other subclasses. The *Heterodera* groups (*schachtii* and *cacti*) with the widest host ranges among dicotyledons are centred on the Caryophyllales and to a lesser extent the Rosales, and both are thought to be the basal orders of their subclasses, Caryophyllidae and Rosidae. Because of its vulval structure and the large number of eggs laid outside the female (i.e. not retained within the cyst) *H. cruciferae* Franklin may represent a group of primitive Heteroderas and this is supported by inclusion of the Capparales in its host-range. Although a climax in the evolution of herbs, crucifers are placed in a relatively low phylogenetic position, other remaining *cruciferae*-like forms may have acquired secondary hosts as the other proposedly ancient group, *Globodera*, appears to have done. The *schachtii* and *cacti* groups may be derived from a *H. cruciferae*-like form which they resemble in the morphology of the juvenile lip and that of the female vulva. It is suggested that the main development of *Heterodera* on dicotyledons was from an *H. cruciferae*-like form (but not necessarily on a cruciferous host) and that radiation occurred early in the evolution of the Caryophyllidae, Dilleniidae and Rosidae so producing a predominance of hosts in the basal orders of these subclasses.

The remaining *Heterodera* groups have narrower host-ranges and usually fewer species: they may have evolved more recently. Because *Globodera* spp. retain the primitive hexaradiate lip condition in the juvenile and differ markedly from the others in cyst morphology, they may have evolved independently from the primitive heteroderid stock, on Solanaceae and Compositae in the subclass Asteridae (*Oxalis* may be an acquired host). It is suggested that groups of cyst nematodes on Cyperales have separated from the other forms and radiated independently on grasses, perhaps in the Miocene during the rapid radiation of their hosts. *Punctodera* may have evolved independently on grasses.

https://doi.org/10.23637/ERADOC-1-135

Because there are no fossil records of intermediate groups, phylogeny can only be inferred from the interrelationships between groups extant to-day. Consideration of host interrelationships is helpful but botanical phylogenies are also derived mainly from comparisons of extant forms. (Stone)

The gene-for-gene relationship. In 1974 (*Rothamsted Report for 1973*, Part 1, 152–153) we reported evidence for a gene-for-gene relationship in *G. rostochiensis* based on the behaviour of two populations, one unable and the other able to develop on the roots of plants with major resistance gene H_1 derived from *S. tuberosum* ssp. *andigena*. Further crosses have been made including some between populations of *G. pallida* which have a similar relationship with gene H_2 derived from *S. multidissectum* Hawkes. Here too the gene-for-gene relationship seems to exist and again females able to grow and reproduce on resistant roots appear to be double recessives (nn); males are normal and can have any constitution (NN, Nn or nn). The basis of the relationship is illustrated in Table 8. Incidentally, it appears that white colour in the females of *G. pallida* is a dominant trait.

TABLE 8

The presumed basis of the gene-for-gene relationship in potato cyst-nematodes

Constitution of host		Gene products in transfer cell (feeding site)			Constitution of female† parasite	Effect
††h	⟶	nil	N factors	⟵	NN or Nn	Female reproduces
H	⟶	H factors ****	N factors	⟵	NN or Nn	Female dies
H	⟶	H factors	nil	⟵	nn	Female reproduces

† Males feed little and can have the constitution NN, Nn or nn (Howard *in litt.*).
†† H, h host genes for resistance; N, n matching genes in nematode.
**** gene products incompatible, feeding site spoiled.

Pooling the matings of both species, 26 of 36 observed results were not significantly different from values calculated assuming that virulent phenotypes were homozygous for a single recessive gene, the genotypes were in Hardy-Weinberg equilibrium, males were normal and the inheritance Mendelian. This was a better fit than that obtained in tests on inbred lines of the nematode populations and supports the hypothesis that virulence genes in the nematode are recessive.

The gene-for-gene relationship seems to be confirmed for nematodes and this lends support to the view that it is general in parasitism throughout the plant and animal kingdoms. (Parrott)

Morphology and function

Scanning electron microscope studies. In *Aphelenchoides*, *Aphelenchus*, *Cryptaphelenchoides*, *Huntaphelenchoides*, *Laimaphelenchus*, *Paraphelenchus* and *Seinura* the lip region has the same basic hexaradiate pattern consisting of a cephalic plate with two lateral, two subdorsal and two subventral sectors. The amphid apertures are located on the dorsal side of the lateral lip sectors at the edge of the cephalic plate and there is a prominent cephalic papilla on the outer margins of each of the other four lip sectors. In many specimens there are six small depressions around and close to the oral aperture and these are probably the openings of the inner labial papillae. There is also a second ring of six raised areas which probably represent the lips (*sensu stricto*). All of the eight *Aphelenchoides* spp. examined except *A. ritzemabosi* (Schwartz) and *A. fragariae* (Ritzema Bos), have a lip region surrounded by a deep groove so that the lips are contained within a labial disc. The cephalic plate patterns of *Aphelenchus* and *Paraphelenchus* are very similar whereas that of *Aphelenchoides* is different but shows little variation within that genus.

https://doi.org/10.23637/ERADOC-1-135 **pp 17**

The oral aperture is round to oval except in *Seinura* and *Cryptaphelenchoides* which have a dorso-ventral slit; these also have the most prominent lips and lip sectors. The *Seinura* sp. also has lip 'flaps' between the oral aperture and the lateral lips. All species examined have fine transverse striations on the head region behind the cephalic plate. (Hooper and Clark)

Spermatogenesis and sperm structure. Studies by us and by others on the ultrastructure of nematode sperm indicate that differences or similarities in structure between and within nematode groups are great enough to indicate phylogenetic relationships.

Differences between sperm of the cyst-nematodes *Heterodera* and *Globodera* contributed to their separation as two distinct genera. The structure of sperm of *Aphelenchoides* (Aphelenchina) is so different from that of the cyst-nematodes that we need to know if the cyst-nematode sperm structure is typical of the Tylenchina, or even of the Heteroderoidea. We have started by comparing those of the closely related genus *Meloidogyne*.

The testis and vas deferens of adult male cyst-nematodes (*Heterodera* and *Globodera*) (*Rothamsted Report for 1972*, Part 1, 157 and *for 1974*, Part 1, 175) contain only spermatids and spermatozoa, cell division having ceased after the last moult. The testis of adult males of *Meloidogyne incognita* (Kofoid & White) contains all stages of sperm development. At its tip are many (about 300–400) spermatogonia. These, as in all observed nematode species, have an ovoid nucleus, complete with a nuclear membrane which after the meiotic division is not reconstituted. The closely packed spermatogonia contain mitochondria, free ribosomes and rough endoplasmic reticulum. The spermatocytes are few at any one time (about 50) and in them the nuclear material is dispersed as moderately electron-dense groups constituting chromosomes. Around these are some apparently degenerate mitochondria, many free ribosomes, a few Golgi bodies and numerous deposits of electron-dense fibrous material. (In cyst-nematodes fibrous bodies do not appear until the spermatid phase.) The spermatocytes have a complex outline with the first stages of pseudopodial and filopodial development already present. The spermatids also are strongly amoeboid and, as do other nematode sperm, they reject excess cytoplasm and ribosomes as a 'residual body' which is then absorbed by the cells of the testis wall. The spermatid nucleus is of condensed chromatin, has a divided outline, is surrounded by many fibrous bodies and by numerous mitochondria now restored to normal appearance. The disposal of the residual body marks the transition from spermatid to spermatozoon. In the newly-formed sperm the centrally positioned nucleus is again of much-condensed, homogeneous chromatin but now more compact in outline. Most of the cytoplasm is occupied by fibrous bodies and mitochondria, and there are very many filopodia over the whole surface. Further down the testis the more mature sperm show a demarcation into a somewhat amoeboid zone containing the nucleus surrounded by the other organelles and a very amoeboid zone of cytoplasm lacking organelles other than microtubules. As far as we can tell, the filopodia, which are very numerous, are not limited to either zone.

The outer membrane of the sperm is lined with microtubules but they seem less definitely attached to the plasma membrane than those of cyst-nematode sperms, and sometimes many are seen dispersed in the cytoplasm of both zones. There are no 'membrane specialisations' as in Rhabditida, Aphelenchoidinae and other groups.

There are some 300–500 sperm in the testis at any one time, which is fewer than the 2000–3000 in cyst-nematodes. However, in *M. incognita* males they can be replenished, which is surprising in an animal which does not feed. The vas deferens is 30–60 μm long, much shorter than in cyst-nematode males where it also acts as a seminal vesicle. In *M. incognita*, sperms pass through the vas deferens during sperm release: they are not stored in it. The wall of the vas deferens is glandular. (Shepherd and Clark)

https://doi.org/10.23637/ERADOC-1-135 *pp 18*

Function of the feeding pump in the stem nematode. Advanced cinemicrography made possible a detailed analysis of the function of the oesophageal pump of *D. dipsaci* (Kuehn) during feeding on bean-leaf epidermis. The lining of the pump consists of six plates joined flexibly to each other edge to edge. The pump does operate as was inferred: the radial muscles unfold the plates from their collapsed configuration, creating a brazil-nut-shaped cavity. In lateral view, equatorial and polar radii of the lining increase and decrease by 15% respectively. The radius at intermediate positions stays the same. A scale model showed similar changes (about 13%). As the radial muscles contract to open the pump lining, they thicken and jam together round the pump periphery like bricks lining a well; from this purchase their inner ends open the pump lining. The operation of the pump is more complex than the above outline suggests and control of the 'outlet valve', movement of gland secretions, and opening and closing the pump lining are all involved in it. Some groups of muscle fibres, though active, do not shorten but rather resist stretching forces exerted on them by nearby fibres. The outlet valve region of the posterior oesophagus closes when its lumen is occluded by surrounding, largely non-muscular, tissues displaced when neighbouring groups of muscle fibres shorten and thicken. Closing of the pump is essentially a return of all the strained elastic tissues, but especially the lining, to their 'preferred configuration'. (Seymour and Doncaster)

Techniques

Refined techniques are important in advancing research into feeding and other behaviour of nematode pests.

Film projection and analysis. It is often necessary to make enlarged copy prints from single frames of ciné film, both for analysis and for illustrations. For the latter a film-copying system using intermediate negatives has already been developed and described (*Rothamsted Report for 1973*, Part 1, 152) but for some analyses time can be saved by using the motion-analysis projector itself to make negative prints directly. An advantage is that the film can be viewed normally and the frame required selected easily and quickly. The new components of the copying system are a remotely-controlled shutter in front of the projector lens, a combined projection screen and holder for photographic paper, and a light-proof duct, over the projector lamphouse, to prevent stray light from reaching the sensitive paper without obstructing the flow of cooling air from the lamp. (Seymour, with Instrument Workshop staff)

Filming speeds. To determine accurately the temporal relationships in filmed behaviour, it is essential to know the original filming speed exactly. Using the remote, low-light recording system (*Rothamsted Report for 1976*, Part 1, 206–207) the marked settings in pictures per second have been checked for the ciné cameras in use. The light-sensitive probe was arranged so that the camera shutter interrupted the light falling upon it, and filming speeds were recorded on a chart. Divergence from nominal speed was sometimes surprisingly large. One camera took up to eight frames to reach a steady speed and about the same number of frames to stop after the camera was switched off. Other variations in speed were also detected. (Seymour)

Because the image from the motion analysis projector is effectively flicker-free, it is possible to record fluctuating behaviour, such as that of the feeding pump of nematodes, directly from the projected image, using the remote recording system previously described (see above), that uses a light-sensitive probe coupled to a pen recorder. Now we can record from many points of interest in a filmed sequence, and check previous recordings, by running the film as many times as necessary with the probe in a different position on the projected image each time. (Seymour)

https://doi.org/10.23637/ERADOC-1-135

In recording successive activities of different speeds it is often essential to be able to switch from one filming speed to a different one without losing continuity. An intervalometer and single-shot pulse gear were built so that time-lapse is now instantly interchangeable with normal-speed filming without affecting exposure. Intervals can also be selected immediately and give from three pictures per second to one every 30 min. (Doncaster, with Forder and Faulkner, Electronics and Instrument Workshops)

Losses of nematodes added to pots. Pot experiments indicated that most of *Pratylenchus* spp. added to pots were washed through the soil and lost, even when watering was carefully controlled. In experiments when varying numbers of nematodes are added to pots it is desirable to prevent losses without impeding drainage. Of several methods tried, sintered glass funnels with a pore size of 5–15 μm (grade 4) retained inoculated nematodes best. (Perry, Webb and Bateson)

Miscellaneous studies

Stunt nematodes. The stunt nematode, *Tylenchorhynchus dubius* (Bütschli) was associated with poor growth of oilseed rape by Graham, ADAS, Reading. The species multiplied well on rape and its pathogenicity to rape and the suitability of the crop as a host was assessed in pots. The population structure of one of the original field populations was mimicked by densities of 0, 300, 700 and 1500 specimens litre^{-1}. Plant growth was significantly increased by increasing nematode densities during the first 6 weeks (see also p. 172) but after 4 months, when plants were harvested, the largest densities gave the smallest yields. (Spaull)

Stubby-root nematodes. The stubby-root nematode *Paratrichodorus* (*Atlantadorus*) *anemones* (Loof) produces patches of poor growth that typically appear in spring-sown cereal crops during May/June. However, the activity of these ectoparasitic nematodes is greatly influenced by external conditions and the plant may be able to compensate for the initial slowing of growth. The tolerance of spring barley (cv. Julia) and spring wheat (cv. Sicco) to exposure to 300 nematodes litre^{-1} was tested by growing plants in infested and sterilised soil and transplanting some replicates to sterilised soil after periods of 2, 4, 6, 8, 12 and 16 weeks.

Exposure for 6 weeks or longer significantly reduced the growth of barley and wheat and the plants had not compensated appreciably 4 weeks later. At harvest, wheat transplanted from infested soil after only 2 weeks under attack yielded more whereas all other attacked barley and wheat plants yielded significantly less. The yield loss increased appreciably for each additional 2 weeks' exposure to attack up to *c.* 8 weeks; thereafter, longer periods did not greatly increase it. The nematode doubled its numbers on both crops during the experiment. (Spaull)

Sex determination of cyst-nematodes. Adding a cyst-nematode juvenile singly to the soil near a host plant removes competition between juveniles and if a root is invaded successfully sexual differentiation continues unhindered. A sex ratio of 1 was achieved when juveniles of *H. avenae* were added to oats cv. Milford, a good host that supports many females, and 75% of the nematodes added were recovered as sexually differentiated juveniles. When the oat cv. Sun II, a poor host that supports relatively few females, was used the number of males was the same but there were fewer females ($P < 0{\cdot}01$), giving a sex ratio of 3. When juveniles from two other populations were tested they invaded less successfully ($P < 0{\cdot}01$) but sex ratios of 1 and 3 were still achieved on Milford and Sun II respectively. In comparable tests, a sex ratio of 1 was found for *G. pallida* and *G. rostochiensis* on tomato, *H. cruciferae* on cabbage and *H. schachtii* on sugar beet.

https://doi.org/10.23637/ERADOC-1-135

Although it did not prove possible to count the numbers of female juveniles in roots that failed to develop and presumably died, there was no evidence that the numbers of males increased proportionately. Contrary to earlier findings (*Nematologica* (1967), **13**, 263–272) the sex of cyst-nematodes seems to be genetically and not environmentally determined. (Bridgeman)

Hatching of the stem nematode. Whereas *A. blastophthorus* Franklin simply breaks through an eggshell gradually degraded by larval movement and *G. rostochiensis* cuts a continuous slit by precise stylet thrusts radiating from a single point, the stem nematode *D. dipsaci* weakens the eggshell by thrusting its stylet where the emergence slit will later form. Stylet thrusting seems relatively haphazard, rarely punctures the shell and occurs in bursts directed from several different centres and separated by bouts of movement of the head and fore-body. Many thrusts are aimed at the two points that will form the ends of the slit. Several hundred thrusts are made in all, at about 2 s^{-1}, and only about 7% of these fall outside the eventual slit.

Just before emerging, the juvenile presses its head against the slit region of the shell and, when the slit opens, the head emerges at about 54 $\mu m\ s^{-1}$, declining to 10–20 $\mu m\ s^{-1}$ within 0·6 s. An avoiding reflex may occur, when the juvenile reacts to the external medium by reversing back into the shell, sometimes almost completely, before finally leaving it.

The main changes in the eggshell from laying to hatching (several days) are a progressive loss of resilience, and wrinkling, detachment and breakdown of a distinct inner shell layer. (Doncaster and Seymour)

Hatching and osmotic stress. Unlike *G. rostochiensis* (Ellenby & Perry, *Journal of Experimental Biology* (1976), **64**, 141–147), there is no significant change in the water content of second-stage juveniles of *H. schachtii* before hatching whether they have been immersed in root diffusate or in water but immediately after hatching juveniles take up water rapidly (Perry, *Nematologica* (1977), **23**, 431–437). This indicates that the hatching process in *H. schachtii* differs in some respects from that in *G. rostochiensis* (Clarke, Perry & Hennessy, *Rothamsted Report for 1977*, Part 1, 177) and we have compared the osmotic tolerance of these two species.

Unhatched juveniles of *H. schachtii* in eggs equilibrated with water contain more water (69%) than those of *G. rostochiensis* (67%). When free juveniles of *H. schacthii* were transferred from distilled water to sugar solutions they lost water in proportion to the concentration of the solute. In 0·3M solutions the water content of the juveniles stabilises at 69%, suggesting that the egg-fluid surrounding the *H. schachtii* juvenile has a lower osmotic pressure than the egg-fluid of *G. rostochiensis* eggs (≡0·4M-trehalose). In various concentrations of sucrose and inositol the percentage of juveniles moving did not substantially decrease compared with juveniles in water unless the concentration was 0·5M or more, whereas 0·4M was sufficient to reduce the percentage of *G. rostochiensis* moving to less than 9%.

The smaller osmotic pressure within the egg and the greater resistance of *H. schachtii* juveniles to inhibition of movement by osmotic stress may explain why *H. schachtii* hatches readily in water. (Clarke, Perry and Hennessy)

The water content of *H. avenae* juveniles before hatch varied only with storage and hatch temperatures. No significant change in water content was found between juveniles from cysts in water and in root diffusate. (Perry and Beane)

Few juveniles hatched from *H. avenae* pathotype 1 cysts collected in October, at 5, 10 or 15°C and hatching was no better after storing cysts at these temperatures for 5 weeks; a storage time greater than 5 weeks is evidently required before eggs hatch.

https://doi.org/10.23637/ERADOC-1-135 *pp 21*

After storage for 17 weeks the influence of the different combinations of storage and hatching temperatures became apparent. The addition of root diffusate to all combinations enhanced hatch, confirming and extending earlier results (Williams & Beane, *Rothamsted Report for 1971*, Part 1, 171). Most hatched after storage at 5 and fewest after storage at 15°C, the best combination was 17 weeks storage at 5 before hatching at 15°C.

This population of *H. avenae* appears to have a temperature mediated diapause but the influence of root diffusate seems to be temperature-independent. (Perry and Beane)

Cysts and free eggs of *G. pallida* exposed to root diffusate for 5 min and then washed in running water for 30 min gave significantly greater hatches than unstimulated controls. This indicates that root diffusate acts more rapidly than previously suspected. (Perry, with Dr. J. Forrest, Scottish Plant Breeding Station)

Visitors and Visits Abroad

Dr. Julia Meredith, Instituto Zoologia Agricola, Universidad Central de Venezuela, Dr. Maria de Scurrah, International Potato Centre, Lima, Peru, Dr. Walter J. Apt, University of Hawaii, Manoa, Mr. M. Storey, Department of Pure and Applied Biology, University of Leeds and Mr. M. Tanveer, Cotton Research Institute, Pakistan, worked for varying periods in the Department. Mr. M. A. Quigley also worked extra-murally as an Open University Ph.D. candidate. Dr. C. Scotto la Massese, Station de Recherches sur les Nematodes, Antibes, France, Dr. M. Brzeski, Institut Warzywnictwa, Skierniewice, Poland and Dr. J. W. Meagher, Plant Research Institute, Victoria, Australia, paid brief visits.

F. G. W. Jones, D. J. Hooper, Sybil A. Clark, R. N. Perry, M. Bridgeman and J. Cuthbert attended the 3rd International Congress of Plant Pathology in Munich, W. Germany in August, D. J. Hooper lectured on virus-vector nematodes at the workshop held in the Department of Plant and Forest Protection, Ultuna, Uppsala, Sweden. A. R. Stone lectured on co-evolution of nematodes and plants at the Institute of Systematic Botany, University of Uppsala, Sweden. A. R. Stone and K. Evans collected round-cyst nematodes in Peru and Bolivia on funds from the Percy Slayden Memorial Foundation, London, the International Potato Centre, Lima, Peru, the Consortium for International Development, La Paz, Bolivia and the Agricultural Research Council. From July K. Evans was seconded to the US Department of Agriculture Golden Nematode Research Program, at Cornell University. Alison Spaull visited nematology centres in W. Germany.

Publications

Thesis

1 Roberts, P. A. (1978) The interrelationships of *Globodera* and some *Solanum* spp. University of Birmingham, 332 pp.

General Papers

2 Evans, K. (1977) Distribution of round-cyst nematodes and their effects on the host. *Biological Journal of the Linnean Society* **9,** 381.

3 Jones, F. G. W. (1978) Cyst-nematodes, biology and background. *Biological Journal of the Linnean Society* **9,** 381.

4 Jones, F. G. W. (1978) Plant nematodes: a neglected group of pests. Clive Behrens Lectures. *Leeds University Review* **21,** 89–115.

https://doi.org/10.23637/ERADOC-1-135

5 KERRY, B. R. (1978) Natural control of the cereal cyst-nematode by parasitic fungi. *ARC Research Review* **4,** 17–21.

6 PERRY, R. N. (1978) Events in the hatching process of the potato cyst-nematode *Globodera rostochiensis*. *ARC Research Review* **4,** 79–83.

7 SEYMOUR, M. K. (1978) Education. *New Scientist* **77,** 105.

8 SEYMOUR, M. K. (1978) The infinite variety of worms. *New Scientist* **77,** 650–652.

9 SEYMOUR, M. K. (1978) Mnemonics. *New Scientist* **77,** 871.

10 STONE, A. R. S. (1978) Taxonomy of round-cyst nematodes. *Biological Journal of the Linnean Society* **9,** 381.

11 WHITEHEAD, A. G. (1978) Progress in the chemical control of plant nematodes. *International Pest Control* **2** (Mar/Apl), 14; and *World Crops and Livestock* **30,** 1078.

PAPERS IN ROTHAMSTED REPORT, PART 2

12 EVANS, K. (1979) Nematode problems in the Woburn Ley-Arable experiment, and changes in *Longidorus leptocephalus* population density associated with time, depth, cropping and soil type. *Rothamsted Experimental Station. Report for 1978*, Part 2, 27–45.

13 WILLIAMS, T. D., BEANE, J., BERRY, M. M. & WEBB, R. M. (1979) The Rotation Fumigation experiment, Woburn Experimental Farm, 1969–77. *Rothamsted Experimental Station. Report for 1978*, Part 2, 47–66.

RESEARCH PAPERS

14 BAINBRIDGE, A., BARDNER, R., COCKBAIN, A. J., DAY, J. M., FLETCHER, K. E., HOOPER, D. J., LEGG, B. J., MCEWEN, J., SALT, G. A., WEBB, R. M. & WILDING, N. (1977) Recent work at Rothamsted on factors limiting yields of field beans (*Vicia faba* L.). In: *Proceedings of the Symposium on the Production, Processing and Utilisation of the Field Bean* (Vicia faba *L.*) held at the Scottish Horticultural Research Institute on 9 March, 1977. *Scottish Horticultural Research Institute Bulletin* No. 15, pp. 28–38.

15 CLARKE, A. J., PERRY, R. N. & HENNESSY, J. (1978) Osmotic stress and the hatching of *Globodera rostochiensis*. *Nematologica* **24,** 384–392.

16 DONCASTER, C. C. & FAULKNER, G. (1978) Apparatus for recording time on film in time-lapse cinemicrography. *Laboratory Practice* **27,** 471–472.

17 EVANS, K. & FRANCO, J. (1979) Tolerance to cyst-nematode attack in commercial potato cultivars and some possible mechanisms for its operation. *Nematologica* **25,** 153–162.

18 FRANCO, J. (1978) Measuring area and perimeter of second-stage larvae and males with the image-analyzing computer to distinguish between *Globodera rostochiensis* and *G. pallida*. *Journal of Nematology* **10,** 278–279.

19 FRANCO, J. (1979) The effects of temperature on hatching and multiplication of potato cyst-nematodes. *Nematologica* **25,** 237–224.

20 FRANCO, J. (1979) Disc electrophoresis of female proteins of British and Peruvian potato cyst-nematode populations, *Globodera* spp. *Nematologica* **25,** 32–35.

21 FRANCO, J. & EVANS, K. (1978) Mating of British and Peruvian populations of potato cyst-nematodes *Globodera* spp. *Nematropica* **8,** 5–9.

https://doi.org/10.23637/ERADOC-1-135

22 FRANCO, J. & EVANS, K. (1979) Effects of daylength on the multiplication of potato cyst-nematode (*Globodera* spp.) populations. *Nematologica* **25,** 184–190.

23 FRANCO, J. & EVANS, K. (1979) Restoring the morphological features of *Globodera pallida* after storage in formalin. *Journal of Nematology* **10**, 370–372.

24 FORDER, D., FAULKNER, G. & DONCASTER, C. C. (1978) A time lapse apparatus for use with 16 mm Beaulieu ciné cameras. *Laboratory Practice* **27,** 383–387.

25 GREET, D. N. (1978) The effect of temperature on the life cycle of *Panagrolaimus rigidus* (Schneider). *Nematologica* **24,** 239–242.

26 HOOPER, D. J. (1978) The identification of stunt nematodes (Tylenchorhynchinae, Merliniinae and Trophurinae) especially those in Western Europe. In: *Spiral and stunt nematodes*. Association of Applied Biologists, Workshop Manual, Harpenden, Rothamsted Experimental Station, 75 pp.

27 JONES, F. G. W., KEMPTON, R. A. & PERRY, J. N. (1978) Computer simulation and population models for cyst-nematodes (Heteroderidae: Nematoda). *Nematropica* **8,** 36–56.

28 JONES, F. G. W. & PERRY, J. N. (1978) Modelling populations of cyst-nematodes (Nematoda: Heteroderidae). *Journal of Applied Ecology* **15,** 349–371.

29 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,** 781–787.

30 SEYMOUR, M. K., (MINTER, B. A.) & DONCASTER, C. C. (1978) A low-light remote recording system used to study nematode behaviour. *Nematologica* **24,** 167–174.

31 SHEPHERD, A. M. & CLARK, S. A. (1978) Cuticle structure and 'cement' formation at the anterior end of female cyst-nematodes of the genera *Heterodera* and *Globodera* (Heteroderidae: Tylenchida). *Nematologica* **24,** 201–208.

32 SPAULL, A. M. & (HAGUE, N. G. M.) (1978) Influence of cereal cultivar on the population dynamics of the cereal cyst-nematode, *Heterodera avenae*. *Nematologica* **24,** 376–383.

33 (TOWLE, A.) & DONCASTER, C. C. (1978) Feeding of *Longidorus caespiticola* on rye-grass, *Lolium perenne*. *Nematologica* **24,** 277–285.

34 YEATES, G. W. (1979) *Hemicycliophora chathami* n. sp. (Nematoda) from Chatham Island, New Zealand with the description of two sub-species. *Nematologica* **24,** 425–435.

https://doi.org/10.23637/ERADOC-1-135 *pp 24*