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"A contribution to the epidemiology of the cyst nematodes *Heterodera schachtii* Schm., *Globodera rostochiensis* Woll. and *G. pallida* Stone in north-west Europe"

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Foreword

This significant unpublished manuscript was written by our late father Dr Frederick G.W. Jones in the early 1990s but remained unfinished after his work on it ceased in 1993. We found it among his belongings following his death in 2003. He emigrated to Western Australia in 1991 at the age of 77 and we believe that most or all of the manuscript was written at his home in Applecross, Perth, in the period 1991-1993.

His first job (1937-1947) was in the Agricultural Advisory Service based at the School of Agriculture at Cambridge University, UK[1,2]. This included the 2nd World War period when he was in a 'reserved' profession dedicated to ensuring 'self-sufficiency' in food. From 1947 to 1955 he was first Demonstrator, then Senior Lecturer in Agriculture at Cambridge University. In his time at Cambridge, his research focussed mostly on nematode pests of crops. He then moved to Rothamsted Experimental Station, Harpenden, UK, where he worked from 1956 to 1979. He was Head of the Nematology Department throughout his time at Rothamsted, taking on the additional role as Deputy Director of Rothamsted in 1971. Following his retirement in 1979, he worked as an Honorary Scientist in the Computer Department at Rothamsted until 1987. During this period, among other things such as producing a third edition of the book *Pests of Field Crops* and acting as Managing Director and Secretary of the International Trust for Zoological Nomenclature (1980-1987), he continued his research on models for cyst nematodes. However, although he obviously collected together many of his ideas on the subject of this manuscript at that time and earlier, as mentioned in the previous paragraph, we believe that it was written after he arrived in Australia.

This manuscript represents a valuable, carefully-considered study of considerable benefit to other researchers. We therefore decided to produce it as the third in a series of historical bulletins containing unpublished

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

manuscripts by members of our family. This unfinished manuscript is published in its entirety without any attempt to bring it up to date by reference to more recent scientific publications since 1993 on this subject. It should, therefore, be viewed as a historical document published posthumously.

Roger Jones
Susan MacDougall
December 2007

This article is available as a PDF file on the family web site,
www.geocities.com/macdougalljones/
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A contribution to the epidemiology of the cyst nematodes *Heterodera schachtii* Schm., *Globodera rostochiensis* Woll. and *G. pallida* Stone in north-west Europe

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1993

Summary

The cyst, a vehicle for dispersal, and the *K*-selected life style and other properties of cyst nematodes, contribute to their persistence and successful transference from their centres of origin to other parts of the world. Dispersal by the migration of 2nd-stage juveniles is trivial, whereas that of cysts due to the activities of mankind is overwhelmingly greater. A simplistic two-dimensional model is developed taking into account both methods. Spread is defined as dispersal modified by competition for available territory. Initially, this is the field, the boundaries of which offer only temporary barriers to further spread. Spread is decidedly contiguous, that is, most often adjacent to existing foci of infestation. Patterns of early spread within fields above or below ground cannot be seen. However, patterns of the kind that might be expected from the passage of harvesting machinery are found in aerial photographs of lucerne (alfalfa) crops infested with the stem nematode. This nematode multiplies rapidly and is dispersed by harvesting machinery in pieces of plant tissue in much the same way as cysts are dispersed with soil during the harvesting of root crops.

Introduction

"Whether within fields or localities, spread by cyst nematodes results in the occupation of territory in the zoological sense, but exploitation of territory is incomplete until populations approach densities of the order of 2.5 x 10^{-10} eggs/ha (10 eggs/g soil)."

The ideas expressed above are illustrated by the history of the beet cyst nematode (*Heterodera schachtii* Schm.) in the English fenlands, where colonisation and exploitation are nearing completion, and by a few examples of experiments and experiences with the two potato cyst nematodes (*Globodera rostochiensis* Woll. and *G. pallida* Stone) and with the beet cyst nematode elsewhere. One feature of the aetiology of these nematodes is the sudden and unexpected appearance of severely damaged crops in places previously thought uninfested. This may be due initially to the slow spread and build up of populations, but a contributing factor is probably the recruitment of cysts during the last stages of competition for territory. These fall increasingly on territory already occupied, boosting populations and speeding the appearance of crop injury. Climatic stress may also contribute in dry years. Although rotations may slow spread and growing crops one year in three may avoid appreciable losses for a time, use of longer rotations seems inevitable eventually, unless assistance from other control measures, such as nematode-resistant cultivars and nematicides, is enlisted. Although the patterns of early spread of cyst nematodes cannot be seen in beet or potato fields, patterns analogous to those expected have been seen in aerial photographs of lucerne (alfalfa, *Medicago sativus* L.) crops infested with the stem nematode (*Ditylenchus dipsaci* Kuhn).

This account deals with means by which cysts are disseminated and infestations initiated. It considers briefly the properties of the cyst and of associated adaptations which make cyst nematodes such successful root parasites of crops. Attention is drawn to the inadequacy of self-dissemination by 2nd-stage juveniles and of the overwhelming importance of harvesting of root crops, such as beet and potatoes, in the colonisation of fields. Spread is defined as dispersal modified by competition for available territory. A

simplistic model combining both means of dispersal is developed and competition is illustrated geographically. Conservative values are applied to the model parameters to avoid complexity and exaggeration of the speed of dispersal. Even so, the model shows that the speed of dispersal is sufficient to colonise large areas within the time span of host crop years found in practice.

Comments are made on world spread from the epicenters where cyst nematodes co-evolved with their host plants. A map of the dispersal of potato cyst nematodes from the Andean epicentre is given.

Initiation of infestations

The means by which cysts are spread are many and various (Table 1), but usually they are carried with soil, often unwittingly. Ploughing tends to invert the soil, whilst ordinary cultivations and other operations also move soil. These operations are far less important than the harvesting of root crops which disperses soil containing cysts within fields and about farms. For potato cyst nematodes, soil adhering to or accompanying seed potato tubers is, perhaps, the most important vehicle for long distance spread. For beet cyst nematode, soil transported incidentally during harvesting and haulage to beet sugar factories plays an important role. Waste soil collects at beet sugar factories and at vegetable grading and packing stations. Careless disposal of these wastes can be a potent source of new, more distant infestations of several species of cyst nematode.

Although some infestations are doubtless founded by single cysts containing viable eggs, probably most infestations are multiple, especially after a local infestation becomes substantial. When the appropriate host crop is grown frequently, much spread is contiguous, that is, to neighbouring areas within the same farm, and to neighbouring farms in the same locality. Far flung infestations are mostly fortuitous, although sometimes hidden connections are revealed on closer study, due to family or commercial connections such as the sale of transplants, bulbs and other horticultural products. For example,

Table 1 *Dispersal of cyst nematodes*

Means	Distances	Speed
Self-dispersal of 2nd-stage juveniles		
- movement through soil	Immediate vicinity only	very slow
Assisted dispersal of eggs within cysts		
natural agencies		
- rain splash	local	slow
- water currents	mostly local)	sometimes rapid
- wind	medium)	
- with seeds)	medium-long	mostly slow
- on animals)		
Human agencies		
- agricultural operations	local	rapid
- commerce	medium and long	rapid
- tourism	long	fortuitous

the isolated infestation of potato cyst nematode on Vancouver Island, Canada, appears to have been connected with the purchase of bulb stocks from The Netherlands.

Colonisation after establishment

Once established in uninfested land, colonisation begins when eggs hatch and 2nd-stage juveniles move through the soil pore system to find and invade host roots. Their migrations depend mainly on pore spaces and moisture (Wallace, 1963; Jones, 1975), being favoured most by sandy soils or well-structured loams and least by dense clays. Apart from the movements of males to find and fertilise females, males play no part in dispersal. The greater part of the cyst nematode life cycle is passed within or attached to plant roots and so is largely uncoupled from the soil itself. Within the roots the females establish territories of a kind, induce syncytial transfer cells and feed on their contents (Jones, M.G.K., 1981). Developing females are immobile, swell greatly, fill with eggs and, on death, become cysts. In some species, a proportion of the eggs may be laid in egg sacs externally (beet cyst nematode and clover cyst nematode, *H. trifoilii* Goff) but mostly they are retained within the cyst.

The cyst and associated adaptations

The cyst is the culmination of female development which, coupled with associated adaptations, contributes to the fitness of cyst nematodes to operate in the root-soil environment and makes them remarkably well attuned root parasites (Table 2). Their *K*-selected lifestyle (Southwood, 1981; Jones & Jones, 1984) has enabled them to follow their host crops wherever they are cultivated so long as they fit within the temperature parameters of the particular soil in any new locality where they are grown.

K-selected organisms are usually ones with modest rates of multiplication and

Table 2 *Properties of the cyst*

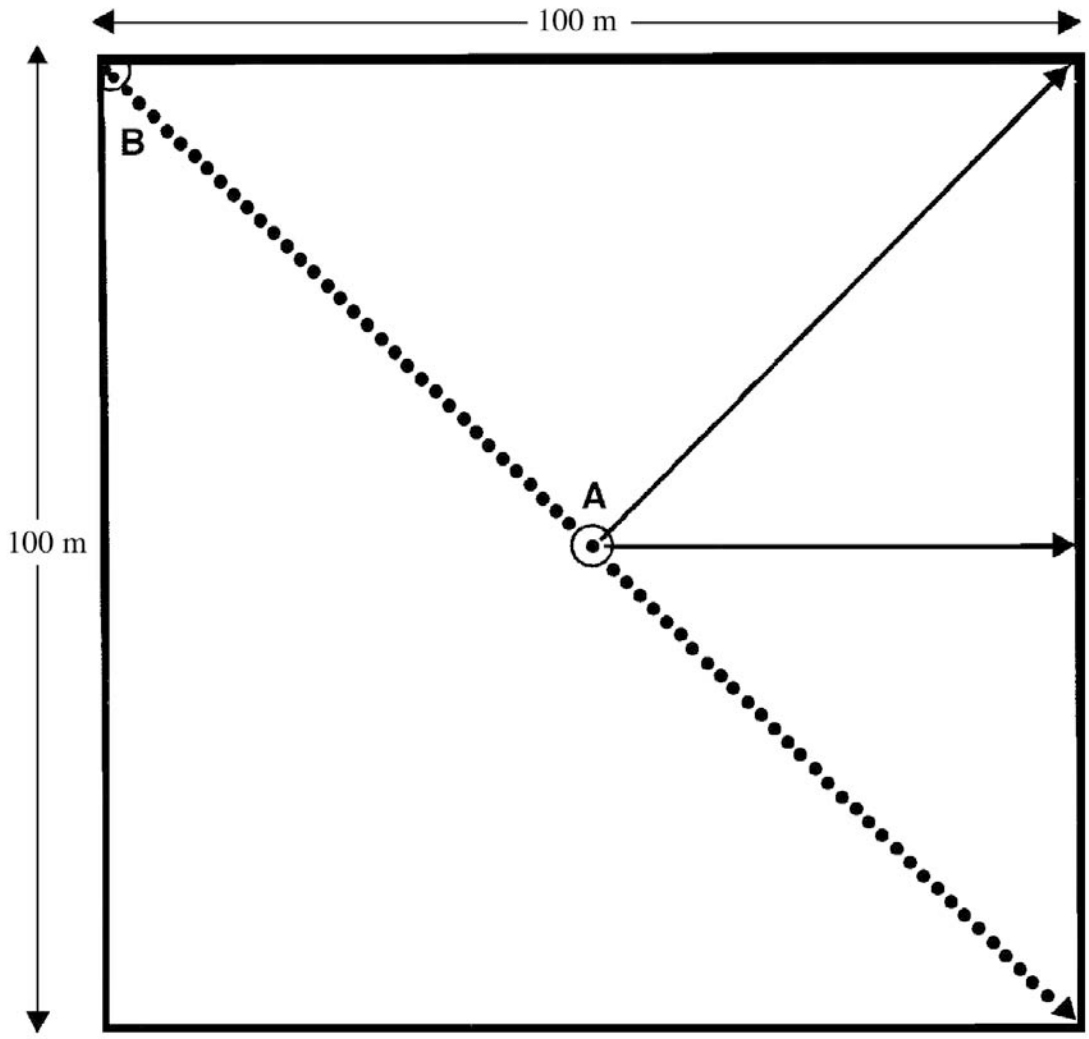
1.	A vehicle for dispersal of an organism that has only limited means of self-dispersal
2.	A means of protection additional to the egg shell and juvenile cuticle
3.	Harbours a community that avoids the perils of under-population
4.	Aids persistence when host is absent or nematode-resistant
5.	An essential part of the life style that is *K*-selected

limited means of dispersal. Consequently they need to avoid damaging their hosts unduly during feeding. Also, ability to persist when the host is absent is a helpful additional adaptation. They contrast with *r*-selected organisms which multiply excessively and possess great mobility. For these species, whether they destroy their hosts or not is immaterial, as they can find new ones elsewhere. They, too, must be able to persist, but not necessarily beyond the next season. In cultivated crops, many of the pressures endured by cyst nematodes during co-evolution with their host plants (isolation in remote localities, scattered hosts) are replaced by the planting of host crops in pure stands, often repeatedly on the same land. These conditions afford opportunities even for *K*-selected species to develop massive and damaging populations unlikely to occur in the wild.

The inadequacy of self-dispersal by 2nd-stage juveniles

In north-west Europe, populations of potato and other cyst nematodes in well-established infestations fluctuate between <10 and >100 eggs/g soil which, translated to cultivated land, range from $<2.5 \times 10^{10}$ to $<2.5 \times 10^{11}$ eggs/ha of topsoil. Populations of this magnitude take time to develop at apparent multiplication rates of 50 times or less and one or few generations per crop year. Much of this time is occupied by spread from initial foci. The slowness of self-dispersal can be imagined by considering a flat, uniform, square field of 1 ha, the four sides of which would measure 100 m (Fig. 1). Assuming that the self-spread of 2nd-stage juveniles is 10 cm per host crop year, it would take the progeny of a gravid cyst arriving in the centre of the field, the most favourable position, some 500 crop years to reach the centre of every side and 707 crop years to reach all four corners. That is, colonisation would be by a series of concentric circles, the last including the whole square field. For a cyst arriving in one corner, it would take 1,000 years for its progeny to reach the two nearest corners and 1,414 years to reach the far corner. Whether the radius of occupation in one crop year is 10 cm or 1 m, and whether there are more than one generation a year, clearly, self-dispersal would be painfully slow.

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



Legend to Fig. 1:

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

The importance of assisted spread

Field experience indicates that colonisation of whole fields may be completed in a relatively few host crop years, as the two following examples show. The ley-arable experiment at Woburn Experimental Farm, Rothamsted, tested the effects on soil fertility of three years of ley crops versus three years of arable crops. It was sited on land not previously planted with potatoes. Between these three year rotations, test crops of potatoes followed by wheat were planted, their yields intended to measure the fertility of preceding crop sequences (Table 3). Block 4 was planted with test crop potatoes in 1938 and potatoes were also grown as the first crop in the arable sequences. Yields of potatoes followed seasonal trends until 1950 (Fig. 2), when those from plots in the continuous arable series dipped slightly. They dipped further in 1953 and failed completely in 1955. These plots had grown eight potato crops in 18 years. Nothing untoward alerted the sponsors of the experiment in 1950 or 1953 and no patches of stunted plants were noticed. One plot in the arable-ley sequences that grew potatoes six times in 16 years was also badly affected, depressing the average yield of that sequence. Those in the ley-arable sequences that also had six potato crops in 12 years were only slightly affected, and those in the continuous ley sequence that had five potato crops in 12 years, effectively a 5-course rotation, yielded normally. When the infestation was imported, presumably with seed tubers, is unknown, but most likely it was in 1938 when the whole of Block 4 was planted with test crop potatoes. So, it took 6 to 8 host crop years, possibly fewer, for the small plots in this experiment to generate highly damaging populations.

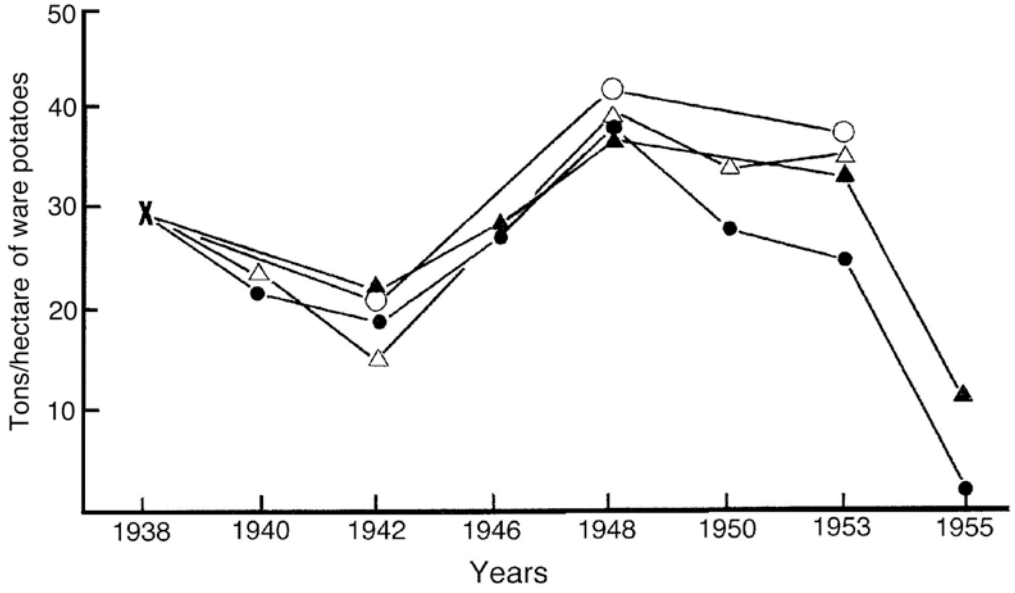
The second example comes from a farm in Norfolk, UK, situated in an area where beet cyst nematode was unknown. The farmer, a member of the Agricultural Extension Service, deprecated the need for crop rotation, saying that he had grown sugar beet on the same field for nine years and that each crop was better than the last. In the ninth year, large beet-sick patches appeared and it was unsafe to grow beet until 6 years later. These and similar experiences underline the fact that the initial spread of cyst nematodes is slow and insidious. Once crop symptoms appear, the pest is well established and may already have spread further locally.

Table 3 *Details of the Woburn Ley-Arable Experiment 1938 - 1955*

		Crop sequences	Potato crops	Post-harvest eggs/g soil
Continuous Arable	AAA	TOSOOTOSOOTOSOOTOT	8	71
Ley - Arable	LAL	TOOOOTOSOOTOOOOTOS	6	60
Arable - Ley	ALA	TOSOOTOOOOTOSOOTOO	6	14 (* 32)
Continuous Ley	LLL	TOOOOTOOOOTOOOOTOO	5	1 (* <1)

T = test crop potatoes, S = arable potatoes, O = other crops
* estimated post-harvest eggs after potatoes 1953

Fig. 2 *Yields of potatoes from crops in Block 4 of the ley-arable experiment, Woburn Experimental Farm, Rothamsthed*



Continuous arable = ●; Ley - arable = ▲; Arable - ley = Δ;
Continuous ley = O; **X** = when whole area planted with potatoes.
For explanation see text and for details of cropping see Table 3.

Modelling dispersal and spread

Dispersal may be defined as dissemination by the migration of 2nd-stage juveniles plus the movement of cysts during agricultural operations. Spread is the occupation of available territory which, in the first instance, is the field or plot with its semi-permanent boundaries. As dispersal proceeds within these or wider boundaries, both migrating juveniles and transported cysts arrive in territory already occupied. A competition for space ensues which becomes increasingly acute until the whole is occupied. Hence, spread may be defined as dispersal modified by competition.

The two-dimensional area occupied by juveniles at the end of one host crop year is defined as the domain, which is a circle of area Pir^2 where r is the radius. Since r is unknown, it may be represented by unity as a dimensionless number to be dimensioned later. One generation a year is assumed.

With these simplifications in mind, we may write:

Host crop years		0	1	2	3	4	…… n
Area occupied	Pi	(0	1	4	9	16	…… n^2)
Domains occupied		0	1	4	9	16	…… n^2

Note that the number of domains may be converted to an area by multiplying by Pir^2 when a value is ascribed to r.

The progeny of a successful gravid cyst introduced into uninfested land will produce concentric circles of 1, 4, 9, 16 …… n^2 domains at the end of successive host crop years. From these, an array of secondary infestations arises as shown in Table 4. Again for simplicity, it is assumed that one cyst is transported from each domain during harvesting and other operations between host crops. When these arrays are totalled, they indicate the area that could be colonised in the corresponding years, assuming unlimited space and no competition. In a similar way, it is possible to derive tertiary, quaternary and higher orders of infestation. These are shown in Table 5 in log. form. Postulating that each domain gives rise to N more, it is only

Table 4 *Dispersal: calculation of secondary dispersal from primary infestation*

Each domain generates one more only

Host crop years	Primary infestation	Array of secondary infestations									Total of secondary infestations
		Number of domains									
1	1										
2	4	1									1
3	9	4	4								8
4	16	9	16	9							34
5	25	16	36	36	16						104
6	36	25	64	81	64	25					259
7	49	36	100	144	144	100	36				560
8	64	49	144	225	256	225	144	49			1092
9	81	64	196	324	400	400	324	196	64		1968
10	100	81	256	441	576	625	576	441	256	81	3333

Table 5 *Dispersal: no competition for space*

Each domain generates one more

Host crop years	**Order of infestations**										**Log. arithmetic totals**
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	
	Log. domains										
1	0.000										0.000
2	0.602	0.000									0.699
3	0.954	0.903	0.000								1.255
4	1.204	1.531	1.204	0.000							1.826
5	1.398	2.017	2.121	1.505	0.000						2.468
6	1.556	2.431	2.876	2.716	1.806	0.000					3.213
7	1.690	2.748	3.523	3.758	3.315	2.107	0.000				4.074
8	1.806	3.038	4.091	4.683	4.651	3.915	2.408	0.000			5.060
9	1.908	3.294	4.597	5.519	5.865	5.549	4.516	2.709	0.000		6.174
10	2.000	3.523	4.054	6.283	6.999	7.059	6.450	5.118	3.010	0.000	7.420

necessary to multiply the column of secondary infestations by N, that of tertiary by N^2, quaternary by N^3 and so on. To apply $N = 10$, a modest rate of cyst transportation, to the columns in Table 5, add 1 (= log. 10) to values in the secondary infestation column, 2 (= log. 100) to those in the tertiary column, and so on. Converting them to arithmetic values and summing the rows gives the results in Table 6. Numbers of domains have also been converted to ha by multiplying them by $Pi \times 10^{-6}$ after assuming a domain radius of 10 cm. The potential rate of dispersal is slightly greater than exponential for, when the log. total numbers of domains in Table 5 are plotted against crop years, the curve produced slopes gently upwards (Fig. 3). With a propagation rate of $N = 10$, the area potentially able to be colonised without the constraints of competition is immense after fewer than 10 host crop years.

Competition

In an area being colonised, competition is slight at first, but then increases and intensifies. So, a coefficient of competition to relate dispersal to spread must bear an inverse relationship to its intensity. It must start with a value ->1 at the end of the initial year, decrease in successive years, and end with a value ->0 when the area under consideration is almost fully colonised. The values of this coefficient are represented notionally in Fig. 3 by the differences between points on the lower curve simulating spread and the horizontal line representing the area being colonised, 1 ha.

Colonisation of English peat fens

The spread of the beet cyst nematode in the English Fenlands, once an extensive swamp, is documented over the last 60 years or so. There, the cultivation of sugar beet began in about 1925 and the first infestation was found in 1934 near Chatteris in the Isle of Ely. Two further infestations were found in Feltwell Fen and Larmans Fen in 1935 and 1936 respectively (Fig. 4A). Subsequent enquiries suggested that the Chatteris infestation originated on land near Billup Siding on the railway south of Chatteris in the 1920s

Table 6 *Dispersal: no competition for space*

Each domain generates ten more

6a

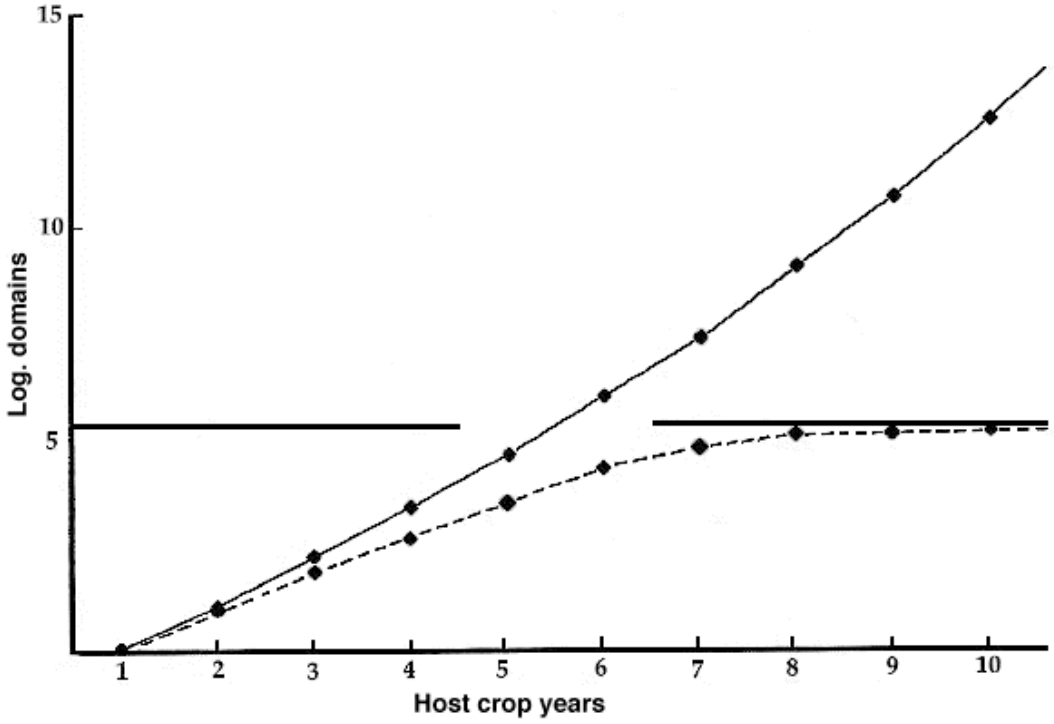
Host crop years	**Order of successive infestations**										**Log. arithmetic totals**
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	
	Log. domains										
1	0.00										0.0000
2	0.60	1.00									1.1459
3	0.95	1.90	2.00								2.2761
4	1.20	2.53	3.20	3.00							3.4701
5	1.40	3.02	4.12	4.51	4.00						4.7494
6	1.56	3.41	4.88	5.72	5.81	5.00					6.1253
7	1.69	3.75	5.52	6.76	7.31	6.11	6.00				7.4686
8	1.81	4.04	6.09	7.68	8.65	8.92	8.401	7.00			9.1984
9	1.91	4.29	6.60	8.52	9.87	10.55	10.52	9.71	8.00		10.9070
10	2.00	4.52	7.05	9.28	11.00	12.06	12.45	12.12	11.01	9.000	12.7366

Table 6 continued

6b

Host crop years	Potential area colonised		
	Domains	**Hectares**	
1	1	0.00	
2	14	0.00	trivial
3	189	0.00	
4	2956	0.01	
5	56265	0.18	
6	1337826	4.20	
7	28987749	91.07	
8	1585168584	4979.95	
9	81085588471	254737.89	extensive areas
10	5480994881430	17219053.25	

Fig. 3 *Potential dispersal rate for the potato cyst nematode*

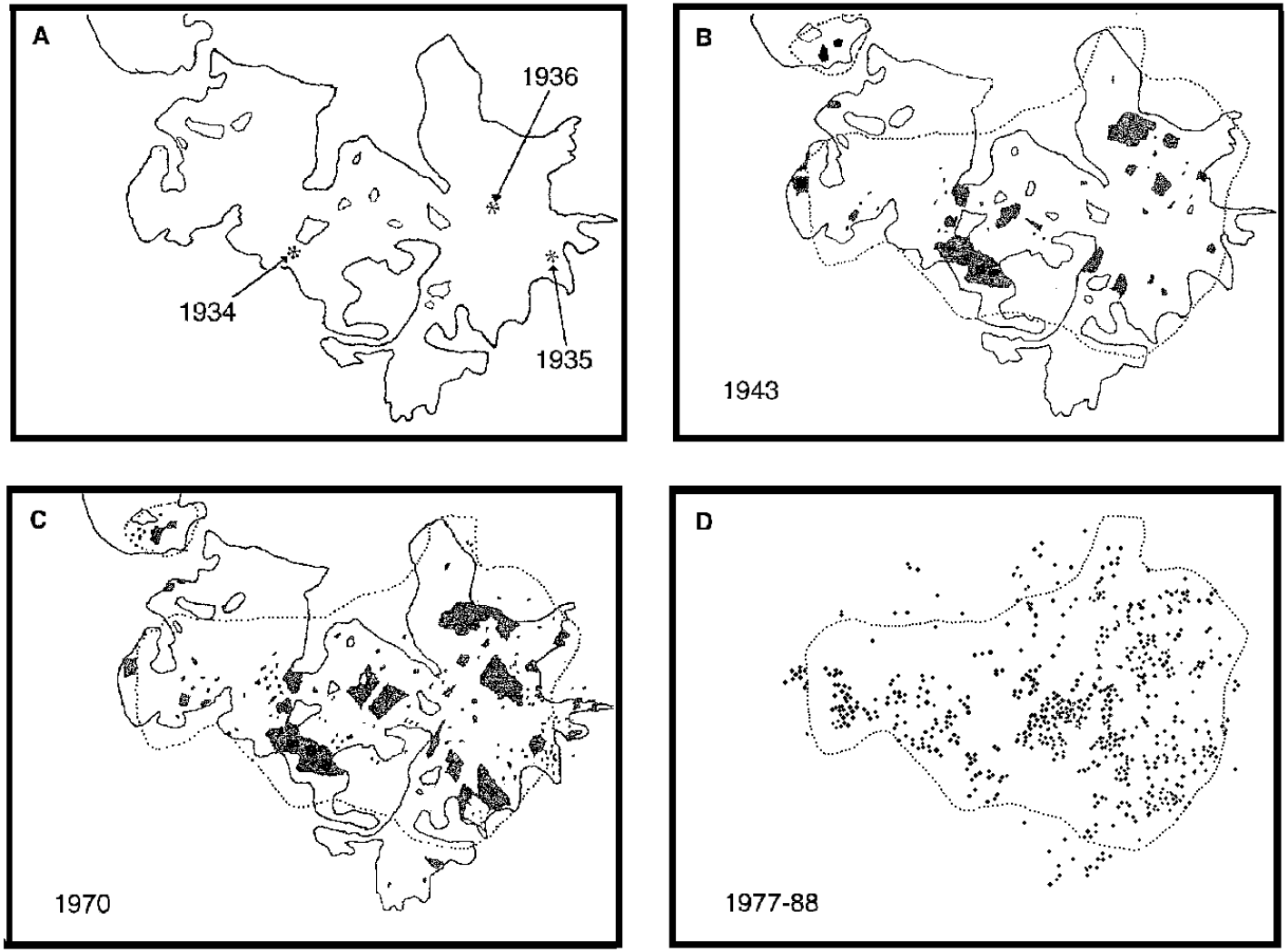


Legend to Fig. 3:

Upper curve: dispersal of cyst nematodes, one generation a year; each domain generates 10 more domains. Plotted values of total dispersal from Table 5.

Lower curve: notional values for colonisation of 1 ha ($\frac{1}{\sqrt{1}}$ x 10^5 domains) represented by the horizontal line. Competition is represented by the differences between the lower curve and the horizontal line (coefficient is the inverse of these differences, $\rightarrow 1$ at the end of year 1 and $\rightarrow 0$ from the end of year 8 onwards).

Fig. 4 *Colonisation of the Peat Fen basin (solid outlines) by the beet cyst nematode*



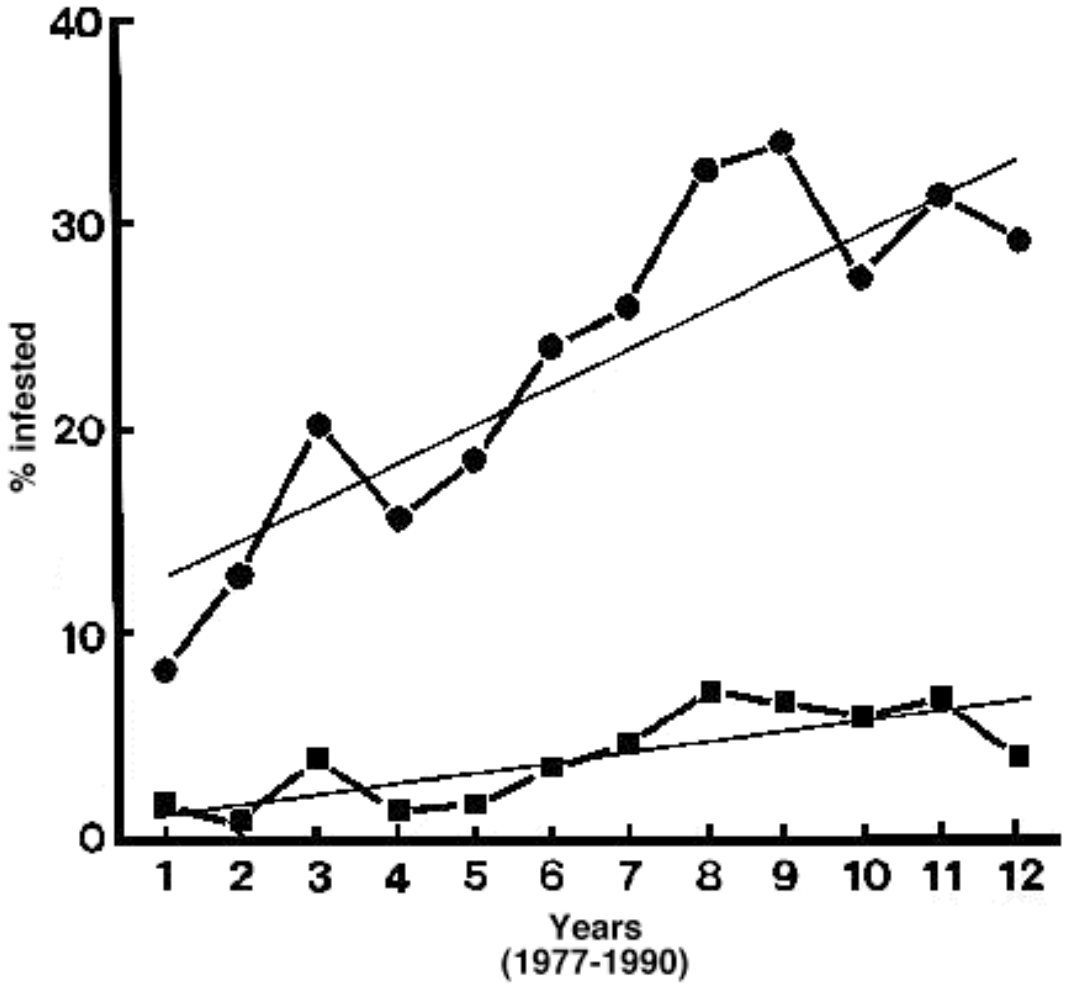
Legend to Fig. 4: A, first infestations found (1934-1936); B, position in 1943; C, position in 1970; D, data from maps in Cotten *et al.* (1992) (1977-1988). Excludes fenland north of Peterborough. Dotted line is the boundary of the area scheduled under the Beet Eelworm Orders.

or earlier. Horse manure was brought there from London by rail for use as fertiliser and loads of mangolds, a different type of beet *(Beta vulgaris* L.), were transported back to London as horse fodder. Consequently mangolds were grown frequently in fields near Billup Siding. Several other isolated infestations on mangolds outside the Fens (Gloucester in 1928; Glamorgan in 1932; Barnfield at Rothamsted in 1944, a field which grew mangolds from 1876 to 1959) suggest that the beet cyst nematode was already sparsely scattered over parts of England and Wales.

Field by field surveys in the Fens using the "fork test" method, that is, lifting plants and examining their root systems at times when females and cysts were visible on the roots, were made from 1937 to the 1950s and less thoroughly thereafter. Attention was directed to places likely to be infested by the frequency with which beet was grown and by testing soil samples from loading sites near roads, rivers and railway lines. Agriculturalists and fieldmen from the beet sugar factories in the area greatly assisted by sending samples from patchy crops and in other ways. The results of these surveys are in Figs 4B and 4C.

Recent sample surveys (Cotten *et al.*, 1992) from 1977 to 1988 (Fig. 4D) suggest that virtually the whole of the Peat Fen basin south and east of Peterborough is now occupied in the zoological sense after a period of beet growing of a little more than 60 years. The "fork testing" method is not expected to detect trivial infestations with any degree of certainty: many "covert" infestations would be missed. When the numerical data in Cotten *et al.* (1992) were plotted against years (Fig. 5), the percentage of infested fields drifted gently but significantly upwards from about 8% to nearly 30%, while the number of substantially infested fields increased more slowly, from about 1.5 to 4%. A regime of crop rotation was included in growers' contracts with beet sugar factories starting in 1936 and legally enforced within Scheduled Areas by successive Beet Eelworm Orders from 1943 to 1977 (Jones, 1951a,b; Southey *et al.*, 1982; Cotten *et al.*, 1992). The final Order enforcing crop rotation was revoked and replaced by the Beet Cyst Nematode Order 1977 reserving powers to reintroduce restrictions, should the need arise. The rotational

Fig. 5 *Incidence of fields infested by the beet cyst nematode in the Peat Fen basin*



Legend to Fig. 5:

Upper curve: % of fields found infested (●).
Lower curve: % of fields found substantially infested (■).
From data in Cotten *et al.* (1992).
Fitted regression lines: upper curve, b = 2.033, t = 6.17, P <0.001; lower curve, b = 0.471, t = 3.774, P <0.01, DF = 10.

clause in growers' contracts was also removed in 1983. These changes led to some narrowing of crop rotations, a drift checked by the appearance of the virus disease beet "rhizomania" vectored by the root-infecting fungus *Polymyxa betae* (Keskin) in 1989 (Hill & Torrance, 1989). This led to the re-instatement of a rotational clause in growers' contracts in 1988.

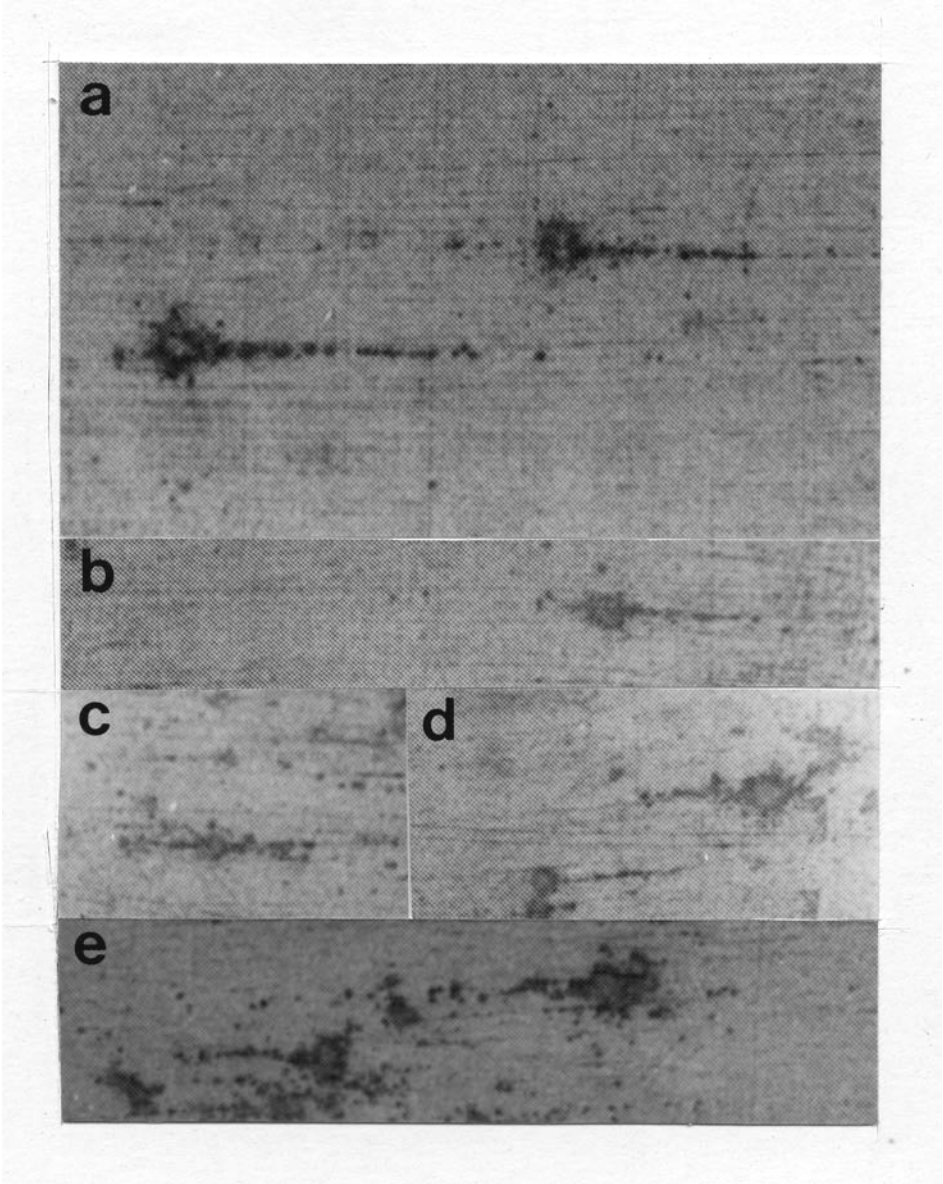
The history of beet cyst nematodes in the Fens shows that crop rotations, however long, are unlikely to prevent the spread of cyst nematodes when conditions are favourable, but they do help avoid serious crop losses. Crop rotation has its cost drawbacks for farmers with suitable land within reach of beet sugar factories. Nevertheless, some farmers adopt longer rotations and find alternative crops to fill the gaps. Others turn to nematicides which bring their own problems. Cyst nematode-resistant sugar beet cultivars are not yet available.

Patterns of spread

The contiguous nature of spread between neighbouring fields and farms can be seen in Figs 4B & C. Here, individual fields cannot be shown in heavily infested localities on the small scale maps: they are depicted as continuous areas bounded on the ground by farm roads, wide drains and other features. Nor do the dots in Fig. 4D record exactly the positions of individual infested fields. The symbols on the maps in Cotten *et al.* (1992) frequently overlap: again, evidence of contiguous spread. Within fields the patterns of spread resulting from the passage of harvesting machinery cannot be seen below or above ground because injurious populations take time to develop and are slow to cause readily visible symptoms in the host crop. The pattern from an isolated focus would be expected to resemble an elongated bunch of grapes with some isolated fruits scattered along the line of passage of the harvesting machinery and a few further away in chance locations.

Such patterns can be seen in aerial photographs of fields of lucerne, where pieces of leaf and stem tissue infested with the stem nematode are scattered above ground by harvesting machinery in a manner analogous to the dissemination of cysts in soil (Fig. 6). Sparse infestations arise from the few

Fig. 6 *Aerial photographs of spread of the stem nematode* (Ditylenchus dispaci*) in fields of lucerne (alfalfa) where pieces of infested plant tissue were scattered above ground by harvesting machinery*



Legend to Fig. 6:

7a- 7d: initial spread around initial focus and along rows.

7e: later spread showing widely scattered infestations.

infested seeds that escape routine fumigation, and crop symptoms appear in the year after sowing (Atkinson & Sykes, 1981) because the stem nematode multiplies more rapidly than *Heterodera* or *Globodera* spp. Further patterns appear in subsequent years and, by the fourth and fifth, are widely scattered and confused, especially in fields where harvesting proceeds in different directions in different years. Much the same invisible patterns would be expected within cyst-nematode infested fields of north-west Europe where surface irrigation (as opposed to spray irrigation) is rare.

Occasionally, sharply defined patches of intensely infested plants are found in sugar beet fields. These seem to be the result of soil being dumped during harvesting, the soil having fallen from the roots of heavily infested plants into the bottoms of haulage vehicles and subsequently dumped. "Dump dirt", long recognised as a potent source of infestations, is retained at sugar beet factories until "safe" to be disposed of.

Exploitation of occupied territory

Territory is not fully exploited until populations of the order of 100 eggs /g soil are established. Initially, populations of *G. rostochiensis* increase within domains, or small groups of domains, with each host crop grown until they oscillate about an equilibrium. In greensand soils at Woburn, UK, this averages about 85 eggs/g soil when potatoes are grown each year. Average population estimates in bulk soil samples collected from large plots or fields obscure such oscillations because domains are out of phase or uninfested (Jones & Perry, 1978). As populations increase the extreme variations in population density within fields decrease, but they still vary appreciably from place to place. Regular rotations of susceptible potatoes, one year in two, three, four, five or six, also tend towards equilibria at the end of each cycle, taking a few cycles to settle down. The next potato crop is subjected to these end-of-cycle population densities. According to the model of Jones & Perry (1978), these equilibria approximate to 57, 38, 25, 17 and 11 eggs/g soil. In practice, because of the effects of aging, the last three densities would probably be somewhat less harmful than the figures suggest. These tentative

values fit with field experience in the potato growing areas of East Anglia, where the nematode is well established. A one year in three rotation leads to appreciable yield loss. Farmers tend to be satisfied with potatoes one year in four, but one year in five or six would be better when relying on crop rotation alone for control. In such fields, where available territory is almost fully exploited, crops on a one in three or one in four rotation may make uniform top growth without much evidence of patchiness but yields may be disappointing (Anon, 1982).

Exploitation of territory proceeds faster than the curve of spread in Fig. 5 suggests because cysts that fall on domains already occupied add recruits to the population already there, effectively increasing the population density (Jones, 1988). This effect increases as competition intensifies and is greatest in the last stages of colonisation. It may help to explain the sudden appearance of stunted patches as, for example, in the potatoes of the ley-arable experiment at Woburn Experimental Farm (Fig. 2) and in the sugar beet in the Norfolk field where beet-sick patches appeared in the ninth year of continuous cropping. Other similar examples are known.

Note: Text on the effect of climatic stress on potato tuber yield was supposed to be inserted here but unfortunately was not located.

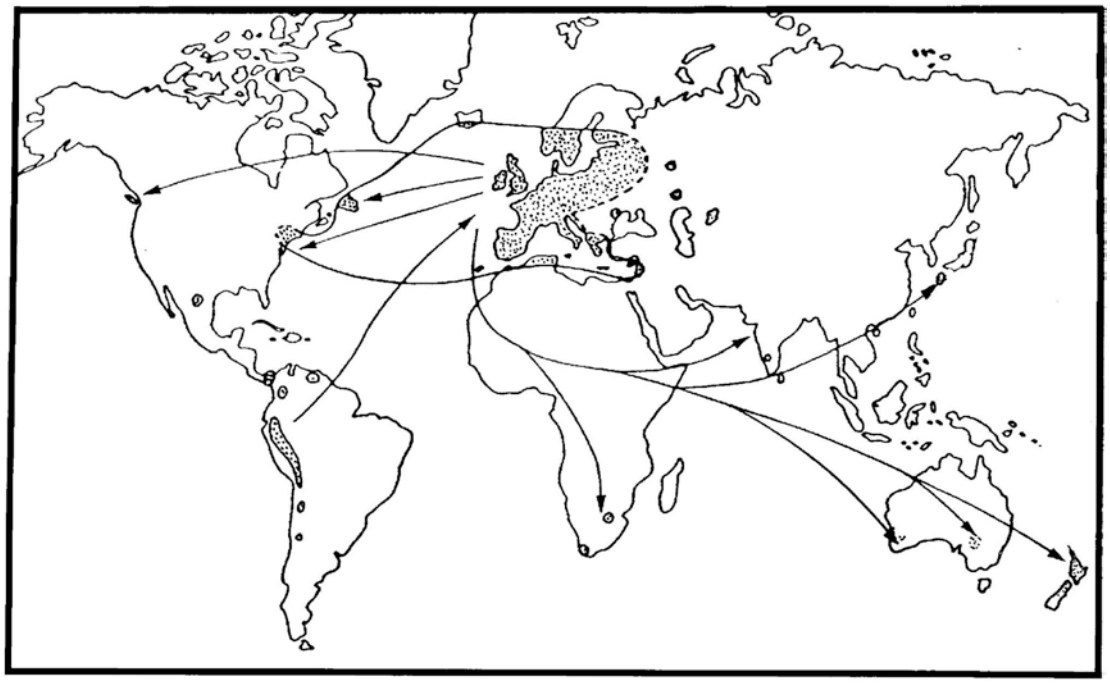
World spread

Cyst nematodes occur widely in many countries throughout the world: their origins are obscure. Some have narrow host ranges confined to a few genera in one plant family, while others have a wide range of hosts in several plant families. For the first group, one may postulate that they co-evolved in a discrete epicentre along with a branch of their host family. The second may have co-evolved in a mixed plant community occupying some special habitat. Incomplete knowledge of host ranges makes it impossible to suggest where. However, there seems little doubt that tuberous Solanums and the two known sibling species of potato cyst nematode co-evolved in the Andes mountains of South America. The first record elsewhere was that of Kuhn

who observed cysts on potatoes in Germany in 1881. The next was from Scotland in 1913, then described as "a common pest of potatoes". Potato cyst nematodes were established in the UK by the 1920s, in the Channel Islands, Sweden and Denmark by the 1930s, and in Long Island, New York, USA by the 1940s (Franklin, 1951). From then on they were found on potatoes increasingly in Europe, around the Mediterranean basin and in other parts of the world. Until *G. pallida* was differentiated from *G. rostochiensis* (Stone, 1973) the two species were confused. The spread of both from their epicentre is shown in Fig. 7. The distribution of the species is not always coincident about the world or within countries. Nor do the introductions include the full range of genetic variations present within the epicentre of both species due to founder effects (Gonzalez-Andujar, 1972). For example, the infestation with *G. rostochiensis* in Long Island, USA, seems to be one race or pathotype that is differentiated by the inability of all but a few individuals to complete female development on potatoes possessing resistance gene H_1. Populations of this type were also the commonest in Scotland and most of the rest of England and Wales, but widespread plantings of potatoes with resistance gene H_1 during the last 30 years have led to its replacement by *G. pallida* where previously it was rarely noticed.

Note: Unfortunately, text remains unfinished beyond this paragraph.

Fig. 7 *Dispersal of potato cyst nematodes from their Andean epicentre*



Legend to Fig. 7:

Map to illustrate the combined spread of *G. rostochiensis* and *G. pallida* from their centre of origin in the Andes to eight other parts of the world (modified from Jones & Jones, 1984)

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