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SPECIAL REVIEWS

THE USE OF STICKY TRAPS AND THE RELATION OF THEIR CATCHES OF APHIDS TO THE SPREAD OF VIRUSES IN CROPS

M. A. WATSON and G. D. HEATHCOTE

In Great Britain aphids are the vectors of many important viruses affecting crops, and their number and distribution determine virus-spread.

Fluctuations in numbers of aphids infesting particular crops can be assessed either by counting aphids at intervals on the plants or by trapping alatae in flight to or from the crop. Many workers (e.g., Davies, 1932 and 1934; Loughnane, 1943; Simpson, 1940) used the plant-counting method, mostly in the potato crop, but the relation between spread of virus and density of aphid infestation on foliage was often obscure. Doncaster and Gregory (1948) suggested that this was because winged migrant aphids in June were mainly responsible for spreading viruses in the potato crop, and numbers of spring migrants were not necessarily closely related to subsequent infestation, which depended to a large extent on local conditions of weather and cultivation.

Doncaster and Gregory's suggestion has been supported by several workers. When Heathcote and Broadbent (1961) exposed potato plants infected with viruses for successive periods in potato crops, leaf-roll and rugose mosaic spread from them early in the season when aphids were few, but not in mid-season when they were numerous. Burt, Heathcote and Broadbent (1964) sprayed potato crops with insecticide at different times, and found that only the earliest spraying decreased spread of leaf-roll virus. At this time there were few apterae on the crop, but fairly numerous spring migrants entering it. Broadbent (1952) also found that leaf-roll and Y viruses spread from infected to healthy potato plants in plots surrounded by sticky boards to prevent inter-plot movement of apterae. All these results suggest that potato viruses depend mostly on spring migrant aphids for their spread.

To try to estimate the aerial aphid population, Doncaster devised "a simple form of adhesive trap, cheap to construct and easy to operate, which could be used in conjunction with the potato fields to be sampled each season". This became the well-known "sticky trap", forms of which are still in general use, although other apparatus has been devised, such as the suction-trap (Johnson, 1950a) and Moericke's water-trap (1949).

Doncaster's original trap, first erected in 1941, consisted of a 3-ft length of galvanised iron chimney-pipe, diameter 5 in., mounted on a stake with its top 6 ft above the crop in a corner of a potato field. The surface was coated with grease-banding material, "pale in colour and of a clear, even consistency". This material remained sticky for considerably longer than the 7- or 8-day intervals at which aphids were removed from it, and it was renewed. Doncaster picked off the aphids *in situ* with the point of a knife or

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a needle, with their embedding grease, which was later dissolved away and the aphids stored in phenol till they could be identified. A disadvantage was that removing the aphids took a lot of time and had to be done when other field work demanded attention. Nevertheless, Doncaster operated the traps for several years in many parts of the country, and the value of the information obtained (Doncaster and Gregory, 1948) can hardly be over-estimated, either for the potato crop itself or for the impetus it gave to the study of other virus diseases of agricultural crops.

Doncaster's sticky traps were adapted for use in sugar-beet fields in 1943. The first were 6 ft × 2 in. timber stakes with the upper 3 ft coated with grease-banding material, giving a surface of 2 sq ft, from which aphids were picked *in situ*. Later, Hull and Watson developed a drum-shaped trap with a detachable cover (10 × 15 in. = 1 sq ft approx.) carrying the grease-banding material. The covers could be sent by post in special containers from anywhere, and required no entomological knowledge to operate. This type of trap, described by Broadbent, Doncaster, Hull and Watson (1948), is still in use, with little modification, except that most are now painted yellow (Broadbent and Heathcote, 1961).

Adhesive traps do not measure the aerial aphid population, because their catches depend too much on topography of the land and height and colour of the traps. The extent to which light colours, particularly yellow, attract aphids differs with species (Moericke, 1962; Broadbent, 1948; Heathcote, 1957a). Comparison of catches on sticky traps with those by suction traps, tow-nets and water traps (Johnson, 1950b; Heathcote, 1957a) showed that, although sticky traps catch fewer aphids than do suction or water traps, they catch enough to show when aphids are flying. Sticky traps have the advantage of requiring much less attention than most other types. Their catch consists of aphids attracted to the trap and those impacted on it by wind. Heathcote (1957b) compared cylinders of different diameter and found large traps preferable because, although they catch fewer per unit area than small traps, their total catch is greater.

Potato Viruses

Broadbent (1948) showed that cylindrical sticky traps set at ground level and at about 2 and 5 ft above potato crops caught different numbers of aphids, particularly of *Myzus persicae* (Sulzer). In 1947, during the peak period of infestation, 249 *M. persicae* were trapped 5 ft above the crop, 75 at 2 ft and only 16 at ground level. This did not reflect the distribution of other species. *Aphis fabae* Scop. was evenly distributed between the three traps, and *Cavariella aegopodii* (Scop.) slightly more numerous on the lowest one. However, similar numbers of all species were caught on four similarly placed traps 80 ft from each other, so comparison from one centre to another seems justified so long as the traps are similar, and similarly sited.

In multiple regression calculations using trap-count and field-count aphids as two independent variants, Broadbent (1950) found the partial regression coefficient for dependence of spread of leaf-roll virus on trap-

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count *M. persicae* to be 0.43 ± 0.020 , whereas the independent contribution of the field-count was negligible; Watson and Healy (1953) found a similar relationship for spread of beet yellows virus; the partial regression coefficient for % plants infected on $\log(n + 1)$ trap-count *M. persicae* was 22.9 ± 4.7 , showing a 20% increase in plants infected for every 10-fold increase in aphids trapped, whereas the contribution of apterae on the plants was small and insignificant (4.0 ± 2.8). It is wrong to assume that these results necessarily preclude spread by apterae, for apterae of all vector species can transmit viruses, and may do so provided they move from infected to healthy plants. Any condition that encourages them to move, such as favourable weather, the passage of agricultural machinery, scientific investigators making frequent observations and some insecticides (see p. 298), can increase spread of virus by disturbing aphids. When apterae become very numerous on plants they probably move frequently of their own accord, but at this time alate generations are produced whose numbers depend on those of the infesting apterae, so that correlation analyses cannot distinguish their independent effects. Apterae move voluntarily within the crop at the time of peak infestation, usually in July and August, when the crop is well grown. If virus has already spread early in the year many plants will be infected by July or August, so only a small proportion of apterae can initiate infections. When virus spreads late more may initiate new infections, but in most crops these will be less important than earlier infections, because older plants tolerate infection better than young ones and are less damaged. Older plants are also usually more difficult to infect and take longer to develop symptoms, which may not show before harvest. Tubers of late-infected potato plants often remain virus-free (Broadbent, Heathcote, McDermott and Taylor, 1957). When virus spreads most rapidly early in the growing season plants are small and apterae are few and cannot easily move from plant to plant. When apterae become numerous and plants are meeting in the rows their contribution is often not reflected in the final virus estimates or crop yields. This explains why the partial regression coefficients relating virus-spread to counts of apterae on plants are sometimes negative.

The very large errors associated with counting aphids on plants result from discontinuity both in time and space. Aphids multiply on crops exponentially and often very rapidly. They can increase by a factor of ten in about a week, and it is impossible to examine all fields at the same stage of infestation. Populations are also far from uniform, even in one crop, and there can be large differences in small areas caused by the direction of aphid immigration or topographical and cultural differences between crops or parts of crops. These sources of error influence catches on sticky traps much less, for the traps operate continuously and can be sited so as to minimise topographical differences.

Sugar-beet Viruses

The importance of early infection in sugar-beet crops introduced by spring migrant *M. persicae* was demonstrated by Watson and Healy (1953) using results from a survey of aphids and virus diseases of sugar beet made

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between 1943 and 1948 (Watson, Hull, Blencowe and Hamlyn, 1951). Healy produced a simple mathematical model which, in effect, predicted spread of virus during the season, knowing only the earliest recorded percentage of plants infected and the totals of alatae of *M. persicae* caught on sticky traps at about 3-weekly intervals, this being the average time in which a sugar beet might be expected to show symptoms after becoming infected in the field. When fitted to results for 95 root crops the calculated values fitted the observed values very closely and accounted for 82% of variance between fields, whereas the regression coefficients fitted to un-

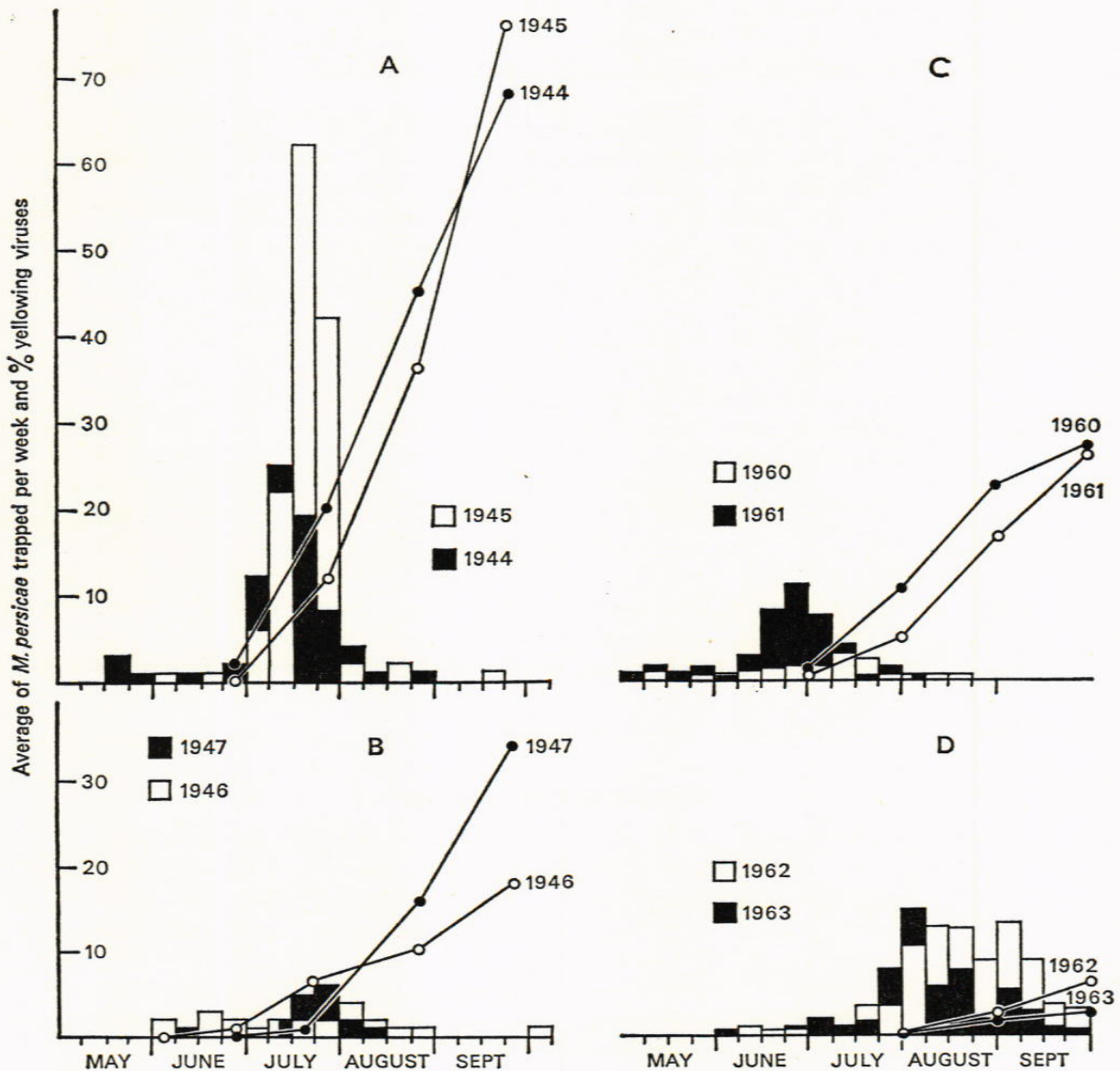


FIG. 1. Spread of beet yellowing viruses in sugar-beet crops showing the effects of time of migration and numbers of *M. persicae* in 1944-47 and 1960-63. (See text, p. 296).

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converted sticky-trap counts accounted for only about 40%, and the contribution of total apterae was again negligible.

Fig. 1 illustrates the effect of time when *M. persicae* migrate on spread of beet yellows and beet mild yellowing viruses together; these although recognised (Watson 1952), were not distinguished from each other in the field until Russell (1962) described methods of doing so. The histograms show average weekly trap-catches of *M. persicae* from May to September, and the curves, increasing percentage of plants infected with yellowing viruses. In 1944 and 1945 (Fig. 1 (a)) and 1960–61 (Fig. 1 (c)) early invasion of the crops by spring migrants led to widespread virus attack, but in 1946–47 (Fig. 1 (b)) and 1962–63 (Fig. 1 (d)) no aphids were caught during May, invasion was late and virus spread more slowly, especially in 1962–63, in spite of moderately large and long-lasting infestation of the crops during late summer.

Plants showing symptoms in July may have their yield halved (Watson, Watson and Hull, 1946), and much of the crop is lost when virus spreads early; delaying infection makes losses progressively less.

Results for all 8 years (Fig. 1 (a–d)) suggest that for a given number of aphids at any time beet yellowing viruses may have spread more in the 1940s than in the 1960s (see also Hull, 1966). This is probably because in 1951 Hull (1952), as a result of the survey made between 1940 and 1948 (Watson, Hull, Blencowe and Hamlyn, 1951), introduced measures to improve the health of the sugar-beet seed crops, which till then had been a large source both of over-wintering virus and of spring migrant *M. persicae*. The direct effect of these measures is difficult to determine, because weather and aphid numbers have varied in relation to the other factors, and because beet yellows may have been partly replaced by the more persistent but less damaging beet mild yellows. However, the non-persistent beet mosaic virus, which was very common up till 1950 and is very dependent on seed-crops for its source (Watson and Healy, 1953), is now rare, which suggests that seed-crops have ceased to be an important source of viruses.

Systemic insecticides, which are now widely used to control beet yellowing viruses, may have contributed to the decline of virus incidence by decreasing the ambient aphid-populations but another decade of trapping will be needed to know whether this is so.

Viruses in Other Crops

The value of sticky traps in providing a simple method of measuring fluctuations in aphid numbers has been amply demonstrated for potatoes, and for sugar beet (Heathcote, 1966). They have also been used successfully in studying aphid vectors of viruses affecting other crops, including carrots, which can be crippled by carrot motley dwarf virus. The vector, *Cavariella aegopodii*, is one of the most numerous British aphids, and often comprises half the total aphids caught on sticky-traps during May, June or July. A large spring migration can infect 100% of carrots by the first week of June (Watson and Serjeant, 1963), in contrast with beet yellowing viruses, which rarely infect more than 5% of the beet crop before the beginning of July. The yields of carrot crops untreated by insecticides can be

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predicted with some accuracy from the numbers of spring migrant *C. aegopodii* caught on sticky traps in their vicinity. Fig. 2 shows the yields of untreated plots in experiments made in different parts of Great Britain during the years 1959–65, plotted against $\log(n + 1)$ sticky-trap catches up

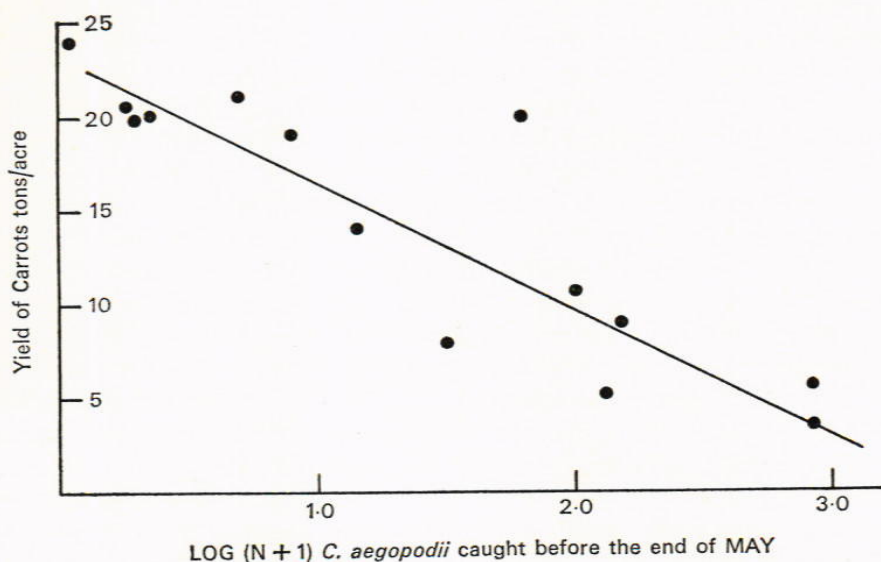


FIG. 2. Relation of yield of untreated plots on carrot experiments for 1959–65 inclusive, to mean numbers of *Cavariella aegopodii* caught per trap before the end of May (N).

Regression coefficient $b = -6.9 \pm 1.11$.

till the end of May. About 6 tons/acre of carrots were lost for each 10-fold increase in number of spring migrants caught.

Whether causally or not, therefore, spread of viruses such as beet yellows and carrot motley dwarf, whose vectors may remain infective for some days, is closely related to the numbers of winged vector-aphids. Estimates of the relationship can be improved by taking account of the time at which virus is first introduced, which emphasises the importance of early spring migrants.

The most damaging virus of cereal crops in Great Britain is barley yellow dwarf (Watson and Mulligan, 1960), but it is less frequent and widespread here than in the U.S.A., Australia and New Zealand, where the warm, dry summers are more suitable for aphid movement. New Zealand has an "early-warning" scheme, forecasting outbreaks of barley yellow dwarf, based on sticky-trap information (Close, Smith and Lowe, 1964).

Barley yellow dwarf was widespread in spring-grown crops in Great Britain in 1960 and 1961, and crops sown in autumn 1961 suffered because they were infected soon after they emerged. Since then it has not seemed to do much damage, although there have probably been small annual losses caused by late infection with virus carried by summer migrations of grass aphids such as *Metopolophium dirhodum* (Walker). Young oat plants placed out of doors in early July 1965 became infested with *M. dirhodum* and were severely affected by virus in August. Maturing plants in field

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crops then showed no obvious virus-symptoms, but many must have been infected.

Non-persistent Viruses

The viruses so far discussed belong to the "persistent" group of aphid-transmitted viruses (Watson and Roberts, 1939), so called because aphids can transmit them for some days after they become infective. Vectors of the contrasting "non-persistent" viruses remain infective for less than an hour while feeding and for a few hours while fasting. Persistent viruses can be carried long distances by aphids, whereas non-persistent ones usually come from a nearby source. A large population of active vectors is needed to spread non-persistent viruses, because most vectors infect only one plant, whereas vectors of persistent viruses may infect many. Conditions favouring the spread of non-persistent viruses are fulfilled when large spring migrations of alate aphids move into crops that already contain some infected plants, grown from vegetative parts of plants, such as tubers or bulbs, or in which virus is seed-transmitted, or biennials such as sugar beet (Watson, Hull, Blencowe and Hamlyn, 1951) and brassicas (Broadbent, 1957) which over-winter to provide the following year's seed-crops. Watson (1937) gave an early example of this last type of spread for the drug-crop, *Hyoscamus niger*; new crops continuously became re-infected with henbane mosaic (Hy 3) and potato virus Y (Hy 2) when old crops were kept for a second year.

Non-persistent viruses cannot spread unless aphids are numerous. As with vectors of persistent ones, this is indicated by trap-catches. However, their spread is less well correlated with trap-catches, for non-persistent viruses spread only from nearby sources of infection, whose incidence differs greatly from place to place. This decreases the variance of virus-spread accounted for by aphid numbers (Broadbent, 1950; Watson and Healy, 1953). The many species able to transmit some non-persistent viruses also contribute to such irregularity, although only a few species usually need to be considered for any particular crop. However, many species are affected by the same conditions, and their numbers are usually correlated.

As non-persistent viruses can be acquired by aphids in a few seconds, and can be transmitted immediately to a healthy plant, their spread is not easily controlled by insecticides and may even be increased. Broadbent *et al.* (1951) attributed increased spread of lettuce mosaic to activity by alatae irritated by an insecticidal dust containing DDT. Broadbent and Heathcote (1957) observed this "disturbance effect" in plots of *Narcissus* treated with insecticides. More plants became infected with yellow stripe (mosaic) virus (Broadbent, Green and Walker, 1963) in plots sprayed with DDT or treated with mazidox (a systemic, organophosphorus insecticide) than in untreated plots (the mean percentages were: unsprayed 7.3; DDT 19.4; mazidox 12.7; S.E. \pm 2.3). The aphids disturbed were almost certainly alatae visiting the plants temporarily, as no apterae were found during the three years the plots were observed. It is not known which species of aphids acted as vectors (Blanton and Haasis in 1942 described seven aphid species

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as vectors in Holland), but more alatae were trapped and virus spread more in 1954 than in 1953 or 1955. Most new infections were in plants near to ones previously infected, providing some evidence both that a nearby source of virus is essential and that many aphid flights within crops are short. Spread of beet yellows virus, which, though persistent, survives only about 36 hours in the vectors, was also shown to be increased by such insecticides as DDT and chlordane (Hull and Gates, 1953; Dunning and Winder, 1965).

This account of the uses of sticky traps shows that, though they do not give accurate enough information for population studies comparing different species of aphids in different localities, their catches can be accurately related to virus spread when proper qualifying assumptions are made. They are, as Doncaster said, a cheap and easy way of assessing the spring migrations of aphids that initiate early and damaging outbreaks of viruses in crops. Accurate evaluation of the meteorological factors that determine their numbers and distribution in time is the first requirement for predicting virus-outbreaks: prediction is a growing need to meet the potential dangers from increasing use of persistent organophosphorus and chlorinated hydrocarbon insecticides by ensuring that they are not used unnecessarily or wastefully.

One advantage of the trapping method over the plant-counting method is that each catch provides information about all migrant species, whether it is wanted for that particular investigation or not. The whole catch is preserved and can be referred to after many years. Collaboration between workers on different viruses already exists, with much economy of labour. It could easily be extended, were there workers to sort and identify the whole catch, and the behaviour of different viruses and their vectors could then be compared. The whole picture would provide a better basis for prediction than the parts.

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

F. G. W. JONES

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

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