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Report for 1962

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NEMATOLOGY DEPARTMENT

F. G. W. JONES

In June H. R. Wallace attended a meeting of the American Society of Parasitology in Washington, D.C.; in July J. B. Goodey, F. G. W. Jones and H. R. Wallace assisted in a nematology course at Cornell University, Ithaca, and afterwards visited research centres in the U.S.A. and Canada. J. E. Peachey visited the Channel Islands in July and September. Several members of the department assisted with the nematology course at Imperial College Field Station, Sunninghill. M. Bravo Lima (Oeiras, Portugal) and D. W. Larbey joined the Department to work for three years on taxonomy and the bionomics of *Xiphinema*, respectively. M. Rafiq Siddiqi (Aligarh, India) was employed from April to October. C. D. Blake and J. M. Webster were awarded Ph.D. degrees of London University.

The revised edition of the late Tom Goodey's book on *Soil and Freshwater Nematodes* appeared in March 1963.

Systematics and Bionomics

Several new species of nematodes were found and have been or are being described. The new subgenus (*Cephalenchus*) has been made for a new species of *Tylenchus* from the Côte d'Ivoire. It has a rounded, offset head, coarse annulation, six lateral incisures and lateral vulval flaps. A new British species of *Boleodorus* from around grass roots shares some characters, which may be of generic value, with *B. thylactus* but not shown by *B. clavicaudatus*. A new British species of *Criconemoides* was described, and the constitution of the family *Criconematidae*, its subfamilies and genera is under review. A new species of *Aphelenchoides* was described from South India. Nematodes from rotting Gardenia buds reported last year as *Aphelenchoides* were found on closer study to be a new species of *Bursaphelenchus*. Species of this genus are usually associated with wood-boring insects, and they live in the tunnel frass. When cultured on the fungus *Botrytis cinerea* at 20–25°, the life cycle lasted about 6 days. Like the dauer larvae of other species of *Bursaphelenchus*, third-stage larvae had a weakly developed oesophagous without a mouth stylet; they predominated in the old cultures and, like dauer larvae, withstood adverse conditions better than other stages of the nematode. (Franklin, Goodey, Hooper, Lima, Siddiqi)

Aphelenchoides blastophthorus from buds of *Scabiosa caucasica*, the type host, readily reproduced on cultures of *Botrytis cinerea*; yet another example of a nematode that includes fungi and higher plants among its hosts. (Hooper)

Nematodes in the families Longidoridae and Trichodoridae, which contain species acting as vectors of soil-borne viruses, received more attention than previously because of this new knowledge of their behaviour. Populations of *Xiphinema* collected around the roots of grape-

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vines in Portugal, previously identified as *X. americanum*, probably contain new species, as do collections from around sugar-cane roots from the same country. These and collections from Britain, Canada, India, Nicaragua, Portugal, Tunisia and the U.S.A. are being studied. A new species of *Longidorus* was described from Florida, and a new genus, *Paralongidorus*, has been made to accommodate species with a stylet and guide ring like *Longidorus* but with wide amphid openings and amphids like *Xiphinema*. The type species, *P. sali* n. sp., came from India; other species are *P. sacchari* n. sp. associated with sugar-cane roots in India and Australia, and *P. citri* with citrus roots in India. New species of *Trichodorus* were described from Britain, India, Nicaragua, North Borneo and Tunisia. Yet another species was found in virus-infective soil in Britain, but is not yet described. (Hooper, Lima and Siddiqi)

Longidorus elongatus, *Pratylenchus crenatus*, *Tylenchorhynchus dubius*, *Aphelenchus avenae*, *Tylenchus* spp. and *Rhabditis* were recovered alive from moist Scottish sandy soils kept for 2½ years in polythene bags in the dark at room temperature. Adults and larvae of *Longidorus* appeared not to have fed recently, for the soil in the bags contained no live roots, and the gut cells of most contained few of the granules usually present. Larvae and adults extracted from some of the soils fed on roots of cucumber seedlings, but did not transmit virus to them, so presumably they had become virus free. (Harrison, Plant Pathology Department, and Hooper)

In plots where populations of soil arthropods were controlled at different levels by insecticides, nematode numbers did not differ significantly from those in untreated controls, but cultivation and fallowing caused a steady decline. (Doncaster and Edwards, Entomology Department)

Feeding and Oesophageal Structure

Improved methods for making serial sections of the oesophaguses of nematodes were devised. Accurate orientation of nematodes for sectioning is possible using double embedding in agar and wax, and marking the "head" of the agar block with Indian ink. Special block holders are drilled to take a plug of wood or cork, the end of which is trimmed off perpendicularly. A wall of adhesive tape is bound around the upper end of the plug to make a cavity with the plug as base. This is filled with molten wax and the marked agar block laid on the base, on its side for longitudinal sections and on end for transverse sections. The wax block is trimmed with accurately parallel sides to ensure straight ribbons, using a lathe as a shaping machine. Parallelism is essential if closely spaced sections are to be readily found under the highest powers of the microscope. The method was used to study the oesophagus of *Rhabditis*, and is being applied to *Diplogaster*, *Plectus*, *Cephalobus*, *Panagrolaimus* and *Tylenchorhynchus*.

Examination of sections of *Rhabditis* confirmed Chitwoods' description of the oesophagus, the oesophageal glands, their ducts and most of the musculature, but longitudinal sections showed no trace in the posterior bulb of muscles supposed to return the bulb flaps to the resting position.

By making working models and taking film sequences of *Rhabditis* and

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Pelodera, especially *R. oxycera*, while feeding on bacteria or yeast grains heavily stained with Janus Green, the method of feeding and the form and function of the bulb flaps were determined. The organ described by the Chitwoods' as the "oesophago-intestinal valve" was renamed "oesophago-intestinal cells" because film sequences show these are inert and the true valve is further forward in the oesophago-intestinal canal. Dilation of the oesophagus during feeding draws water and particles in suspension through the stoma. On collapsing, the oesophagus holds the food particles while water is expelled through the mouth. Later dilation sweeps the particles backwards. Ingested spores sometimes prevent the flaps in the posterior bulb from inverting. In one worm a spore that caused obstruction was crushed and passed on into the intestine. Usually, however, stained yeast grains are not crushed. Whether or not the flaps crush the food particles, they assist transport of larger particles backwards to the haustrulum (the chamber behind the bulb flaps) and, during inversion, form part of the inlet valve. The valvular function of the three-rayed, oesophageal lumen has not previously been sufficiently appreciated. It can be closed completely or dilated widely, yet the bulb flaps and the oesophageal cells have wrongly been considered as important valves. (Doncaster)

Biology of *Tylenchorhynchus macrurus* and *T. icarus*

The frequency distribution of the body length of male and female *T. macrurus*, from a grass plot in Great Field, indicated that there were two distinct size groups in each sex. This introduced a complication into field studies, because differences between the small form and other nematodes of a similar size, such as *Rotylenchus*, were too small for accurate and rapid counting under a low-power microscope. Examination of the two size forms indicated that there were differences other than body length, and the large and small forms were distinguished as *T. icarus* n. sp. and *T. macrurus*, respectively. Later field and laboratory observations were confined to adults of the easily distinguishable large form, *T. icarus*.

Soil samples taken from the soil profile after a week of rain (0·8 cm) and after a week when no rain fell indicated that: (*a*) most *T. icarus* occurred about 5 cm deep corresponding to the greatest root concentration; (*b*) there were few nematodes below 24 cm, the boundary between top- and sub-soil; and that (*c*) numbers in the top 5 cm decreased during the dry period. When the top 5 cm of soil was sampled at intervals during July and August 1961 the numbers fell after a period with little rain and rose again after rain, showing the importance of soil moisture on populations of *T. icarus*.

Laboratory experiments showed that: (*a*) in a soil moisture gradient, a population of *T. icarus* migrated to the wet end; (*b*) movement in soil was greatest at a moisture content corresponding to field capacity; (*c*) the optimum temperature for movement was about 20°; and (*d*) that nematode movement decreased only when the osmotic pressure of the soil solution was equivalent to that of 10^{-1} *M* urea, i.e., 2·24 atmospheres. An osmotic pressure of 22·4 atmospheres inhibited movement completely; nevertheless, *T. icarus* recovered when transferred to water after 4 days at this high

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osmotic pressure. About 35% of a population of *T. icarus* survived after being in soil without host plants for 32 weeks. These observations suggest that the vertical distribution of *T. icarus* in the soil profile may result from migration to different zones under the influence of environmental stimuli. The migratory habits of other free-living stages of plant nematodes may be similar. (Wallace)

Tests with the Cartesian diver microrespirometer showed that the apparatus was a useful tool for studying the influence of various factors on nematode metabolism. The oxygen consumption of *T. icarus* increased with increase in osmotic pressure up to about 22 atmospheres in urea, after which it decreased. At 45 atmospheres oxygen consumption was very small, and examination of the nematodes at the end of the experiment showed that they were probably dead. These results confirm that adults of *T. icarus* can withstand osmotic pressures up to about 22 atmospheres and suggest that they actively oppose the drying effect of the environment.

In damp sand at 10° oxygen consumption of *T. icarus* was steady for 16 weeks, but by 32 weeks it had decreased, indicating the possible onset of senescence. After 48 weeks the body contents of the nematodes were disorganised and, as the nematodes showed no sign of movement, they were presumed to be dead. The oxygen consumption of the dead nematodes was greater than that of the living ones, presumably because of bacterial and fungal activity within the decaying bodies. This result shows that in experiments using lethal treatments, measurements of oxygen consumption to have any meaning in terms of nematode respiration should be taken as soon as possible after the start of the treatment. (Greet and Wallace)

Biology of *Panagrolaimus rigidus*

The best way of observing the behaviour of single individuals was in a drop of Nigon's nutrient agar in the well of a cavity slide. Nematodes and eggs of known history could be observed directly, and the rate of egg laying, hatching and moulting could be counted accurately.

At 24° the life cycle of *P. rigidus* was 6 days from newly laid egg to the first eggs of the next generation. The eggs hatched about 48 hours after laying, and the new generation reached maturity and were laying eggs themselves 4 days later. The average rate of egg laying was about two per hour per female; over 230 eggs were laid per female in 120 hours, when the experiment was discontinued.

Experiments were also done to see whether individuals of different sexes attracted each other. Tubes of clear water agar were divided in half by a cellophane barrier. Nematodes, which had been reared singly, were introduced on to the agar at the mid point of each half of the tube and their distribution along the tube was determined after about 17 hours. When males and females were introduced into opposite halves of the tube both sexes tended to aggregate at the cellophane barrier. No aggregation occurred when nematodes of the same sex, male or female, were introduced into opposite halves of the tube. These results indicate that: (*a*) males and females of *P. rigidus* attract each other; (*b*) the attractant is probably a

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chemical of small molecular weight because it diffused through the cellophane; and (*c*) each sex produces a specific attractant.

Observations on dense mixed populations of *P. rigidus*, however, also indicated tactile response of males to females. Thus, contact between a female and the posterior third of the male appeared to initiate an involuntary coiling response around the female which sometimes led to copulation. The duration of copulation ranged from 30 seconds to over 30 minutes. These experiments required nematodes of known sexual history, and so each individual had to be reared in a separate culture chamber. (Greet)

Biology of *Ditylenchus dipsaci*

The oat race of the stem eelworm *D. dipsaci* invaded resistant and susceptible oats and formed cavities in both by withdrawing cytoplasm from the cells and causing the walls to collapse. In the susceptible oat, Sun II, separation and hypertrophy preceded the breakdown of cell walls, whereas in the resistant variety Manod cavities formed without cell separation, and growth and reproduction were restricted, presumably because feeding was restricted or the cytoplasm lacked an essential growth substance. The number of larvae invading Sun II seedlings was proportional to the inoculum level. Many larvae remained in the spaces between enfurled leaves of Manod, where they caused little tissue disturbance.

When inoculated while germinating, 33% of Manod and 45% of Sun II seedlings were killed. Lucerne and oat races of *D. dipsaci* both invaded lucerne and oat seedlings but reproduced only in their original host. Fewer larvae invaded roots than pseudostems, and the nematodes reproduced only in pseudostems.

The body and gonads of nematodes from Manod were shorter than those from Sun II, but the sex ratio was the same on both varieties. Growth was in steps corresponding to moults. The growth curve in Manod was the same as in Sun II, except that growth was slower. Gonads lengthened rapidly in the late-fourth-stage larvae and early adult stage, as though they had received some stimulus that increased their growth rate relative to other organs.

Larvae separated by a dialysis membrane accumulated around seedlings growing in sand or aseptically on agar. In the rhizosphere, larvae seemed to orientate along a concentration gradient of secretions from roots, but elsewhere they moved at random. The optimum temperature for migration was 15–20°, more larvae invaded plants at 20° than at 8°, and reproduction was fastest at 20° in carrot callus tissue, but at 8° in oats. (Blake)

Tulip is resistant to the narcissus race of *D. dipsaci*. In a pot experiment in which the narcissus race was inoculated into narcissus and tulip bulbs the population increased sixfold in the narcissus bulbs but did not rise above the level of the original inoculum in the tulip bulbs. Nevertheless, as in the resistant oat Manod, some nematodes reproduced. (Webster)

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Egg-hatching Factors

The bioassay techniques long used to assay potato-root eelworm hatching-factor (see page 105, Biochemistry Department Report) were made more rapid and less tedious by a simple pipette devised to set up batches of cysts and by estimating the number of larvae that hatch by absorptiometry. Counting is no longer essential. Using the pipette and increasing replication to give dense suspensions of hatched larvae has increased the number of cysts used per week to 80,000, and 9 months' supply of cysts has been extracted from about 10 tons of soil.

In setting up batches with the pipette an aqueous suspension of cysts is thoroughly mixed with a vibrator. For reasons unknown this treatment sometimes upsets hatch. Hand-picked cysts from Woburn give a mean of 120 hatched larvae/cyst in undiluted root diffusate; vibrated and pipetted cysts give only 37 larvae/cyst, but vibrated cysts dried overnight and then presoaked, give an almost normal hatch (104 larvae/cyst). Many years of experimentation with cysts have shown how sensitive hatching is to the laboratory environment, and for reasons unknown hatch from cysts of the same source often fluctuates widely.

In estimating larval hatch by absorptiometry errors occur mainly from absorption of light by bacterial and fungal debris. Provided readings are taken quickly, the sedimentation of larvae from the suspension does not affect readings. The method is unsuitable with fewer than 300 larvae/ml. Attempts are being made to lessen microbial contamination by using bacteriostatic and fungistatic substances to prevent the organisms affecting either the hatch or the estimation of hatch by absorptiometry. (Gander and Jones)

After finding that some dyes stimulate the hatching of eggs of *H. schachtii*, other compounds with more simple structures were tested to try to identify the structural features associated with hatching activity. For this the bioassay technique was simplified so that many compounds could be tested. Each compound was first used at a single dilution within the range 10^{-2}–10^{-3} *M*. If compounds with hatching activity affect the same mechanism the molecular concentration required for activity might be similar for all of them. The threshold concentration (i.e., that at which hatch approaches that in water) for partially purified *H. rostochiensis* hatching factor is between 10^{-8} and 10^{-9}. The threshold concentrations for auramine and nile blue sulphate as hatching agents for *H. schachtii* are between 3×10^{-7} and 3×10^{-8}, and 7×10^{-7} and 7×10^{-8} respectively in absolute concentrations. Compounds which showed activity at 10^{-3} *M* are being tested over a range of dilutions to find their threshold concentrations and maximum activity.

The degree of activity of artificial hatching agents can be expressed in various ways. The simplest method is to express the hatch as a percentage of that in a standard root diffusate. This was done in the work with dyes, but it does not take into consideration differences in the water hatch of *H. schachtii*, which can range from 5 to 60% of the diffusate hatch even with cysts from the same source. An alternative is to express hatch as a percentage of cyst contents, taking neither water hatch nor diffusate hatch

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into consideration, but this makes no allowance for the different reactions of cysts to environmental conditions at different times. A hatch rating which covers these contingencies is obtained from the following formula, which applies to hatches greater than in water:

$$\text{Hatch rating} = \frac{h_n - h_w}{h_r - h_w} \times 100$$

where h_n is the hatch in the test compound, h_w the simultaneous hatch in water and h_r the simultaneous hatch in root diffusate. For hatches smaller than in water the degree of inhibition is expressed as follows:

$$\text{Inhibition } \% = 100 - \frac{100h_n}{h_w}$$

Of more than 250 compounds tested, 138 were inactive or inhibitory and 64 active. At their optimum concentrations 19 compounds gave hatches equal to or greater than standard root diffusate. The highest hatch rating was obtained from tolylene blue (329). Methyl ethyl ketone, acetone and picric acid, all relatively simple compounds, had hatch ratings of 162, 138 and 114 respectively, and the dye new blue R, useful in distinguishing living from dead nematodes, had a rating of 100.

Amino acids, sugars and common plant organic acids are not effective hatching agents. As these compounds, many of them common metabolites, do not initiate hatching, the lack of a specific metabolite is probably not a controlling factor in the hatching process. Certain characters recur among active compounds. They mostly have lipophilic properties and either weakly acidic groups, as in benzoic acid, or reducible groups such as nitro, carbonyl or indophenol. Other reducible groups, however, seem not to be active, for example the disulphide group, as in cystine, and some simple quinones and aldehydes. The compounds with weakly acidic groups also contain reducible groups, and the reducible property may be the significant feature rather than the acid function, or the two may be additive.

The dyes that have hatching activity also possess conjugated systems able to undergo oxidation and reduction, but many less-active dyes also have these features, so that other structural characteristics are also important. The active systems are modified by substituent groups and by their spatial arrangement, as in the indophenol systems, where *o*-cresol indophenol (59) is less active than *m*-cresol indophenol (99). Picolinic acid (pyridine-2-carboxylic acid) (-5) is less active than nicotinic acid (pyridine-3-carboxylic acid) (68). In the dyes hydrophilic groups such as sulphonate and hydroxyl lessen activity, as in the series Janus green (124), Janus black (32) and Janus blue (9). Not all the active compounds contain benzene ring systems. Some are aliphatic compounds, such as acetone, and methyl ethyl ketone.

When some of the substances tested with *H. schachtii* were tested with *H. rostochiensis* only four showed slight hatching activity; all four were inactive with *H. schachtii*. Anhydrotetronic acid had a rating of 95 for *H. rostochiensis*, but was almost inactive with *H. schachtii*. Thus, like natural hatching factors, artificial agents show specificity. (Clarke, Biochemistry Department, and Shepherd)

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Distinguishing between Living and Dead Tylenchida

New Blue R, a water-soluble, non-toxic strain, was found useful for distinguishing living from dead nematodes. Dead individuals of *Meloidogyne*, *Ditylenchus*, *Aphelenchoides*, *Aphelenchus* and *Anguina* stained mauve to deep purple after 1–24 hours in a 0·05% solution; living nematodes were unstained. The simplest method with eggs of *Heterodera* is to place cysts in stain for a week and to release the eggs into water by pressure. When the egg suspension is left to stand for a few hours the egg shells destain, and the stained and unstained larvae inside the eggs can then be counted using a magnification of about ×50. The stain enters the body of freshly killed nematodes through the oral and anal openings. (Shepherd)

Biotypes and Biological Races

Work on biotypes of the potato-root eelworm, *Heterodera rostochiensis*, continued, and the ability of different populations to infest different potato hybrids is reported in reference 8.32. When *Solanum nigrum* was grown for 3 years in soil inoculated from 40 populations of the eelworm, cyst numbers fell during the first year but rose above the initial level during the second year: hence biotypes able to reproduce on this resistant race of *S. nigrum* were selected rapidly. In a similar experiment using resistant *S. vernei* for 4 years and a resistant *S. vernei* hybrid for 2 years cyst numbers fell at first, but most populations began to increase again in the fourth and fifth years. In the sixth year the average cyst numbers were one and a half times the initial level: several populations produced 200–600 cysts, increases of five and eight times the initial number. Although resistance in *S. vernei* is stronger than in *S. andigena*, biotypes able to reproduce freely on it will probably be selected in time, although it will take longer than with *S. andigena* which, in the field, requires 4–6 years of continuous cultivation.

This series of tests suggests that different populations of potato-root eelworm from different localities differ greatly in their ability to reproduce on marginal hosts, despite the fact they have all undergone much selection by the past growing of one type of host, cultivated *Solanum tuberosum* ssp. *tuberosum*. For this reason, attempts to divide populations into well-defined physiological races, as has been done for some pathogenic fungi, may prove difficult, because nematodes are not haploid, and the variations observed are probably more the result of recombination in sexual reproduction than of genetic mutation. (Jones)

Attempts are being made to interbreed individuals from different types of potato-root eelworm population to determine the genetics of ability or failure to reproduce on a given host. Cultures of potato-tuber callus and of roots were made in an effort to establish suitable media. The parallel problem of biological races in *Ditylenchus dipsaci* is being studied in cultures of callus tissue. (Webster)

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Nematicides

Over the last three years several experimental and commercial nematicides have been tested against potato-root eelworm in fields and glasshouses. The glasshouse work has been mostly in collaboration with the National Agricultural Advisory Service. Treatment of field infestations of this nematode, and of most others, is uneconomic at present, but this may not always be so, and the results of field trials are of value for glasshouse practice. Field trials are easier to lay down and the results less influenced by previous soil treatments or the diseases prevalent in glasshouses.

Outdoors, methyl bromide applied under a gas-tight sheet was the best treatment; it killed most nematodes, and gave the biggest increase in yield and greatest increase in ammonia-nitrogen. A dust formulation of dimethyl tetrahydrothiadiazine thione (dazomet, "Boots Soil Steriliser"), diluted formulations of sodium methyl dithiocarbamate (metham-sodium, "Vapam") and methyl isothiocyanate ("Trapex", "Trapexide"), all mixed into the soil, were the next best treatments. Dichloropropene-dichloropropane ("D-D") and sodium methyl dithiocarbamate injected into the soil were less effective. Late summer application of "D-D", when the soil temperature at 6 in. was 20°, was better than spring application when the temperature was 10°.

In experiments under glass at seven centres dazomet applied as a dust mixed into the soil did better than liquid formulations of metham-sodium, methyl isothiocyanate or "D-D" injected. At the eighth centre, in Lancashire where the soil was derived from peat moss, the results were different. In another glasshouse experiment methyl isothiocyanate ("Trapex") injected was superior to the same material sprinkled on the surface and covered with waterproof paper. (Peachey)

To assess the effects of nematicide treatments on potato-root eelworm, several assay methods were used. Live eggs were estimated by staining with new blue R, hatchable larvae by plying batches of cysts with potato-root diffusate, and the larvae invading plants were estimated by macerating root systems of indicator plants. The indicator plants were grown in pots containing either soil from treated plots or a sterilised loam : sand mixture to which known numbers of cysts extracted from the soil had been added. Pot-grown indicator plants were also used to assess the numbers of new cysts formed, either by counting the cysts visible on the mat of roots surrounding the soil ball or extracting the cysts from the soil in which the plants were grown. New cysts were also estimated directly from soil samples taken from the plots after harvest.

The percentage kill calculated from estimates of live eggs was somewhat less than those from the other assay methods, but all assays selected the same treatments as best. Assays based on live eggs, larval invasion and cyst counts on external roots of potted plants were less laborious than estimating hatchable larvae or final cyst numbers. Assays of live eggs and larval invasion enable estimates of kill to be computed within a short time of the completion of treatment, and are less affected by all those factors that influence the host plant during growth and modify the final cyst count in the field. (Peachey and Rao)

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Field experiments showed that "D-D" and methyl bromide control *Xiphinema diversicaudatum* in strawberries and greatly lessen the incidence of soil-borne arabis mosaic virus. Two years after planting, strawberries at one site were less affected by virus where the plots had been treated by "D-D" in the summer of 1960. Untreated control plots gave no yield at all. In another experiment, where "D-D" and methyl bromide had been applied to different plots in the summer of 1961, the numbers of *Xiphinema* in soil samples taken down to 2 ft a year later were still less than 1% of the controls. Plant growth was better on these plots and the incidence of virus less. These results were confirmed in other experiments in Hampshire and in Geescroft Wilderness. (Harrison, Plant Pathology Department, and Peachey)

After experiments at the Royal Horticultural Society's Gardens, Wisley, a trial of carrot varieties was duplicated on land fumigated with chloropicrin. Only the carrots on fumigated soil were of sufficient size and quality to assess the varieties. The cause of poor growth on the unsterilised soil is unknown, but the symptoms resembled those of "Docking disorder" in sugar beet. Routine disinfestation of banana stocks held in quarantine at the Royal Botanic Gardens, Kew, confirmed that regular drenching with emulsified dibromochloropropane ("Nemagon") killed plant-parasitic nematodes infesting "sets" and roots. (Peachey)

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