Tribune

A partir du présent fascicule, une nouvelle rubrique, *Tribune*, figurera au sommaire de la *Revue de Nématologie*.

Cette rubrique, que nous souhaitons voir paraître au moins une fois l'an, est dévolue aux publications autres que les articles de recherche, les notes brèves et les revues bibliographiques. Elle comprendra notamment les articles traitant de données socio-économiques ou historiques, de points de vue plus ou moins ouverts à la controverse dans les différentes branches de la nématologie. De ce fait, ces articles pourront être beaucoup plus spéculatifs qu'habituellement admis, pourvu qu'ils contiennent des éléments susceptibles d'apporter une impulsion nouvelle aux recherches.

Tribune ouvre ainsi à la nématologie une nouvelle voie pour la publication des faits et l'expression des idées.

Starting with this issue, a new item is introduced in the Revue de Nématologie. Tribune, *which is expected to appear at least once a year, is devoted to papers other than the normal research papers, short notes and review articles. In particular it covers socio-economical or historical data in nematology, controversial views in various branches of nematology, and the articles may be more speculative than usual so as to afford an additional impulse to research.*

Tribune *thus opens a new avenue for the publication of facts and expression of ideas in the field of nematology.*

Les Éditeurs Scientifiques
Michel Luc Georges Merny
Editors

NEMATODES IN AN OVERCROWDED WORLD [1]

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We are a heavily populated, overcrowded world and, except for the energy we receive from the sun, our resources are limited to the confines of this globe. As scientists, we might reasonably be expected to be able to identify our resources, maximize their use and, perhaps, aid society to adjust the rate of expansion of the world population to that of the available resources.

Mankind has not done this. Rather our social, political and economic desires have modified the optimum route to one that, in the eyes of many, is heading for disaster; albeit not in our life time.

Our population growth increases by leaps and bounds. Its rate of increase, which was only about 1 % per year around the turn of the century, is expected to be about 2 % per year by the year 2000. For the sake of nematological readers, it could be claimed that by the turn of the century, the world population will have doubled since the European Society of Nematologists had their first meeting, in Wageningen, in 1955.

This increasing human population directly effects our food and energy requirements and waste production. The amount of food that is consumed worldwide is influenced by the level of personal income and, this varies greatly with the different regions of the world but, nevertheless, overall food consumption is rapidly increasing. Expenditure on food by an individual is greater in some countries than in others. In Canada, for instance, only about 15 % of the average individual's spending goes on food whereas in some regions of the world this figure is as high as 60 % (Anon., 1974).

Food consumption and, hence demand, is not

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evenly spread across all food products. Although agricultural productivity is likely to satisfy the world needs for wheat and root crops in 1985, there are projected deficiencies in many major food products. This deficiency seems certain to increase greatly by the year 2000.

The main sources of human food are crops, animal products and fish. Although animal products and fish provide about 35 % of the total protein needs of man, only 1 % of mankind's calories come from fish (Anon., 1974). Hence, 99 % of the calorific requirements of man and his domestic animals come from terrestrial plants as either crops or rangelands. Therefore, our increasing population is almost wholly dependent on the availability of arable and range land, together with adequate water. Good land is at a premium. Canada, for instance, which is the second largest country in the world, has only 10 million acres of prime agricultural land. About 50 % of its food lands are suitable only for pasture or marginal cropping, and we know that animal production is an inefficient way of producing protein.

Ironically, of course, the larger the human population, the less land there is available for growing crops due to increased urbanization. Even in Canada we are expecting to lose, by the turn of the century, another 20 % of our best agricultural land in the most populace provinces, Ontario and Quebec.

The energy problem, of which we are all very conscious but somewhat delinquent in our responsiveness, has a direct bearing on our ability to provide adequate nutrition for our population. In the twenty years from 1950 to 1970 world energy consumption rose by 175 %. This rise reflects the population growth plus a 75 % *per capita* increase in consumption (Anon., 1974). The greater the energy shortage, the higher the costs and, hence, the higher the costs of fertilizers, pesticides and mechanization associated with plant and animal production. All forms of energy production decrease the amount of land available for food production and often increase pollution of our land and water resources as well as modifying the climate. It would seem, therefore, that as our population grows, we not only are using up our food supplies because of our increased nutrient needs, but we are using up the land and spoiling the land upon which our growth and survival depends. Fortunately, our methods of agriculture have intensified so as to obtain more food from less land. We are more conscious of our environmental dependency and are taking steps to protect it, and health authorities help us to live in a more overcrowded state by successfully overcoming more diseases.

Where do nematodes fit into this picture of an overcrowded and resource limited world?

There are plenty of them and you may remember the quotation in the book by the American zoologist, Bucksbaum (1953) :

> « If all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable, and if, as disembodied spirits, we could then investigate it, we should find its mountains, hills, vales, rivers, lakes, and oceans represented by a film of nematodes. »

When we sample the top 5 mm of good arable soil, we can expect a nematode population of many millions per hectare. Their abundance in the sea is almost legendary and Tietjen (1966) claims that nematodes comprise 83 % of the total number and 64 % of the biomass of the marine meiofauna. However, it is not our existence side by side with nematodes that has been man's major concern but rather the existence of one inside of the other. The widespread debilitating and devastating nematode diseases of man, his domestic animals and crops has resulted in the study of nematodes as a major discipline. In 1977, over 1,700 papers were published in the field of plant nematology alone, and this was 140 % greater than ten years earlier.

Having set the scene of man's dilemma, I now will give an impression of the importance of nematodes in this scene by discussing their role in four different areas, namely :

As disease organisms of plants and animals.
As biological control agents of pest insects.
As environmental indicators.
As basic research tools in studying biological systems.

Nematodes as disease organisms

Nematode diseases of animals

Nematode parasites are one of the great scourges of man and domestic animals. Man himself is host to heavy infections of *Ascaris lumbricoides*, and to the two species of human hookworm. It has been estimated by Sprent (1966) that hookworm infections alone consume enough human blood to exsanguinate 1.5 million people every day and that in densely populated mainland China human infections of *Ascaris* produce 18,000 tons of eggs per annum. In addition to the hundreds of millions of people infected with hookworm and *Ascaris*, the World Health Organization estimated, in 1972, that another 250 million were infected with the nematodes which caused elephantiasis and, another 20 million are blinded as a result of *Onchocerca* — induced river blindness. Ironically, Onchocerciasis is an increasing problem in Ghana, as a result of building the Volta dam to increase the energy supply for industrial development.

Despite the fact that we have known about these nematode parasites of man since before biblical times, we still cannot control them, and, as they tend to be debilitating rather than lethal, the resulting increase in size of the feeding but non-productive human work force emphasizes the economic importance of these diseases. Hence, control of *Onchocerca* and its black fly vector would not necessarily produce more mouths to feed, but would release whole communities from misery and free vast fertile areas for agricultural development. The common human infections of *Ascaris* and *Enterobius* are more prevalent in overcrowded conditions. Indeed, the pinworm is a frequent problem in crowded primary schools in temperate climate countries where its affect on school children can be severe. *Toxocara canis* infection of dogs is an increasingly common zoonosis, especially in the increasing numbers of overcrowded apartments and slum dwellings in urban areas where families commonly live in close contact with their pet dogs. In such situations it is common for the humans, especially children, to become afflicted by visceral larva migrans as a result of cross contamination from parasitized dogs (Sprent, 1963).

Research into nematode control has made considerable advances but our best hopes are sometimes slow to pay-off as has been poignantly illustrated in North America in their attempts to more readily control the dog hookworm, *Ancylostoma caninum*. It is common practice to take ones dog to the vet for a deworming for hookworm. In recent years, scientists developed a vaccine against dog hookworm which, once applied, would last the dog's lifetime. Unfortunately, this breakthrough has proved to be so unprofitable for the vet, who gets paid only $10 for the « one-shot visit », instead of an average of $300 over a dog's life, for many « deworming visits », that such vaccination is slow to become an established procedure (Miller, 1977).

Human population pressures continue to result in emigration and this together with the general increased intercontinental travel, and at faster speeds, is causing increasing concern among world health and quarantine authorities, as nematode infected people and plants and, nematode infective insect vectors, carry nature's dispersal methods to extremes. Perhaps the increased frequency of reports of human nematode parasites by the Vancouver medical authorities reflects this jet-age dispersal of parasites. For instance, the number of reports of human hookworm have increased from 94 to 2,989 and, of *Ascaris*, from 46 to 877 for the five year period ending 1975, compared with the five year period ending in 1960 (Bowmer, 1979). Some of this increased frequency of helminth parasitism in western Canada is associated with the relatively large influx of people from the heavily populated Asian countries. African students in Canada have been found to be suffering from Onchocerciasis and although Canadian blackflies (of which there are many!) are unlikely to become infective vectors, these human infections far away from source emphasize that such reservoirs of infection readily travel the globe, and might be a problem in another location. Marshall Laird (1975), in one of his peripatetic reflexions, reminds us that man's voluminous literature on the quarantining of produce and people from flying machines commenced when authorities in the United States appropriated the flowers of a lady traveller as she stepped down from one of the Graf Zeppelin's first trips from Germany in the 1920's.

There is an urgent need to intensify the researches on the parasitic diseases of domestic animals from the standpoint of parasitic zoonoses and human nutrition. One of the reasons for low productivity of livestock and poultry, especially in Third World countries, is the widespread occurrence of nematode parasites. Calf mortality in some countries may be as high as 30 % of the annual calf crop (Griffiths, 1978) and in addition to this is the extensive invisible loss such as lower milk and meat yields and reduced length of productive life caused by nematode parasites.

Nematode diseases of plants

We have, during the last 40 years, improved our methods of control of plant-parasitic nematodes and, it can be reasonably claimed that the use of nematicides saved the Hawaiian pineapple industry, the Rhodesian tobacco industry and, possibly the citrus industry of Florida. Interestingly, these are crops of major economic and social significance in the countries concerned implying, perhaps, that man can find the necessary answers to crop disease problems if the price is right! Some years ago, I (Webster, 1972) advocated a closer look at the economics of nematode induced plant diseases as our knowledge of the subject was inadequate. In 1973, Jones presented a paper to the British Insecticide and Fungicide Conference in which he gave a cost-benefit analysis of the chemical control of potato sickness. He emphasized that a high level of productive potential was necessary, before considering nematicidal treatment, as for instance, even an increase from 15 to 28 t/ha of potatoes could be insufficient an increase to be profitable. In high value crops, our reliance upon nematicides has been increasing as the consumer more readily absorbs the cost of treatment. Currently, the use of some of our most successful nematicides is being curtailed due to public pressure and the greater awareness of possible environmental hazards.

It is surprising, therefore, that despite the substantial increase in research in plant nematology in the last ten years, the percentage of publications on nematicides during this period has increased by only about 4 %. If the number of papers is a true reflection of research vigour this is an unsatisfactory state of affairs. It is gratifying, however, that some of this increase in nematicidal research has been on integrated control and on nematicidal hazards.

Crop rotation is one of the oldest and most effective methods of nematode control in annual crops as the appropriate nematicide is often too costly and, particular nematode resistant varieties are unavailable. Unfortunately, the best rotation sequences often include fallowing and, at a time of urgent food needs, this is increasingly unacceptable.

In view of the shortage of land pressuring our use of crop rotation, and of the environmental concerns pressuring our use of nematicides, the control of nematodes by manipulating the genetics of the host plant is a route that must be pursued vigorously. Breeding for resistance to plant nematodes began with Nilsson-Ehle (1920) who crossed resistant and susceptible barley varieties and studied the host response to what we now call *Heterodera avenae*. We have gone some way since 1920 in finding resistant or tolerant varieties of many of our important crops to the more specialized nematodes such as *Ditylenchus*, *Meloidogyne* and *Heterodera* species. In doing so, we have increasingly had to face the problem of resistant breaking strains or races of the pathogen, and in no group was this struggle to combat new strains as intensive, as well documented or as confusing as with the *Globodera rostochiensis* complex. Fortunately, thanks to Jones *et al.* (1970), Stone (1972), Kort (1974), and others, this taxonomic problem has been clarified (Kort *et al.*, 1977) and we have incorporated major genes for resistance into commercial potato stocks.

The basis of specificity lies in the interacting genomes of the host and the parasite. These interactions are basically antagonistic and are controlled by the resistant genes in the host, and the virulent genes in the parasite, the classic gene-for-gene phenomenon.

Under natural conditions, as distinct from in the laboratory, plants are attacked by many incidental and true parasites and, together, the interactions between these parasites result in disease complexes. Symbiotic relationships between various species of parasite on the same host plant may lead to susceptibility through predisposition or to resistance through pre-induction of a host to a particular parasite. The genetic basis of the *Meloidogyne incognita-Fusarium oxysporum lycopersici* disease complex of tomatoes has now been determined (Sidhu & Webster, 1974). F_2 progeny derived from a cross between a tomato cultivar resistant to both the pathogens and one susceptible to both the pathogens were tested against each pathogen singly and, against both pathogens sequentially. Each F_2 genotype was multiplied by taking cuttings and, from the single inoculations of the pathogens, two independently segregating dominant genes were identified, one effective against the nematode and the other against the fungus. From sequential inoculations of each F_2 plant, a 9 : 3 : 4 ratio was obtained showing resistant to both, resistant to the nematode but susceptible to the fungus, and susceptible to both the pathogens respectively. Such a ratio was possible due to the modification of the response of the F_2 plants which were genetically susceptible to the nematode but resistant to the fungus. The nematode predisposed these plants to the fungus, and so they exhibited a susceptible reaction to the fungus. Hence, the classic 9 : 3 : 3 : 1 Mendelian ratio is modified. It is important to note that if the F_2 progeny had been inoculated only with the wilt fungus without the knowledge of the presence of the root-knot nematode in the soil, the observed ratio probably would have been misinterpreted as 9:7 (Sidhu & Webster, 1977). Such ratio artifacts occur in the literature and are probably due to the mistaken belief of the experimentor that he/she was working with a single pathogen rather than a disease complex of a host.

Modified ratios similar in nature to these also occur in those disease complexes where one parasite preinduces resistance against the other. Although, as yet, no nematode has been found to induce resistance in a plant to another pathogen. These interactions have important implications on the practice of plant breeding against nematodes and other disease causing organisms. These changes in genetic ratios obtained due to parasite-parasite interactions are not brought about by corresponding changes in the genome of the interacting organisms. Rather, the modification is essentially biochemical and physiological which influences the phenotypic response of the host to the parasite.

Nematode parasites, therefore, likely influence the host response to many soil borne fungal and bacterial parasites (Webster, 1975) and Estey (1977) reminds us of the converse situation where fungal mycorrhiza may protect plant roots from attack by nematodes. Breeders of resistance against plant pathogens should, therefore, be striving to achieve long-term disease control of several potentially interacting parasites in the rhizosphere. They should remember also that the shorter life spans of cultivars in relation to certain parasites, such as nematodes, may be due to predisposition rather than to the occurrence of a virulent race with the relevant major virulence gene(s).

Nematodes as biological control agents

Some nematodes are potentially of great benefit to man in that they attack pest insects and so cause their death, sterilization and/or modified behaviour and development (Webster, 1972).

Research in Australia and North America in particular has resulted in some species, namely *Deladenus siricidicola*, *Romanomermis culicivorax* and *Neoaplectana* spp., being marketed commercially or applied extensively by government agencies in the control of major pest insects. *Deladenus* has been introduced successfully into southeast Australia by Bedding and his co-workers to control the woodwasp, *Sirex noctilio*, a serious pest of *Pinus radiata* (Bedding, 1968, 1972; Bedding & Akhurst 1974). Since 1952 the *Sirex* pest has spread rapidly killing as many as 40 % of the trees in some locations. After releasing *Deladenus* at a *Sirex*-infected site in 1972 Bedding and Akhurst (1975) found that as the levels of parasitism in *Sirex* increased there was a dramatic drop in the number of trees killed by this pest. By 1977 no *Sirex* infested trees could be located by ground or aerial surveys of the original 400 hectare site (Bedding & Akhurst, 1977). The nematodes have started to move into adjacent *Sirex* infested plantations naturally. However, it appears to be important to aid the spread of the nematode by transferring *Sirex* infested timber from areas of high nematode parasitism to those of fresh *Sirex* outbreaks, as the natural dispersal of the nematode parasite is not rapid.

It seems likely that *Deladenus* has become established at a level sufficient to keep the pest woodwasp at an acceptable level. Further, from an environmental point of view this method of control is preferable to aerial spraying of large areas with a chemical insecticide, especially in water catchment districts.

I am hopeful that the high expectations that many have had for the success of *R. culicivorax* as a biological control agent against some mosquito species will be realized. Many years of research on this nematode (formerly known as *Reesimermis nielseni*) by Petersen and his colleagues (see Petersen, 1973*a* and *b*; Petersen, Chapman & Woodward, 1968 ; Petersen, Hoy & O'Berg, 1972; Petersen & Willis, 1972) and supplemented by Nickle (1979), Platzer (see Brown & Platzer, 1977; Platzer & MacKenzie-Graham, 1978) and Gordon (see Gordon, Bailey & Barber, 1974) have brought it to the verge of commercial application. It is an effective biological control agent of several species of mosquito which breed in permanent and semi-permanent habitats. In the United States the overall cost of application (including culture costs) was estimated by Petersen and Willis (1972) to be as low as 50 cents per acre. The preparasitic stage is resistant to many of the common insecticides, including abate and malathion and the synthetic growth hormone altosid, and so this nematode could be used in an integrated control programme.

Neoaplectana spp., and especially *Neoaplectana carpocapsae*, have been advocated extensively as biological control agents against several pest insects by many research groups. They can be readily cultured on a large scale (Poinar, 1975; Bedding, 1976) and sprayed onto a wide range of crop plants to control phytophagous insects. In order to apply these nematodes successfully against insect pests of crops, they have to be able to resist desiccation. The technique (Bedding, 1976) of spraying *Neoaplectana* spp. onto plants in oil (Shell Talpa 60) with high melting point wax (Shell 140/145) at concentrations of 500,000 per ml. ensures that the nematodes remained viable for at least four weeks. Over 90 % kill of several pest species has been achieved using concentrations of 50,000 nematodes per square metre of foliage sprayed on in a 0.1 g oil/wax mixture.

Nematodes as environmental indicators

We have become conscious of our environment in the last 10 years as the pressure on our limited resources has increased. The scientist has responded to public pressure by exploring more fully the physico-chemical requirements and the toxicity levels in the marine, terrestrial and freshwater habitats.

Freshwater is at a premium in many parts of the world and its quality and supply comes under close scrutiny especially when chemical toxicants can commonly change the biological behaviour of filter beds and so cause a change in water quality. Cobb (1918) reminded us of the many millions of nematodes in filter beds which, together with the bacteria, play an important role in its overall biological stability. Undoubtedly nematodes add a quality and flavour to our water if one follows some of Cobb's reflections on their activities in filter beds :

> « Each of these nemas is excreting material of which the soluble portions must pass into the city's water supply ... [and] must play a role in imparting to the water its flavour and other qualities. This is enough to make one wish that we had connoisseurs to assist us in the selection and control of drinking-water, as we have connoisseurs in wine and tea, — experts capable of distinguishing minute differences in the flavour... »

It is, however, on our shorelines and in our oceans that man's environmental concern is also being expressed, encouraged on the one hand by camera-eye views of spectacular ocean-depths and, on the other, by news media photographs of the latest oil-slick clinging to our shores. As currently only 1 % of our food comes from the sea, it behoves us to safeguard this environment as a future food source. The pioneering work being done on free-living marine nematodes by De Coninck and Gerlach in Europe (see Gerlach & Riemann, 1973) and by Hope in the United States is providing the foundation for future developments in this resource rich habitat.

Our mining and sewage disposal habits are still quite primitive and waste a significant portion of our land, lakes and streams. Many substances that are toxic to nematodes are found in sewage such as, the PCB - Aroclor 1254 (a contaminant of oil) which decreases the fecundity (Wasilewska, Oloffs & Webster, 1975) of *Acrobeloides nanus*, copper, lead and zinc which slow the development of *Caenorhabditis elegans* (Popham & Webster, 1976) and methyl mercuric chloride which slows development and prematurely kills *C. elegans* in laboratory tests (Thong, pers. commun). Many of the heavy metals build-up in the soil and streams due to their presence in processed sewage fertilizers.

Interestingly, cadmium treated *C. elegans* closely resemble starved and overcrowded specimens (Popham & Webster, 1979). Specifically, such nematodes are smaller, their ovaries are smaller and there is delayed egg-laying, as compared with normal specimens. An electron microscope examination shows that in the cadmium treated nematodes the cytosomes of the intestinal cells are disrupted and the microvilli are smaller than in the controls. Further, in the oesophagus the mitochondria are grotesquely shaped and electron-dense. These various ultrastructural modifications suggest that the cadmium treated nematode is no longer able to take-up and utilize nutrients and is, consequently, physiologically starved. Similar ultrastructural changes occur in cadmium intoxicated vertebrates. Nematodes can be useful laboratory organisms upon which to study subcellular effects of heavy metal toxicity even though high doses are needed in order to exhibit such phenomena.

Nematodes as basic research tools

I have left until last comment on what some call « basic research » to remind us that without it the so-called « applied research » has no foundation. We are fortunate that in the last thirteen years, there have been some very significant strides made in our understanding of basic nematode genetics, development, neurobiology and behaviour. These advances are likely to be of great importance in our control of nematode pests by the next generation of anthelminthics and nematicides and by integrated control.

An ever-growing group of researchers, commonly with background training in molecular biology and genetics, have developed the ideal model system for many biological studies by using nematode, *C. elegans*. Factors such as the small number of cells, small number of genes, short generation time, large number of progeny and ease of culture have enabled us to understand a living system that is more complex than *Escherichia coli* but simpler than *Drosophila*. We now know, through the use of mutants and clearly visable, non-lethal genetic markers, a great deal about the genetic map, know the precise function of some genes as well as the time that these genes operate in the development of *Caenorhabditis* (Brenner, 1974; Riddle, 1978; Moerman & Baillie, 1979).

Hence, we are getting a better understanding of the regulation of muscle development (MacLeod *et al.*, 1977), of the genetic organization of the eukaryote and of the mode of operation of the nervous system (Ward *et al.*, 1975). The more we understand about such systems in the *Caenorhabditis* model, the better chance man has of resolving the human problems of muscular dystrophy, aging, effects of drugs and prenatal abnormalities.

The study of nematodes has come of age by being a vital discipline in its own right rather than being merely a component of medical, veterinary and plant pathology.

Conclusion

Our world is overcrowded, it is going to get worse and the human population is sensitive to this. The research that we do as nematologists is directly related to ways of easing some of the problems that man faces in this increasingly overcrowded world. It is important, therefore, that we take a positive and vigorous research approach. Our research is usually dependent on institutional, government or industrial funding and these sources must be informed of our research needs and of their significance to science and society. We owe it to society to talk openly and with confidence of the advances and of the significance of our discipline.

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