World Dissemination of the Cereal-Cyst Nematode (Heterodera avenae) and Its Potential as a Pathogen of Wheat[1]

J. W. MEAGHER[2]

Abstract: World distribution of the cereal-cyst nematode is herein reviewed. It is suggested that *Heterodera avenae* originated in Europe and has been widely disseminated, largely by the activities of Man but also by wind movement of cysts. So far, it may not have spread to some major wheat-growing regions of the New World, but a non-friable soil structure limits population level and disease. Yield loss could result from the introduction of new cultivars to developing countries where *H. avenae* has not been detected or where existing cultivars possess tolerance. *Key Words:* wheat, barley, oats, rye, ecology, nematode-fungus interactions, resistance.

Over the last 20 years, there has been an increased awareness in many countries regarding the occurrence and economic importance of the cereal-cyst nematode (*Heterodera avenae* Woll.) as a cause of disease in wheat (*Triticum aestivum* L.). Oats (*Avena sativa* L.), barley (*Hordeum vulgare* L.), and rye (*Secale cereale* L.) are also hosts of *H. avenae* but, although their importance is well recognized in some regions of the world, the acreage and production of wheat exceeds that of any other grain crop. It is the principal food of about one-third of the world's people and ranks next to rice (*Oryza sativa* L.) in importance as a food crop. Rice, however, is not a host of *H. avenae*.

My personal knowledge of diseases caused by this nematode is based primarily on Australian experience. Until recently, however, most of the literature on the morphology, ecology, symptomology, and yield loss associated with this nematode was based on observations and experiments in Europe and Ontario, Canada. In the last few years, indications of some important differences have emerged from research in other wheat-growing regions. These differences have provided information on the ecology and survival of the nematode. Increased insight into host-parasite relationships and pathogenesis of disease, and information on yield losses and economic control measures have resulted from experiments in different countries. Using information obtained from research in both the Old and New World, I will discuss, in this paper, the present world distribution of this nematode, its role as a disease agent, and its potential as a factor limiting cereal production, particularly wheat.

DISTRIBUTION

The cereal-cyst nematode was first recognized as a parasite of cereals in Germany (29) and is now recorded in most wheat-growing regions of the world (52). Recognized for many years as the cause of yield loss in cereal crops in most European countries and in the Province of Ontario, Canada (17, 27), it was known in most of these countries as the oat-cyst nematode because the greatest effects of disease were observed in oats. In recent years, however, most attention in Europe has been directed toward control of the disease in barley (9).

Heterodera avenae has been described as a parasite of crops grown in the cool-temperate zone (16, 24), but it is by no means confined to cool temperate regions as it has also been recorded in Italy (40), Tunisia (11), Spain (56), Portugal (30), Greece (21), Yugoslavia (19), Israel (41), and Australia (10). In India, it is known as the cause of "Molya" disease, an important problem in wheat and barley crops in that country and particularly so in the states of Rajasthan, Haryana, and Punjab (51). This nematode species is common in Japan and in the USSR as far west as Siberia, but it is not known in China. It was recorded in 1975 in New Zealand (18), but the most recent record of major significance is the discovery of its presence in a limited area in Washington County, Oregon, U.S.A. (23). *H. avenae* had not previously been recorded in the U.S.A. and is still unknown in the prairie provinces of Canada.

There is only one record of *H. avenae* occurring on the South American continent

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[2]Victorian Plant Research Institute, Burnley Gardens, Burnley, 3121, Victoria, Australia.

—at one location in Peru (28), and it has not been recorded in South Africa (van den Berg, private communication) despite statements to the contrary (17, 23, 27).

DISSEMINATION

Those countries in which *H. avenae* has been detected are listed in chronological order according to the year of record (Table 1). This list should not be expected to provide a clear indication of the nematode's origins or its dissemination pattern. Nevertheless, there does appear to be good evidence that *H. avenae* is indigenous to northern Europe and possibly to Germany where it was originally detected in 1874.

If this hypothesis is correct, it would indicate that the original host of *H. avenae* is either oats or rye rather than wheat or barley. Oats and rye are both believed to have had their origins as a cultivated crop in Europe, whereas wheat and barley originated in Asia Minor and are the oldest known cultivated plants (3).

If the areas in which *H. avenae* is known to occur are examined (Fig. 1), it is evident that the nematode is widespread in Europe. With the exception of Israel, however, it has not been recorded in countries around Asia Minor or in any of the other ancient centers of wheat production such as Iraq,

TABLE 1. The occurrence of the cereal-cyst nematode *(Heterodera avenae)*.

Country	Year	Reference
East Germany	1874	29
Holland	1891	47
Denmark	1897	20
Sweden	1897	25
England	1908	55
West Germany	1923	58
U.S.S.R.	1925	15
Norway	1926	50
Australia	1930	10
Canada (Ont.)	1935	45
Scotland	1946	7
Tunisia	1953	11
Italy	1953	40
Japan	1954	22
Israel	1956	41
Belgium	1957	4
Peru	1958	28
India	1959	44
Poland	1960	59
France	1961	46
Eire	1962	13
Spain	1963	56
Portugal	1963	30
Northern Ireland	1964	1
Switzerland	1965	49
Greece	1966	21
Yugoslavia	1966	19
Bulgaria	1967	53
Czechoslovakia	1967	26
U.S.A.	1975	23
New Zealand	1975	18

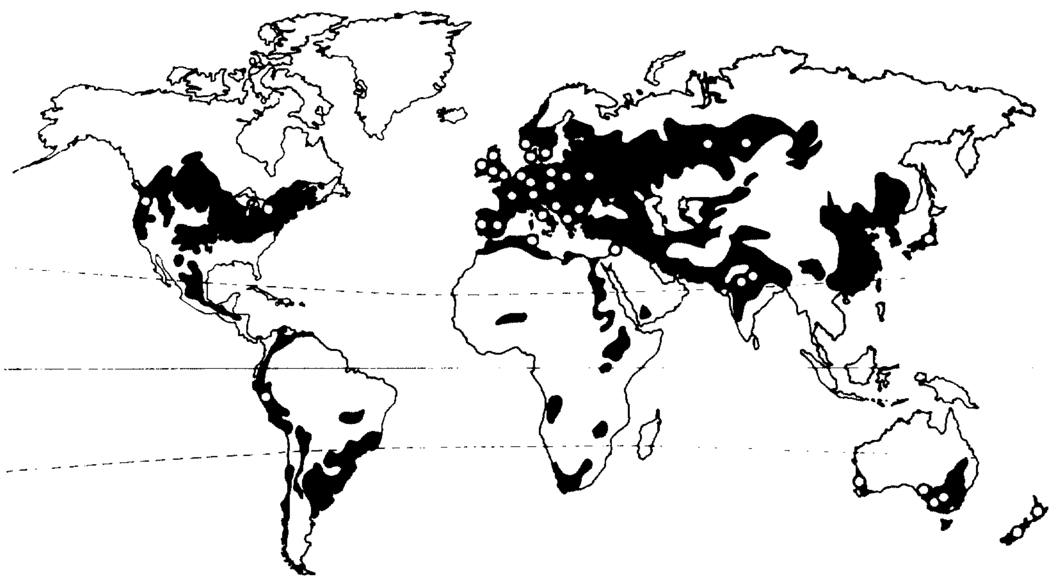

FIG. 1. Areas of wheat production and world occurrence of the cereal-cyst nematode *Heterodera avenae*. White dots show countries or regions where the nematode has been recorded (cf. Table 1).

Iran, and Afganistan. This apparent distribution may merely reflect the number of nematologists in these areas, but evidence for a European origin is also supported by the presence of a greater number of *H. avenae* biotypes there. In addition, *Heterodera hordecalis*, a cyst-forming species which also attacks cereals, has recently been found in northern Europe (2). The identification of five biotypes of *H. avenae* in India (31), however, suggests that it has also been present in that country for many years.

The spread of wheat and barley production in the Old World coincides with the Neolithic Revolution, when Man first began to practice farming, so wheat was introduced to Northern Europe by about 4,000 B.C. The dissemination of *H. avenae* throughout the Old World would have commenced about the same time.

Today, wheat is the most widespread cereal crop. It accompanied the Europeans in the course of their overseas expansion and partly adapted to cold climates (through vernalization and hardening) and to hot climates (by growth at higher altitudes). The environmental conditions to which wheat has become adapted have not always been suitable to *H. avenae* and may be the reason that its distribution in some wheat-growing regions of the New World is limited; or, it may not have been introduced at all as wheat has been intensively cultivated in many of these areas for less than 100 years.

Thus, the known distribution of *H. avenae* in the Australian wheat belt and its recent detection in New Zealand and the U.S.A. adds importance to the question of dissemination and its potential for future spread.

MEANS OF DISSEMINATION

In the Old World, there is little doubt that Man, in his migration and cultivation of new land for cereals, was largely responsible for the long-distance transport of cysts—either in soil attached to boots, tools, and equipment, or through his deliberate movement of soil, alone or with plants. Cysts could have been transported in the same way to the New World.

Once established within a field, cysts or larvae may be disseminated by cultivation or the movement of water. In Australia, however, the rapid dissemination of cysts appears to have been due largely to movement by wind. In that country, the nematode was first described as a parasite of cereal crops in South Australia in 1930 (10). There is no evidence that *H. avenae* is indigenous, but herbarium specimens show that it has been present since at least 1904 (34). It was probably introduced from Europe in the nineteenth century and it is already widespread in the wheat belt of southeastern Australia (34). For about 8 years, *H. avenae* has also been recognized as a cause of poor growth of wheat near Geraldton, Western Australia.

It has been shown that cysts of *Heterodera rostochiensis* Woll. can be moved by wind over limited distances (57), and eggs in cysts of this species can survive long periods of desiccation (43). Until recently, eggs within cysts of *H. avenae* were thought to be very sensitive to desiccation, but it is now known that eggs within mature cysts can survive in air-dry soil for at least 13 months (33), or in a dry atmosphere (75-40% RH) for at least 5.5 years (35, 36).

The Mallee soils of southeastern Australia vary in texture from sands to sandy loams. During periods of drought, they are often subject to wind erosion and, in some seasons, violent dust storms develop with every strong wind. By means of dust traps, viable eggs have been recovered from cysts carried by the wind (35). With the demonstrated capacity of eggs to survive long periods of desiccation and the frequency of dust storms in this area, it is not surprising that infestation is widespread, even though much of the Mallee was only settled in the past 50-60 years.

FACTORS LIMITING DISTRIBUTION OF THE NEMATODE

Soil: Despite the apparent ease of dissemination of *H. avenae* by wind or other means, all wheat-growing regions adjacent to diseased areas may not become infested. Both distribution of the nematode and symptom expression are clearly influenced by soil type (14, 17, 32, 34). In Victoria, *H. avenae* could only be detected in the sandy, solonized, brown soils of the Mallee and the grey clay, but friable, soils of the Wimmera district (32, 34). This nematode species is widespread on similar soils in South Australia and in a limited area of New South Wales. These soils are characterized by good physical structure. *H. avenae* has not been detected on the heavy, poorly-structured soils in other wheat-growing regions of Victoria which are adjacent and climatically similar to the infested areas.

There is a consistent association of increased disease severity with lighter soil types within infested areas in Victoria (34). This association has also been observed in Canada (45), Europe (27), and India (51). Structural properties of lighter soils (14, 34), which provide good drainage and aeration, appear to favor the maintenance of nematode populations, perhaps by greater emergence and mobility of larvae or survival of higher numbers of eggs. However, in Australia, disease symptoms on the lighter soils are also intensified by increased leaching of nutrients, particularly nitrogen (34).

Climate: Patterns of larval emergence appear to be related to the soil temperatures that exist during the different seasons of the year (33). Thus, in the cool-temperate zones of the world (northern Europe or Ontario) where winter temperatures are low, *H. avenae* is able to over-winter as eggs within cysts. By contrast, the infested areas of Australia experience a Mediterranean climate, and eggs remain quiescent throughout a hot, dry summer and early autumn (fall). It is likely that eggs over-summer in other semi-arid climates, including India, where spring cultivars are sown in autumn and growth continues throughout a mild winter.

In Australia, crops are sown and larvae emerge after rains in late autumn, and soil temperatures are at the optimum range (around 15 C) for hatching. In Europe, larvae emerge as temperatures rise in spring. As a result, although the seasons in Australia and northern Europe are opposite, larval emergence takes place during the same months (33). In both of these situations, there is only one generation per year.

In general, high temperatures (above 20 C) do not favor the long-term survival of *H. avenae*. In the laboratory, eggs in cysts survive at high temperatures (21 C) for at least 1 year when stored dry (75-40% RH) but rapidly lose viability when stored at 21 C under moist conditions (36). Also, few larvae are able to survive in moist soil for more than 8 weeks at temperatures above 20 C (Meagher, unpublished data). If these results can be extrapolated to field conditions, they indicate that survival is not favored by continually high temperatures and moist soil, as are present in tropical regions.

There may be little requirement for the long-term survival of either eggs or larvae in soil under certain climatic conditions and cultural practices. For example, maize (*Zea mays* L.) is an efficient host of *H. avenae* and, in India, both wheat and maize crops are equally attacked when grown in rotation (60). Under these circumstances, there may be two generations of the nematode per year, but this has not yet been observed in the field.

FACTORS AFFECTING ECONOMIC DAMAGE

Cyst and larval populations: In Australia, the rapid increase in nematode population, which follows the intensive cropping of infested land with susceptible cereal species, has been described from both field (39) and microplot experiments (37). These results have also emphasized the correlation between nematode population levels and yield loss.

Symptom expression in the seedling stage can be more accurately correlated with larval populations than with cyst populations. This relationship occurs because seedling growth may sometimes precede a mass larval emergence so that plant growth can be well established before a massive invasion of roots occurs (33, 35). In Australia, disease may be minimized when crops are sown soon after rain falls in autumn. Crops sown some weeks later, in late autumn or early winter, are often severely damaged. During the mild winter, which favors larval emergence, plant growth is slow and seedlings are less able to offset damage caused by the continual invasion of nematode larvae.

Geographic and soil fertility differences: The previously described relationships explain the reports that wheat is more severely damaged in Australia (34) and

India (42) than in Europe (17) or Canada (16). Winter wheats are not grown in Australia but are commonly grown in Europe and Canada where they escape invasion during the winter months. In Europe, however, spring wheat cultivars may also be badly damaged (12).

Gair stated that, in this century, the nematode has caused increasingly more yield loss to crops in Europe because of the more intensive cultivation of cereals (17). Also, mechanization has increased the spread and occurrence of the very susceptible wild oat (54). Yield losses caused by *H. avenae* in Europe and Canada are much less than those in India or Australia where yield losses of 50% (51) or higher (6) are often experienced, possibly because winter wheat is usually grown in Europe and Canada and because barley cultivation has increased. Barley cultivars are usually more tolerant of invasion than spring wheat cultivars (34), except in India (31). In addition, nematode resistance has been bred into some European cultivars (8).

Other factors which may partially account for the observed differences in Europe are: *(i)* higher soil fertility and the more widespread use of nitrogen fertilizer offsets nematode symptoms; *(ii)* there is less moisture stress during the growing period and *(iii)* perhaps most important, wider crop rotations are more generally practiced.

Nematode-fungus interaction: Research in Australia has shown that the most severe economic damage caused by *H. avenae* is the result of nematode-fungus interactions (35, 38). Because of its widespread occurrence, *Rhizoctonia solani* Kühn may be the most important fungus involved, but other cereal root-rot fungi may also be associated in a root-rot complex (Meagher, unpublished data).

POTENTIAL FOR THE FUTURE

Heterodera avenae is now recognized as one of the most important diseases limiting wheat yields in southeastern Australia and, in future years, a similar situation may be recognized in Rajasthan, India. Presently, we can only speculate on the likely spread of this species and the resultant yield effects that it will cause in the North American wheat belt.

In Victoria, Australia, we have attempted to measure the potential for yield improvement in wheat that might be achieved either by the elimination of nematodes through the use of nematicides (6) or the elimination of all soil-borne pathogens by the use of a broad-spectrum fumigant (chloropicrin 50%, methyl bromide 50%). The use of nematicides trebled grain yield in comparison with yield on nontreated plots and CP, MeBr (450 kg/ha) produced a four-fold increase (0.95 tonnes/ha to 4.02 t/ha). Large yield increases have also resulted from experiments with chemical-control tests in India (42). The Australian experiments were not planned to provide economic control, but the extent of the yield response obtained has stimulated experimentation to test more economic methods of chemical control.

There is little doubt that the development of "resistant" wheat cultivars provides the greatest potential for economic control and yield improvement. In Europe, the value of resistant barley cultivars is already accepted (9). In Australia, microplot experiments have shown that yield increase is possible by the use of trophic resistance. This term is suggested to describe resistance to nematode reproduction rather than resistance to larval invasion and plant damage (trophos = feeding, reproduction).

Nevertheless, the danger exists that, with incentives such as those provided by the "green revolution," it is possible that new cultivars may be introduced to a region where the occurrence of *H. avenae* is not recognized or that they may replace existing cultivars which possess tolerance. For example, in India, some native cultivars are claimed to be tolerant (42), whereas Australian experiments (5) indicate that some, and possibly all, of the high-yielding dwarf wheats are susceptible. This situation, combined with the more intensive cultivation of wheat, could lead to "genetic vulnerability," and it emphasizes the need to evaluate all varieties to endemic pathogen populations (48).

Much is yet to be learned about the occurrence of *H. avenae* biotypes in some regions (31), but it is hoped that cultivars produced from current breeding programs, including those in Australia, might assist in providing healthy plants in a hungry world.

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