

Chapter 2

Current Nematode Threats to World Agriculture

J. M. Nicol, S. J. Turner, D. L. Coyne, L. den Nijs, S. Hockland
and Z. Tahna Maafi

2.1 Key Nematodes Threatening Major Agricultural Crops of Importance Worldwide

A major global challenge in the coming years will be to ensure food security and to feed the increasing human population. Nowhere will the need to sustainably increase agricultural productivity in line with increasing demand be more pertinent than in resource poor areas of the world, especially Africa, where populations are most rapidly expanding. Although a 35% population increase is projected by 2050 (World Bank 2008), an increase in food demand in the order of 75% is anticipated, due to economic development and changes in food preferences (Keating et al. 2010). Significant improvements are consequently necessary in terms of resource use efficiency. In moving crop yields towards an efficiency frontier, optimal pest and disease management will be essential, especially as the proportional production of some commodities steadily shifts. For example, over half the global potato production (>150 million t) now occurs in Asia, Africa and Latin America, as a result of steady increases in recent years (FAO 2010). With this in mind, it is essential that the full spectrum of crop production limitations are considered appropriately, including the often overlooked nematode constraints. For example in a recent review of intractable biotic constraints in Africa, not a single mention of nematodes was made (Gressel 2004), while for the potato crop in the UK alone, it is estimated that the cyst nematodes, *Globodera rostochiensis* and *G. pallida*, account for an estimated ~\$70 million per annum or 9% of UK production (DEFRA 2010). Given the current withdrawal from use of inorganic pesticides (UNEP 2000), the primary source of pest and disease management over the past decades, the need to consider nematode pests is more acutely brought into focus.

Although over 4,100 species of plant-parasitic nematodes have been identified (Decraemer and Hunt 2006), new species are continually being described while

J. M. Nicol (✉)
CIMMYT International Maize and Wheat Improvement Centre,
P.K. 39 Emek, 06511 Ankara, Turkey
e-mail: j.nicol@cgiar.org

others, previously viewed as benign or non-damaging, are becoming pests as cropping patterns change (Nicol 2002). However, the plant parasitic nematodes of economic importance can be grouped into relatively restricted specialized groups that either cause direct damage to their host or act as virus vectors (Table 2.1). Most affect crops through feeding on or in plant roots, whilst a minority are aerial feeders. In addition to direct feeding and migration damage, nematode feeding facilitates subsequent infestation by secondary pathogens, such as fungi and bacteria (Powell 1971).

On a global scale the distribution of nematode species varies greatly. Some are cosmopolitan, such as certain *Meloidogyne* spp. while others are particularly restricted geographically e.g. *Nacobbus* spp. or are highly host specific, such as *Heterodera carotae* which attacks only carrots. Some crops may have very few nematode pests while others have a particularly wide range of genera and species associated with them, such as sugar cane and rice, leading to difficulties for nematode control strategies. Distribution maps and host range data are available and updated regularly as a useful source for determining nematode damage potential (<http://www.cabi.org/dmpd>).

Although plant parasitic nematodes are among the most widespread pests, and are frequently one of the most insidious and costly (Webster 1987), data on their economic impact remain less than comprehensive, especially for crops produced in resource poor areas. In the tropical and sub-tropical climates, crop production losses attributable to nematodes were estimated at 14.6% compared with 8.8% in developed countries. Perhaps more importantly, only ~0.2% of the crop value lost to nematodes is used to fund nematological research to address these losses (Sasser and Freckman 1987). One difficulty with assessing nematode impact is that damage resulting from nematode infection is often less obvious than that caused by many other pests or diseases. Losses that result from nematode attack may not necessarily be as a consequence of direct cell death, necrosis or 'diseased' tissue but may derive from other more insidious aspects, such as interference with the root system, reducing their efficiency in terms of access and uptake of nutrients and water; to the unaware, nematode-affected plants present typical drought and nutrient stress symptoms, which are easily and often misdiagnosed. On *Musa* spp. (bananas and plantains) nematode damage affects root efficiency on the one hand, but additionally leads to root necrosis and death, undermining plant anchorage; heavily infected bunch-bearing plants can topple due to poor root anchorage leading to total loss of the unripe fruit (Gowen et al. 2005). Moreover, nematode manifestation over time leads to a gradual decline over seasons with misdiagnosis common. Plants are rarely killed outright, although impressive exceptions of full scale crop devastation can occur; *Ditylenchus angustus*, for instance, which causes Ufra disease on deepwater rice in Asia (Cox and Rahman 1980). More generally, Sikora and Fernández (2005) suggest that vegetable production in tropical and sub-tropical environments cannot be considered without some form of nematode management.

In the USA a survey of 35 States on various crops indicated nematode-derived losses of up to 25% (Koenning et al. 1999). More recently Handoo (1998) estimated global crop losses due to nematode attack in the region of \$80 billion, which, given

Table 2.1 World Food Production for major food commodities and main nematode pests of importance

| Crop | Total production (million metric tonnes) | Top 3 producers | Production (million metric tonnes) | Main nematode pests (Luc et al. 2005; Evans et al. 1993; McDonald and Nicol 2005; Nicol and Rivoal 2007) |
|--|---|---|---------------------------------------|---|
| Coarse Grains | 856.2 | | | |
| Maize (<i>Zea mays</i>) | 681.5 | United States of America China Mexico | 331.2 152.4 23.4 | <i>Meloidogyne</i> spp., <i>Pratylenchus</i> spp., <i>Heterodera</i> spp., <i>Punctodera chatcoensis</i> , <i>Paratrichodorus</i> spp., <i>Longidorus breviamulatus</i> |
| Barley (<i>Hordeum vulgare</i>) | 92.3 | France United States of America Australia | 9.5 4.7 5.9 | <i>Heterodera avenae</i> , <i>Meloidogyne</i> spp., <i>Anguina</i> <i>tritici</i> , <i>Pratylenchus</i> spp. |
| Sorghum (<i>Sorghum bicolor</i>) | 49.4 | United States of America Nigeria India | 12.6 9.1 7.2 | <i>Belonolaimus longicaudatus</i> , <i>Paratrichodorus</i> spp., <i>Pratylenchus</i> spp., <i>Criconemella</i> spp. |
| Oats (<i>Avena sativa</i>) | 19.3 | Canada Finland United Kingdom | 4.7 1.2 0.7 | <i>Heterodera avenae</i> , <i>Meloidogyne</i> spp., <i>Ditylenchus</i> <i>dipsaci</i> , <i>Pratylenchus</i> spp. |
| Rye (<i>Secale cereale</i>) | 13.7 | Russian Federation Poland Germany | 3.9 3.1 2.7 | <i>Anguina tritici</i> , <i>Heterodera avenae</i> , <i>Pratylenchus zeae</i> |
| Rice (<i>Oryza sativa</i>) | 621.6 | China India Indonesia | 187.4 144.5 57.2 | <i>Ditylenchus angustus</i> , <i>Aphelenchoides besseyi</i> , <i>Het-</i> <i>erodera</i> spp., <i>Meloidogyne</i> spp., <i>Hirschmanniella</i> spp., <i>Pratylenchus</i> spp. |
| Roots & Tubers | 554.5 | | | |
| Potatoes (<i>Solanum tuberosum</i>) | 255.8 | China Russian Federation India | 64.8 36.8 28.6 | <i>Globodera</i> spp., <i>Meloidogyne</i> spp., <i>Nacobbus aber-</i> <i>rans</i> , <i>Pratylenchus</i> spp., <i>Trichodorus</i> spp., |
| Cassava (<i>Manihot esculenta</i>) | 203.6 | Nigeria Thailand Indonesia | 43.4 26.9 20.0 | <i>Pratylenchus brachyurus</i> , <i>Rotylenchus reniformis</i> , <i>Helicotylenchus</i> spp., <i>Meloidogyne</i> spp., <i>Scutel-</i> <i>lonema bradyi</i> |
| Sweet potatoes (<i>Ipomoea batatas</i>) | 95.1 | China Uganda Nigeria | 75.8 2.6 2.4 | <i>Meloidogyne</i> spp., <i>Pratylenchus</i> spp., <i>Rotylenchus</i> <i>reniformis</i> , <i>Ditylenchus destructor</i> |

Table 2.1 (continued)

| Crop | Total production (million metric tonnes) | Top 3 producers | Production (million metric tonnes) | Main nematode pests (Luc et al. 2005; Evans et al. 1993; McDonald and Nicol 2005; Nicol and Rivoal 2007) |
|--|---|---|---------------------------------------|--|
| Wheat (<i>Triticum aestivum</i>) | 525.8 | China India United States of America | 109.3 75.8 55.8 | <i>Heterodera</i> spp., <i>Pratylenchus</i> spp., <i>Meloidogyne</i> spp., <i>Anguina tritici</i> , <i>Ditylenchus dipsaci</i> |
| Oil crops | | | | |
| Soybeans (<i>Glycine max</i>) | 291.2 217.3 | United States of America Brazil Argentina | 72.9 57.9 47.5 | <i>Meloidogyne</i> spp., <i>Heterodera glycines</i> , <i>Rotylenchulus reniformis</i> , <i>Hoplolaimus columbus</i> , <i>Pratylenchus</i> spp. |
| Rapeseed (<i>Brassica napus</i>) | 48.7 | China Canada India | 10.6 9.6 7.4 | <i>Heterodera schachtii</i> |
| Sunflower seed (<i>Helianthus</i> spp.) | 25.2 | Russian Federation Ukraine Argentina | 5.7 4.2 3.5 | <i>Meloidogyne</i> spp. |

the more subtle effects of low infestation levels is probably a vast underestimate. Globally, a wide range of crops are produced, with some grown in specific areas (Table 2.1). Others have a broader geographical plasticity, which can result in a greater range of pests, varying according to region, continent and climate. Moreover, some crops are produced in regions of varying levels of economy, leading to different levels of nematode management, often as a consequence of awareness as well as the availability of options for their management. The degree of damage a nematode causes can also be dependent upon host and age. In addition, prevailing soil, environmental and climatic conditions all influence the threshold population density, above which measurable damage occurs. For example, *Tylenchorhynchus martini* causes damage on sugarcane at populations between 600 and 6,400/plant, whilst on onions just 5 individuals per seedling of *Pratylenchus penetrans* will result in serious damage (www.encyclopediaalive.com).

Nematode attack can also predispose plants to attack by other pathogens either through mechanical damage but also on a genetic basis. For example, Sidhu and Webster (1974) determined the genetic basis of the *Meloidogyne incognita*—*Fusarium oxysporum lycopersici* disease complex on tomatoes, from sequential inoculations of F₂ progeny and further demonstrated the role of nematodes in disease interactions through the breakdown of resistance to *F. oxysporum lycopersici* in the presence of *M. incognita*.

In addition to the immediate concerns surrounding global food security issues, there is growing concern for pest and disease management under the predicted climate changes and the threat of the emergence of new pests, including nematodes. The Intergovernmental Panel on Climate Change (IPCC) assessments (2007) have concluded that, even if concentrations of all greenhouse gases had been kept constant at the levels present in 2000, a further overall warming of ~0.1°C per decade would be expected, due to the slow response of the oceans. About twice as much warming would be expected if emissions are within the range of scenarios used in IPCC assessments. Resulting changes would include an increase in frequency of heat extremes, heat waves and heavy precipitation; changes in wind, precipitation and temperature patterns; precipitation increases at high latitudes and decreases in most sub-tropical land regions. This would impact on species range shifts; water scarcity and drought risk in some regions of the dry tropics and sub-tropics; and coastal damage from floods combined with sea-level rise. For example, *Radopholus similis* occurs only below ~1,400 m altitude in the East African Highlands where it is a principal pest of banana and plantain, a regional key starch staple for over 20 million people. A small raise in temperature would result in *R. similis*, which is cold-sensitive, infecting millions more bananas grown at higher altitudes. In an alternative example the rice root knot nematode, *Meloidogyne graminicola*, can be maintained under damaging levels through good water management. However, with reduced availability of water following climatic changes and/or competition for urban use, reduced quality of water management, or the introduction of water saving mechanisms such as direct wet seeding is favouring the development of high populations of *M. graminicola*, drastically raising its economic significance as a damaging pest (de Waele and Elsen 2007).

Nematodes are excellent bio-indicators for environmental change as once they are present in a habitat and in proximity of hosts conducive to their development, they may rapidly multiply. Indigenous species that have remained in balance may emerge to pest status on agricultural crops with small changes to their habitat, either through changes in cropping practice (crop, cultivars, rotation cycle, etc.) or climate. A good example of this is illustrated by the rapid and alarming emergence of *Meloidogyne minor* in Europe (Karszen 2004). Plant damage symptoms were first observed in The Netherlands on sports turf in 1997 and on potato in 2000 (Karszen 2004). Since then this nematode has been recovered from a range of pasture, amenity turf and potato crops in mainland Europe and the British Isles (PRA 2007). Its varying morphology on different hosts creates confusion with the quarantine root knot species *M. chitwoodi* and *M. fallax*, with both morphological and molecular characterisation essential for accurate diagnosis (C. Fleming, personal communication). Consequently, we can be sure that nematodes will continue to emerge as new or more aggressive pests of crops as farming practices adapt to fashion, as climate change occurs and as cropping systems intensify in response to an increasing global demand for food. In a world of limited means for nematode management, focus on plant parasitic nematodes as a significant affliction of crop production is highly pertinent.

2.2 Quarantine Nematodes of Global Importance

2.2.1 Potato Cyst Nematodes

Cyst forming nematodes, or cyst nematodes, are one of the most specialized and successful plant-parasitic nematode pests of agriculture. These nematodes usually have a very narrow host range. In the case of the potato, the potato cyst nematodes (PCN), *Globodera rostochiensis* and *G. pallida* are able to infest potato crops and some other Solanaceae such as tomatoes and woody nightshade (bitter sweet). These nematodes belong to the family Heteroderidae and originated in South America and were probably introduced to Europe along with potato breeding material around 1850 (Turner and Evans 1998).

The life cycle of cyst nematodes is well adapted towards the host and they can survive in various environments. The cyst, the dead body wall of the female, contains the eggs which hatch in the presence of the host. Root exudates from Solanaceae activate these juveniles and this can cause hatch of up to 80% of the nematodes under suitable environmental conditions. The juveniles enter the roots near the root tip and induce a feeding cell or syncytial “transfer cell” (See Chap. 4). The juveniles become sedentary and feed from the syncytia, until their development is complete after four moults. After the 4th moult the female is round and swollen and protrudes from the root. The males are slender, leave the roots, mate and fertilize the females. After mating the female forms eggs and when the female dies the cuticle tans to

form a protective cyst with 200–500 eggs within. The life cycle is complete and may take up to three months. The cyst (pinhead size) falls off the roots, waiting for the next suitable host plant.

Damage is related to the level of nematode infestation. Infested plants show retarded growth and heavily infested fields normally show badly growing patches, especially under dry conditions, and as a result yield can be decreased by up to 50%. Apart from the yield reduction, the financial benefits of growing potatoes are also reduced by the costs of control measures and reduction of marketable products.

Sampling soil on land prior to planting of seed potatoes is one way of minimizing spread of these nematodes and forms part of the statutory measures for the production of seed potatoes of all countries. However, when the cysts are present at low density they are often overlooked, or below detection level, whilst the population is spread, mainly by machinery. The difference between the status “not known to occur” and “known not to occur” is not always clear.

When PCN is present in the field there are several ways to minimize the population to such an extent that growing potatoes is feasible although complete eradication is not possible due to the persistence of the cysts in the soil. Available management tools include growing resistant potato varieties, using a lengthened crop rotation, applying chemicals, using biological methods such as solarisation or bio-fumigants or growing catch (trap) crops. The most reliable method in recent years has been the growing of resistant potato varieties.

Potato varieties can differ greatly in the extent to which the nematodes can multiply on them. On a fully susceptible cultivar the nematodes can multiply freely on the roots, stolons and even on the tubers. On resistant cultivars no multiplication can take place and partially resistant cultivars give intermediate multiplication, thus reducing the rate at which the nematode population builds up in the soil. The multiplication of the nematodes depends on the resistance genes present in the potato and on the virulence genes present in the nematodes. When the same resistant potato variety is grown successively, selection for virulent nematodes that can overcome the resistance source may occur. A prime example of this has occurred in the UK since the introduction of commercially viable cultivars carrying the H1 gene. This gene gives complete control against the pathotypes of *G. rostochiensis* present in the UK and whereas *G. rostochiensis* was the prevalent species present in the UK in the past, repeated use of cultivars containing H1 has led to an increase in the prevalence of *G. pallida*, which was previously rarely encountered (Minnis et al. 2002).

Outbreaks of potato cyst nematodes have now occurred in most of the potato growing areas of the world. PCN remains rare in some countries with extensive potato acreages, most notably Australia, Canada, USA, India and, probably, some parts of the former USSR. Most outbreaks involve *G. rostochiensis* or both species. The relative scarcity of commercially acceptable varieties with full resistance to *G. pallida* makes the control of this species much more difficult to achieve. Identification of the species, generally based on morphology, is now being taken over by molecular methods as these techniques are easier to learn and adapt than the more specialised knowledge of taxonomy. The EPPO Diagnostic

protocol for identification of potato cyst nematodes (OEPP/EPPO 2009a) gives an overview of the more recent identification tools and this topic is also covered in Chap. 21.

2.2.2 *Endoparasitic and Free-Living Parasitic Nematodes*

Endoparasitic and free-living plant-parasitic nematodes present a different challenge to plant health services. Endoparasites spend most of their life inside bulbs, corms, roots or tubers and hence can be unknowingly spread and escape detection, whilst free-living species are found in soil residues that need to be processed to confirm their presence. There is more potential for unlisted species in these groups to be assigned quarantine status because international trade is facilitating the spread of species that were not known to have potential to become economic pests when most international plant health legislation was first implemented; it usually takes several years to collect evidence with a Pest Risk Analysis (PRA) that a species should be listed as quarantine. The challenge to plant health services is to detect and identify not only listed species but also new or unusual species that might pose a threat to agriculture should they be allowed to establish and spread. Nematologists specialising in identification largely rely on morphological characters for identification, but molecular techniques offer potential for a new range of tools to facilitate this. This is especially important when frequently samples only contain a few or immature specimens that cannot be identified by morphological means.

The root-knot nematodes, *Meloidogyne* species, are endoparasitic species widespread throughout the world and usually have a wide range of host plants. *Meloidogyne chitwoodi* was first described from the Pacific Northwest of the USA in 1980 (Golden et al. 1980), but it is not clear if this is its area of origin. It was causing damage to potato tubers and a few years later was also detected in potatoes in The Netherlands, although there is evidence that it may have been present in Europe for some time (OEPP/EPPO 1991). It has a wide host range including other economically important crops such as carrots and other root crops such as salsify. *M. chitwoodi* lowers the market value of such crops as a result of internal necrosis and external galling and yields are reduced. A PRA (Tiilikkala et al. 1995; Braasch et al. 1996) led to the pest being listed as a quarantine organism in the EU in 1998. This meant that plant health service inspectors were alerted to look specifically for symptoms of this pest, particularly on potato tubers, and samples were submitted to quarantine laboratories for detection and identification.

It is important to distinguish *M. chitwoodi* and *M. fallax*, listed species in Europe and elsewhere, from other nematodes, particularly related, unlisted species, that might also be found in potato tubers and roots. In addition, survey work has demanded that large numbers of samples are dealt with quickly so prompt action on control could be taken. This has led to the development of molecular

tools to assist identification, most recently using TaqMan technology. The EPPO standard on *M. chitwoodi* and *M. fallax* gives additional information (OEPP/EPPO 2009b).

The free-living pine wood nematode, *Bursaphelenchus xylophilus*, is associated with pine wilt disease but depends on bark beetles (*Monochamus* spp.) to spread from tree to tree. It is native to North America and is thought to have been carried to Japan at the beginning of the twentieth century on timber exports. In Japan, it is causing massive mortality of native pine trees. In 1999, *B. xylophilus* was found in Europe for the first time, in Portugal. Quarantine nematologists were already researching the identity of this species in order to be able to distinguish it from the many species of *Bursaphelenchus* that inhabit wood. Unfortunately there is a variation in characters between species in the *Bursaphelenchus* group, which makes morphological identification particularly difficult, so biomolecular tools are highly recommended (OEPP/EPPO 2009c).

The majority of plant-parasitic nematodes are free-living species that feed ectoparasitically on roots; this group contains thousands of species, some well known to science but others not. Quarantine is concerned with the detection of any species that may pose an economic risk to agriculture, horticulture and, increasingly, the native biodiversity of recipient countries. This demands specialist skills in nematode identification in order to distinguish such species from native ones. Nematodes in the EU-listed group, *Xiphinema americanum sensu lato*, are listed in many countries because of the ability of some species to transmit viruses. The identification of this group is in a state of flux, but recent work in Europe has led to the development of an EPPO Diagnostic protocol (OEPP/EPPO 2009d). It is hoped that research into molecular tools will provide further tools to facilitate the harmonisation of protocols worldwide.

Control programmes may be aimed at eradication or suppression of intercepted pests, but in the long term the development of certification schemes to produce nematode-free material is important. The development of hosts with resistance to quarantine species is a prolonged and expensive process but may be justified for economically important species. Sustainable methods of control are receiving more attention as chemical controls become scarce and this stimulates research into biological control methods. Combined with knowledge of the biology and life-cycle of the species such research offers the potential to minimise the effect of plant-parasitic nematodes spread in trade.

2.3 Key Nematodes on Food Staples for Food Security in Developing Countries

Cereals constitute the world's most important source of food. Amongst cereals, rice, maize and wheat occupy the most prominent position in terms of production, acreage and source of nutrition, particularly in developing countries (Table 2.1). It has

been estimated that about 70% of the land cultivated for food crops is devoted to cereal crops. The global population is projected to increase steadily to around 9 billion by 2050 and with this demand for the staple cereals of rice, maize and wheat will increase (Dixon et al. 2009). Projections suggest that over this period the demand for maize will grow faster than that for wheat due to the use of maize as animal and poultry feed and the increasing demand for biofuel. The demand for wheat will grow faster than that for rice and is likely to follow closely the growth in global population over this period (FAO 2006; Dixon et al. 2009).

In order to meet the expected food demand, further research is required on how to produce more from less. Research will need to also focus on the less understood and appreciated nematodes which are known to be economically important on all three cereal crops. As described above, there is a void of representative information from developing countries for nematodes on many crops, which has affected recognition by the scientific and policy community with respect to agriculture research. As time advances the challenge to meet food security for developing countries is more acute. As their economic situation improves consumption of meat based products is increasing, resulting in greater demands for cereals for animal feed. It is also predicted that there will be reductions in irrigation water for agriculture as the value of this compared with other industries is challenged. This is further compounded by the climate change scenarios and extremes of drought and floods which have been forecast (IPCC 2007).

2.3.1 Maize

2.3.1.1 Introduction

Maize (*Zea mays*) has the highest production of all three cereal staples (752 Mt). It is grown largely in tropical and subtropical regions with the three largest producers found in North America Asia and Europe (Tables 2.1 and 2.3). Over 60 nematode species have been found associated with maize in different parts of the world. Most of these have been recorded from roots, or soil around maize roots, with information on the biology or pathogenicity of many of these species not readily available. The most important groups of plant parasitic nematodes demonstrated to be important limiting factors in maize production from all over the world include the root knot nematodes, *Meloidogyne* spp., the root lesion nematodes, *Pratylenchus* spp. and the cyst nematodes, *Heterodera* spp. A questionnaire survey to agricultural research institutions in South Africa put *Pratylenchus* species second overall after root knot nematodes in terms of economic importance (Keetch 1989). *Pratylenchus*, along with *Meloidogyne* and *Hoplolaimus* were the most frequently reported genera on maize in the USA. (Koenning et al. 1999). There are also reports of other plant parasites on maize (Table 2.2), but knowledge of their importance and distribution is limited.

Table 2.2 Plant Parasitic Nematodes of Economic Importance. (Adapted from Handoo 1998)

| Genus | Common Name | Type | Plant tissue |
|------------------------|---------------|----------------------------------|----------------------|
| Primary damage (15) | | | |
| <i>Anguina</i> | Seed gall | Migratory endoparasite | Seeds, stems, leaves |
| <i>Bursaphelenchus</i> | Wilt | Migratory ectoparasite | Seeds, stems, leaves |
| <i>Cricanemella</i> | Ring | Sedentary ectoparasite | Roots |
| <i>Ditylenchus</i> | Stem and Bulb | Migratory ectoparasite | Stems, leaves |
| <i>Globodera</i> | Cyst | Sedentary endoparasite | Roots |
| <i>Helicotylenchus</i> | Spiral | Migratory ecto-, endoparasite | Roots |
| <i>Heterodera</i> | Cyst | Sedentary endoparasite | Roots |
| <i>Hirschmanniella</i> | Root | Migratory endoparasite | Roots, tubers |
| <i>Hoplolaimus</i> | Lance | Migratory ectoparasite | Roots |
| <i>Meloidogyne</i> | Root-knot | Sedentary endoparasite | Roots |
| <i>Pratylenchus</i> | Lesion | Migratory ecto-, endoparasite | Roots |
| <i>Radopholus</i> | Burrowing | Migratory endoparasite | Roots, tubers |
| <i>Rotylenchulus</i> | Reniform | Sedentary semi-endoparasite | Roots |
| <i>Scutellonema</i> | Spiral | Migratory ecto-, endoparasite | Roots, tubers |
| <i>Tylenchulus</i> | Citrus | Sedentary semi-endoparasite | Roots |
| Virus vectors (3) | | | |
| <i>Xiphinema</i> | Dagger | Migratory ectoparasites | Roots |
| <i>Longidorus</i> | Needle | Migratory ectoparasites | Roots |
| <i>Trichodorus</i> | Stubby | Migratory ectoparasites | Roots |

Table 2.3 World and regional production of key staple cereals. (Sourced from the FAO website, www.fao.org May 2010. Figures represent five years average 2004–2008)

| Continent | Total production (million metric tonnes) | | |
|---------------------------|--|--------|--------|
| | Maize | Rice | Wheat |
| World | 752.05 | 645.18 | 633.14 |
| Africa | 49.57 | 21.23 | 21.68 |
| Asia | 209.61 | 584.92 | 273.52 |
| Australia and New Zealand | 0.56 | 0.41 | 18.78 |
| Central America | 25.28 | 1.12 | 3.26 |
| Europe | 84.01 | 3.46 | 211.49 |
| North America | 307.54 | 9.55 | 82.77 |
| South America | 74.86 | 23.43 | 21.64 |

2.3.1.2 Economic Importance and Distribution

Several species of root knot nematodes including *M. incognita* and *M. javanica* have been detected at damaging levels in almost all maize growing regions of the world (McDonald and Nicol 2005). *M. africana* and *M. arenaria* have been

recorded on maize in India and in Pakistan, and *M. arenaria* has also been reported by several authors from the USA (McDonald and Nicol 2005). Above ground symptoms include stunting, leaf chlorosis and patchy growth. Root galls may be small or large, terminal or sub-terminal or in some cases totally absent. For this reason maize has often mistakenly been considered a poor host or even a non-host for root knot nematodes (McDonald and Nicol 2005). Although root knot nematodes occur frequently in maize fields, information on economic losses is lacking and requires further study. However, indirect observations when nematicides are applied in root knot nematode infected soils, suggest that these nematodes are economically important (Riekert 1996; Riekert and Henshaw 1998). It is important that growers are alert to the possibility of root knot nematode infestation of maize, particularly in low input production conditions (Table 2.2).

Many more reports exist for the lesion nematodes which have a cosmopolitan occurrence in maize fields with several of these species reported to be associated with poor growth and yield reduction (McDonald and Nicol 2005). The most commonly occurring species include *Pratylenchus brachyurus*, *P. zae* and *P. penetrans* in subtropical and tropical regions but many other species have been noted. Lesion nematodes have wide host ranges which can affect the selection of the crop used to control nematodes in rotations. In addition, the presence of weed hosts in a field can strongly influence lesion nematode (and indeed root knot nematode) densities. The nematode species, population density and environmental conditions affect symptom expression of root lesion nematodes and hence the aboveground symptoms are not specific. Nematode damage is associated with lesions to the root as a result of the destruction of cortical parenchyma and epidermis, which may cause sloughing-off of the tissue and severe necrosis (McDonald and Nicol 2005). In addition, severe root pruning as well as proliferation of lateral roots may occur. More definitive yield loss studies have been conducted for root lesion nematodes on maize. Smolik and Evenson (1987) found direct relationships between *P. hexincisus* and *P. scribneri* and maize yield loss, with *P. hexincisus* more damaging to dry land maize than *P. scribneri* to irrigated maize. In Nigeria, *P. brachyurus* has been reported to be responsible for a 28.5% yield reduction, with this reduction being correlated with a 50% increase in nematode density (Egunjobi 1974). Indirect evidence has been obtained with nematicides where detected yield increases suggest that lesion nematodes are important limiting factors in maize cultivation with yield increases of 33–128% in South Africa, 10–54% in the USA and a two-fold increase in Brazil reported (reviewed by McDonald and Nicol 2005).

The third group of nematodes of importance for maize are the cyst nematodes. Although more than nine species of cyst nematodes have been recorded as being associated with maize in subtropical and tropical countries, only three (*Heterodera zae*, *H. avenae* and *Punctodera chalcoensis*) are considered economically important (Luc 1986). *Heterodera cajani*, *H. delvii*, *H. gambiensis*, *H. graminis*, *H. oryzae* and *H. sorghi* have been recorded sporadically, but their role as parasites of maize remains uncertain (reviewed by McDonald and Nicol 2005). As with other nematodes the above ground symptoms are relatively non-specific. *H. zae* infested plants exhibit poor growth and are stunted and pale green in colour (Koshy and

Swarup 1971). *Punctodera chalcoensis* is limited in distribution to Mexico where it has been given the local name of Mexican corn cyst nematode and is considered of extreme importance. The symptoms of *P.chalcoensis* are the same as those for *H. zaeae*, with the chlorotic leaves also exhibiting pale colour stripes (McDonald and Nicol 2005).

Pathogenicity of the cyst nematode *H. zaeae*, has been demonstrated on maize but data on economic damage to the crop is lacking (Koenning et al. 1999). Plant growth reductions are directly correlated with initial nematode population density and maize growth and yield are suppressed by 13–73% in the presence of *H. zaeae* with this damage more profound under hot and dry conditions (reviewed by McDonald and Nicol 2005). It is also important to note the wide host range of *H. zaeae* and the need to select crop rotations carefully in order to minimize population increase (Ismail 2009). There is limited published information about the importance of *H. avenae* on maize but this could be very important in wheat & maize production systems as this is a well acknowledged pathogen on wheat. Unlike the other two cyst species the host range of *P. chalcoensis* is highly restricted with only two plants, *Z. mays* and *Z. mexicana* (Teosinte), considered hosts (Stone et al. 1976). Damage by *P. chalcoensis* can be severe and is dependent on cultivar susceptibility, nematode density and adequate soil moisture levels in the later part of the growing season. Under glasshouse conditions, Sosa-Moss and Gonzales (1973) obtained a reduction of about 60% in yield in heavily infested soils. Although yield loss in the field is considered to be high, experimental data is lacking.

2.3.1.3 Major Methods of Control

Although there are limited groups working on controlling nematodes in maize production systems there have been many local reports identifying resistance against not only the 3 main groups described above but also many other genera and species (reviewed by McDonald and Nicol 2005). Some of these are in commercial varieties but most are within breeding lines and land races.

Cultural practices such as crop rotation, planting time, application of organic amendments and biological control have been tested and in many cases were demonstrated to be effective in reducing various nematode populations but these are genera and species specific (McDonald and Nicol 2005). For example in Mexico early sowing dates and adequate fertilization reduces damage caused to maize by *P. chalcoensis* (Sosa-Moss and Gonzalez 1973; Sosa-Moss 1987). In terms of rotation maize has been suggested as a good ‘rotation crop’ that can help reduce populations of some nematodes but little is actually known about the effects of rotation on root knot population densities in a maize crop. Crop rotations or sequences where maize was involved demonstrate the dangers of ineffective crop choices in rotations due to the susceptibility of maize to various species of nematodes (McDonald and Nicol 2005). Biological control has been investigated against several species of plant parasitic nematodes of importance to maize (McDonald and Nicol 2005), with many of these offering potential. However, none of

these biocontrol agents can be used economically at the present time in extensive cereal crops.

2.3.2 Rice

2.3.2.1 Introduction

Rice (*Oryza sativa* L) belongs to the Graminae family and as a cereal grain is the most important food resource for a large part of the world's population. As with maize, rice is grown in most tropical and subtropical regions. Rice is grown in 114 countries throughout the world in Asia, Africa, Central and South America and Northern Australia. Asia accounts for 90% of world rice production with China, India, Indonesia, Bangladesh and Vietnam the five highest rice-producing countries (FAO 2008; Tables 2.1 and 2.3).

There are different systems of cultivating rice that have evolved to suit specific environments, including irrigated, rainfed lowland, deepwater, tidal wetlands and upland. Irrigated rice is the dominant growing system in the world. Plant parasitic nematodes have adapted to each cultivation system with both foliar and root parasites being important.

2.3.2.2 Economic Importance and Distribution

Parasitic nematodes on rice can be divided into two groups: the foliar parasites and the root parasites. The foliar parasites include two well known species. *Aphelenchoides besseyi* Christie, 1942 the causal agent of 'white tip disease' in rice is widely spread throughout the rice growing areas of the world. *A. besseyi* is seed borne in rice and hence the infested seed acts as a primary source of infestation. The characteristic symptom caused by *A. besseyi* in rice is a whitening of the leaf tip that turns to necrosis, there is also distortion of the flag leaf that encloses the panicle. Infected plants are stunted, have reduced vigour and their panicles contain small and distorted grain (Ou 1985). Two other species, *A. nechaleos* and *A. paranechaleos* have been reported from rice stems in Sierra Leone and Vietnam. Both have a similar morphology and biology to *A. besseyi* (Hooper and Ibrahim 1994; Ibrahim et al. 1994). However, both species show marked differences in their pathogenicity to rice and the inconsistencies observed in the damage caused by *A. besseyi* to rice might be due to incorrect nematode identification (Ibrahim et al. 1994). The economic damage threshold density was determined to be 300 live nematodes per 100 seeds (cited by Bridge et al. 2005). Yield losses of up to 60% due to *A. besseyi* have been widely reported from various infested regions (Bridge et al. 2005). Such high losses are probably rare as the disease is now easily controlled by seed treatment and resistant cultivars (Whitehead 1998).

The other major foliar nematode pest in rice is *Ditylenchus angustus*, which is mostly limited to the south and southeast of Asia where deepwater and lowland cultivation systems are used (Table 2.3). Although it has been suggested that *D. angustus* cannot survive severe desiccation (Ibrahim and Perry 1993; Sein 1977), a recent survey indicated the recovery of live nematodes from dried seeds three months after harvest, mainly located in the germ portion (Prasad and Varaprasad 2002). This finding emphasises the importance of seed (and nematode) exchanges between different regions as a source of infection. *D. angustus* causes 'ufra' disease in rice and the most prominent symptoms of infected plants are chlorosis, twisted leaves and swollen lower nodes. Infected panicles are usually crinkled with empty, shrivelled glumes, especially at their bases, the panicle head and flag leaf are twisted and distorted (Bridge et al. 2005). The annual yield loss due to *D. angustus* has been estimated at 4% in Bangladesh (Catling et al. 1979) and 10–30% in Assam and West Bengal, India (Rao et al. 1986). However, the importance of *D. angustus* has reduced as the area sown to deep-water rice has declined (Plowright et al. 2002).

Nematode parasites of rice root systems include migratory endoparasites, sedentary endoparasites (cyst and root knot nematodes) and ectoparasites. Many species of *Hirschmanniella*, known as the rice root nematodes, have been reported from the majority of rice growing regions which are irrigated, lowland and deep water rice. Seven species are reported to damage rice, with the most commonly reported species being *H. oryzae*. The symptoms caused by *Hirschmanniella* species are not specific and include poor growth, leaf chlorosis, reduction of tillering and yield. Nematodes invade roots and migrate through the cortical tissues causing cell necrosis and cavities with infected roots, which turn brown and rot. The crop losses due to *Hirschmanniella* spp. have been estimated at 25% (Hollis and Keoboonrueng 1984).

Four cyst nematodes species are known to affect rice; *Heterodera oryzicola*, *H. elachista*, *H. oryzae* and *H. sacchari* on upland, lowland and flooded rice in Japan, India, West Africa and Iran. As with *Hirschmanniella* the infected plants show reduced growth, chlorosis, fewer tillers and a reduction in root growth. The crop losses due to cyst nematodes have been documented by Bridge et al. (2005), *H. elachista* decreases yield by 7–19% and even higher yield losses have been attributed to *H. oryzicola* in India. In Côte d'Ivoire increasing *H. sacchari* populations are expanding rapidly with intensive wet season rice cropping, leading to yield losses of up to 50% (Bridge et al. 2005).

Although several species of root knot nematodes have been reported on rice, the key species is *M. graminicola* which is mainly distributed in South and South East Asia. This species has also been reported from the USA and some parts of South America (Table 2.2). *M. graminicola* causes damage to upland, lowland, deepwater and irrigated rice. The most prominent symptoms of *M. graminicola* on the root system are swollen and hooked root tips which are characteristic for *M. graminicola* and *M. oryzae* (Bridge et al. 2005). Typical above ground symptoms include stunting and chlorosis leading to reduced tillers and yield. The effects of *M. graminicola* on grain yield in upland rice has been estimated at 2.6% for every 1,000 nematodes

present around young seedlings (Rao and Biswas 1973). The tolerance limit of seedlings has been determined as less than one second stage juvenile/cm³ of soil in flooded rice (Plowright and Bridge 1990).

2.3.2.3 Major Methods of Control

Using clean seed is the most effective means of preventing yield loss due to *A. besseyi*. Fumigating seed with methyl bromide, gamma radiation, seed dressing with effective nematicides, hot water or chemical seed treatment are the most useful methods for reducing crop losses. There are many reports on seed treatment of rice by hot water but the most effective control requires pre-soaking seed in cold water for 18–24 h followed by immersion in water at 51–53°C for 15 min (Bridge et al. 2005). Using resistant or tolerant cultivars and low seed planting densities are other control measures for reducing the crop losses due to *A. besseyi*.

There are many different methods to control ‘ufra’ disease in rice caused by *D. angustus*. These include destroying or removing the infested stubble or straw, burying crop residues, growing non-host crops such as jute or mustard in rotation with rice, using early maturing cultivars, removing weed hosts and wild rice to prevent the build up of nematodes for the next crop and improving water management to prevent spread of the nematodes. There are good sources of resistance to *D. angustus* and advanced generation breeding material is available for development of resistant cultivars suitable for lowland and deep-water environments (Plowright et al. 2002).

Management of *Hirschmanniella* spp. comprises various methods including soil solarisation, fallow, weed control, use of resistant cultivars and rotation with non host plants (Bridge et al. 2005). For *H. sacchari*, there are good sources of resistance in the African rice *O. glaberrima*. Flooding of soil reduces the population density of this nematode. Soil solarization and use of resistant cultivars are the main methods used for control of root knot nematodes in rice cultivation (Whitehead 1998).

2.3.3 Wheat

2.3.3.1 Introduction

Wheat (*T. aestivum* and *T. durum*) is the third largest cereal staple with production of 633Mt each year. The three largest producers are China, India and the USA (Table 2.1). It is considered the key crop of importance for food security in the regions of West Asia and North Africa. This section will focus on the primary nematodes of global economic importance on wheat: Cereal Cyst Nematode (*Heterodera*) and Root Lesion Nematode (*Pratylenchus*). Other important nematode genera including Root Knot (*Meloidogyne*), Stem (*Ditylenchus*) and Seed Gall (*Anguina*) will not be described here. However, further information on all these nematodes can

be found in the reviews of Kort (1972), Griffin (1984), Sikora (1988), Swarup and Sosa-Moss (1990), Rivoal and Cook (1993), Nicol (2002) and McDonald and Nicol (2005), Nicol and Rivoal (2007) and Riley et al. (2009).

2.3.3.2 Economic Importance and Distribution

The most globally recognized and economically important nematode on wheat is the Cereal Cyst Nematode (CCN). The CCN complex is represented by a group of twelve valid and several undescribed species. Three main species, *Heterodera avenae*, *H. filipjevi* and *H. latipons*, are thought to be the most economically important. One of the complexities of the CCN is the presence of pathotypes, making the use of genetic control challenging. The above ground symptoms caused by CCN occur early in the season as pale green patches, which may vary in size from 1 to more than 100 m², with the lower leaves of the plant being yellow and in which plants generally have few tillers. The symptoms can easily be confused with nitrogen deficiency or poor soils and the root damage caused by CCN exacerbates the effect of any other abiotic stress, e.g. water or nutrient stress. The below ground symptoms may vary depending on the host. Wheat attacked by *H. avenae* shows increased root production such that roots have a 'bushy-knotted' appearance, usually with several females visible at each root. The cysts are glistening white-grey initially and dark brown when mature. Root symptoms are recognisable within one to two months after sowing in Mediterranean environments and often later in more or less temperate climates (Tables 2.1 and 2.3).

As reviewed by Nicol and Rivoal (2007), *H. avenae* is the most widely distributed and damaging species on cereals cultivated in more or less temperate regions. *H. avenae* has been detected in many countries, including Australia, Canada, South Africa, Japan and most European countries, as well as India, China and several countries within North Africa and Western Asia, including Morocco, Tunisia, Libya and Pakistan, Iran, Turkey, Algeria, Saudi Arabia and Israel. *Heterodera latipons* is essentially only Mediterranean in distribution, being found in Syria, Cyprus, Turkey, Iran, Italy and Libya. However, it is also known to occur in Northern Europe, and Bulgaria. Another species with an increasingly wide distribution is *H. filipjevi*, formerly known as Gotland strain of *H. avenae*, which appears to be found in more continental climates such as Russia, Tadjikistan, Sweden, Norway, Turkey, Iran, India, Pacific North West USA and Greece. A relatively new report also describes this species from Himachal Pradesh in India (SP Bishnoi, pers. com.). There are also several other species of *Heterodera* reported on wheat but these are not considered to be of major economic importance (Nicol and Rivoal 2007).

In terms of economic importance the review of Nicol and Rivoal (2007) provides a long list of published yield loss studies. Interpretation of the damage threshold between specific nematological studies should be done with extreme caution, as very few studies are truly comparable, with inherent differences in sampling protocol, extraction procedure and nematode quantification. Several authors have

reported that water stress is one of the key environmental conditions that can exacerbate damage caused. Yield losses due to *H. avenae* on wheat are reported to be 15–20% in Pakistan, 40–92% in Saudi Arabia, 23–50% in Australia, 24% in the Pacific North West of the USA and 26–96% in Tunisia. It has been calculated that *H. avenae* is responsible for annual yield losses of 3 million pounds sterling in Europe and 72 million Australian dollars in Australia (Wallace 1965; Brown 1981). The losses in Australia are now greatly reduced due to their control with resistant and tolerant cultivars.

Little is known about the economic importance of the species *H. latipons*. As reviewed by Nicol and Rivoal (2007) there is one report from Cyprus on barley that indicated 50% yield loss. Recent studies in Iran in field microplots reported yield losses of up to 55% on winter wheat (Hajihassani et al. *in press*). Because the cysts of *H. avenae* and *H. latipons* are similar in size and shape it is possible that damage caused by this recently described nematode species has previously been attributed to *H. avenae* (Kort 1972). Similarly, *H. filipjevi* is most likely an economically important nematode on cereals due to its widespread distribution but has previously been misidentified as *H. avenae* in the former USSR and Sweden. In Turkey significant yield losses (average 42%) in several rainfed winter wheat locations have been reported. In Iran under microplot field trials yield losses of 48% were found on common winter wheat over two wheat seasons (Hajihassani et al. 2010). Natural field trials conducted over several seasons have clearly indicated greater losses under drought conditions. Given increased recognition and incidence, *H. filipjevi* and *H. latipons* are now being identified as a constraint to cereal production (Philis 1988; Oztürk et al. 2000; Scholz 2001).

The second group of nematodes considered economically important on wheat production systems is the migratory endoparasitic genus *Pratylenchus*. At least eight species infect small grains and the four most important species *P. thornei*, *P. neglectus*, *P. penetrans* and *P. crenatus* are polyphagous and have a worldwide distribution (Rivoal and Cook 1993). *P. thornei* is the most extensively studied of these species on wheat and has been found in Syria, Yugoslavia, Mexico, Australia, Canada, Israel, Iran, Morocco, Tunisia, Turkey, Pakistan, India, Algeria, Italy and the USA (Nicol and Rivoal 2007). *P. neglectus* has been reported in Australia, North America, Europe, Iran and Turkey while the other species have only been reported from local studies.

In terms of economic importance *P. thornei*, causes yield losses in wheat from 38 to 85% in Australia, 12–37% in Mexico, 70% in Israel and has also recently been reported to cause losses on wheat in the Pacific North West of the USA. *P. neglectus* and *P. penetrans* appear to be less widespread and damaging on cereals compared to *P. thornei*. In Southern Australia, losses in wheat caused by *P. neglectus* ranged from 16 to 23% while at sites infested with both *P. thornei* and *P. neglectus* yield losses of 56–74% were reported. In North America and Germany, *P. neglectus* has been shown to be a weak pathogen to cereals. Sikora (1988) identified *P. neglectus* and *P. penetrans* in addition to *P. thornei* on wheat and barley in Northern Africa, and all these as well as *P. zaeae* in Western Asia. Further work is necessary to determine the significance of these species in these regions.

The life cycle of *Pratylenchus* is variable between species and environment and ranges from 45 to 65 days (Agrios 1988). Eggs are laid in the soil or inside plant roots. The nematode invades the tissues of the plant root, migrating and feeding as it moves. Feeding and migration of *Pratylenchus* causes destruction of roots, resulting in characteristic dark brown or black lesions on the root surface, hence their name 'lesion' nematodes. Secondary attack by fungi frequently occurs in these lesions. Aboveground symptoms of *Pratylenchus* on cereals, like other cereal root nematodes are non-specific, with infected plants appearing stunted and unthrifty, sometimes with reduced numbers of tillers and yellowed lower leaves.

2.3.3.3 Major Methods of Control

The major method of control for both Cereal Cyst Nematode and Root Lesion Nematode is the use of non-hosts in rotation with wheat and also genetic host resistance. Since CCN is host specific, rotation with non-cereals offers good potential to reduce nematode density. However, as *Pratylenchus* is largely polyphagous, rotational options for these nematodes are far fewer (Nicol and Rivoal 2007). Successful use of rotation requires a thorough understanding of the effectiveness of a particular rotation and, in the case of *Pratylenchus*, a clear understanding of the host status of the other plants used in the rotation.

Resistance is one of the most cost effective and straightforward methods for nematode control. Many sources have been reported and reviewed for CCN and *Pratylenchus* (Nicol and Rivoal 2007). Genetic resistance is favoured with the addition of genetic tolerance (the ability of the plant to yield despite attack by the nematode). The progress in understanding and locating resistance sources in cereals is more advanced for cyst (*H. avenae*) than lesion (*Pratylenchus* spp.) nematodes, in part due to the specific host-parasite relationship that cyst nematodes form with their hosts (Cook and Evans 1987). In contrast, the relationship of migratory lesion nematodes with their hosts is less specialized and therefore less likely to follow a gene for gene model. The identified sources of resistance to *H. avenae* have been found predominantly in wild relatives of wheat in the *Aegilops* genus and have already been introgressed into hexaploid wheat backgrounds for breeding purposes. Unlike cereal cyst nematode, no commercially available sources of cereal resistance are available to *P. thornei*, although sources of tolerance have been used by cereal farmers in Northern Australia for several years (Thompson and Haak 1997).

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