

Nematological Abstracts

The past, present and future of plant nematology in International Agricultural Research Centres

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1. INTRODUCTION

The International Agricultural Research Centres (IARCs) constitute an association of 16 research institutes coordinated by the Consultative Group on International Agricultural Research (CGIAR). The establishment of "The CG System" in 1971 grew largely out of the earlier successes of the Ford and Rockefeller Foundation funded research in rice, wheat and maize, successes that came to be termed the "Green Revolution". The two Institutes most involved in this work, the International Rice Research Institute (IRRI) and the Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT), together with the International Institute of Tropical Agriculture (IITA) and the Centro Internacional de Agricultura Tropical (CIAT) formed the original members of the CGIAR. They have now been joined by other crop-based Institutes (Table 1). These IARCs make up the principal international component of what is becoming termed the "Global Agricultural Research System" with their activities focused on research and training in developing countries while working in close partnership with other "players"; notably the National Agricultural Research Systems (NARS) of these countries (Nickel, 1996; CGIAR, 1997 a).

The CGIAR itself is an informal (hence "Consultative") grouping of national governments, and public and private sector donors. With facilities and a secretariat supplied by the World Bank, the CGIAR receives core funding of over US \$300 million a year to support the IARCs. Additionally the IARCs may receive complementary and special project funding directly from donors. The CGIAR views its mission, as stated in the recent "Lucerne Declaration and Action Plan" (CGIAR, 1995), as being "to contribute, through its research, to promoting sustainable agriculture for food security in the developing countries". Of the 16 IARCs, 8 are essentially crop-based (although CIAT has a major livestock research component) with each institute generally having responsibility for specific "Mandate Crops" (Table 1). Major and well-recognised efforts in the investigation and alleviation of various biotic and abiotic constraints to production of these crops, notably pests and diseases, and the associated programmes for the breeding of improved varieties of these crops, form a large part of the IARCs work. In addition, the IARCs place a strong emphasis on the strengthening of national research and development organisations in the countries they operate in and on the training of these organisations personnel.

Table 1: The Crop Based International Agricultural Research Centres.

CGIAR Centres	Founded	Location of Headquarters	Mandate Crops Discussed
Original CGIAR Members			
IRRI (International Rice Research Institute)	1960	Los Banos, Philippines	Rice
CIMMYT (Centro Internacional de Mejoramiento de Maiz y Trigo)	1966	Lisboa, Mexico	Maize, Wheat
CIAT (Centro Internacional de Agricultura Tropical)	1967	Cali, Colombia	Cassava, Common Beans, Rice
IITA (International Institute of Tropical Agriculture)	1967	Ibadan, Nigeria	Cassava, Maize, Yam, Banana and Plantain, Cowpea, Soybean
Adopted after 1971			
CIP (Centro Internacional de la Papa)	1970	Lima, Peru	Potato, Sweet Potato
WARDA (West Africa Rice Development Association)	1970	Bouaké, Cote d'Ivoire	Rice
ICRISAT (International Crops Research Institute for the Semi-Arid Tropics)	1972	Hyderabad, India	Sorghum, Millets, Pigeonpea, Chickpea, Groundnuts
ICARDA (International Centre for Agricultural Research in the Dry Areas)	1975	Aleppo, Syria	Wheat, Barley, Lentils, Faba Beans

At present a major global debate, both within and outside the CGIAR system, is taking place over both the past achievements and future organisation and directions of the IARCs, exemplified in the appearance of articles with titles such as "Does International Agricultural Research Pay Its Dues?" (Walker, 1992) and "The CGIAR: What Future for International Agricultural Research?" (ODI, 1994). There is widespread concern that the initial, and significant, advances of the green revolution may have been only temporary and that future advances will be much harder to achieve. Scientifically there has been a greater recognition of the complexity of the process controlling both agricultural and overall economic development and of the role of agricultural research in these processes. This, together with heightened concern for the environment and for issues such as the conservation of genetic resources and biodiversity, have resulted in CGIAR viewing 'sustainability of agricultural development' as its broad research agenda. Increases in food output are considered to be one of many components within this (von der Osten-Sacken, 1992).

The purpose of this paper is first, to draw attention to the significance of plant parasitic nematodes as yield constraints to the major mandate crops of the IARCs. Second, to highlight the need for considering plant parasitic nematodes in developing approaches to the improvement in yield and yield sustainability of these mandate crops, and the agricultural systems in which they are grown.

This paper gives an overview of nematological research on those crops that have been adopted as mandate crops by the IARCs and attempts to highlight the inadequate attention paid to plant nematology within these IARCs. It is beyond the scope of this paper to do more than briefly comment on a particular crop in the most general terms. In addition to drawing on standard published literature, review articles and our own experiences, this contribution is also based on assessments of the scientific literature as abstracted in CABPEST-CD derived from CAB Abstracts, providing a coverage of published research from 1973 to the present, essentially covering the period since the establishment of the CG System. Some crops have a large body of published research devoted to their nematode pests (e.g. potato) whereas other crops have been so little studied that the papers resulting from a single Ph.D. project may constitute a significant contribution. We shall show that there are compelling arguments for emphasizing the importance of nematology even within, and in fact because of, the present context of severe funding constraints facing international agricultural research particularly in the IARCs.

2. PLANT PARASITIC NEMATODES

Plant parasitic nematodes, the 'unseen enemies' of crops, have been recognised since the earliest days of microscopy, and were studied as agricultural pests in Europe as early as the late 19th century. However, it was not until the discovery in 1943 of the soil fumigants dichloropropane and dichloropropene mixture (DD) that scientists were able to empirically demonstrate the crop damage some nematode species can cause, and thus the benefits nematode control can bring. This stimulated a great expansion in nematological research (Dropkin, 1989) and established nematology itself as a scientific discipline, complete with its own university departments, scientific journals, and learned societies. Nematologists have estimated plant parasitic nematodes to cause crop yield losses at nearly 9% in the developed world, but at over 14% in developing countries (Sasser & Freckman, 1987). Although these authors attributed a value of US \$78 billion to these losses (in 1987 terms) such simple values are clearly inadequate in assessing or describing the potential impact of such losses to resource poor farmers in the worlds developing regions.

The crop damage caused by nematodes and the symptoms of this damage are often poorly recognised; their microscopic size further reduces their chances of being identified as the causal organism of any disease. Specialised endoparasites, such as the cyst nematodes (e.g. *Heterodera* spp.) cause reduced and altered root growth and a consequent inability of the plant to explore the soil adequately for water and nutrients. This form of nematode damage can often constitute an interaction with soil conditions and become particularly serious in conditions of water shortage or poor soil nutrition. The closely related root-knot nematodes (*Meloidogyne* spp.) may cause galling and hypertrophy of root tissues, constituting a diversion of plant biomass and production. Some more general feeders (e.g. *Pratylenchus* spp.) can cause physical disruption in roots as well as promote invasion by other root pathogens that lead to a general necrosis of affected root tissues. In some situations, nematode damage to roots can predispose plants to other pathogens (the best known such interaction being that between root-knot nematodes and *Fusarium* wilt). Some nematodes act as virus vectors. Although most recognised plant parasitic nematodes affect plant growth and harvested yield, some (e.g. *Scutellonema bradyi* on yams) are principally post-harvest pests, whereas others (e.g. *Rotylenchulus reniformis* on sweet potato) can affect the marketability of the harvested crop. Although plant growth and crop yield responses to nematicide treatment are often used to illustrate nematode damage, this may present difficulties. Nematicides are often general biocides. The killing of soil fauna after treatment with nematicides can lead to a liberation of organic compounds and nitrogen, and thus

create a general fertilizer effect that can increase plant growth (Dropkin, 1989). Other nematicides may have more direct and favourable effects on plant physiology independent of any control of parasitic nematodes. Thus the empirical assessment of plant parasitic nematodes as "production constraints" can present considerable difficulties in experimental design and interpretation.

3. THE MAJOR MANDATE CROPS OF THE INTERNATIONAL AGRICULTURAL RESEARCH CENTRES AND THEIR IMPORTANT NEMATODE PESTS.

3.1 Rice

Rice (*Oryza sativa*) is the staple food of more than two billion people, predominantly in Asia where more than 90% of the world's rice is grown and consumed (Bridge *et al.*, 1990). Of the total rice area, about 53% is irrigated, 31% is rainfed lowland, 13% is upland, and 3% is deepwater (Khush, 1984).

Worldwide, rice yield losses due to plant parasitic nematodes are estimated at 10% (Sasser & Freckman, 1987). Major nematode pests of rice are *Aphelenchoides besseyi*, *Criconelella onensis*, *Ditylenchus angustus*, *Heterodera* spp., *Hirschmanniella* spp., *Hoplolaimus indicus*, *Meloidogyne* spp., *Paratylenchus* spp., *Pratylenchus* spp., and *Xiphinema fucolium* (Bridge *et al.*, 1990). Two species, *A. besseyi* (the white tip nematode) and *D. angustus* (the ufra disease nematode) are foliar parasites. Damage due to *A. besseyi*, which is a seed-borne nematode, is more severe on irrigated lowland and deep water rice because at the high relative humidity found in these situations the nematode easily migrates into the panicle. Crop damage caused by *A. besseyi* depends on the amount of infested seed sown and number of nematodes per seed. Extensive damage caused by this nematode has been reported from Bangladesh and India. The stem nematode, *D. angustus*, causes severe damage in years of high rainfall and it is a major pest in deepwater and lowland rice systems in the great river deltas of Vietnam, India, Bangladesh and Myanmar. Although of localised occurrence, it can cause complete yield loss. The nonparasitic root-knot nematodes (*Meloidogyne* spp.), particularly *M. graminicola* and *M. incognita* are important arsites of rice. *M. graminicola* is mainly found in South and E. Asia (Bangladesh, Laos, Myanmar, Philippines, Thailand, Vietnam, India), and also in the USA. Both *M. incognita* and *A. javanica* cause damage to upland rice in Africa as well as their areas of the world. *Meloidogyne salasi* is reported from Costa Rica and Panama. *Hirschmanniella* spp. (rice root nematode) are virtually cosmopolitan in lowland rice production systems. These migratory endoparasites of roots produce cavities and channels in the cortex (Hollis & Leboonrueng, 1984). They are very well adapted to constant flooding (Fortuner & Merny, 1979) and cause greater damage in low fertility soils. The lesion nematodes, *Pratylenchus* spp., are also migratory endoparasites and have been reported on rice throughout the world. *Pratylenchus zeae* and *P. indicus* cause significant damage to upland rice (Bridge *et al.*, 1990). Nematode parasitism destroys the root cortex and extensive damage greatly hampers root growth and function. The cyst nematodes, *Heterodera* spp., have been found on upland rice although are of restricted distributions and thus localised importance (Table 2).

The major contributors to research in rice nematology have been the national institutes within the producing countries. Both India and Bangladesh have National Rice Research Institutes and a large proportion of the research published on rice nematodes has emanated from the subcontinent. This has included surveys (e.g. Rahman & Taylor, 1983; Prasad *et al.*, 1987), yield loss assessments (e.g. Jonathan & Velayutham, 1987); evaluation of chemical and non-chemical control (e.g. Rahman & Miah, 1989; Rahman, 1990; Jonathan & Pandiarajan, 1991); and screening and breeding for nematode resistance (e.g. Rahman, 1987; Sahu & Chawla, 1988). Within Asia, the

other major producers, principally Japan (especially in the area of chemical control) but also China and Thailand, have generated research information (e.g. Uebayashi *et al.*, 1971; Feng, 1986; Aravurangsant *et al.*, 1986). Other prominent rice producing countries such as Myanmar and Vietnam also have established rice nematology research programmes (e.g. Kinh & Ngoc, 1982). The United States, a major rice exporter, has also undertaken some research in rice nematology (e.g. McGawley *et al.*, 1984). By contrast IRRI, the longest established IARC, although influential in disseminating findings generated by national programmes in the Asian region, has only recently itself begun to conduct nematological research. The IRRI programme started with surveys and attempts at prioritizing the influence of nematodes on rice production (e.g. Prot, 1994; Prot *et al.*, 1994b) as well as investigations of nematode-plant relationships (Prot *et al.*, 1995). Of the other IARCs mandated to study rice, the West Africa Rice Development Association (WARDA) has recently initiated a research programme (WARDA, 1995) whereas CIAT, situated in Colombia, a region where rice is rapidly increasing in importance as a crop, has not.

3.2 Wheat

Wheat (*Triticum aestivum*) originated in southwest Asia from wild grasses, became an important plant to the ancient civilizations of Egypt, Greece, and Persia and is now the world's most widely grown staple food (Purseglow, 1972; Kochlar, 1981).

A large number of nematodes are associated with wheat in different agro-ecological regions. Annual yield losses due to damage by plant parasitic nematodes to wheat on a global basis are estimated at 7% (Sasser & Freckman, 1987). The major nematode pests of the crop are *Anguina tritici*, *Heterodera* spp., and *Pratylenchus* spp. Of these, the most important is the cereal cyst nematode *Heterodera avenae* and the foliar parasite, *Anguina tritici* (Table 2). *H. avenae*, previously thought to occur mainly in temperate countries, has now been reported from more than 31 countries (Griffin, 1984). It is the most important pest of wheat in southeastern Australia and serious yield losses have been reported in India and Pakistan. Another cyst nematode species, *H. latiposa* occurs mainly in the Mediterranean region and in northern Europe and causes considerable damage in semi-arid temperate environments. *Anguina tritici* is a problem in the Indian subcontinent, China, in parts of eastern Europe and temperate semi-arid north Africa and West Asia (Swarup & Sosa-Moss, 1990; Sikora, *et al.*, 1988). Infective juveniles of this species present in the soil invade the host plant and are carried up to the inflorescence by the growing point. The nematodes mature inside galls or cockles that replace the kernels, and can survive in an anhydrotic state for many years. Additionally, this nematode is vector of a bacterium, *Corynebacterium michiganense* pv *tritici*, which causes yellow ear rot and whose presence significantly increases yield loss (Swarup & Gokte, 1986). Strict laws regulating seed and seed certification procedures can virtually eradicate this nematode. The endoparasitic lesion nematode, *Pratylenchus thornei*, is potentially important in India, Mexico, and Australia (Meisner *et al.*, 1992). The cereal root-knot nematode, *Meloidogyne naasi*, is widely distributed on wheat, particularly in Europe.

Wheat is grown in both temperate and semi-arid subtropical regions, in countries of both the developed north and the developing south. Within Europe, nematological research has taken place in most countries, including those of Eastern Europe, but most prominently in France and Italy (e.g. Rivoal & Sarr, 1987; Greco & Brandonisio, 1987). Although a range of nematode species affect wheat in the United States and studies on nematode resistance (e.g. Kaloshian *et al.*, 1989) and pathogenicity assessments (e.g. Nyczepir *et al.*, 1984) have been conducted, most research here has focused on the use of wheat in the control of more serious nematode pests of other crops (e.g. Mai & Abawi, 1980; Koening & Anand, 1991). It is in Australia, where the cereal cyst nematode

Table 2. Major plant parasitic nematode pests of mandate crops.

Crops	Nematodes	Symptoms	Distribution
Rice	<i>Aphelenchoides besseyi</i>	Leaves with chlorotic tips	Worldwide
	<i>Ditylenchus angustus</i>	White speckles or patches at the base of young twisted leaves and panicles; crinkled, empty glumes	Bangladesh, Myanmar, India, Madagascar, Malaysia, Thailand, Vietnam
	<i>Meloidogyne graminicola</i>	Poor growth. Swollen and hooked root tip galls	Myanmar, China, Bangladesh, India, Laos, Philippines, Thailand, Vietnam, USA
	<i>Hirschmanniella</i> spp.	No specific symptoms. general poor growth and delayed flowering	Worldwide in lowland rice growing areas
	<i>Pratylenchus</i> spp. (<i>P. zaei</i>)	General poor growth. Dark elongated lesions on roots	Worldwide in upland rice growing areas
Wheat	<i>Heterodera</i> spp. (<i>H. elachista</i> , <i>H. oryzae</i> , <i>H. oryzicola</i> , <i>H. sacchari</i>)	Poor growth. Cysts/white females on roots	Localised. <i>He</i> - Japan, <i>Ho</i> - Bangladesh, <i>HS</i> - mainly W. Africa
	<i>Heterodera avenae</i>	Poor growth. Cysts/white females visible on roots	Temperate climates
Maize	<i>Anguina tritici</i>	Swelling of basal stem of seedlings, twisting of leaves. Seed replaced by black nematode galls	Temperate/Mediterranean climates
	<i>Pratylenchus</i> spp. (<i>P. brachyurus</i> , <i>P. zaei</i>) <i>Punctodera chalcensis</i> , <i>Heterodera zaei</i>	Poor growth. Small brown elongate lesions on root surface Poor growth. Cysts/white females on roots	Worldwide <i>Pc</i> - C. America, <i>H.z</i> - Egypt, India, Pakistan, USA.
Sorghum	<i>Tylenchorhynchus</i> (<i>T. martini</i> , <i>T. nudus</i>)	General stunting, non-specific symptoms	Worldwide
	<i>Pratylenchus</i> spp. (<i>P. zaei</i>)	Poor growth, brown lesions on roots	Worldwide
	<i>Heterodera</i> spp. (<i>H. gambiensis</i> , <i>H. sorghi</i>)	Poor growth, cysts visible on roots	<i>H.s</i> - India, <i>H.g</i> - Gambia, Niger, India
Pearl millet	<i>Meloidogyne acrona</i>	Poor growth, swollen females on roots	Southern Africa
	<i>Meloidogyne incognita</i>	Poor growth, galls on roots	Worldwide
Barley	<i>Pratylenchus zaei</i>	Poor growth, brownish lesions on roots	Worldwide
	<i>Heterodera avenae</i>	Poor growth, cysts/white females visible on roots	Temperate climates
Potato	<i>Anguina tritici</i>	Swelling of basal stem of seedlings, twisting of leaves. Seed replaced by black nematode galls	Temperate Asia
	<i>Globodera</i> spp. (<i>G. pallida</i> , <i>G. rostochiensis</i>)	Poor growth, leaf chlorosis, cysts/white females visible on roots and tubers	Temperate climates now worldwide
	<i>Meloidogyne</i> spp. (<i>M. incognita</i> , <i>M. javanica</i>)	Poor growth, leaf chlorosis. Galls on roots, knobby tubers	Tropical climates worldwide
	<i>Nacobbus aberrans</i>	Poor growth, rosary-bead-like root galls	S. and C. America
	<i>Ditylenchus destructor</i>	Small white or light brown spots just below surface of tuber, dark brown rotting of tuber	Temperate climates, Europe, N. and S. America
Sweet potato	<i>Meloidogyne</i> spp. (<i>M. incognita</i>)	Poor growth, leaf chlorosis. Galls on roots, distortion of developing tuber roots	Tropical, worldwide
Cassava	<i>Rotylenchulus reniformis</i>	Poor growth. Cracking of storage tubers	Tropical, worldwide
	<i>Pratylenchus</i> spp. (<i>P. brachyurus</i> , <i>P. coffeae</i>)	Lesions on roots	Tropical, worldwide
	<i>Meloidogyne</i> spp. (<i>M. incognita</i> , <i>M. javanica</i>)	Galls on roots, poorly formed storage roots	Tropical, often localised
Yam	<i>Scutellonema bradyi</i>	Dark brown/black dry rot of tubers below surface of skin (initially light yellow lesions)	W. Africa, Caribbean, S. America
	<i>P. coffeae</i>	Dry rot of tubers (as above with <i>S. bradyi</i>)	Caribbean, Pacific, C. And S. America
Banana	<i>Meloidogyne</i> spp.	Galling of roots and knobby tubers	Worldwide
	<i>Radopholus similis</i>	Toppling of plants. Yellow, purple and black lesions throughout root cortex	Tropical, worldwide
	<i>Pratylenchus coffeae</i>	Toppling of plants. Yellow, purple and black lesions throughout root cortex	Tropical, worldwide, but mainly Pacific, C. And S. America, Caribbean
	<i>Pratylenchus goodii</i>	Toppling of plants. Yellow, purple and black lesions throughout root cortex	Subtropical/Mediterranean climates. E. Africa, Cameroon, Canary Islands, Crete
Cowpea	<i>Helicotylenchus multicinctus</i>	Dark brown lesions mainly in outer root cortex	Worldwide
	<i>Meloidogyne</i> spp. (<i>M. incognita</i> , <i>M. javanica</i>)	Galls on roots	Worldwide
	<i>Meloidogyne</i> spp. (<i>M. incognita</i> , <i>M. javanica</i>)	Stunted growth, chlorosis. Galls on roots	Tropical, worldwide
	<i>H. cajani</i>	Cysts/white females visible on roots	Egypt, India
Soybean	<i>R. reniformis</i>	Poor growth. Roots with mucilaginous egg sacs	Worldwide
	<i>Meloidogyne</i> spp. (<i>M. incognita</i> , <i>M. javanica</i>)	Stunting, chlorosis. Galls on root	Worldwide
	<i>H. glycines</i>	Severe stunting, chlorosis. Cysts/white females visible on roots	Egypt, S. America, Korea, Indonesia, Japan, USA
	<i>R. reniformis</i>	Stunting, chlorosis	Worldwide

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geonpea	<i>H. cajanii</i>	Stunting, chlorosis. Cysts/white females on roots	India
	<i>Rotylenchulus</i> spp. (<i>R. reniformis</i> , <i>R. parvus</i>)	Chlorosis, reduced root system	India, E. and C. America, Caribbean, Pacific, Kenya
	<i>Meloidogyne</i> spp. (<i>M. incognita</i> , <i>M. javanica</i>)	Poor growth. Galls on root	India, E. And C. Africa, Nepal, USA
roundnut	<i>Meloidogyne</i> spp. (<i>M. hapla</i> , <i>M. brachyura</i> , <i>M. arenaria</i>) <i>P. brachyurus</i>	Severe stunting, chlorosis. Galls on roots, pegs and stems. Malformed, warty pods Unthrifty growth. Dark spotted lesions on roots, pegs and pods	Worldwide Australia, Egypt, India, USA, Zimbabwe
	<i>Criconebella ornata</i>	Stunting, chlorosis. Brown necrotic lesions on pegs and pods	Egypt, India, USA
	<i>Tylenchorhynchus brevitarsus</i>	Pod discolouration	India, South Africa
	<i>Aphasmatylenchus straturatus</i>	Chlorosis. No specific symptoms	W. Africa
	<i>Aphelenchoides arachidis</i>	Discolouration and crinkling of seed coat	Nigeria
	<i>Scutellonema spp.</i> (<i>S. cavense</i> , <i>S. clathricaudatum</i>)	Poor growth, chlorosis. No specific symptoms	W. Africa
	<i>Ditylenchus africanus</i>	Testa with distinct brown necrotic tissue at pod base, discolouration of veins beneath pod surface	South Africa
	<i>Meloidogyne</i> spp. (<i>M. incognita</i> , <i>M. javanica</i>) <i>M. artiellia</i>	Poor growth, chlorosis. Galls on roots	Tropical, worldwide
	<i>Pratylenchus</i> spp. (<i>P. thornei</i>) <i>Heterodera ciceri</i>	Poor growth. Dark brown lesions on roots Severe decline. Cysts/white females visible on roots	Worldwide Syria
	<i>H. ciceri</i>	Stunting, chlorosis. Cysts/white females on roots	Syria
'aba bean	<i>Ditylenchus dipsaci</i>	Swollen and deformed stem with dark brown lesions, blackened pods and seeds	Temperate climates, Europe, Mediterranean, E. Asia
	<i>Heterodera goettingiana</i>	Poor growth, leaf chlorosis, cysts/white females visible on roots	Temperate climates, Europe, Mediterranean, E. Asia
Common Beans	<i>Meloidogyne</i> spp. (<i>M. incognita</i> ; <i>M. javanica</i>) <i>Heterodera glycines</i> <i>Rotylenchulus reniformis</i>	Severe stunting, chlorosis, root galling Stunting, yellowing, cysts on roots General poor growth, yellowing	Worldwide N & S America, Asia Tropical Americas

avenae is a pest of major economic importance on wheat (rennan & Murray, 1988), where the largest contribution to research on this pest has been made. This has included work on chemical and cultural control (Brown, 1987) and ant breeding (e.g. Wilson *et al.*, 1983). Work has also been conducted on other nematode pests of wheat (e.g. *Pratylenchus tritici* (Doyle *et al.*, 1987)). In the developing world, a considerable amount of research has arisen from the national programmes of both India and Pakistan. A number of nematode species affect wheat on the sub-continent (Swarup Gokte, 1986; Maqbool, 1987), principal among them being *avenae*. The effects of this nematode on the crop are referred to as "molya" disease. Investigations of damage thresholds and yield loss assessment have been conducted (e.g. Bhatti *et al.*, 1981), chemical and cultural control methods evaluated (e.g. Kaushal & Seshadri, 1989) and screening for resistance has been done (e.g. Jain & Sehgal, 1979). Work on other important nematode species on wheat in the region has also been done. These include *A. tritici*, the cause of "ear-cockle" or "tundu" disease (e.g. Shahina *et al.*, 1989; Paruthi & Bhatti, 1990), and root-knot nematodes (e.g. Patel & Patel, 1991). Wheat is also a major crop both in the Mediterranean region and the Middle East/West Asia (the area of the "fertile crescent"). Work has been conducted by various national programmes, notably that of Israel (e.g. Orion *et al.*, 1984; Mor *et al.*, 1992). The basis for research in other countries of the region has been established (Saxena *et al.*, 1988) and survey work (e.g. Ibrahim *et al.*, 1988a), and experimentation (e.g. Zek *et al.*, 1987; Ibrahim *et al.*, 1988b) have been conducted. Within the CGIAR, the mandate for wheat is shared between the International Centre for Agricultural Research in the Dry Areas (ICARDA) in Syria and CIMMYT in Mexico. ICARDA has contributed to establishing nematological links between, and with, national programmes (e.g. Saxena *et al.*, 1988). Wheat nematodes are not considered serious pests in North America, although *Pratylenchus thornei* has been shown to

attack wheat in Mexico (Van Gundy *et al.*, 1974). Although the second oldest IARC, CIMMYT has never conducted sustained research in nematology.

3.3 Maize

Maize (*Zea mays*) is the third most important cereal crop after rice and wheat in terms of world production. Annual production is about 570 million tons of which 256 million tons is produced by the United States and a further 100 million tons by China (FAO, 1995). Brazil, Mexico, Argentina and India are also major producers. This crop is used in more ways than perhaps any other cereal; for human consumption, as a feed grain, a fodder crop, and as raw material for many industrial products.

Although nearly 120 species of plant-parasitic nematodes have been reported associated with maize the significance of most species is undocumented. Additionally, as polyspecific communities of plant-parasitic nematodes are generally found on maize it may be more appropriate to consider the pathogenicity of the nematode community rather than of a single species (Singh, 1976; Norton, 1984). Of these the most important are the lesion nematodes, *Pratylenchus* spp. and the cyst nematodes (*Heterodera zae* and *Punctodera chalcensis*) (Table 2). Worldwide, the loss in yield of maize due to plant parasitic nematodes is estimated at over 10% (Sasser & Freckman, 1987). More than 15 species of *Pratylenchus* are associated with maize. *P. brachyurus*, *P. hexincisus* and *P. zae* being the most damaging. *Punctodera chalcensis* and *H. zae* cause significant damage to maize but accurate loss figures are not available (Swarup and Sosa-Moss, 1990). Parasitism of maize roots by polyspecific nematode communities is very common and evaluation of crop damage and yield losses caused by any one nematode species is difficult (Norton, 1984).

Parasitism by *Pratylenchus* sp. can lead to root destruction, with above ground symptoms of stunted growth, chlorosis and yield reduction. Unattributed losses due to *Pratylenchus* are considered as widespread and in the United States experiments in nematode (principally *Pratylenchus*) control on maize have resulted in yield increases of 10–54%, and in South Africa of up to 100% (Norton, 1984).

The ectoparasitic genera *Beloniolaimus*, *Longidorus* and *Paratrichodorus* are considered pests in the United States. *Beloniolaimus longicaudatus* in particular is a serious pest in the south eastern states and nematode control resulted in average yield increases of 73% in Florida (Johnson & Dickson, 1973). In Europe, where maize production has increased greatly in recent years, the cereal cyst nematode, *Heterodera avenae*, can cause yield reductions of up to 50% (Rivoal & Cook, 1993). The stem nematode, *Ditylenchus dipsaci* can also cause severe losses, particularly when plant topping results (Rivoal & Cook, 1993).

In regions of the tropics and sub-tropics where maize is a major starchy staple in smallholder agriculture, in addition to *Pratylenchus* sp. various species of endoparasitic nematode can be serious pests. Generally very little information is available on the status of nematode problems of maize in the developing countries. The cyst nematode *Heterodera zea* is considered a serious pest in the Indian sub-continent and has also been recorded in Egypt, Thailand and the USA (Swarup & Sosa-Moss, 1990; Chinnasri *et al.*, 1995). Although the nematode can provoke typical symptoms of poor growth and cause plant growth reductions of over 63% in pot experiments (Srivastava & Sethi, 1984) field losses have not yet been adequately assessed. A closely related species, *Pimodera chalcensis* is considered a serious pest in Mexico. Certain species of root knot nematode, *Meloidogyne*, can cause damage to maize, and considering the cosmopolitan distribution of this genus in the sub-tropical and tropical regions, nematodes of this genus are concluded to be causing yield losses (Norton, 1984). However, although plant growth reductions due to *M. incognita* of over 80% have been obtained in pot experiments (Di Vito *et al.*, 1980), field data on losses is lacking. Complications arise as maize is resistant to some species of *Meloidogyne*, and may be a poor host to certain races, for example, *M. incognita*. Populations of these nematodes decline under maize and inclusion of this crop is recommended in certain cropping sequences designed to control these nematodes on other crops (e.g. Baldwin & Barker, 1970; Rodriguez-Kabana, *et al.*, 1991).

Research on nematodes of maize has been conducted almost exclusively within the various national programmes. Of these by far the most work has been conducted in the United States. Here, in addition to work on the influence of maize on nematode populations of the whole cropping system, there has been work on cultivar evaluation (e.g. Windham & Williams 1988; Hashmi *et al.*, 1994) as well as on chemical control (e.g. Todd & Oakley, 1995). A similar range of research has taken place in Brazil, with resistance screening (e.g. Brito & Antonio, 1989), chemical control (e.g. Lordello *et al.*, 1992) as well as the use of maize in crop rotations. Outside of the Americas most research on nematodes of maize has taken place within the national programmes of India and Pakistan. Surveys (e.g. Haider & Nath, 1992; Anwar *et al.*, 1973) as well as more detailed studies of nematode biology (e.g. Parihar & Yadav, 1992) have been conducted. Limited research has taken place in various countries of Africa, notably South Africa (e.g. Jordaan *et al.*, 1989) and also Nigeria (e.g. Afolami and Fawole, 1991) and more recently Egypt (e.g. Ismail *et al.*, 1994).

Within the CGIAR, responsibility for research on maize is shared between CIMMYT in Mexico and IITA in Nigeria. Neither centre has ever conducted sustained or significant work on the plant parasitic nematodes of the crop.

3.4 Sorghum

Sorghum (*Sorghum vulgare*), a crop of African origin, is the world's fifth most important grain crop (Doggett, 1988), and is often grown for forage and silage. Approximately

40% of the world's area devoted to sorghum is in Asia, 33% in Africa, and over 20% in the Americas. Yields in Africa and Asia are generally below 1t/ha but can be three times greater in China and the Americas (Doggett, 1988). Sorghum is one of the most important cereals of the semi-arid tropics.

Although more than 115 species of plant parasitic nematodes have been associated with sorghum in different production systems (Sharma & McDonald, 1990) and nematodes have been estimated to cause nearly 7% loss to sorghum yield (Sasser & Freckman, 1987), very little work has been done to characterize and manage the important nematode pests of sorghum. This crop is a host of the stunt nematodes (*Tylenchorhynchus* spp.), the lesion nematodes (*Pratylenchus* spp.), and also some root-knot nematodes, *Meloidogyne* spp. (Sharma & McDonald, 1990). *Tylenchorhynchus martini*, *T. nudus*, and *T. acutus* in the USA, and *T. mashoodi* and *T. vulgaris* in parts of Asia are important. Yield increases of as much as 55% after nematode treatment were reported where *T. martini* was the dominant population (Hafez & Clafin, 1982). Lesion nematodes (*Pratylenchus* spp.) are important parasites of sorghum in Australia, Brazil, Egypt, India, Pakistan, Sudan, Thailand, USA, and Zimbabwe. The root-knot species *M. acrota* is a pest of sorghum in southern Africa and pot experiments have demonstrated that it can cause a 56% loss in yield. Other genera and species particularly *Heterodera gambiensis*, *Paralongidorus bullatus*, *P. duncani*, *Scutellonema cavense*, and *S. clathricaudatum* in West Africa and *Heterodera* spp. in India are potentially important nematodes. Although experiments with nematicides have increased yields of grain sorghum and of sorghum/millet forages by 50% or more (Johnson & Burton, 1973, 1974; Hafez & Clafin, 1982), little field work has been done to assess the overall significance of nematodes in yield suppression. Of the work done on sorghum nematology, a large proportion has been conducted in the southern United States. However, in this region interest in sorghum is primarily in its potential in rotations to reduce populations of nematode species, such as *Heterodera glycines* (Rodriguez Kabana *et al.*, 1991) and *M. incognita* (McSorley & Gallaher, 1992) considered serious on other crops. In other parts of the world, most published research on sorghum nematodes has consisted of survey work and host records (e.g. Germani *et al.*, 1984, West Africa; Hasan & Jain, 1986, India). Research on pathogenicity and varietal screening has also taken place in some National Institutes, principally in India (e.g. Srivastava & Sethi, 1988).

The IARC mandated to work on sorghum is ICRISAT. Although involved in survey work (Sharma & McDonald, 1990), ICRISAT at present has no active research programme on sorghum nematodes.

3.5 Millets

Finger millet (*Setaria italica*) and pearl millet (*Pennisetum glaucum*) are grown widely in the semi-arid areas of Africa and the Indian sub-continent (Kochlar, 1981). Finger millet is an important food crop in the highlands of eastern and southern Africa and in parts of India and Nepal. Pearl millet is used as a grain food in both India and Africa and also provides a good source of fodder for livestock.

On a worldwide basis, annual losses to millets due to damage by plant parasitic nematodes are estimated at nearly 12% (Sasser & Freckman, 1987). Little work has been done on nematode parasites of these crops. *Helicotylenchus indicus* (spiral nematode), and *T. vulgaris* in India, *M. javanica* and *Paratrichodorus minor* in Brazil, *Pratylenchus zea* and *Rotylenchulus* spp. in Zimbabwe, *P. zea* in the United States, and *Tylenchorhynchus* spp. and *Hoplolaimus* spp. in Pakistan, are considered as important nematode pests of pearl millet (Sharma & McDonald, 1990). Information on nematodes associated with finger millet is limited, but three species of cyst forming nematodes (*Heterodera gambiensis*, *H. sorgii* and *H. deluii*), and the reniform nematode, *Rotylenchulus reniformis*, have been reported as parasites (Seshadri, 1970; Krishna Prasad & Krishnappa, 1982). Some research in West Africa has shown yield increases in millet following nematicide

reatment (Germani *et al.*, 1984). Work has also occurred within national institutes in India (e.g. Tiyagi *et al.*, 1987). Apart from contributing to nematode surveys of various crops, including millets (e.g. Sithole & Mtsi, 1987), the mandated IARC, CRISAT, has no active research programme on the nematode parasites of millets (Sharma & McDonald, 1990).

3.6 Barley

Barley (*Hordeum vulgare*) is one of the world's major grain crops. Its principal uses include animal feed and malting. It may also be milled and used in baked foods. The crop is grown widely in northern Europe and as a winter crop in the semi-arid regions of the Mediterranean and the Middle East/West Asia.

Plant parasitic nematodes, on a global basis, are estimated to cause over 6% yield loss in barley (Sasser & Freckman, 1987). The nematode pests of this crop are similar to those of wheat; *H. avenae* is the most serious and occurs in many parts of the world (Swarup & Sosa-Moss, 1990). Another cyst nematode, *H. latipons*, affects barley in north Africa and the Middle East/West Asia. Other nematodes known to attack barley include *Pratylenchus* spp. (including *P. thornei*) and root-knot nematodes (including *Meloidogyne naasi*). Research on the nematodes (principally *H. avenae*) of barley is conducted in most of the countries of Europe. This includes Scandinavia (e.g. Andersson, 1976; Sweden; Hansen, 1986; Denmark) and also countries of eastern Europe and Russia (e.g. Glaba, 1985; Carpova, 1987). Most work concerns damage assessments (e.g. Magi, 1989; Romero *et al.*, 1991) and resistance breeding (Ewertson & Lundin, 1985). The national programmes of both India and Pakistan have conducted research on the control of *H. avenae* on barley (e.g. Handa *et al.*, 1985; Pankaj & Dhawan, 1991). Within the Mediterranean and the Middle East/West Asia, survey work and some experimentation has been conducted in several countries (e.g. Romero *et al.*, 1991; Spain; Vesikine & Abbad, 1993; Morocco; Al-Hazmi *et al.*, 1994; Saudi Arabia). ICARDA has the crop mandate for barley and has done much to facilitate work in the Middle East/West Asia region (Saxena *et al.*, 1988) and establish linkages with other research programmes to conduct nematode surveys (ICARDA, 1995). However, much basic work remains to be done, not least in assessing the pest status of the major nematode parasites of barley observed in these regions.

3.7. Potato

Potato (*Solanum tuberosum*) originated in the high Andes of South America (Simmonds, 1971). Since its introduction to Europe in the 16th century, and in particular following the emergence of adapted varieties in the 18th century the potato has become the leading starchy staple of northern temperate countries. The crop is now grown world-wide, in tropical highlands (e.g. the Andes, Himalayas and in East Africa), as a cool season crop in tropical lowlands, as well as a spring-sown crop in temperate regions (Horton, 1990). In sub-Saharan Africa, production has increased by 150% since 1961 (Scott, 1993), greater than for any other major food crop except rice and yams.

Annual yield losses to potato due to damage by plant parasitic nematodes are estimated to exceed 12% worldwide (Sasser & Freckman, 1987). The major nematode pests of potato are the cyst nematodes (*Globodera rostochiensis* and *Globodera pallida*), the root-knot nematodes (*Meloidogyne* spp.) and the stem and tuber nematodes (*Ditylenchus* spp.). Lesion nematodes (*Pratylenchus* spp.) may also cause yield loss and the false-root knot nematode (*Nacobbus aberrans*) is a serious pest in South and Central America (Brodie *et al.*, 1993). Potato cyst nematodes originated in the Andean highlands but have been spread worldwide during the last 150 years (Jones & Kempton, 1982). *Globodera* spp. are established in all potato growing areas of Europe and are now found in at least 59 countries worldwide including South Africa, India, Australia and Japan (Brodie *et al.*, 1993). Strict quarantine measures at first prevented, and have subsequently retarded the spread of potato cyst nematode in the United States, which is confined to one pathotype of the species *G. rostochiensis* (Brodie *et al.*, 1993). Both *Meloidogyne* spp. and *Pratylenchus* spp. occur worldwide, the particular species present in a location generally depending on ecological factors: *M. incognita* is the most important root-knot nematode species in the warm tropics; *M. hapla* and *M. chitwoodi* are found in cooler regions (Jatala & Bridge, 1990). *Ditylenchus* spp. causes a dry rot of potato tubers. Although found widely, species of *Ditylenchus* are considered serious pests in Europe, particularly in eastern Europe. The nematodes feed on sub-epidermal tissues and this may promote attack by secondary rot organisms. Such attack may continue on stored tubers (Jatala & Bridge, 1990; Brodie *et al.*, 1993).

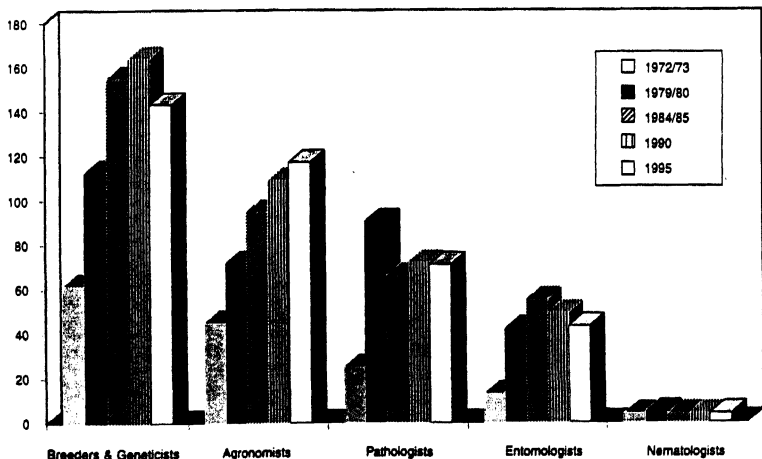


Figure 1. Numbers of senior staff by specialism in seven International Agricultural Research Centres (IARC's): CIAT, CIMMYT, CIP, ICARDA, ICRISAT, IITA, IIRRI.

The major importance of potatoes is reflected in the vast body of scientific literature, going back over 100 years, on their nematode pests. A bibliography prepared in 1979 lists 1798 publications on potato nematodes (Jensen *et al.*, 1979). At this time, it was estimated that an eighth of all scientific literature concerning nematodes dealt with potato nematodes, and 70% of these with potato-cyst nematodes (Winslow, 1978). Several comprehensive reviews are available on nematodes of potatoes (Winslow & Willis, 1972; Brodie, 1984; Jatala & Bridge, 1990; Brodie *et al.*, 1993). Over the years, work on potato cyst nematodes has covered all aspects of the pests' biology and host-parasite relationships. Control measures investigated include crop rotations, chemical control, the use of resistant varieties and more recently biological control. Over the last 50 years, considerable effort has been directed at the development of cyst nematode resistant varieties. This effort has been particularly successful against *G. rostochiensis*. In New York State (USA), for example, virtually complete control is now possible with the use of resistant varieties (Brodie, 1995). Potato breeding programmes, including the development of cyst nematode resistant varieties, exist in both the national programmes and within the commercial private sector of many developed countries. In the developing world, many countries conduct research on potato nematodes. In the countries of the Andes where potatoes remain a major staple, research has also concentrated on the cyst nematodes indigenous to the region (e.g. Fernandez, 1988; Chile; Nieto and Barriga, 1976; Colombia; Franco, *et al.*, 1991; Bolivia; Llontop *et al.*, 1989; Peru). The national programme in India has conducted research on nematodes of potato, reviewed by Prasad (1986). Root-knot nematodes are major pests of potato in India and it was here that the earliest attempts at developing *Meloidogyne* resistance were made (Khanna & Nirula, 1964). More recently, work has been conducted in the United States (e.g. Ingham *et al.*, 1991) where the species, *M. chitwoodi*, is causing concern (O'Bannon *et al.*, 1982). Research on *Ditylenchus* spp. has occurred mostly in Europe, in particular in eastern Europe (e.g. Kornobis & Stefan, 1991). Some work has also been done in South Africa (e.g. De Waele *et al.*, 1991). *Ditylenchus* spp. are considered serious pests of sweet potato in China (see section 3.8); however, nothing is known of their influence on *S. tuberosum* in China. *Nacobbus aberrans* is being studied within the national programmes of various South American countries (Brodie *et al.*, 1993). The IARC mandated to conduct research on potato is CIP and, of the international centres, CIP has conducted the most work in nematology, and has been the only Institute to recognise the discipline administratively (with a Department of Nematology and Entomology). At one stage, a number of nematologists were included in the programme (Fig. 1) and over the years CIP has generated a large amount of research information on various aspects of potato nematology (CIP, 1978; Jatala & Bridge, 1990). Much of this work was conducted in close collaboration with research groups in the United States or the United Kingdom. A large part of this effort was directed at germplasm collection, screening and evaluation, and this has contributed significantly to the successful development of the cyst nematode resistant varieties referred to earlier. With the recognition of the potential of potatoes in the lowland tropics (e.g. Simmonds, 1971), the importance of research on root-knot nematodes was recognised (Jatala & Mendoza, 1978). Such work was developed further (e.g. Iwanga *et al.*, 1989) as a component of CIP's overall efforts in this area. Recently, however, the CIP nematology programme has been much reduced (CIP, 1996).

3.8 Sweet Potato

Sweet potato (*Ipomoea batatas*) originated in the New World, and was being grown in Mexico and other parts of tropical America in pre-Columbian times. Sweet potatoes are presently grown throughout the humid tropics and many sub-tropical regions (Purseglowe, 1968). Globally, sweet

potato production is concentrated overwhelmingly in Asia (Chandra, 1994). Of the total world production of over 130 million tons, over 75% is produced in China alone and the crop is also of major importance in Japan and Taiwan. Sweet potato is becoming increasingly important as a subsistence crop in Africa, particularly in the East and Central African Highland countries of Uganda, Burundi and Rwanda where annual per capita consumption may be over 100 kg (Scott & Ewell, 1993). The Americas produce about 3 million tons per year, some 0.5 million tons of which are grown in the southern United States.

The major nematode pests of sweet potato are *Meloidogyne* spp., *Rotylenchulus reniformis*, and *Pratylenchus* spp. *Ditylenchus dipsaci* and *D. destructor* are reported as serious pests in China. Root-knot nematodes are distributed worldwide, the most important species in sweet potato growing regions being *M. incognita* and *M. javanica*. *Rotylenchulus reniformis* is found throughout the tropics and sub-tropics (Siddiqui, 1972). Among the species of *Pratylenchus* known to attack sweet potato are *P. coffeae*, *P. brachyurus*, *P. penetrans*, *P. vulnus* and *P. zaei*. *Meloidogyne* spp. fail to induce the prominent galls on sweet potato as they do on many other crops. Neither does *R. reniformis* induce obvious root symptoms. Consequently, field assessments are inadequate, and laboratory examinations are required to register the presence of these pests. Two factors may influence losses caused by *Meloidogyne* spp. and *R. reniformis*. Plant growth and the weight of roots harvested may be reduced. Additionally, physiological stresses associated with nematode parasitism can induce longitudinal cracking of roots during development (Clark & Moyer, 1988). These cracks become deep fissures with a surface of callus or periderm, and the market value of such sweet potatoes is reduced. For example, in North Carolina yields of sweet potatoes grown in sandy soils infested with *M. incognita* were up to one-third that of nematocide treated plots. Additionally, there were 18% of cracked roots in infested plots compared to less than 3% in treated plots (Nielsen & Sasser, 1959). Pre-plant nematocide treatments of *M. incognita* infested soil both doubled the yield of marketable sweet potato roots and also reduced the proportion of cracked tubers by over 40% (Hall *et al.*, 1988). Similar benefits can occur with the control of *R. reniformis*. In two years of field tests with eight sweet potato varieties, nematocide treatments increased yield overall by 40% and reduced the percentage of cracked sweet potatoes from 27% to 21% (Clark & Wright, 1983). Tuber damage may be of importance in assessing economic losses (CIP, 1992) and nematode effects on quality and grade (Johnson *et al.*, 1992) are of significance in developed countries. The importance of such factors in other agricultural systems, where the crop may be viewed as a low status food, or is grown for uses such as animal feed (Clark & Moyer, 1988; Scott & Ewell, 1993), needs to be assessed. The best studied lesion nematode is *Pratylenchus coffeae*, a serious pest of sweet potato in Japan. Here significant losses may occur particularly on volcanic ash soils, and although no data are available, they have been serious enough to warrant significant sweet potato breeding programmes against this nematode (Marumine & Sakamoto, 1979; Suzuki, 1989). *Ditylenchus* spp. provoke "brown ring", a brown to brownish black layer within the storage root. Eventually the entire root may become decayed, especially following secondary invasion by fungi. The disease is generally considered a storage problem. No information is available on the incidence of the problem in China, the world's largest producer of sweet potatoes, although it is the subject of plant health management (Li & Guo, 1992) and breeding efforts (Xie *et al.*, 1992). Internationally, most nematological research on sweet potatoes has been conducted in the United States, which produces less than 0.5% of the world's output. Work on *Meloidogyne* spp. and *R. reniformis* has predominated. Nematode population dynamics, studies on pathogenicity and breeding for resistance have taken place at a number of universities and institutes in the southern states since the earlier part of this century. A significant component of research in the United States has involved

the evaluation of nematicides. Such work continues and references cited by Clark & Moyer (1988) give an introduction to this body of research. Outside the United States surveys have been conducted in Burundi (Hendy *et al.*, 1989a & b), Niger (Sikora *et al.*, 1988), China (Ying *et al.*, 1994) and New Guinea and other Pacific island countries (Bridge, 1988). Breeding has taken place over many years in Japan (Kondo *et al.*, 1972; Suzuki, 1989) and programmes also exist in India (Mohandas & Palaniswami, 1990) and China (Xie *et al.*, 1992; Lin *et al.*, 1995). In Africa, breeding work has taken place in South Africa (Kirstner *et al.*, 1993) and work on the nematodes of sweet potato has been published from Egypt: Kassab & Taha, 1990). The IARC mandated to conduct research on sweet potatoes is CIP which took over responsibility for the crop within the CGIAR from IITA in 1988 (CIP, 1988). IITA continues work on sweet potato within the context of developing root and tuber crops within national programmes. Since assuming the mandate for sweet potato, CIP has initiated basic screening of its germplasm collection for resistance to root-knot nematode species *M. incognita* and *M. javanica* (CIP, 1988; 1989). More recently, such work has involved collaboration with national institutes in China to screen germplasm for resistance to the storage rot nematode, *D. destructor* (CIP, 1992).

3.9 Cassava

Originating in tropical America, cassava (*Manihot esculenta*) is now grown in all tropical regions. Total production is estimated at over 150 million tons, all in the developing countries. Introduced to Africa by the Portuguese explorers in the 15th century, its cultivation has developed rapidly (Purseglove, 1968), it is now one of the continent's most important crops, with an annual production in excess of 70 million tons. In some countries of central Africa, cassava constitutes 80% of the per capita consumption of starchy staples. Brazil, with 22 million tons per annum accounts for nearly 80% of the production of Latin America. Production is rapidly growing in importance in Asia, now producing over 80 million tons per annum.

Cassava is host to a wide range of nematodes (McSorley *et al.*, 1983); however, relatively little work has been done on these nematodes or the losses they may cause. Root-knot nematodes, in particular *M. incognita* and *M. javanica*, found widely on cassava are the most important. Other important plant-parasitic nematodes associated with cassava are *P. brachyuris*, *R. reniformis* and the yam nematode, *Scutellonema bradys* (McSorley *et al.*, 1983). Although work has shown that the root-knot nematodes are capable of causing significant reductions in root weight (Caveness, 1981; Crozoli & Hildago, 1992), nematodes have not always been regarded as a major constraint to cassava production (Jatala & Bridge, 1990). However, survey work reporting severe field symptoms of root-knot damage in cassava (Sikora *et al.*, 1988; Bridge *et al.*, 1991) suggests that serious losses may be occurring in certain countries. At present very little research is conducted on the nematodes of cassava. Some evaluation of varietal differences in resistance to root-knot nematodes and methods of control has been conducted in Latin America (Crozoli & Hildago, 1992; Medina *et al.*, 1992). Research programmes on cassava exist in both Brazil and Thailand. One may hope that investigations on plant-parasitic nematodes will be incorporated into these programmes as the crop's importance increases.

Both CIAT and IITA have cassava among their mandate crops. Although CIAT has a major breeding programme for the improvement of cassava (Hershey & Jennings, 1985; glesius & Hershey, 1994), susceptibility or resistance to plant-parasitic nematodes are not included in assessments. IITA, with a mandate covering that part of the world where cassava has assumed its greatest importance as a food crop, has also played a major role in cassava research. Work on agronomy and pest control have been conducted for many years.

Success in the biological control of the cassava mealybug (*Phenacoccus manihoti*) has received international recognition (CGIAR, 1997 b) and improved cassava varieties arising from the breeding programme are having a significant impact in the region (Dahniya *et al.*, 1994). However, although work at the Institute has shown that root-knot nematodes could cause significant reductions in root yield (Caveness, 1981) and the importance of incorporating nematode resistance into breeding programmes has been recognised (Hahn *et al.*, 1989), no further work on cassava nematology has as yet been done.

3.10 Yam

Yams (*Dioscorea* spp.) are one of the world's most widely grown crops. At least 10 species of the genus have been cultivated in Asia, America and Africa (Coursey, 1967). Worldwide, yam production was estimated at 30.3 million tons in 1994, well behind that of cassava and sweet potato (at 152.5 and 124.3 million tons respectively; FAO, 1995). However, over 90% of the world's yams are grown in Africa, in particular in the "yam belt" stretching from Nigeria to the Côte d'Ivoire. In this region, yams are of major dietary, and also considerable cultural importance. Yams are also important food crops in South-East Asia, the Pacific and the Caribbean. The most important species of yam in West Africa is *D. rotundata*.

On a worldwide basis, plant parasitic nematodes are estimated to cause nearly 18% loss in yield of yams per annum (Sasser & Freckman, 1987). The most important nematodes of yams are *Scutellonema bradys* and *Meloidogyne* spp., in particular *M. incognita*. The lesion nematode *P. coffeae* is a pest of yams in the Caribbean and the Pacific (Bridge, 1988; Coates-Beckford & Brathwaite, 1977; Jatala & Bridge, 1990). *S. bradys* causes a "dry rot" disease of yam tubers. As a migratory endoparasite, the nematode enters young growing tubers and feeds in the tissues of the outer 1 - 2 cm. Feeding is on the harvested portion of the plant and yield loss is directly related to the damage caused. It has been found that *S. bradys* damaged tubers may weigh 10% less than healthy tubers and the amount of diseased tissue discarded in food preparation may be 20% more. Losses by continued feeding of the nematode during the storage of yams, particularly when associated with fungal diseases, reached 80-100% (Adesiyun *et al.*, 1975). Control methods have not been developed. All the major yam species are susceptible to *S. bradys* and the nematode has a wide range of alternate hosts restricting the scope for fallow or crop rotation. Both chemical control and hot water treatment of tubers have been evaluated (Bridge, 1982) but their applicability for small scale farmers is limited. Root-knot nematodes attack both roots and tubers of the plant. As with *S. bradys* the major cause of loss is due to attack of the tubers. Damage is less due to absolute yield loss than is a reduction in marketable value due to the abnormal, warty or knobby tubers resulting from root-knot attack (Nwauzor & Fawole, 1981). Root-knot nematodes have wide host ranges, restricting, as in the case of *S. bradys*, the scope for control by fallow or crop rotation. There are reported differences in susceptibility to *M. incognita* and *M. javanica* between different species of yam (Adesiyun & Odihirin, 1978; Jatala & Bridge, 1990). In those regions of Central America and Asia where *P. coffeae* occurs, the nematode is found commonly on yams (Jatala & Bridge, 1990). A migratory endoparasite like *S. bradys*, *P. coffeae* also attacks tubers, in the field and in storage. A reduction in the edible portions and in marketability can result. Severely attacked planting material may fail to sprout (Coates-Beckford & Brathwaite, 1977). As with *S. bradys* and root-knot nematodes, *P. coffeae* has a wide host range. Most research on nematodes of yams (mainly *P. coffeae*) has been conducted in Central America and the Caribbean. Work has also been done in Asia, including India and Japan. The review by Bridge (1982) referred to work conducted in Nigeria, the world's biggest producer of yams. Since this period, however, published research from Africa on yam nematodes has been negligible. The IARC with

the mandate to conduct research on yams is IITA, but little research on yam nematology, apart from some early surveys, has been reported from the Institute. In a record of work published by the institute (IITA, 1992) some 54 citations deal with yams; but only one of these (Badra *et al.*, 1980) is devoted specifically to nematodes. However, the authors are aware of new detailed studies on resistance in yams to *S. bradyi* and *Meloidogyne* at IITA and it is hoped that this work will develop and continue.

3.11 Banana and Plantain

Bananas and plantains (*Musa* spp.) are grown world-wide in tropical regions, principally in lowland areas where rainfall is in excess of 1,250 mm per year. Most commonly grown varieties are triploid hybrids of the naturally occurring species *M. acuminata* and *M. balisiana* (Simmonds, 1966). The export trade by large plantations represents less than 15% of the estimated annual production of 76 million tons (Price, 1995). The vast majority of production is by smallholders and subsistence farmers in the developing world. In Africa, in particular, plantains in the lowland tropics, and highland bananas in highland East Africa are important crops in smallholder agriculture.

Estimated annual yield losses caused by plant parasitic nematodes to bananas and plantains worldwide approach 20% (Sasser & Freckman, 1987). The most serious nematode pest of bananas and plantains is the "burrowing nematode" *Radopholus similis*, partly due to its status as the major nematode pest of export plantations (Gowen & Quénehervé, 1990). *Radopholus similis*, and species of *Pratylenchus*, are principally spread on infected planting material. The worldwide spread of *R. similis* is attributed to the dissemination of infected planting material, principally connected with the establishment of plantations for the export trade over the last century. *Pratylenchus coffeae* also has a worldwide distribution and has probably been spread in the same way. Another *Pratylenchus* species, *P. goodeyi* is found in Africa in the highlands of East Africa and in Cameroon, in the Canary Islands and in a few localities in the Mediterranean. It is important principally in those areas of East Africa where bananas provide a starchy staple. *Helicotylenchus multicinctus* is also found worldwide on bananas. *Meloidogyne* spp. (principally *M. incognita* and *M. javanica*) also occur widely on bananas and plantains. Available data, reviewed by Gowen and Quénehervé (1990) suggest that yield increases in export bananas over 100% can result from nematicide treatment to control *R. similis*. In India yield losses caused by this species are estimated at 30 - 40% (e.g. Koshy, 1986; Reddy, 1994). The spiral nematode (*H. multicinctus*) occurs widely in Africa, Asia and South America (Bridge, 1993) and may predominate in mixed populations with *R. similis* (Gowen & Quénehervé, 1990). In Nigeria, nematicide treatment of plantains infested principally with *H. multicinctus* and *M. javanica* (Badra & Caveness, 1983) led to increases in bunch weight of nearly 100%. In India, *H. multicinctus* reduced banana yield by 34% (Reddy, 1994).

Until recently research on *Musa* has concentrated almost exclusively on problems of the export sector (Buddenhagen, 1993) and banana nematology focused, almost exclusively, on one species (*R. similis*) and primarily on nematicide testing. The development of improved varieties with nematode resistance is still awaited, a difficulty being that transferable resistance has so far only been found from one source and only against *R. similis* (Pinochet, 1988). Little breeding effort has thus far been directed towards other nematode species. The IARC that assumed the mandate for bananas and plantains (in 1987) is IITA in Africa, the continent where the crop assumes its greatest importance in food security and where there has been some work done on yield losses caused by nematodes (Caveness & Badra, 1980; Badra & Caveness, 1983). IITA's plantain breeding programme has hitherto concentrated principally on sigatoka (*Mycosphaerella fijiensis*). Attention is being turned towards nematodes with IITA's

recent appointment of a nematologist, based in East Africa working mostly on bananas (Anon., 1995). The diagnostic surveys being undertaken (Gold *et al.*, 1994) are an important first step in attempting to establish the relative importance of nematode species in smallholders' plantains in Africa. Similar work is needed elsewhere, particularly in Asia where most bananas and plantains are produced.

3.12 Cowpea

Cowpea (*Vigna unguiculata*), is of African or South-East Asian origin. The plant shows wide varietal differences and is mainly grown for its seed although it may also be grown as a vegetable or for fodder. Grown in the tropics, subtropics and semi-arid tropics, some 90% of the world's annual production is in Africa, with substantial amounts also being grown in India and the United States. In the subsistence farming of the developing world, the crop is well suited to rainfed semi-arid conditions where it is often intercropped with cereal crops such as sorghum and millets.

Yield losses due to plant parasitic nematodes are estimated at over 15% worldwide (Sasser & Freckman, 1987). The root-knot nematode species, *M. incognita* and *M. javanica*, are the most serious pests of cowpea worldwide (Sikora and Greco, 1990). In glasshouse experiments, growth and yield of cowpea were reduced by 90% by root-knot nematodes (Sharma & Sethi, 1975). Field trials have shown grain yield increases of 14% in nematicide treated plots (Patel *et al.*, 1990). Infection can also increase the incidence of fusarium wilt in wilt resistant or tolerant cultivars (Harris & Ferris, 1991) and has been shown to reduce rhizobial nodulation and nitrogen fixation (Ali *et al.*, 1981).

Other major nematode pests include the pigeonpea cyst nematode, *Heterodera cajani*, found mainly in India (Koshy & Swarup 1971), and *R. reniformis*, a world-wide pest of cowpea which has been investigated in various countries, including India (Gupta & Yadav, 1980), the United States (Heald & Robinson, 1987), Brazil (Ponte, 1987), Egypt (Badra & Elgindi, 1979), Nigeria (Egunjobi *et al.*, 1986) and the Philippines (Castillo *et al.*, 1977). Published research on cowpea nematodes and their control has come predominantly from the national institutes of India and the United States. In India, survey work (e.g. Sen & Dasgupta, 1976), pathogenicity studies and resistance screening (Khan & Husain, 1988a) have been done. Work on nematode-plant relationships, (e.g. Sirohi & Dasgupta, 1993) interactions with other organisms (e.g. Kanwar *et al.*, 1987) and on nonchemical methods of control (e.g. Khan & Husain 1988b) has also taken place. In the United States, published research has often investigated the role of cowpeas in overall studies of a particular nematode species and its management (e.g. Southards & Priest, 1973). In addition, resistance screening (e.g. Swanson & Van Gundy, 1984) and plant breeding (e.g. Ferry & Dukes, 1995) have been conducted.

Within the CGIAR, the crop mandate for cowpea is held by the IITA which has conducted a substantial amount of research on the crop, encompassing aspects of cowpea agronomy, breeding, and entomology (IITA, 1992). Within Nigeria various national institutes have studied cowpea nematology, including varietal screening (e.g. Onyeigwe and Ogbuji, 1991) and nematode control (e.g. Egunjobi and Olaitan, 1986). Although some of this work was in collaboration with IITA (e.g. Egunjobi *et al.*, 1986) and the institute has conducted germplasm screening for nematode resistance (e.g. Caveness, 1975), no sustained research programme on cowpea nematodes has been developed at IITA.

3.13 Soybean

Soybeans (*Glycine max*) originated in China and the first domestication is thought to have occurred some 3000 years ago (Hymowitz, 1970). The crop has since attained major importance in the agriculture (and culture) of the region. During the last century cultivation of the crop has spread and

increased, most notably in the United States, and soybeans have become one of the world's major food crops and a significant commodity in international trade. World production now exceeds 136 million tons per year, of which 50% is from the United States, with the world's second biggest producer, Brazil, producing over 24 million tons per year. China (16 million tons), Argentina (11 million tons), and India (3 million tons) are also major producers (FAO, 1995).

More than 100 species of plant-parasitic nematode have been associated with soybean (Schmitt & Noel, 1984), the major pest species being *Heterodera glycines*, *Meloidogyne* spp., *M. incognita*, *M. arenaria* and *M. javanica* and *R. reniformis*. These nematodes are estimated to cause annual yield losses of over 10% to soybean on a worldwide basis (Sasser & Freckman, 1987). Over the last 20 years by far the greatest contribution to soybean nematology has been made by numerous research groups in the United States. Here work has very largely concentrated on the soybean cyst nematode, *H. glycines*, considered the most serious single pest of soybeans in the country. Of pest and disease losses overall, 19% are attributed to "nematodes" and over half of these to *H. glycines* alone (Mulrooney, 1986). A voluminous literature has developed on this nematode, for example, one in eight abstracts presented at a recent conference (SON, 1995) concerned *H. glycines*. All aspects of the species biology and host-parasite relations are being studied and resistance breeding is being actively conducted in many states. The species is of such importance that a book, specifically devoted to *H. glycines*, has been published (Riggs & Wrather, 1992). Research on *H. glycines* including the breeding of nematode resistant soybean varieties is also being done in China and Japan where the crop, and the nematode, are considered to have originated (e.g. Lin, 1985; Nakamura *et al.*, 1982). Research on *Meloidogyne*, considered of increasing importance to soybean production in the world's warmer regions (Schmitt & Noel, 1984), has been conducted again principally in the United States (e.g. Koening & Barker, 1992) but also in many other countries including India (e.g. Meena & Mishra, 1993), Brazil (e.g. Tihohod *et al.*, 1988), Nigeria (Caviness, 1975) and Egypt (e.g. Mohamed & Elgindi, 1990).

Within the CGIAR, the crop mandate for soybean is held by IITA. Although at a little over 500,000 tons per year, Africa accounts for less than 0.5% of world production, the crop is considered to have great potential in the continent (IITA, 1990; IITA 1991). Although some research has recently been conducted in Egypt (e.g. Mohamed & Elgindi, 1990) virtually no work on the nematodes of soybeans has been done in sub-Saharan Africa. Apart from an initial yield loss study (Caviness, 1987), no work on soybean nematodes has been conducted at IITA.

3.14 Pigeonpea

Pigeonpea (*Cajanus cajan*) originated in India and presently it is grown in over 50 countries. It is an important grain legume in the semi-arid tropics with about 90% of the world production in the Indian subcontinent, principally in northern, central and eastern India (Nene & Sheila, 1990). The crop is also of considerable importance in Africa, Latin America and the Caribbean. One of the characteristics of pigeonpea is the diversity of its uses. In addition to dry grain, pods and seeds may be consumed green as a vegetable, the leaves may provide fodder and the stems used as fuel-wood. For these reasons, and the genetic diversity available, the crop is considered to have significant worldwide potential (Nene & Sheila, 1990; Remanandan, 1990).

Although many species of plant-parasitic nematodes have been found associated with pigeonpea (Nene *et al.*, 1996) the major nematode pests are *Meloidogyne* (*M. incognita* and *M. javanica*), *Heterodera cajani* and *R. reniformis* (Sharma *et al.*, 1992). *Meloidogyne* spp. and *R. reniformis* are distributed worldwide, and *H. cajani* has so far been found in the Indian

subcontinent and in Egypt. However, with pigeonpea production being concentrated overwhelmingly in India, this species is considered the crop's most serious nematode pest. The plant parasitic nematodes cause an estimated annual loss of over 13% in pigeonpea yield (Sasser & Freckman, 1987; Sharma *et al.*, 1992). Nematode parasitism may directly affect plant growth and also reduce the formation of rhizobial nodules on root systems (Mohanty & Padhi, 1987). In addition, interactions between nematode parasitism and increased incidence of *Fusarium* wilt have also been reported (Hasan, 1984; Sharma & Nene, 1989; Singh *et al.*, 1993). Research on nematodes on pigeonpea has been conducted largely within India. This has been both within national institutes and at ICRISAT, the IARC mandated to research on pigeonpea. In addition to surveys (e.g. Velayutham, 1988a), work on the biology of the major nematodes, on host-parasite relationships (e.g. Patel & Patel, 1990) and pathogenicity studies and crop loss assessments (e.g. Mohanty & Padhi, 1987; Saxena & Reddy, 1987) have been conducted. Application of nematicides in *H. cajani*-infested fields results in a 20-30% increase in pigeonpea yield. Screening of pigeonpea for resistance constitutes the major element of published research on pigeonpea nematode control (e.g. Patel *et al.*, 1987; Velayutham, 1988b; Sharma, 1995). Field evaluations have been conducted by various national research groups within India (e.g. Ravichandra *et al.*, 1988). Control measures evaluated include chemical control (e.g. Zaki & Bhatti, 1986). ICRISAT's work has concentrated on the identification of nematode constraints of pigeonpea, identification of the distribution and role of nematodes in the modification of *Fusarium*-wilt resistance, and the development nematode management practices such as host-plant resistance, cultural practices, and natural control (e.g. Chauhan *et al.*, 1988; Sharma *et al.*, 1992; Sharma *et al.*, 1996). Some investigations on pigeonpea nematodes have also taken place outside India, notably in East Africa, a secondary centre of diversity for the crop (Saka, 1985; Hillocks & Songa, 1993). Some of this work has been conducted in collaboration with ICRISAT (Daudi *et al.*, 1995).

3.15 Groundnut

Groundnut (*Arachis hypogaea*), a native of South America, is grown widely in 108 tropical and sub-tropical countries. Production exceeds 28 million tons per annum worldwide,

among the major producers of groundnut. Nigeria, Senegal and the Sudan are major producers in Africa. The crop is grown at both subsistence and commercial levels for its oil and as a protein rich source of food for humans and livestock.

Plant parasitic nematodes are estimated to cause annual yield losses of 12% to groundnut worldwide (Sasser & Freckman, 1987). The most important nematodes of groundnuts are *Meloidogyne* spp. (principally *M. arenaria*, *M. hapla* and *M. javanica*) and the lesion nematode, *P. brachyurus* (Sharma & McDonald, 1990). In addition to attacking roots, *P. brachyurus* also infects and weakens the peg and pods (Minton & Baujard, 1990). Other nematode species considered important in specific regions include, *Belonolaimus longicaudatus* and *Cricomonella ornata* in the United States (Minton & Baujard, 1990), *Aphelenchoides arachidis*, *Aphasmatylenchus straturatus* and *Scutellonema* spp. in West Africa (Bridge *et al.*, 1977; Germani, 1981; Germani & Luc, 1982; Minton & Baujard, 1990), *Tylenchorynchus brevilineatus* in India (Reddy *et al.*, 1984), and *Ditylenchus africanus* (= *D. destructor*) in S. Africa (DeWaele *et al.*, 1989). As yet, little nematode resistance has been identified in *Arachis hypogaea* germplasm (e.g. Joshi & Patel, 1990; Smith *et al.*, 1978), although research work is in progress (e.g. Holbrook & Noe, 1990; Smith *et al.*, 1978; Mehan *et al.*, 1993). Most research has therefore been directed at chemical control and the use of crop rotations and soil

amendments. Of published research over the last two decades, nearly half has come from the United States. Research on nematodes (e.g. Phipps *et al.*, 1988), cropping systems (e.g. Rodriguez-Kabana *et al.*, 1988), and varietal improvement (e.g. Holbrook & Noe, 1990), have all been conducted. National institutes within India and China have also investigated chemical control of nematodes in groundnuts (Mahapatra & Padhi, 1988) although other management techniques are also used (Zhang, 1989). Groundnuts are of major importance (once constituting a major export crop) in the sub-sahelian regions of West Africa. Here research has been conducted over many years by ORSTOM (Office de la Recherche Scientifique et Technique Outre-Mer) researchers, mainly evaluating nematicides (e.g. Baujard *et al.*, 1989). The IARC mandated to research groundnuts is ICRISAT which has initiated various surveys in India (e.g. Sharma, 1988), West Africa (Sharma *et al.*, 1991) and Vietnam (e.g. Sharma *et al.*, 1994). This has for example, shown that plant-parasitic nematodes contribute to the crop growth variability problem of groundnut in West Africa. Presently, ICRISAT's groundnut nematology is focused on root-knot nematodes.

3.16 Chickpea

Chickpea (*Cicer arietinum*) originated in the Mediterranean region and presently it is the world's third most important pulse crop. Although grown in many countries, principally in the Mediterranean region and Asia (van der Maesen, 1987) world production occurs overwhelmingly in the developing countries of the semi-arid tropics and exceeds 7.8 million tons per year (FAO, 1995). India is the world's major producer, others include Pakistan, Turkey and Mexico. The crop produces relatively low yields mainly due to being often grown on marginal lands but yield potential can be high. A lack of economic competitiveness with more profitable crops has led to considerable declines in production over past decades, particularly in Europe (Jodha & Subba-Rao, 1987) and similar declines are being observed in India (ICRISAT, 1995a).

Nematodes are an important constraint to chickpea production and they are estimated to cause annual yield losses of nearly 14% worldwide (Sasser & Freckman, 1987; Sharma *et al.*, 1992). The major nematode pests in the Indian sub-continent are the root-knot nematodes (*M. incognita* and *M. javanica*) and the lesion nematode (*P. thornei*). *Rotylenchulus reniformis* may also cause damage (Sharma & McDonald, 1990). In the Mediterranean - Middle Eastern region *Meloidogyne artiellia*, *P. thornei* and *Heterodera* spp. (*H. goettingiana* and *H. ciceri*) are important (Greco & Di Vito, 1988; Di Vito *et al.*, 1994a). Published research on chickpea nematology reflects the crop's geographical importance. The majority of work arising from various national institutes in India is devoted to *M. incognita* and *M. javanica* (e.g. Ahmad & Naimuddin, 1988). A substantial body of Indian research has investigated possible interactions between root-knot nematodes and *Fusarium oxysporum* f. sp. *ciceri* (e.g. Goel & Gupta, 1986; Khan & Hosseini-Nejad, 1991). Described as a "poor crop for poor people in poor environments" (Jodha & Subba-Rao, 1987) research into chemical control is insignificant. Considerable attention has been given to screening germplasm for resistance (e.g. Mishra & Gaur, 1989). Research on other non-chemical control methods, notably the use of soil amendments, (e.g. Pandey & Singh, 1990), of biological control agents (e.g. Zaki & Maqbool, 1991) or of cultural methods (e.g. Kanwar & Bhatti, 1992), has been conducted.

Within the CGIAR, research on chickpea is conducted at ICRISAT in India and at ICARDA in Syria. Close links in chickpea research exists between the two centres, focusing on the West Asia - North Africa region (WANA). Within ICRISAT, surveys of chickpea nematodes (e.g. Sharma *et al.*, 1990), pathogenicity, interactions with *Fusarium* wilt, and germplasm screening (e.g. Sharma *et al.*, 1993; Uma Maheswari *et al.*, 1995) have been conducted and chickpea cultivars tolerant to the root-knot nematodes identified. Research on

chickpea nematodes by ICARDA has largely taken the form of collaboration with researchers in Italy (itself a producer of chickpea). Field work has taken place in Syria, ICARDA's host country (e.g. Di Vito *et al.*, 1992). There has been an emphasis on the most important chickpea nematode in Syria, *H. ciceri* (e.g. Greco *et al.*, 1988) and field work has been complemented by laboratory studies in Italy (e.g. Di Vito & Vovias, 1990).

3.17 Lentils

Lentils (*Lens culinaris*) are one of Man's oldest food crops, originating in the "fertile crescent" region of the Middle East (Webb & Hawtin, 1981). Grown as a cool season/early season crop, principally in the Near East and the Indian subcontinent, production, although minor compared with some legumes, is increasing and exceeds 2.8 million tons annually (FAO, 1995). Lentils are grown for human consumption in a variety of ways and the straw may be used for animal fodder. Occasionally the crop is cut green for this purpose (Nygaard & Hawtin, 1981).

Very little attention has been given to nematode pests of lentil, the discussion in a 1981 review consisting of just three sentences (Khare, 1981). Most published research has been conducted in the national institutes of India where attention has been devoted mainly to the root-knot nematode, *M. incognita*, and the reniform nematode, *R. reniformis*. Both pathogenicity assessments (e.g. Fazal *et al.*, 1991; Devi & Gupta, 1993) and screening for resistance (e.g. Bernard *et al.*, 1990; Fazal & Husain, 1991) have been reported. Research on lentil nematodes in the Middle East - Mediterranean region has been conducted by ICARDA, the IARC mandated to conduct research on lentils. This research has principally consisted of surveys in collaboration with Italian scientists (e.g. Di Vito *et al.*, 1994a; Di Vito *et al.*, 1994b). This work has shown that the lesion nematodes, *Pratylenchus* spp., are the most widespread nematodes of lentils in the region.

3.18 Faba bean

Faba bean (*Vicia faba*) is grown widely in temperate and subtropical regions. In the subtropics it is grown as a winter/cool season crop. As well as for human consumption, it is also widely used as animal feed in industrialised countries, and the crop may be grown for fodder and as green manure (in China in particular, Saxena & Weigund, 1993). China, Egypt, Ethiopia, Morocco and Italy are major producers of faba bean.

Although many species of plant-parasitic nematode have been associated with faba beans (Hooper, 1983), the most important nematode pest in temperate and subtropical regions is the stem nematode, *Ditylenchus dipsaci*. As the name implies this species does not attack roots but feeds on stems, petioles, leaves and pods. Feeding dissolves the middle lamellae of parenchyma and results in stem swelling and deformation, leaf and petiole necrosis and the production of smaller, distorted seed (Sikora & Greco, 1990). The nematode may be transmitted by infected seed, and it is one of the most serious plant-parasitic nematodes of temperate agriculture (Hooper, 1983), and a wide range of crops worldwide have been reported to be attacked (Hooper, 1972). Research into the nematode's biology and control on a range of crops has been conducted in many countries of Europe over many years (Hooper, 1972). Reflecting the high value of some of these crops, control has often consisted of chemical treatments. Hot water treatment of infected plant material has also been used (Hooper, 1972). Faba bean is attacked both by the "oat race" and the "giant race" of *D. dipsaci*. The former predominates in temperate regions and the latter (considered the more damaging) in subtropical and semi-arid regions (Sikora & Greco, 1990). Other nematodes reported attacking faba bean include the pea-cyst nematode, *Heterodera goettingiana*, various *Pratylenchus* spp. (including *P. penetrans*, *P. thornei* and *P. vulmus*) and *Meloidogyne* spp. in the Middle East and uplands of Africa. In recent years, research on faba beans and *D. dipsaci*

has been conducted principally in the countries of western and eastern Europe. In the United Kingdom chemical control methods (e.g. Whitehead & Tite, 1937), and in France resistance screening (e.g. Cabel & Leclercq, 1989) have been conducted. In many areas, regulatory measures such as the use of certified clean seed for planting are used in the control of the pest (e.g. Knuth, 1993). Outside Europe, faba bean nematodes have been investigated in various countries, particularly in Egypt where attention has been directed at the root-knot nematodes (e.g. Gazar & Morad, 1981).

The International Centre which is mandated to conduct research on faba bean is ICARDA. Surveys conducted by ICARDA and its collaborators (e.g. Di Vito *et al.*, 1994a & b) have identified nematodes attacking faba beans in the region. Some experimental work such as cultivar screening (Hanounik *et al.*, 1986) and the evaluation of cultural control techniques (Linke *et al.*, 1991) has also been conducted by ICARDA. Overwhelmingly the world's largest producer of faba beans is China. Considerable research effort is directed to the crop within that country (see Saxena & Weigund, 1993) and in collaboration with ICARDA (e.g. ICARDA, 1995).

3.19 Common bean

Common bean (*Phaseolus vulgaris*) is a New World crop arising from multiple domestications of wild ancestors (Debouck, 1991; Gepts & Debouck, 1991). Approximately half of the world's production of 18 million tons is in Asia, China being a major producer (FAO, 1995). In the Americas, major producers are Brazil, the USA and Mexico. The crop has attained major importance in subsistence agriculture and food security in Africa, for example in the countries of the East African highlands. Although produced industrially for processing (e.g. in the USA), there is also interest in the potential of snapbeans in peri-urban agriculture.

The most serious nematode pests of common bean are the root-knot nematodes, in particular the species *M. incognita* and *M. javanica*, one or both of these species probably affect common bean in most of the tropics or subtropics (Sikora & Greco, 1990). Losses of up to 60% have been attributed to root-knot nematodes in experimental work conducted both in Kenya (Ngundo & Taylor, 1974) and Colombia (Mullin *et al.*, 1991a). The wide genetic variability present within the crop (Silbermagel *et al.*, 1991) is reflected in a wide range of responses to root-knot nematodes (de Moura & Regis, 1987) with galling in some cases nearly undetectable and in others severe (e.g. Mullin *et al.*, 1991b). In addition to reduced plant growth resulting from stunting and galling of the root system, root-knot nematodes may influence bacterial nodulation and increase the incidence of some diseases (Al-Hazmi, 1985; France & Abawi, 1995). Various species of lesion nematode (*Pratylenchus* spp.) have been found associated with beans (Sikora & Greco, 1990). During severe infestations, yield losses may reach 10-80% with root-lesion nematodes and 50-90% with root-knot nematodes (de Agudelo, 1980). The reniform nematode, *R. reniformis* damages beans, causing 50% reduction in shoot dry weight in pot experiments and yield increases have followed nematicide control of *R. reniformis* in field trials (McSorley *et al.*, 1981). *Phaseolus vulgaris* is also host to *H. glycines* (Melton *et al.*, 1985). *Heterodera glycines* has been recorded parasitizing beans in China, Japan, USA and Colombia (Liv, 1986; Gomez-Tovar & Medina, 1983) and recently in Brazil (Farraz, *pers. comm.*). The influence of this nematode on yield reduction has yet to be established. Beans may however maintain populations of *H. glycines* in the absence of soybeans (Nishiiri *et al.*, 1981) and planned crop rotations need to consider this (Sikora & Greco, 1990). Most research on the nematodes of *P. vulgaris* has been conducted in the USA. The biology of nematode-plant relationships has been investigated (e.g. Melton *et al.*, 1986; Wilcox and Loria, 1986) as has nematode control. Research on control has largely investigated the use of nematicides (e.g. Rhoades, 1983; Abawi & Czerny, 1982), but also the development of nematode resistant varieties (e.g. Wyatt *et al.*, 1983; Hagedorn

& Rand, 1986; Omwega & Roberts, 1992). There has also been research on the integration of beans in cropping systems and crop rotations and the influence this may have on plant-parasitic nematode populations (e.g. Rhoades & Forbes, 1986; Johnson *et al.*, 1983). Brazil has also conducted research on nematodes of *Phaseolus*. In addition to survey work (e.g. Machado-Menten *et al.*, 1980), biological studies and investigations of disease interactions (e.g. Huang & Pereira, 1994; Costa-Manso & Huang, 1986) have been done. Nematode control measures studied have included use of chemicals (e.g. Carvalho *et al.*, 1981) cultural methods (e.g. Sharma & Scolari, 1984) and resistance screening. National institutes in India have published research on common bean although most research has been on the more important *Vigna* species, in particular mung bean, *Vigna radiata*. Chemical control (e.g. Singh & Reddy, 1981), the use of soil amendments (e.g. Srivastava & Singh, 1991), and resistance screening (e.g. Singh *et al.*, 1981) have all been conducted. Many other countries in the world have published research on beans. Within Africa, after initial investigations of pathogenicity (e.g. Ngundo & Taylor, 1974) and varietal screening, there has been no sustained research effort. More recently further survey work (e.g. Asefa, 1987) and nematode control studies (e.g. Ogallo, 1988) have been published.

The IARC with the world mandate for *Phaseolus* is CIAT, based at Cali in Colombia. Some research on bean nematodes was initiated with the launching of the Institute's Field Beans Programme in 1973 (CIAT, 1974) and some resistance screening was conducted (CIAT, 1978). Nematodes were identified as important pathogens of mandate forage legumes (*Desmodium* spp.), but this work was apparently not sustained (Lenne & Stanton, 1990; Stanton, 1994). Although, more recently, some collaborative research has been conducted (e.g. Mullin *et al.*, 1991a & b), no substantive research on bean nematodes has been conducted by CIAT.

4. DISCUSSION

4.1 The Institutional Neglect of Nematology

The preceding sections have described the role plant parasitic nematodes may play as production constraints to most of those crops selected as mandate crops by the IARCs. It is evident that, with some exceptions, the effort and resources directed towards research on plant parasitic nematodes within the IARCs has been and remains much less than even a conservative assessment of their significance as crop pests would merit. An examination of Annual Reports from some selected IARCs (Fig. 1) shows that as "The CG System" has grown and numbers of Senior Scientific Staff within these institutes have increased by 250% over the last twenty years, numbers of nematologists have remained unchanged, at what can only be described as a bare minimum. Although there have been occasional nematology projects at some Centres only CIP has ever employed more than one core staff nematologist and most IARCs have never employed nematologists at all.

Why has nematology remained so under-represented, particularly in organisations which place such importance on the careful consideration and establishment of research priorities and goals, the assessment of research impacts and not least in presenting well argued research justifications and strategies to donors?

Fundamentally the general absence of specific clearly recognisable and attributable above ground symptoms make the unambiguous demonstration of nematode damage difficult to achieve. It has been shown that some observers are unable to visually assess nematode caused reductions in crop growth of up to 50% (Mai, 1985) and most smallholders will not detect a loss of less than 20% in yield caused by nematodes. Even when nematode attack produces clear symptoms these may be indistinguishable from those of, for

example, nutrient deficiency. Thus it is not always possible to present dramatic examples of nematode damage to administrators, policy-makers and donors. Such difficulties apply equally to, and influence, the most fundamental stages of the project cycle and research process. It is recognised that farmers have little or no perception of invisible pests (e.g. Cauquil & Vaissavie, 1994) including nematodes (e.g. Bentley, 1992; Bridge, 1996). This may then result in the best intentioned of PRA exercises either overlooking or mis-attributing nematode problems (Gold *et al.*, 1993).

A scarcity in nematological expertise or lack of awareness of nematode problems may also influence more formal assessments. In a recent Priority Setting exercise at CIP (Collion & Gregory, 1993) the "Management of Cyst Nematodes" was included (and given a score of zero) in Project Ranking for potato in the Sub-Tropical Lowland and the Arid and Mediterranean Agro-ecological Zones. As these nematodes are ecologically unsuited, and essentially absent from the two Agro-ecological Zones considered the ranking is, on nematological grounds, spurious. However, root-knot nematodes, *Meloidogyne* spp. are widely recognised as among the most serious nematode pests of solanaceous crops (including potatoes) in the sub-tropics and tropical highlands (Kibata, 1994). This exercise thus resulted in nematode pests that were essentially absent from certain agro-ecological zones (potato cyst nematodes) understandably being ranked as unimportant, whereas the importance of nematodes of potentially major significance (root-knot nematodes) was obscured by their being subsumed in another project category (Bacterial Wilt Project) (Collion & Gregory, 1993).

These difficulties are integral to, and are compounded by, the general scarcity of trained nematologists (and ex-nematologists) which is then further reflected in a general lack of nematological experience or awareness in the agricultural research community particularly in the tropics (Luc *et al.*, 1990). The comment that "systems for priority setting are generally weak, and that overcoming this weakness was imperative" (Walton, 1994) is particularly relevant to nematode research. The circularity of this problem has long been recognised. "Because there are few trained nematologists many nematode problems remain to be diagnosed, so that policy-making agencies in both governmental and private sectors are not aware of the need to encourage expansion" (Hague, 1969). This statement is as relevant today as it was in the years preceding the establishment of the CGIAR.

This leaves nematologists with the task of continually needing to draw the attention of others to the pest potential of nematodes, with all the suspicion of self-interest this might promote.

The limited, and in many cases, absence, of any consideration of the role of plant parasitic nematodes is a serious shortcoming, and one that should be recognised. A lack of knowledge and understanding allows the possibility of the misinterpretation of research findings and also increases the potential for both erroneous and misdirected research activities, sometimes in areas considered priorities by the CGIAR. A simple illustration will suffice: to what extent might nematode problems be implicated in the "yield gaps" so often seen between on-station and on-farm trials or between intensive and extensive cropping systems (e.g. Becker *et al.*, 1994)?

4.2 Research in Plant Nematology and Sustainable Agriculture

There are compelling arguments for emphasising the importance of research on plant-parasitic nematodes in any holistic approach to improved agricultural productivity. Plant parasitic nematodes affect many components of plant growth and yield and as agricultural production in the worlds developing regions continues to increase and intensify the influence of plant nematodes can be expected to increase. This

influence will also, we suggest, be directly relevant to aspects of the future CGIAR Research Agenda as outlined in the recent Lucerne Declaration (CGIAR, 1995).

Increased crop production may come from either, or both, increasing yield or increasing the land area under cultivation. The relative contribution each of these has made to increased agricultural production in the developing world over the last 35 years has varied greatly with geographic region. In Asia 90% of the increases in cereal production over this period has resulted from increased yields (notably of "Green Revolution" derived rice and wheat varieties). By contrast in Latin America and Africa a large proportion of increased production (30%-50%) has resulted from increased land area under cultivation (Pinstrip-Anderson & Pandya-Lorch, 1994). The potential for these components to contribute to the future increases in food production the world will require, are subjects of pressing concern to the development community. There is a widespread recognition that the past rate of yield increases produced in "Green Revolution" crops is unlikely to be sustained (Anon, 1996) and that future research to raise the "yield barrier" (CIMMYT, 1994) or "yield plateau" (IRRI, 1996) will only produce steady increments in the yields of these major staples. The potential for further expansion of cropland is also limited. In South Asia, for example, agricultural land is almost totally developed and only 4% of increased production between now and 2010 is expected to come from land expansion (Anon, 1996).

Future increases in crop production will thus need to derive largely from agricultural intensification of those areas already under use (Anon, 1996). However, agricultural intensification can generate a whole range of concerns, not least in aggravating pest problems (Waage, 1993). This applies particularly to plant parasitic nematode pests, which, with some notable exceptions (and in contrast to many insect pests) are generally indigenous to the regions in which they occur. Conversion of land to cropping, or shortening of fallows can increase or maintain plant parasitic nematodes at damaging levels; levels that would decline during extended fallows (Caveness, 1972; Ogbuji, 1979; Prot *et al.*, 1994a). Many view the build up of plant parasitic nematodes, rather than a loss of soil fertility, as a major component of the phenomenon of "sick soils" (Steiner & Buhner, 1964; Ferris & Ferris, 1974). The development of plant parasitic nematode problems may then be viewed as both a cause and a symptom of a lack of sustainability in a cropping system (Page & Bridge, 1993). An IRRI publication (Gupta & O'Toole, 1986) provides both a clear illustration both of the phenomenon, and also of the shortcomings of a lack of nematological input in assessing such problems. Describing yield declines in continuously cropped rice, the authors describe a "soil-sickness" associated with root residues, predominantly in the upper soil layers. This "soil-sickness" could be mitigated by crop rotation, or by soil sterilisation or flooding, or by replacing top soil with subsoil. All these observations point overwhelmingly to the involvement of plant parasitic nematodes in the phenomenon the authors are only able to describe as "soil sickness". With the recognition that the sustainability and stability of crop-yields are major developmental and research goals (CGIAR, 1991) there is a need to consider the contribution plant parasitic nematodes make to yield decline and the fundamental role these organisms may play in "shifting" and "slash and burn" agriculture.

The effects of some plant parasitic nematodes on plant growth, and hence yield, are largely the result of the disruption these organisms cause to the normal processes of plant root growth and soil exploration for both water and nutrients. IARCs are directing increasing research effort at investigating mechanisms of drought tolerance in crops. The development of drought tolerant varieties (e.g. ICRISAT, 1993) with deeper rooting and improved root architecture are important characteristics under investigation (e.g. beans, CIAT, 1985; rice, IRRI,

1995a; cowpea, IITA, 1994; chickpea, ICRISAT, 1995b). Plant parasitic nematodes should clearly be incorporated into any such programmes investigating both the causes of drought susceptibility and in developing and evaluating any observed mechanisms of drought tolerance.

Nutrient (in particular phosphorus) deficiencies, also resulting from the failure of the plant root system to explore and exploit the soil adequately, can also be major consequences of plant parasitic nematode attack. Additionally it is recognised that nematode parasitism may influence *Rhizobium* nodulation and thus nitrogen fixation in legumes (Hussey & McGuire, 1987; Sharma & Khurana, 1991). Fertility levels themselves may influence the degree of damage nematodes cause to plants (Balogun & Babatola, 1990; Swain & Prasad, 1991). With increasing concern over both the economic and environmental cost of fertilizers (Pinstrip-Anderson & Pandya-Lorch, 1994) and a search for low-fertility tolerant varieties (e.g. Suprihatno *et al.*, 1995; CIAT, 1996) there is a clear relevance to incorporating consideration of plant parasitic nematodes into future research programmes. A recent aspect of concern, micro-nutrient malnutrition, and the effects on human nutrition and performance of dietary shortages of elements such as zinc and iron (Graham & Welch, 1996), may also benefit from nematological input. Nematode parasitism has been shown to reduce concentrations of various elements (including zinc and iron) in plants (Melakeberhan *et al.*, 1987; Haseeb *et al.*, 1990).

Soil fertility may also have more direct influences. It is widely recognised that the nutrient content of the soil, in particular urea (and hence ammonia) can sometimes reduce nematode populations (Stirling, 1991). Plowright and Hunt (1994) working in Côte d'Ivoire, examined a field trial comparing fertilizer regimes on rice. Numbers of root-knot nematodes on plants grown with low fertilizer were 30 times greater than numbers on plants grown under complete fertilizer. It is clear that no full interpretation or understanding of observed plant growth or yield responses in such work can be made without incorporating some consideration of the possible effects of plant parasitic nematodes.

The widely recognised existence of interactions with other pathogens (Hussey & McGuire, 1987) the best known being between root-knot nematodes *Meloidogyne* spp. and *Fusarium* wilt also demonstrates the necessity for nematological input in assessing both the incidence and yield losses due to such pathogens and in developing cultural strategies, or breeding programmes against them.

Soil-dwelling plant parasitic nematodes are a biotic constituent of the soil environment. Geographic distributions of nematode species differ (Table 2), some species are widespread, some of localised occurrence. In Africa for example, two species of root-knot nematode (*Meloidogyne* spp.) occur widely, *M. incognita* appearing to predominate in hotter soils and *M. javanica* in cooler, wetter soils (Whitehead, 1969). With a developing emphasis on producing crop varieties with adaptation to different agro-ecological zones (Serageldin, 1994) there is a consequent need for multi-local evaluation and a consideration of Genotype x Environment (G x E) interactions in breeding programmes (Quin, 1996). Any comparison of cultivar performance in different environments, in particular attempts at evaluating responses to soil conditions, should consider the possible influence of different nematode species in these different environments. Plant-parasitic nematodes themselves may be viewed as a fundamental constituent of the "E" component in any "G" x "E" interaction evaluated.

4.3 Institutional Potential of Plant Nematology

As part of a recently instigated process of renewal the CGIAR is assessing both its place as an "actor" within a "Global Agricultural System" and the nature of its relationship with other constituents of such a Global System (Serageldin, 1997). Such a Global System is considered to embrace a whole range of research and development organisations capable of

contributing to a "New Green Revolution" (CGIAR, 1997a). These organisations include universities and advanced research institutes (ARIs) of the "developed North" as well as national research organisations, extension services and also non-governmental organisations of countries of the "developing South", collectively considered as the National Agricultural Research Services (NARS).

This recognition of the complementarity of activities by a range of "players" to the CGIARs mission has direct relevance to nematological research. The range and scope of research needs in plant nematology compliment both the varied contributions the different and diverse institutions within the Global Agricultural Research System could bring to such research and the special role the IARCs have to play in its achievement.

It is recognised that practices do exist that can successfully manage plant parasitic nematodes and achieve sustainable crop production even with poor resource farmers (Bridge, 1996). Further research is needed in developing and assessing nematode management strategies such as crop rotations or improved fallows, to minimise losses in different crops and cropping systems. These activities fall within the "adaptive research cycle" of the "idealised research paradigm" described by Collinson & Tollens (1994) and are ideally suited to the close partnerships existing between IARCs and NARS. The activities of ICRISAT, and more recently IIRRI, in collaborating in the conduct of nematode surveys and assisting NARS to prioritize nematode problems are examples.

The plant breeding necessary to develop new varieties is the major part of IARC activities in crop research (Fig. 1). In the past the most sustained commitment to nematology research within the IARCs has been that of CIP where a major contribution was made to developing potato varieties resistant to cyst nematodes (*Globodera* spp.). Jatala and Mendoza (1978) have drawn attention to the long term research investment needed in this work, success being achieved in close collaboration with American and European institutes (regions where the crop, and the pest achieve major significance). Although some of the Mandate Crops reviewed here may be described as "orphan commodities" (Platais & Collinson, 1992) others are, like potato, of importance in the agriculture of many countries of the "developed North". Significant nematological research, in particular in the United States, has been conducted on some of these crops. Soybeans are a particular example, but also groundnuts, sweet potato and beans have all been investigated. Other countries, notably Australia and India, have made significant contributions to strategic research on nematodes of cereals, notably wheat. In considering the real need for strategic research on the "orphan commodities", the CGIAR IARCs, with their ecoregional structures and perspectives, have clear advantages.

The potential for "spill-over effects" to smallholders of a current research programme (a programme that involves IITA) on an export commodity crop, bananas, has recently been highlighted (Persley, 1996a). The application of "on the shelf" research findings (Collinson & Tollens, 1994) in nematology from the "developed North" and its adaptation by the IARCs to the needs of the "developing South" could have significant impact in plant nematology. This has particular relevance in the application of biotechnology (itself of major potential in developing countries; Cohen, 1994) to the development of nematode resistant varieties (De Waele, 1993; De Waele, 1996). Root-knot nematode resistance is available in many crop cultivars (Sasser & Kirkby, 1979; Hadisoeganda & Sasser, 1982; Lehman & Cochran, 1991) and the incorporation of this resistance, for example by transfer of the *Mi* gene (Aarts, 1993), into Mandate Crop varieties would be a major advance. Compared to the era described by Jatala & Mendoza (1978), the application of such "on the shelf" techniques to the considerable research effort on nematode resistance screening already conducted on many Mandate Crops has the potential to considerably reduce the scientific investment needed in such work.

There are also potential "spillover effects" of IARCs using other more applied aspects of plant nematology such as crop rotations, or cultural practices, developed elsewhere (e.g. Dunn, 1987; McSorley & Gallaher, 1995). The IARCs are in a unique position to establish the institutional and research linkages that can, in collaboration with NARS collaborators, enable such inherently applied research to be adapted to the needs and conditions of smallholders in the developing countries.

In much basic research there is a clear complementarity between the often regional nature of many nematode problems and the increasingly regional focus of IARC activities. There is great potential for building links with NARS counterparts and collaborators to develop such research. Many developing countries however, have few plant nematologists, and those present may be functioning in relative isolation. The IARCs could play a significant role both in "capability building" and in enhancing and co-ordinating the activities of nematological research in these countries. It should be emphasised that much nematological research, be it in an International Centre or National Programme can be accomplished with limited facilities. The capital investment necessary to establish, or enhance, nematological capacity need not be great.

As the concept of a Global Agricultural System takes hold the IARCs are establishing new research structures to optimise the contributions of various "players" in the system. Such structures include "Networks" of scientists co-operating on a particular problem and "Consortia" of institutes entering into more formal collaborative arrangements. The potential contribution of research capability and expertise available in ARIs of the "developed North" has long been recognised, for example by CIP in its work on potato. This has been formalised as the concept of "Shuttle Research" involving close collaboration between IRI and expertise in ARIs (Bernardo, 1993; IRI, 1995b). The potential for the close co-ordination of geographically and institutionally separate research groups via e-mail and the internet has even led to the concept of "Virtual International Centres" (Pearsley, 1996b).

Fundamental to any, and all attempts at increasing the effort and resources devoted to plant nematology to an appropriate level by the CGIAR is the continuing need for a recognition and awareness of the existence and potential significance of plant parasitic nematodes as crop pests. This is essentially the same problem articulated by Hague nearly 30 years ago (Hague, 1969). That such a recognition and awareness are both lacking, and are needed is seen at some of the highest levels. By way of example, during the 1996 CGIAR Mid-Term Meeting the activity "Plant protection and pest management" was defined as limited to "diseases, insect pests and weeds" with no mention of plant parasitic nematodes (CGIAR, 1996).

Nematologists, in particular those involved in developing countries, must continue to emphasise both the potential importance of plant nematodes, as well as highlighting the possible failings of ignoring nematodes. As this paper has attempted to demonstrate, all involved in agriculture in developing countries, not only researchers, but equally administrators, decision-makers and policy-makers should recognise the possible influence of plant nematodes on crop production, and the contribution research effort on these pests can make to the development of the more intensive, yet sustainable, agriculture the world is going to need.

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