Sustainability in Plant and Crop Protection

Sergei A. Subbotin
John J. Chitambar *Editors*

Plant Parasitic Nematodes in Sustainable Agriculture of North America

Vol.1 - Canada, Mexico and Western USA

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Foreword

Nematodes are invertebrate roundworms that inhabit marine, freshwater, and terrestrial environments. They comprise the phylum Nematoda which includes parasites of plants and of animals, including humans, as well as species that feed on bacteria, fungi, algae, and other nematodes. Estimates are that four out of every five multicellular animals on the planet are nematodes. The majority of nematodes are microscopic, but some of the animal parasites are quite large and readily visible to the naked eye. Most soil nematodes are 1 mm or less although some species may be several times that length. They are aquatic organisms, living and moving in the water films that surround the soil particles. They are adapted to moving through the soil pore spaces without having to move the particles or to create burrows.

Nathan Cobb is often described as the “father” of the discipline of Nematology in North America. To illustrate the abundance of soil nematodes, he famously wrote, in 1914, that if the nematodes resident in a single acre of soil near San Antonio, Texas, USA, were to proceed in head-to-tail procession to Washington, D.C., some 2,000 miles away, the first nematode would reach Washington before the rear of the procession left San Antonio! So, select a field of interest and, on a map, draw around it a circle of radius 2,000 miles. Where might the procession of nematodes from an acre of your field extend? And, how many nematodes of average length 1 mm will be in the procession when it reaches its destination? While a first reaction might be one of horror at the magnitude of the nematode-pest problem in the field, if the source is a healthy soil, the majority of species present in the procession are beneficial and contribute to essential ecosystem services. In fact, most nematodes in our environment are not parasites of plants or animals. Nematodes that feed on other organisms are important participants in the cycling of minerals and nutrients in the ecosystem that is fundamental to other biological activities. Consequently, the incidence and abundance of nematode species with different feeding habits and life-history attributes provide useful indicators of environmental quality and soil health.

North America, the geographic purview of this book, is the third largest continent on the planet, stretching from arctic regions in the north to tropical zones in the south. The continent encompasses an enormous diversity of geographic features, soil conditions, and climatic variation and, consequently, supports a concomitantly enormous diversity of agricultural production systems and crop commodities. Specific cadres of pest and disease organisms, well adapted to the local conditions, exploit most of crop commodities in North America and, indeed, in the world. Many species of plant parasitic nematodes are among those pests and, because of their usually belowground habitat and microscopic sizes, are often the last to be diagnosed as the root cause of poor crop performance. Except for the few species that cause plants to exhibit characteristic symptoms, the development and availability of the microscope had enormous impact on our study and knowledge of plant parasitic and other soil nematodes. The diagnostic tools provided by modern molecular methods further enhance our ability to identify nematode species and to diagnose causes of crop damage.

One could argue that the magnitudes of nematode and other pest problems in North America largely are due to the design of cropping systems that are monocultures or at least center on the continuous production of a specific crop type. That lack of diversity in cropping systems is, of course, dictated by climatic, social, and economic factors; it is determined by which crops will grow in an area, whether there is a market demand, and what investments have been made in expensive farm machinery designed for use in specific crops. The limited diversity of crop species or varieties in an area favors pest and disease organisms that are well adapted to local conditions, and it tends to deplete rather than build the nutrient status of the soil. Consequently, agricultural systems become driven and protected through the use of mineral fertilizers and synthetic pesticides, which further disrupt the natural balance of organisms in the ecosystem.

Agricultural sustainability is based on the fusion of agricultural, environmental, and social sciences with evolving advances in technology. Sustainability is a goal that we pursue for the health of our planet and the preservation of living organisms that it supports. Sustainability is, and must be, a moving target, ever changing with environmental shifts and advances in our experiences and understanding. As we pursue the goal, we need to evaluate our past and intended trajectories, where we have come from, where we are now, and where we are trying to go. In this book, you will find documentation of these three components of the journey with regard to the impact and management of plant parasitic nematodes in agricultural systems of North America. You will find details of our understanding of nematodes as pests of plants and the evolution of management tools from those physically and chemically disruptive of the environment to strategies that are less disruptive and more information intensive.

Cumulative experience and evolving technology, both digital and mechanical, provide tools for assessment, analysis, and dissemination of information and advice and for changes in agricultural practices. With the fusion of the component sciences of sustainability comes a renewed realization that everything is connected. At one scale, the physical, chemical, and biological components of our planet are interdependent. At a finer scale, assemblages of organisms are interconnected with each other and with their environment. Through their life processes, as they acquire resources, grow, produce, die, and decompose, their component molecules return to states that are available to other life forms. Those functions that we consider beneficial to the pursuit of sustainability can be termed ecosystem services. The recycling of nutrients through mineralization and the regulation of pest species through predation and parasitism that we term biological control are important ecosystem services. Management practices that disrupt the delicate balances underlying such ecosystem services are non-sustainable.

We are developing a greater understanding of the interconnectedness of soil organisms in agricultural production systems. As a proxy for understanding interconnectedness, there exists on the planet, in soils, water, and plant material, a vast and diverse array of soil nematodes with wide ranges of ecological adaptations, activity, feeding habits, and ecosystem functions. Some of the species are parasites of domestic and wild animals, human, and plants, including agricultural crops. Many others are beneficial in their contributions to ecosystem services, participating in decomposition and mineralization cycles, as predators of pest species or as resources that sustain other predator organisms.

Sustainable management seeks to conserve and enhance the activities of beneficial organisms in the agricultural production system by minimizing physical and chemical disruption of their environment and by providing continued availability of resources. A diversity of plant species in space and time offers a greater array of resources to soil organisms. Cover-crop mixtures present different spatial patterns of root systems and provide resources in different microhabitats for organisms of the soil food web. Therefore, plant diversity supports greater diversity of soil organisms with differing behavior, activity, sizes, and temporal dominances, which must enhance the service capacity of the whole assemblage by accessing different locations, depths, and aggregations of the soil matrix. The assemblage of beneficial organisms provides top-down regulation of pest species in agricultural systems. In the same systems, bottom-up regulation of pest species can be provided by diversifying resource availability in time and space through non-host and resistant varieties, crop rotation, and cover cropping with non-host or even antagonistic plants that are sources of toxic compounds. Of course, the design of such multifactorial, holistic management systems requires information, including rapid and accurate diagnosis of organism habits and functions and the availability of plants with desired attributes. Chemical, physical, and resource disruptions of agricultural systems have major impact on soil organisms. It is important to conserve and enhance healthy systems; it is easier to destroy the systems than it is to rebuild them.

In the descriptions of plant parasitic nematodes in cropping systems documented in these chapters, you will find examples of the evolution of knowledge and tools to facilitate pursuit of the goals of sustainability. You will find documentation of where we came from, where we are now, and where we hope to go. You will read of systems in all phases and stages of sustainable transition. In addition, you will gain understanding of the forces and advances that have allowed and driven these changes.

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June 4, 2018

Howard Ferris

Preface

The main idea behind this book is to document the nematological problems and their solutions implemented in various regions of North America. There are several wonderful and useful books and reviews written on nematode disease problems and their control measures for various crops of certain countries, but we could not find a single book that presented the reader a broad and detailed view of nematological problems throughout North America. To have such a book to remove from the shelf, so that on opening the table of contents, the reader could immediately obtain all the important information on nematode diseases provided by highly qualified nematologists, would be an invaluable resource. The importance of plant parasitic nematodes in each region is determined by the selection of crops grown and the structure of agriculture, so we asked our authors to include this information in their respective chapters. The history of nematological research is also included in most chapters. To understand the present and to anticipate nematological problems in future agricultural practices, one must know, remember, and learn from the past. We also asked the authors to address related management strategies of their regions with a perspective of "Sustainability of Agriculture," which we try to follow and regard as our future goal. Obviously, not all nematological problems of each region could be fully represented nor could complete lists of plant parasitic nematode species be given due to limitation of the edition volume; however, the most important ones are well described. The reader can also find extensive lists of references and links on the Internet if he or she wants to delve deeper into any problem in detail. Due to extensive information received, *Plant Parasitic Nematodes in Sustainable Agriculture of North America* is incorporated in two volumes. Volume 1 includes Canada, Mexico, and the Western USA, while Volume 2 covers the Northeastern, Midwestern, and Southern USA.

In conclusion, we would like to thank all our 55 authors for their enormous contribution to this project, Howard Ferris for the Foreword to the first volume, Aurelio Ciancio for the Preface to the second volume of our book, many of our colleagues for their constant support and valuable advices and comments, and Springer Publisher and their editorial staff for publishing this book.

Sacramento, CA, USA
June 4, 2018

Sergei A. Subbotin
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Sergei A. Subbotin obtained an M.Sc. degree in Plant Protection in 1981 from the Moscow Agricultural Academy in Russia. In the same year, he joined the Plant Pathology Laboratory in the V. R. Williams All-Russian Fodder Research Institute, Moscow region, and later All-Russian Scientific Research Institute of Fundamental and Applied Parasitology of Animals and Plants named after K. I. Skryabin (former VIGIS), Moscow, where he was awarded the Ph.D. degree in Helminthology (Nematology) in 1987. Dr. S. A. Subbotin has worked as a researcher in the Center of Parasitology of the A. N. Severtsov Institute of Ecology and Evolution (Moscow, Russia), IACR-Rothamsted (UK), Institute for Agricultural and Fisheries Research (ILVO, Merelbeke, Belgium), Julius Kühn-Institut (Münster, Germany), and Department of Nematology, University of California (Riverside, USA). Presently, he serves as Senior Nematologist in the Plant Pest Diagnostic Center, California Department of Food and Agriculture, Sacramento, California, USA, and has affiliation positions as Scientist in the Center of Parasitology, Russia; Visiting Professor in Ghent University, Belgium; and Associate Scientist in the University of California, USA. Dr. S. A. Subbotin is one of the Founders and Chief Editors of the *Russian Journal of Nematology*. He has published more than 180 scientific articles in peer-reviewed journals on different aspects of molecular systematics and diagnostics of nematodes. Dr. S. A. Subbotin is the author of 21 chapters and 2 books, one of them in co-authorship with J. Baldwin and M. Mundo-Ocampo titled *Systematics of Cyst Nematodes (Nematoda: Heteroderinae)*, 2010 (two volumes), and another one in co-authorship with Dr. J. J. Chitambar titled *Systematics of the Sheath Nematodes of the Superfamily Hemicycliophoroidea*, 2014, published by Brill in *Nematology Monographs and Perspectives* series. His research studies have been focused on molecular systematics, diagnostics, and phylogeography of nematodes. Dr. S. A. Subbotin has a wide range of collaborative projects with nematologists across the world.

John J. Chitambar obtained an M.Sc. degree in Plant Pathology in 1977 from the University of Allahabad, Agricultural Institute, in India. In 1983, he obtained a Ph.D. degree in Plant Pathology from the University of California at Davis, USA, with specialization in nematology under the guidance of Dr. D. J. Raski. Following this, he was an Associate Scientist at the Nematology Department of the University of California at Riverside, USA, for a short term and then traveled to India to teach courses in plant pathology and nematology at the Allahabad Agricultural Institute for a year. He then worked as Postdoctoral Researcher at the Department of Nematology, University of California, Davis, after which he was employed as Associate and Senior Nematologist at the Plant Pest Diagnostic Center, California Department of Food and Agriculture. Presently, Dr. J. J. Chitambar serves as Primary Nematologist/Plant Pathologist at the State of California Department of Food and Agriculture and has worked for the State for over 31 years. He is also an Associate Scientist at the University of California, Davis. Dr. J. J. Chitambar is a specialist in the field of nematode diagnostics and morphology. His credits include at least 50 articles in nematological journals and co-authored chapters in professional books plus a book on sheath nematode systematics with Dr. S. A. Subbotin. As lead nematologist for the State Department, he has also produced several nematological reports, training manuals, advisory articles, and state legal documents. In addition, he has produced numerous pest risk assessments of plant parasitic nematodes and other pathogens for regulatory action in California. In collaboration with federal, state, and county government agencies, Dr. J. J. Chitambar has served on several committees presenting scientific basis in dealing with many regulatory nematology issues. He has trained state and county regulatory officials in nematode sampling, processing, identification, and laboratory methods for handling nematodes for diagnostics.

Chapter 1
Current State of Plant Parasitic Nematodes in Canada

Guy Bélair, Tom Forge, Benjamin Mimee, Mario Tenuta, and Qing Yu

1.1 Introduction

In Canada, there is a consensus among experienced nematologists that although crop losses related to plant parasitic nematodes (PPN) have not been exactly estimated, they could be in the range of 5–15% (Potter and McKeown 2003). Similar to many countries, the damages caused by PPNs are most often overlooked, mainly because the typical above ground symptoms of yellowing and stunting are often confused with other diseases, environmental factors such as drought and nutrient deficiencies. A relatively small portion of Canada's land is suitable for agriculture, or about 7% (65 million ha). Across the country, the character of agriculture differs from one province to the next, with climates and soil types influencing the commodities produced. Over 80% of arable land in Canada is located in the Western Prairie provinces. Saskatchewan accounts for almost 38% of farmland, with Alberta

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and Manitoba accounting for 31% and 11%, respectively. Ontario accounts for 8% of the land, Quebec 5%, British Columbia 4%, while Nova Scotia, New Brunswick and Prince Edward Island each contain only 1%, and Newfoundland and Labrador account for less than 1% of Canada's total arable land.

The area per farm continues to increase with great variation from one region to another reflecting regional differences in commodities grown according to differences in soil, climate, topography and markets. Larger farms are located in the Canadian Prairies, where the crops produced are mainly grains, cereals with wheat by far the largest crop and pulses, oilseeds, mainly canola, and tame or native pasture for backgrounding of cattle. The average farm size in Saskatchewan is approximately 675 ha, more than twice the national average. In Alberta, the average farm size is about 472 ha, a little over one and a half times the national average. In the other Prairie province, Manitoba, it is 459 ha (Statistics Canada 2014). Compared to farms of the Prairies, the average size of farms is much smaller elsewhere; British Columbia (132 ha), Quebec (113 ha), Ontario (99 ha) and the Atlantic Provinces (ranging from 161 ha in Prince Edward Island to 62 ha in Newfoundland and Labrador) (Statistics Canada 2014). In terms of area, corn and soybean are the major crops in Ontario and Quebec, but specialized crops such as greenhouse, floriculture and nursery trees are also produced. Fruit and vegetable production is concentrated in Ontario, Quebec, British Columbia and the Atlantic Provinces. Canada is 1 of the 20 largest potato-producing countries in the world. In fact, potatoes are the largest vegetable crop in the country (162,515 ha). They are grown in all provinces and are economically important in several provinces. Prince Edward Island is the largest producer (about 39,512 ha), followed by Manitoba (32,630 ha), New Brunswick (24,228 ha) and Alberta (22,160 ha) (Statistics Canada 2014). Alberta is poised to increase its potato production with the establishment of more processing facilities. Thus, the Prairies are set to become the major growing region in Canada.

Canadian agroecosystems have historically been less affected by PPNs when compared to other countries, mainly because Canada has a relatively cool climate. Winters are sufficiently severe in most agricultural areas of Canada to prevent survival of many of the most pathogenic PPN species found in more southern regions of North America. The cool climate also restricts cropping to one annual crop per year in most agricultural areas, which limits population buildup of those PPN species that do persist in Canada. Diverse crop rotations are often used allowing for breaks in susceptible hosts. Thus, the climate directly and indirectly dictates the PPN species and their severity.

The most common and damaging groups are root lesion nematodes (*Pratylenchus* spp.), and cyst nematodes (*Heterodera* spp., and *Globodera* spp.). With the acceleration of climate change, quarantined and invasive alien nematode species pose greater challenges, for example the stem and bulb nematode (*Ditylenchus dipsaci*) has become a serious pest in recent years, illustrating the need for development of nematology programs and extension in Canada. It is likely that the most devastating PPNs in the future will be different from the ones being dealt with at the present.

For the management of PPN, Canada, like other developed countries, has transitioned from the wide use of broad spectrum fumigant nematicides in the 1990s and early 2000s, to the adoption of integrated pest management (IPM) practices such as rotation with non-host crops and resistant varieties, and the use of green manure cover crops and other types of organic amendments.

Canada faces great challenges, as does the rest of the world, in understanding and controlling PPN in order to increase productivity for an ever-increasing human population while minimizing impacts of agriculture on the environment. This chapter attempts to read the past in order to understand the present, with some hints for the future, related to PPN in Canada.

1.2 Root Lesion Nematodes, *Pratylenchus* spp.

Root lesion nematodes are migratory endoparasites, and the most common PPN in Canadian agroecosystems. Twelve species have been recorded: *Pratylenchus alleni, P. crenatus*, *P. fallax*, *P. flakkensis*, *P. hexincisus*, *P. macrostylus*, *P. neglectus*, *P. penetrans*, *P. pratensis*, *P. sensillatus*, *P. thornei*, and *P. zeae*. The most common and destructive species is *P. penetrans* and the highest diversity of species is observed in the province of Ontario, followed by the province of Quebec (Townshend et al. 1978; Yu 2008; Bélair et al. 2013). In Manitoba, *P. neglectus* was found to be the predominant species, and *P. penetrans* was reported decades ago near the USA border but not currently (Mahran et al. 2010a). *P. neglectus* is present in every Prairie Province in about a quarter of commercial crop fields (Tenuta et al. unpublished). Elsewhere, co-infestations by multiple species are common, e.g., *P. neglectus, P. crenatus*, and *P. penetrans* were found in the same potato fields in Ontario (Olthof et al. 1982), while *P. crenatus* and *P. penetrans* were found to be sympatric in Prince Edward Island (Kimpinski 1979). Interestingly *P. neglectus* has never been detected in Prince Edward Island, while this species is found in large populations in Ontario (Olthof 1990). Surveys for PPN in golf courses, in different climate regions within Ontario and Quebec, also revealed that *Pratylenchus* was the most frequently detected genus (Yu et al. 1998; Simard et al. 2008). These nematodes are ubiquitous in all provinces and affect many crops (Potter and McKeown 2003). As an illustration of the ubiquitous nature of this genus, a survey of nematodes associated with highbush blueberry in British Columbia and other areas of the Pacific Northwest reported that 73% of fields were affected by PPN and that *Pratylenchus* was the most common genus (Zasada et al. 2010).

1.2.1 Pratylenchus penetrans

Overall, *Pratylenchus penetrans* is the most serious pest in Canada, attacking most of the high-value horticultural crops (Table 1.1). In addition, *P. penetrans* interacts with pathogenic fungi to cause serious replant disease complexes of tree-fruit crops such as the peach replant disease and the apple replant disease (Patrick 1955;

Table 1.1 The agriculturally important plant parasitic nematodes and their associated hosts in Canada

Nematode	Province[a]	Crop	Reference
Anguina agrostis	NS, NW, ON, SK	Turfgrass	Baker (1955, 1957, 1959)
Ditylenchus destructor	ON, PE	Garlic, potato	Baker (1946) and Yu et al. (2012)
D. dipsaci	AL, BC, MN, ON, PE, QC, SK	Alfalfa, garlic, onion	Mountain (1957), Vrain and Lalik (1983), Vrain (1987), CABI/EPPO (2009), Réseau d'avertissements phytosanitaires (2013), and Hajihassani and Tenuta (2017)
Globodera pallida	NF	Potato	Stone (1977)
G. rostochiensis	BC, NF, QC	Potato	Olsen and Mulvey (1962), Orchard (1965), and Sun et al. (2007)
Heterodera avenae	ON	Corn, oat	Putnam and Chapman (1935) and Fushtey (1965)
H. carotae	ON	Carrot	Yu et al. (2017)
H. fici	ON (greenhouse)	Fig	Sun et al. (2017)
H. glycines	ON, QC	Soybean	Anderson et al. (1988) and Mimee et al. (2014a)
H. schachtii	AL, ON	Sugar beet	Baker (1942) and Lilly et al. (1961)
Longidorus diadecturus	ON	Peach	Eveleigh and Allen (1982)
L. breviannulatus	ON	Apple, cherry, peach, raspberry, turfgrass	Van Driel et al. (1990) and Simard et al. (2009)
L. elongatus	BC, ON	Strawberry, turfgrass	McElroy (1977), Allen and Ebsary (1988), and Pedram et al. (2010)
Meloidogyne hapla	BC, MN, NB, ON, PE, QC	Cabbage, carrot, cauliflower, lettuce, onion, potato, strawberry, tomato	Olthof and Potter (1972), Potter and Townshend (1973), Sayre and Toyama (1964), Vrain et al. (1981), Bélair (1992), and CABI/EPPO (2002)
M. incognita	ON, QC (greenhouse)	Tomato, cucumber	Bird (1969), Johnson and Boekhoven (1969), and Bélair (unpublished)
M. microtyla	ON	Grass	Mulvey et al. (1975)
M. naasi	QC	Turfgrass	Bélair et al. (2006)
Paratrichodorus renifer	BC	Blueberry, potato	Kawchuk et al. (1997), Xu and Nie (2006), and Forge et al. (2009, 2012)
Pratylenchus alleni	QC	Soybean	Bélair et al. (2013)

(continued)

Table 1.1 (continued)

Nematode	Province[a]	Crop	Reference
P. crenatus	BC, ON, PE	Blue berry, potato	Kimpinski (1979), Olthof et al. (1982), and Zasada et al. (2017)
P. fallax	ON	Turfgrass	Yu et al. (1997)
P. neglectus	AL, BC, MN, ON, QC	Potato	Olthof et al. (1982), Mahran et al. (2010a), and Forge et al. (2015a)
P. penetrans	AL, BC, SK, MN, NB, NS, ON, PE, QC	Apple, barley, bluberry, carrot, corn, grapes, oat, onion, pea, peach, pear, plum, potato, raspberry, soybean, strawberry, tabacco, wheat	Baker (1955), Potter and Townshend (1973), Oltholf et al. (1982), Kimpinski (1987), Dauphinais et al. (2005), Yu (2008), Forge et al. (2012), and Bélair et al. (2018)
P. thornei	ON	Wheat	Yu (1997)
Trichodorus primitivus	ON	Turfgrass	Pedram et al. (2010)
Xiphinema americanum	ON, QC	Apple, blueberry, peach	Vrain and Rousselle (1980), Allen et al. (1984), and Ebsary et al. (1984)
X. rivesi	ON	Apple	Ebsary et al. (1984)

[a]Names of the provinces and territories of Canada are represented by two letter. *AL* Alberta, *BC* British Columbia, *MB* Manitoba, *NB* New Brunswick, *NL* Newfoundland and Labrador, *NS* Nova Scotia, *NW* North West Territory, *ON* Ontario, *QC* Quebec, *PE* Prince Edward Island, *SK* Saskatchewan

Wensley 1956; Mountain and Boyce 1958a, b; Ward and Durkee 1956; Mountain and Patrick 1959; Potter and Olthof 1974, 1977; Braun et al. 2010; Forge et al. 2016a). It also interacts with particular fungal pathogens to cause brown root rot of tobacco (Olthof 1967, 1971; Elliot and Marks 1972), and early dying disease on potato (Kimpinski et al. 2001; Bélair et al. 2005; Dauphinais et al. 2005). In Prince Edward Island, *P. penetrans* has been recognized as a widespread constraint on potato production since the 1970s (Kimpinski et al. 1992). In Quebec, severe symptoms of early dying have been observed in potato fields (Bélair unpublished). A similar interaction with *Verticillium dahliae* was also observed in strawberry fields (Bélair et al. 2018). In soybean, *P. penetrans* was found in 42% of the tested fields (78 out of 185) in the province of Quebec and 8% of the fields showed a population density exceeding the theoretical economic threshold (Dauphinais et al. 2018).

1.2.2 Pratylenchus neglectus

In Manitoba, *P. neglectus* was recently found in a third of 31 commercial potato fields examined (Mahran et al. 2010a). However, the dominant potato cultivar 'Russet Burbank' was not a good host for the Manitoba populations of *P. neglectus*, or if the nematode had significant effects on yields (Mahran et al. 2010a). The studies in Manitoba suggested that rotation crops other than potato such as canola and wheat, were likely primary hosts to the nematode, as shown in the U.S.A. (Smiley et al. 2004; Johnson 2007). More recently, a survey of pulse fields across the Prairies found widespread distribution of *P. neglectus* (Tenuta et al. unpublished). In Alberta, high level of *P. neglectus* populations was associated with potato yield losses in a study where short crop rotations, with wheat preceding potato, resulted in the greatest expression of potato early dying disease symptoms and the lowest yields of several alternative rotations (Forge et al. 2015a). It is unclear if the apparent differences between the Manitoba and Alberta studies are due to differences in the inherent pathogenicity of *P. neglectus* populations or the environments (e.g. soil texture, irrigation) and crop rotations. Previous research also suggests that there may be differences in the ability of *P. neglectus* populations to parasitize and damage potato (Olthof 1990; Hafez et al. 1999).

Worldwide, *P. neglectus* is recognized as a significant pest of small grain and oilseed crops (Taylor et al. 1999; Smiley et al. 2004; Johnson 2007). Considering the importance of these crops to agriculture in Western Canada, research on the impacts of *P. neglectus* on small grain and oilseed crops in Western Canada is urgently needed. The species was also recently found north of Quebec City, which lies outside of what was previously known as the northern limit of its distribution (Bélair unpublished).

1.2.3 Other **Pratylenchus** *Species*

Even though *P. penetrans* is still the most common species in Canada, Canadian nematologists should remain vigilant for any outbreaks of other species. *Pratylenchus thornei*, a serious pest on wheat in some countries, was found in wheat in Ontario (Yu 1997). The recent isolation of *P. alleni* in a Quebec soybean field has also raised some concerns about the possible establishment of species that are more aggressive. The yield losses from *P. alleni* in diseased areas ranged from 38% to 54% (Bélair et al. 2013). In USA, the pathogenicity of *P. alleni* in soybean has been established (Acosta and Malek 1981), but the species is also known to affect other crops such as corn and wheat (Wartman and Bernard 1985). Recently, *P. crenatus* was found to be the main species parasitizing highbush blueberry in British Columbia, as well as, in other areas of the Pacific Northwest (Zasada et al. 2017).

1.2.4 Management of **Pratylenchus penetrans**

Given the ubiquitous presence of *Pratylenchus penetrans* in Canadian fruit and vegetable production systems, a major focus of research has been the identification of cultural practices that may minimize impacts of *P. penetrans* on high-value fruit and vegetable crops. Crop rotation is a challenging approach for *P. penetrans* management due to its wide host range, which also includes many weed species (Bélair et al. 2007). In their comprehensive analysis of weed hosts, Bélair et al. (2007) found that the family Brassicaceae was shown to be the best hosts while representatives of the Cyperaceae were the worst. Annual bluegrass crops were shown to be tolerant to *P. penetrans* under controlled conditions (Bélair and Simard 2008). Despite its wide host range, Canadian research has shown that rotation with suppressive cover crops can be a successful approach to managing *P. penetrans* in annual cropping systems. Ball-Coelho et al. (2003) and Bélair et al. (2005) demonstrated that rotating to a specific variety of forage pearl millet, CFPM 101, prior to planting the potato cash crop resulted in lower *P. penetrans* populations at the time of potato planting. As a consequence, they observed increased yields relative to other types of cover crops including other varieties of forage pearl millet. The cultivar CFPM 101 has been shown to be a poor host to *P. penetrans* that does not allow population buildup. It is not clear if it may also stimulate active suppression via toxic metabolites, or perhaps, by stimulating the development of a suppressive soil food web. Mahran et al. (2008a, b), in a laboratory and field study found that volatile fatty acids in pig slurry and acidified pig slurry could kill the nematode. In British Columbia, however, frequent modest applications of dairy manure slurry to tall fescue resulted in greater *P. penetrans* population densities than a corresponding fertilizer treatment or an untreated control, presumably, as a result of enhanced nutritional value of root tissue (Forge et al. 2005). This research indicates that the utility of manure slurries for *P. penetrans* control will depend on the interplay of application rates with growth responses of the crops. Brassica "bio-fumigant" green manures have also been evaluated extensively for control of *P. penetrans* in Canadian vegetable rotations. In related Canadian research, glucosinolate-containing *Brassica* seed meals suppressed *P. penetrans* under greenhouse conditions (Yu et al. 2007a) but not in corn fields (Yu et al. 2007b).

As part of an integrated replant management program for perennial fruit crops, Forge et al. (2015a, b, 2016b) have shown that heavy applications (>50 Mg/ha) of poultry manure or compost can suppress populations of *P. penetrans* through at least two full growing seasons after replanting raspberry (Forge et al. 2016b) or sweet cherry (Forge et al. 2015b; Watson et al. 2017). The authors speculated that the poultry manure could have bio-fumigant effects owing to the relatively high amounts of ammonia released into the soil environment at such high application rates, but the duration of suppression suggests that stimulation of suppressive soil food webs or rhizosphere communities could also be involved. The researchers demonstrated that the reductions in numbers of *P. penetrans* in compost-treated soil was associated with increased colonization of the cherry rhizosphere by bacteria with nematode suppressive activity but speculate that other biological antagonists could also be involved in the suppression (Watson et al. 2017).

Options for cultural management in perennial fruit crops are constrained by the lack of annual tillage to facilitate incorporation of organic amendments, antagonistic cover crops or control agents. The use of paper mulch in an apple orchard reduced *P. penetrans* populations and could explain the increased root growth of the apple trees (Forge et al. 2008). Other types of organic mulches, including, alfalfa hay

(Forge et al. 2003, 2013) seem to give similar results. Concomitant increases in food web structure suggest that organic mulches may increase the presence of nematode antagonists, creating a suppressive food web, thereby decreasing the damage caused by *P. penetrans* (Forge and Kempler 2009).

1.3 Root Knot Nematodes, *Meloidogyne* spp.

Root knot nematodes are sedentary PPN and among the most damaging of soil-borne pests of horticultural and field crops. Most damages are attributed to these four species: *Meloidogyne incognita*, *M. arenaria*, *M. javanica*, and *M. hapla*, with *M. chitwoodi* being a major pest of potato (Nicol et al. 2011). However, because of our temperate climate, the problems associated with root knot nematodes are far less important in Canada; *M. incognita*, *M. arenaria* and *M. javanica* are unable to persist where the soil freezes, and *M. chitwoodi* has not been introduced to Canada. Consequently, the main species of concern for Canadian agriculture is currently the northern root knot nematode (*M. hapla*), which has been reported in British Columbia, Manitoba, Ontario, Quebec and Prince Edward Island parasitizing a range of horticultural crops (Zimmer and Walkof 1968; Potter and Townshend 1973; Willis et al. 1976; Vrain and Dupré 1982; Bélair 2005) and alfalfa (Townshend et al. 1973).

Several other root knot nematode species are potential concerns on limited crops in Canada, or pose a risk of establishment. In a survey nematodes in golf course turf in Quebec, *M. naasi* was isolated from severely damaged annual bluegrass plants (Bélair et al. 2006). Although it is a common species in Europe and in several states in the USA where it causes significant damage, *M. naasi* has rarely been observed in Canada. *Meloidogyne microtyla*, a new species at the time was found on grass in Southwestern Ontario in 1975 (Mulvey et al. 1975).

Southern root knot nematode (*M. incognita*) has, so far, only been found on several vegetable crops in greenhouses in Southwestern Ontario (Mountain and Sayre 1961) and Southern Quebec (Bélair unpublished). This species could take advantage of climate change to move to open fields, or spread from nearby USA states of New York and Pennsylvania (Walters and Barker 1994) to the neighbouring provinces.

The Columbia root knot nematode (*M. chitwoodi*), which is on the quarantine list of the Canadian Food Inspection Agency (CFIA), was first described in the Columbia River basin of Oregon and Washington in 1980 (Santo et al. 1980). This nematode is substantially more damaging to potato than *M. hapla* (Van Der Beek et al. 1998). It also has a very wide host range that covers many crop species, including tomato and cereals (Ferris et al. 1994). Thus, this species is more difficult to control by means of crop rotation than *M. hapla*, which has a narrower host range and does not reproduce on cereals. Considering the proximity of *M. chitwoodi*-infested areas in the US to Canadian potato production areas, Canadian nematologists must continue to be vigilant. Other species of concern include *M. fallax, M. minor, M. enterolobii, M. exigua,* and *M. paranaensis,* because they have only recently been described (Elling 2013).

1.3.1 Management of Meloidogyne hapla

Meloidogyne hapla has been reported in the provinces of New Brunswick, Ontario, Prince Edward Island, British Columbia and Quebec (CABI/EPPO 2002). Although the nematode is widespread, the populations are generally low. Many vegetable crops such as cabbage, cauliflower, onion and tomato have been shown to be affected by the nematode (Olthof and Potter 1972; Sayre and Toyama 1964), but it is on carrots cultivated in muck soils that the pest has received most attention. Crop rotation with a non-host crops such as cereals or grasses are used to maintain *M. hapla* densities below damaging levels, which are extremely low for carrots (Bélair 1992; Bélair and Parent 1996). Even at the detectable level of 1 infective juvenile per 100 ml soil, severe forking and stunting of the tap root are induced in carrots, which are rendered unmarketable (Bélair 1992).

Several nematicides were effective in reducing the *M. hapla* populations and increasing yields of marketable carrot (Vrain et al. 1981). In strawberry production, the presence of multiple root pathogens including *M. hapla,* justifies preplant fumigation with chloropicrin and metham sodium to increase vigor and yields over the 2-year production period. In potato production, *M. hapla* is not considered to be a primary problem. However, soil fumigation using chloropicrin, metham sodium, or metham potassium is occasionally performed by some growers to manage other soil-borne pathogens, especially *Verticillium dahliae* and root lesion nematodes which together cause the potato early dying disease complex (Celetti and Al-Mughrabi pers. comm.). The planting of certified seed also contributes to limiting the dispersal and losses caused by PPN in potato production. Occasionally, potato tubers containing *M. hapla* females can be observed causing some necrosis underneath the potato peel during storage, but no direct actions are taken by the growers to manage this disorder in Eastern Canada (Bélair unpublished).

With the withdrawal of dichloropropene from the registered list of nematicides, combined with additional restrictions on the use of chloropicrin and metham sodium in Canada, growers have been forced to consider more sustainable cultural practices to control *M. hapla*. A small number of studies were done in Canada in recent years to find alternative and sustainable methods of controlling *M. hapla*. Seed exudates of *Tagetes* spp. (Riga et al. 2005) and oriental mustard bran (Yu et al. 2007a) demonstrated nematicidal activity on root knot nematodes. The effect of nicotine was also studied and proved to be toxic to several species of nematodes including *M. hapla* (Yu and Potter 2008). Soil amendment with *Streptomyces lydicus* significantly decreased *M. hapla* juveniles in soil (Bélair et al. 2011).

Market garden production of vegetables is increasing rapidly in areas around most major Canadian cities. As *M. hapla* can parasitize many of the popular crops in market garden production, the impact of this nematode on market garden production is likely to increase. At this point in time, however, there is limited awareness of the prevalence of root knot nematodes in small-scale vegetable production in Canada.

1.4 Cyst Nematodes, *Heterodera* spp. and *Globodera* spp.

Heterodera spp., and *Globodera* spp. commonly known as cyst nematodes, are sedentary endoparasites that are well adapted for cold-temperate climate regions such as Canada. They infect the roots of many plants including many important crops grown in Canada such as cereals, corn, soybean and potato. They are very difficult to control because of the ability of eggs in dried cysts to survive in soil for extended periods.

1.4.1 Heterodera *spp.*

Heterodera species of significance in Canada include soybean cyst nematode (*H. glycines*), sugar beet cyst nematode (*H. schachtii*), cereal cyst nematodes (*H. avenae* and *H. filipjevi*) and carrot cyst nematode (*H. carotae*).

The soybean cyst nematode is particularly important as soybean production has been expanding in Canada. The pest was first reported in Southwest Ontario in 1987 (Anderson et al. 1988). Since then it has spread north and northeastwards along the St. Lawrence River and, in 2013, was found in Quebec (Mimee et al. 2014a). It is currently present at low population densities in all areas producing soybean in Quebec (Mimee et al. 2016). It is considered likely that soybean cyst nematode was present and causing soybean yield losses in Southwest Ontario by the 1970s, but had gone undiagnosed (Tenuta pers. comm.). The nematode has expanded northward in North Dakota and Minnesota to the Manitoba border though surveys of soybean conducted in Manitoba between 2013 and 2015 did not find the nematode (Tenuta et al. unpublished). Surveys continue in Manitoba as the area of production has increased from insignificant in the early 2000 and expected to cap at 1.2 million hectares within 30 years. Soybean cyst nematode was a regulated pest in Canada until the fall of 2013 when it was de-regulated (CFIA 2013).

The sugar beet cyst nematode, *H. schachtii,* was a serious pest in Southern Ontario in the early 1950s when the crop was widely cultivated (Baker 1942). It was first found in Alberta in 1961 (Lilly et al. 1961) and has become recognized as a significant pest for the sugar beet industry in Southern Alberta. Currently, the nematode is successfully managed using a 4-year rotation. The Manitoba Sugar Company conducted extensive surveys for *H. schachtii* when sugar beet was grown in the province. The nematode was first reported in 1976 and over several years, found on light soils near the city of Winkler (Zednai 1979). The pest has recently been reported in North Dakota where sugar beet is still grown in the Red River Valley, which is contiguous with Southern Manitoba (Nelson et al. 2012).

The cereal cyst nematode, *H. avenae,* was first reported damaging oat in Ontario in the 1930s (Putnam and Chapman 1935), with further investigation occurring through the 1940s (Baker and Chapman 1946). Later, the nematode was found infesting corn in the same regions (Fushtey 1965; Fushtey and Johnson 1966). *Heterodera avenae* is widespread on wheat in the Northwestern US states of Washington, Idaho and Montana that border British Columbia, Alberta and Saskatchewan (Smiley and Nicol 2009). A closely related species, *H. filipjevi,* is also present in Washington (Smiley and Yan 2015) and recently reported in Montana (Dyer et al. 2015). Neither species appears to have become established in the major Canadian cereal-producing regions of Saskatchewan and Alberta despite the proximity to infestations in nearby Washington, Idaho and Montana. Considering this precarious situation and the long-recognized importance of the nematode in Ontario, surprisingly little research has been directed at this nematode in Canada.

The carrot cyst nematode, *H. carotae,* was recently reported in the Holland Marsh region in the province of Ontario (Madani et al. 2017; Yu et al. 2017). These are the first reports of the pest in Canada. A preliminary survey indicated that the pest is wide spread in the region (Vander Kooi et al. 2017). A diagnostic conventional PCR method was developed based on populations of *H. carotae* from Ontario and Italy using primer sets based on the *coxI* gene sequence in real-time PCR and melt curve analysis (Madani et al. 2017).

1.4.1.1 Management of *Heterodera* spp.

Plant resistance remains the most effective and economically viable strategy to control soybean cyst nematode, but the presence of new virulent populations, or HG types, can reduce the efficacy of this strategy (Niblack et al. 2002). A recent phenotypic characterization of soybean cyst nematode populations in Ontario reported 24 different HG types (Faghihi et al. 2010). This diversity of HG types is a major concern, given that the number of resistance genes available in commercial cultivars is very limited. Fortunately, 73% of the populations did not reproduce well on PI 88788, which is the resistance source used in the vast majority of resistant cultivars. However, the study also demonstrated that 15% of the populations developed well on PI 548402 (cv. Peking), even though that source of resistance is not generally present in commercial cultivars in Ontario. Thus, the development of new cultivars based on novel resistance sources is necessary. Fortunately, future breeding will be facilitated by new technologies such as marker-assisted selection (MAS) and genotyping by sequencing (GBS). These techniques have already been used to identify early maturity genes (Tardivel et al. 2014), another meaningful trait for Canadian productivity, as soybean is grown farther north each year.

Unfortunately, a modelling of the soybean cyst nematode life cycle under current and future (2041–2070) conditions in Quebec predicts that it could survive in all soybean-growing areas (Mimee et al. 2014b). Because the optimal temperature for soybean cyst nematode is warm (27 °C) and the production of cysts is directly influenced by temperature (Da Rocha et al. 2008), it will be interesting to see if this pest will really become problematic in colder regions. If so, these environmental conditions will likely exert a strong selection pressure on the pest, and the resulting HG types may be difficult to predict. New methods for studying the population genetics of cyst nematodes (Mimee et al. 2015a) and current studies to rapidly quantify their abundance in soil using real-time PCR (Tenuta et al. unpublished) will be very useful for monitoring. Another popular management tool in managing the pest is through rotating soybean with non-host crops. We must also remain vigilant on the potential spread of the pest to the new soybean producing provinces of Manitoba and the Atlantic Maritime Provinces.

The cereal cyst nematode has not warranted the development of management strategies in Canada because oats were historically grown mostly for animal feed and the economic impact of the nematode was low. This situation could change as oats are increasingly being grown for human consumption and therefore, considered to be of greater economic value. Wheat is the most important crop to Canada. Although the cereal cyst nematodes have not yet been found infesting wheat in Canada, in recognition of the fact that they are serious pests on the crop in many countries of the world, Canadian researchers must remain vigilant for the possibility that they could one day become serious pests of the most valuable crop for the nation.

1.4.2 Globodera *spp.*

The genus *Globodera* comprises several species, including golden cyst nematode (*G. rostochiensis*) and pale cyst nematode (*G. pallida*), that are major pests of potato in the world. They are both of high economic importance, and quarantined under strict regulations in Canada by the Canadian Food Inspection Agency (CFIA) as well as in many other countries. In Canada, *G. rostochiensis* has been present on the Saanich Peninsula of Vancouver Island, British Columbia, since 1965 (Orchard 1965), and both *G. rostochiensis* and *G. pallida* have been present on the Island of Newfoundland since 1962 (Olsen and Mulvey 1962; Stone 1977). In 2006, *G. rostochiensis* was reported from potato in the Saint-Amable region, Quebec (Sun et al. 2007), confirmed by morphological and a phylogenetic analysis (Yu et al. 2010c) and later determined to be pathotype Ro1 (Mahran et al. 2010b). Genetic analyses strongly suggest that both species were probably introduced to Canada from Europe, and that multiple introductions of *G. rostochiensis* occurred (Madani et al. 2010; Boucher et al. 2013). In the bioclimatic condition of Quebec, the species was found to do a single life cycle each year, however, a second hatching cohort was observed each year and could soon result in a full second generation in light of climate change (Mimee et al. 2015b). A few G. *rostochiensis* cysts were recovered from a sample from each of two farms out of 2721 samples taken in Alberta in 2007 by CFIA (unpublished). As a result, CFIA and USDA-APHIS instituted a bi-lateral monitoring program and guidelines for declaration of a field containing PCN (CFIA USDA-APHIS 2014).

1.4.2.1 Management of *Globodera* spp. in Canada

The potato cyst nematodes have a narrow host range, and their distribution in Canada remains limited to a few well-defined sites. The management of the pests includes containment and population reduction by using resistant varieties. Immediately after the finding of the pests either in Newfoundland, BC, and Quebec, delimitation surveys were carried out establishing the boundaries of the infestations, followed by strict phytosanitary measures. A minimum measure was a ban on planting susceptible cultivars of potato. Good outcomes have resulted. On the Saanich Peninsula a recent survey did not reveal any positive samples for *G. rostochiensis* with the exception of one field with a history of quarantine infractions (Rott et al. 2010). In Saint-Amable, CFIA has authorized a 1-year production of resistant cultivars followed by a 2-year rotation with a non-host crop (Mahran et al. 2010b). This strategy appears to have been effective, given that population densities quickly dropped below detection levels (Bélair et al. 2016) and very few viable eggs remain 10 years after the establishment of the quarantine area (Mimee et al. 2017). However, the implementation of quarantine measures was shown to modify the biodiversity and abundance of weeds in the regulated fields, resulting in a significant increase of nightshade weed species (*Solanum* spp.) that could support and serve as pest refuges for *G. rostochiensis* (Mimee et al. 2014c). *Globodera rostochiensis* was already known to reproduce on Canadian nightshades, and interestingly, the nematode populations in the different provinces showed dissimilar host preferences for these weeds (Rott et al. 2011).

Detection and precise species-level identification are critical issues in potato cyst nematode management. For this purpose, a multiplex quantitative polymerase chain reaction (qPCR) assay was developed for the simultaneous differentiation of *G. rostochiensis, G. pallida,* and *G. tabacum* (Madani et al. 2008; Mimee et al. 2017). The same team also developed a method based on the heat shock gene *hsp*90 (Madani et al. 2011). It was recently shown that potato cyst nematode pathotypes could be differentiated with specific single-nucleotide polymorphisms (Mimee et al. 2015a). Thus, the next step will be to replace the long and expensive pathotyping assays in greenhouses with rapid and simple allele-specific oligonucleotide PCR assays.

Even though the current Canadian populations have been characterized and strict containment and monitoring is in place, awareness and vigilance is required moving forward. Recently, a new species of potato cyst nematode, *G. ellingtonae*, was described in Oregon (Handoo et al. 2012), and *G. pallida* was found in numerous fields in Idaho (Skantar et al. 2007). These findings serve as reminders that understanding of the phylogenetic and geographic origins of potato cyst nematodes is not complete and additional research is needed. Especially, new strategies effective against all the pathotypes should be explored. For that, the recent publication of the genome sequence of *G. rostochiensis* (Eves-van den Akker et al. 2016) and the transcriptome variation during hatching and survival (Duceppe et al. 2017) will be very useful.

1.5 *Ditylenchus* spp.

1.5.1 Stem and Bulb Nematode, Ditylenchus dipsaci

Stem and bulb nematode is one of the most destructive nematode pests especially in temperate regions. If not controlled, it can cause complete failure of host crops such as onions, garlic, cereals, legumes, strawberries and ornamental plants, especially flower bulbs. It is also an international quarantined nematode pest. In Canada, *Ditylenchus dipsaci* was first reported on onion in one area of Ontario in 1957 (Mountain 1957) and then was found in nearby counties of Ontario in subsequent years (Sayre and Mountain 1962; Johnson and Kayler 1972; Fushtey and Kelly 1975). It was reported in Saskatchewan on creeping thistle in 1979 (Watson and Shorthouse 1979), then in British Columbia on alfalfa in 1983 (Vrain and Lalik 1983), Alberta in 1987 (Vrain 1987), and then in Quebec and Prince Edward Island (CABI/EPPO 2009). The reported finding in Saskatchewan was likely a find of a closely related *D. weischeri*. Although widely distributed, *D. dipsaci* was not considered to be a serious pest in Canada until the recent outbreak on garlic in Ontario. The identity of the nematode in the outbreak was confirmed (Yu et al. 2010b), and a subsequent survey showed that it was widespread in most garlic growing fields in Ontario (Qiao et al. 2013). It has since spread to the neighbouring provinces of Quebec (Réseau d'avertissements phytosanitaires 2013) and Manitoba (Hajihassani and Tenuta 2017) and is an ongoing economic concern in Ontario (Celetti 2011).

One of the main challenges is the precise identification of *D. dipsaci,* which has several races, each of which exhibits a different host preference, and thus managing this nematode is complicated. A recent study showed that two distinct introductions of this parasite into Ontario likely occurred and found genetic differences within a race (Qiao et al. 2013). Sequence analyses of *D. dipsaci* and *D. destructor* (potato rot nematode), initiated by Agriculture and Agri-Food Canada and the CFIA (Yu et al. 2014), should make it easier to develop specific molecular diagnostic tests in the future.

Recently, *Ditylenchus* populations that parasitize creeping thistle in Russia (Chizhov et al. 2010) as well as Manitoba and Saskatchewan (Watson and Shorthouse 1979; Tenuta et al. 2014) were recognized to be *D. weischeri*. This species has a very different host preference than *D. dipsaci* with specialization to creeping thistle and no host compatibility with onion and strawberry (Chizhov et al. 2010), common bean, chickpea, lentil, canola, wheat and garlic (Hajihassani et al. 2016). Yellow pea seems to be a very weak host for *D. weischeri*, with Hajihassani et al. (2016) reporting that the nematode could survive but not reproduce on two of five varieties of yellow pea examined. A follow-up study failed to show development and reproduction of the nematode on yellow pea at 17 and 22 °C but at a very high average temperature of 27 °C (Hajihassani et al. 2017). Further, the nematode did not reproduce or cause yield damage to yellow pea in a field study (Hajihassani et al. 2017). Madani et al. (2015) reported species-specific PCR primers to differentiate *D. dipsaci* and *D. weischeri* to aid screening of export and import commodities for the former. More recently, Madani and Tenuta (2018) provided additional molecular evidence of several genes further substantiating recognition that *D. weischeri* is a distinct species from *D. dipsaci*.

1.5.1.1 Management of the Stem and Bulb Nematode

With cooperation from major seed suppliers, the Ontario Ministry of Agriculture, Food and Rural Affairs (OMFRA) introduced a program producing and distributing garlic seeds free from the stem and bulb nematodes in Ontario (Hughes and Celetti 2011). In 2013, Quebec growers were worried about the introduction of *D. dipsaci*–infected seed pieces, which raised the potential threat of PPN to the garlic industry (Réseau d'avertissements phytosanitaires 2011, 2013). Stem and bulb nematode can also be spread by irrigation and contaminated equipment (Celetti 2009).

Several chemicals have been tested in field trails to control this pest in Ontario, and several have shown promising results (Celetti and Paibomesai 2015). For example, Agri-Mek®, an abamectin-based insecticide, was effective in reducing nematode populations and increasing yields when garlic cloves were soaked in the compound at the labelled rate prior to the planting.

1.5.2 Potato Rot Nematode, **Ditylenchus destructor**

Potato rot nematode is a serious nematode pest in a number of root and tuber crops, primarily in potatoes, and is an internationally quarantined pest. In Canada, this pest was found in Prince Edward Island on potato in 1946 (Baker 1946), and in Ontario on garlic in 2012 (Yu et al. 2012). Fortunately, the species has effectively been contained.

1.6 Virus Vector Nematodes

1.6.1 Dagger Nematodes, **Xiphinema** *spp.*

Ectoparasites, dagger nematodes are known to damage roots and directly affect plant growth. However, dagger nematodes are perhaps most important due to their ability to vector viruses that cause more significant economic losses than the nematodes alone (Van Driell et al. 1990; Brown and Trudgill 1998; Singh et al. 2013). Several species are present, and damage to several crops has been reported in British Columbia, Quebec, and Ontario (The Canadian Phytopathological Society 2005, 2006, 2008, 2009, 2010, 2011, 2012, 2013, 2014). The dominant species in Canada are part of the *Xiphinema americanum sensu lato* complex, and *X. rivesi* (Graham et al. 1988; Robbins 1993; BCMA 2013). In Yu et al. (2010a), the authors formally identified *X. chambersi* for the first time in Canada, in Turkey Point Provincial Park, Ontario. This species is commonly found on ornamental trees but is also known to cause significant damage in strawberry (Perry 1958; Ruehle 1971). The Canadian National Collection of Insects, Arachnids and Nematodes now lists nine species from Canada*: X. americanum, X. bricolensis, X. pacificum, X. chambersi, X. bakeri, X. diversicaudatum, X. occiduum* and *X. rivesi*. Damages caused by dagger nematodes are expected to worsen as climate changes. For example, increased soil temperatures will likely influence population densities, hosts phenology, geographic distribution, and habitats suitable for introduced nematodes (Neilson and Boag 1996; Boag et al. 1997).

In the 1980s, Vrain and Rousselle (1980) confirmed the high occurrence of *X. americanum sensu lato* in Quebec apple orchards. This species is known to be a vector of the *Tobacco ringspot virus* (TRSV) which in apple causes apple union necrosis, a severe girdling of affected apple trees resulting from the disorganisation of tissue at the scion/rootstock interface (Lana et al. 1983). In Southwestern Quebec, near the USA border, numerous apple orchards have been replaced by highbush blueberry fields. Symptoms of ringspot-type virus in some highbush blueberry plantings have been observed but the presence and role of *X. americanum* in those plantings has not being confirmed (Lambert pers. comm.). In the nearby State of New York, Fuchs et al. (2010) successfully isolated both TRSV and *Tomato ringspot virus* (ToRSV), and also recovered *X. americanum* from the soil in diseased highbush blueberry plants in various plantings.

Xiphinema index is the primary vector of *Grapevine fanleaf virus* which is a serious concern for growing wine industries in Ontario and BC. *X. index* has not been found so far in Canada, but preventive measures related to imports are a high priority (CFIA 2009).

1.6.2 Needle Nematodes, **Longidorus** *spp.*

The Canadian National Collection of Insects, Arachnids and Nematodes currently lists three species of the ectoparasite *Longidorus* from Canada: *L. breviannulatus, L. diadecturus* and *L. elongatus*. These species are widely distributed in Canada and are of economic importance because they parasitize many plants and vector viruses (Eveleigh and Allen 1982; Ebsary et al. 1984; Brown and Trudgill 1998; Simard et al. 2008, 2009). *Longidorus* spp. is frequently found in apple and peach orchards as well as in grape, strawberry, corn, and turfgrass (The Canadian Phytopathological Society 2005 to 2014). *Longidorus diadecturus* was found from peach fields in Ontario and was proven to be a vector for peach rosette mosaic virus (Allen et al. 1982a; Stobbs and Van Schagen 1996). It is listed as an A1 quarantined nematode pest by the European and Mediterranean Plant Protection Organization. In 2009, Simard et al. (2009) confirmed the pathogenicity of *L. breviannulatus* to creeping bentgrass in Quebec. This needle nematode species was already known for transmitting mosaic viruses to peach trees in Ontario (Van Driell et al. 1990). The species *L. elongatus*, known to damage a wide range of crops including beet, barley, potato, and raspberry (Singh et al. 2013), was reported in 2010 in Ontario (Pedram et al. 2010). In various horticultural crops, virus diseases are on the rise across the country. Growers should be aware of nematodes that are potential vectors from infested hosts and/or reservoir weedy plants, so that these pests can be detected early in the field.

1.6.3 Stubby Root Nematodes

Stubby root nematodes (*Paratrichodorus* spp., *Trichodorus* spp. and *Nanidorus* spp.) are other ectoparasites parasiting a wide range of hosts (Riga and Neilson 2005; Davis 2012). *Paratrichodorus renifer*, which was identified for the first time in Canada in 2009 (Forge et al. 2009) and *N. minor*, which is widespread in Canada (Anderson 2008), are responsible for economic losses in turfgrass and berry crops (Zasada et al. 2010; The Canadian Phytopathological Society 2005 to 2014). Recent greenhouse and microplot studies indicate that *P. renifer* can reduce growth and yield of blueberry and could become a greater concern as the relatively young blueberry industry in British Columbia continues to expand and mature (Forge et al. 2012). Stubby root nematodes are also known to be vectors of tobacco rattle *virus* in potato fields in Eastern Canada and a small area of coastal British Columbia (Xu and Nie 2006; Kawchuk et al. 1997). In Ontario, Pedram et al. (2010) identified for the first time *T. primitivus* in the rhizosphere of grasses (*Poa* spp. and *Festuca* spp.). The members of the genus *Trichodorus*, most likely *T. primitivus*, are currently known to cause direct damage to roots and also transmit tobraviruses such as the *Tobacco rattle virus* present in potato fields in British Columbia (Kawchuk et al. 1997; Xu and Nie 2006). Other species listed in the Canadian National Collection of Insects, Arachnids and Nematodes are *P. nanus* and *P. pachydermus*.

1.6.4 Management

Historically, research attention has been focused on plant resistance to nepoviruses rather than the nematode vectors. Grape cultivars and rootstocks have been evaluated for resistance to the *Tomato ringspot virus* (Allen et al. 1982b) and several rootstocks have been found to be resistant to the virus.

Fumigation of soil is recommended when replanting fruit trees in Canada, primarily for management of *P. penetrans* and other components of replant disease complexes. Fumigation is also recommended when *Xiphinema* populations exceed 100/kg soil and/or when nepoviruses were present in the old planting (OMFRA 2017; BCFGA 2017).

1.7 Conclusion and Future Perspectives

Canadian agriculture will undergo numerous changes in the coming decades. The development of sustainable and resilient production systems continues to be a major goal and whole-system approaches to food, feed, and other fiber production that balance environmental impacts, social equity and economic viability are being promoted across the country. Climate change will create some opportunities for Canadian agriculture to grow and diversify, and the adoption of more sustainable practices such as minimum tillage, winter cover cropping and organic production will also grow. However, climate change and corresponding changes in the extent and intensity of cropping systems will also present numerous new challenges, particularly with respect to pests and diseases.

This review has revealed several emerging PPN issues in Canada that will be grafted to these elaborate agricultural challenges. The continual expansion of soybean cyst nematode to Manitoba and Quebec and Maritimes poses a very serious threat to soybean production in Canada. Recent reporting of the golden nematode in Quebec highlights how the potato industry needs to prevent potato cyst nematodes from establishing in other important potato-growing regions of Canada. Improved understanding of the importance of *P. neglectus* in potato, canola, wheat and pulse crops in the Canadian Prairies is required. Similarly, the role of cereal cyst nematodes on wheat in the Canadian Prairies is unexplored. *Ditylenchus* spp. have emerged in recent years as significant concerns in Canada as *D. destructor* has been reported but contained near Ottawa, *D. dipsaci* infestation of garlic farms has spread from Ontario to farms in Manitoba and Quebec, and *D. dipsaci* infestation of garlic has become more prevalent in British Columbia.

Rising temperatures and increasing commercial trade could also bring surprises. Species such as *Pratylenchus alleni* are being discovered, and long-established species could become more problematic. For example, Tenuta (2014) estimated that the within-season potential for population buildup of *P. penetrans* will increase with climate change. Exotic species of significance such as *M. incognita* could become established as average soil temperatures rise, and the impact of climate change on established but unproblematic species is yet to be determined. Indeed, the expected mean annual temperature increases of 2 °C by 2050 and 4–5 °C by 2100 if greenhouse gas emissions are not controlled (Price et al. 2013) could have a major impact on all nematode species in the cool climate of most agricultural areas in Canada (Fig. 1.1).

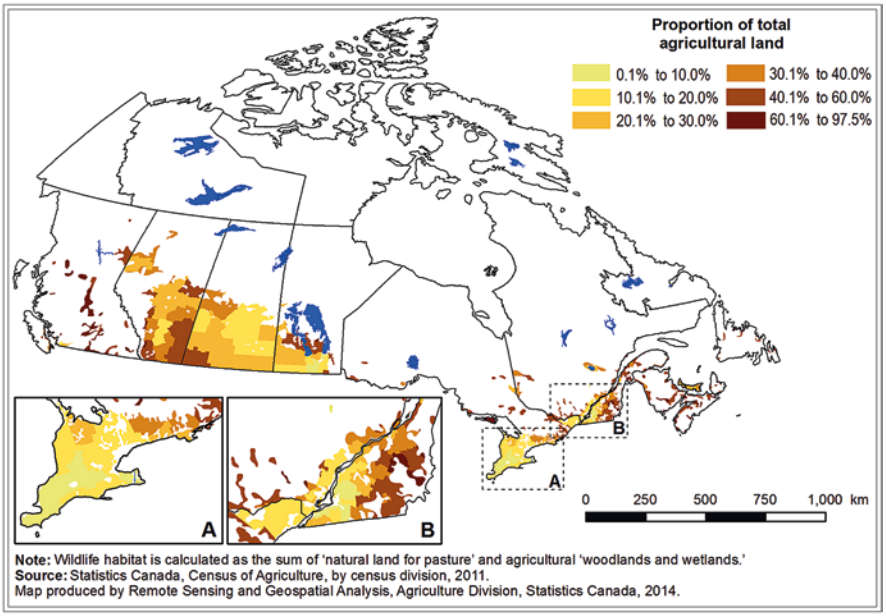

Fig. 1.1 Distribution of agricultural land across Canada (2011)

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Chapter 2
Plant Parasitic Nematodes and Management Strategies of Major Crops in Mexico

Ignacio Cid del Prado-Vera, Francisco Franco-Navarro, and Damaris Godinez-Vidal

2.1 Introduction

Plant parasitic nematodes are recognized as one of the most important limiting factors in crop production worldwide and Mexico is not an exception. Economic losses caused by nematodes are influenced by growing system type (multicropping, mono-cropping, crop rotation in open-field and greenhouse conditions, among others), species involved and their population densities. In Mexico, damages and losses are caused mainly by lesion nematodes (*Pratylenchus* spp. and *Radopholus similis*), the stem and bulb nematode (*Ditylenchus dipsaci*), root knot nematodes (*Meloidogyne* spp.), false root knot nematode (*Nacobbus aberrans*), cyst nematodes (*Globodera* spp. and *Punctodera chalcoensis*), the citrus nematode (*Tylenchulus semipenetrans*), virus transmitting nematodes (*Xiphinema* spp.), foliar nematode species (*Aphelenchoides* spp.) and red ring nematode (*Bursaphelenchus cocophilus*). Some of these nematodes have been observed in commercial plantations, crop fields and greenhouses where mono-cropping is more common and crop rotation is not practiced.

The lack of trained nematologists in Mexico has often meant a lack of awareness of the importance of plant parasitic nematodes in both tropical and temperate environments. This in turn, has led to the uninhibited movement of plant parasitic species into new non-infested areas. Good examples are the dissemination of *Globodera*

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rostochiensis, *Meloidogyne* spp., *Nacobbus aberrans*, *Ditylenchus dipsaci*, *Pratylenchus* spp., *Radopholus similis* and *Bursaphelenchus cocophilus*. The spread of economically important plant parasitic nematodes in major crops such as citrus, tomato, chili, potato, cucumber, bean, corn, banana, guava, coconut, garlic, onion and others has occurred in the past and continues today in Mexico. The detection and accurate identification of species already known, and the description of new species, are highly relevant for knowledge of nematode distribution in the country. Distribution maps of important species of nematodes are needed to either make decisions on the inclusion of new species to a quarantine species list, or simply to monitor relevant species on the most important crops.

In this chapter, we have summarized information on the most important plant parasitic nematodes affecting major crops in small and large fields found in different regions of the country. Moreover, some main aspects of distribution, damages, hosts and control measures of these parasitic nematodes are briefly discussed.

2.2 Overview of Agriculture in Mexico

Mexico is a country with a high diversity of soil types, climates and ecosystems throughout its territory. This ecological diversity allows for numerous options for agricultural production and makes Mexico a country where there are suitable conditions to grow a wide variety of high quality plants. In Mexico, characteristic crops of temperate and semi-temperate zones as well as crops typical of tropical areas can be found. Therefore, agricultural products for domestic consumption and export are available throughout the year.

Despite the fact that many crops are produced in the country, that there are those that, because of their level of production and monetary value, are considered the most agriculturally important crops in the nation. Table 2.1 lists the main economically important agricultural crops grown in Mexico, according to official reports.

Grain cultivation is the most important component of agriculture in Mexico and accounts for almost 50% of agricultural production. In general, the main crops of the country are corn, sugar cane, avocado, sorghum, wheat, tomato, chili, potato, lemon, strawberry, berries, mango and other tropical fruits, beans, alfalfa, cucumber, broccoli, coffee, among many others. The most important crops for domestic consumption are wheat, beans, corn and sorghum. On the other hand, the most important export crops are sugar cane, coffee, fruits such as avocado, strawberry and mango, and vegetables (mainly tomato, chili, cucumber, broccoli), which are exported to the United States. Regarding crops grown for animal feed, the most important are alfalfa, sorghum and corn. Most of these crops are not alien to damages caused by plant pathogens including plant parasitic nematodes, so this group of organisms is extremely important in the production of crops in Mexico.

Table 2.1 Area, yield and value of production of economically important agricultural crops grown in Mexico

Crop	Area (1000 ha)	Yield (1000 ton)	Value (US$1 mill)
Corn	7794	75,000	4114
Avocado	204	1880	1622
Sugar cane	823	7220	1485
Pastures	1435	28,181	1200
Sorghum	1532	4629	1142
Chili	172	2922	1029
Tomato	49	2769	857
Alfalfa	388	4805	800
Berries	4	73.5	742
Wheat	729	3842	686
Potato	65	1718	650
Strawberry	10	398	456
Lemon	180	2439	373
Broccoli	32	499	333
Cucumber	17	614	222
Mango	197	1911	214
Onion	52	1494	203

Source: SAGARPA and SIAP (2017)

2.3 Presence and Distribution of Plant Parasitic Nematodes in Major Crops

The first record of plant parasitic nematodes in Mexico was made by Gándara (1906) who reported a root knot nematode *Meloidogyne* sp. (known as *Heterodera marioni*) in coffee plantations. In 1920, a root knot nematode was also reported by Gandara in citrus. In 1951, staff reserachers of the recently founded Dirección General de Defensa Agrícola made the first report of the causal agent of the red ring of coconut. It was complemented by the findings of Alcocer (1955), who formally reported the disease in the Gulf of Mexico and attributed it to *Bursaphelenchus cocophilus* (= *Rhadinaphelenchus cocophilus*). By 1953, customs inspectors of the United States Department of Agriculture detected cysts of *Globodera rostochiensis* in soil samples taken from a truck transporting Mexican products to USA (Brodie 1998). Despite the report of this important nematode, the knowledge of other species was scarce, and in 1963, Alcocer and Gotwald published the first list of plant parasitic nematodes in Mexico. The list highlighted the report of *Heterodera schachtii* infecting sugar beet, a crop whose seed came from Europe. A couple of years later, *Tylenchulus semipenetrans* was first reported in citrus roots from Oxqutzcab, Yucatán state.

In the following years, many confirmed detections and new descriptions of plant parasitic nematodes were made such as the presence of *G. rostochiensis* in localities from Guanajuato and Nuevo León (Camacho 1977; Rodríguez 1973; Quiñonez 1979), or *Punctodera chalcoensis* (identified as *Heterodera punctata*) from the corn production region of Huamantla, Tlaxcala state (Stone et al. 1976). After that, the most extensive and complete compilation of different genera and species of nematodes of low and high importance present in Mexico, was made by Montes-Belmont in 1979 and 1988 and the last version in 2000. In Table 2.2 are listed the plant parasitic nematodes that have been found in the major crops cultivated across the country for over 100 years. Figure 2.1 shows the distribution of the main species of plant parasitic nematodes in Mexico.

Since those first reports of plant parasitic nematodes up to very recent years, nematode identifications have been based on their morphological and morphometric characteristics. The application of molecular techniques in the identification of nematodes started only in the past few years; as in the case of *Belonolaimus maluceroi*, found in a tropical forest at La Mancha, Veracruz State, Mexico (Cid del Prado and Subbotin 2012) or *Cactodera torreyanae*, a new species of cyst nematode parasitizing romerito plants (*Suaeda torreyana*) in Mexico State, Mexico (Cid del Prado and Subbotin 2013). Jaramillo-Pineda et al. (2015) identified one population of *Meloidogyne* from infested tomatoes as *M. incognita* using sequences of ITS (internal transcribed spacer) regions of rDNA. The identity of *M. enterolobii* parasitizing watermelon in Veracruz State (Ramirez-Suárez et al. 2014) and chili pepper in Sinaloa state, Mexico (Villar-Luna et al. 2016) was confirmed by DNA sequencing of the IGS2 rDNA fragments and PCR with specific SCAR primers. Also, a population of *Meloidogyne* infecting tomato plants in Sinaloa was identified as *M. enterolobii* using PCR with primers Me-F and Me-R specifically amplifying the region rDNA-IGS2 for this species (Martínez-Gallardo et al. 2015). Identification of the nematode *Orrina phyllobia* parasitizing *Solanum elaeagnifolium* was confirmed by sequencing of amplification products obtained with two molecular markers ITS1-5.8S-ITS2 and the D2-D3 expansion segments of 28S rRNA gene (Medina-Gómez et al. 2016).

2.4 Main Plant Parasitic Nematodes in Mexico: Impact and Control

2.4.1 Root Knot Nematodes, Meloidogyne *spp.*

At the beginning of the previous century, Gandara (1906) reported the first plant parasitic nematode in Mexico namely, a *Meloidogyne* sp. in coffee plantations and, some years later, in citrus (Gandara 1920). Since then, there have been many reports of *Meloidogyne* species attacking different crops in open areas and greenhouse environments in almost all states (Fig. 2.1). *Meloidogyne* spp. have been found in

Table 2.2 Some plant parasitic nematodes reported to be associated with major agricultural crops in Mexico

Nematode	State	Crop	Reference
Aorolaimus mexicaniensis	Mexico State	Corn	Cid del Prado (1994)
Aphelenchoides fragariae	Michoacán, Guanajuato	Strawberry	García (1967), Szczygiel and Cid del Prado (1981), Sandoval (1984), and Montes-Belmont (1988)
A. ritzemabosi	Michoacán, Guanajuato	Strawberry	Szczygiel and Cid del Prado (1981), Sandoval (1984), Montes-Belmont (1988), and Cid del Prado and Sosa-Moss (1978a)
Cactodera galinsogae	Hidalgo	Barley	Tovar-Soto et al. (2003)
C. rosae	Hidalgo	Barley	Cid del Prado and Miranda (2008)
Ditylenchus dipsaci	Guanajuato, Puebla, Aguascalientes, Veracruz	Onion, garlic	SENASICA (2013b)
Helicotylechus digonicus	Mexico State	Corn	Hernández (1965) and Becerra (1978)
H. dihystera	Veracruz	Banana	Montes-Belmont (1988)
H. erythrinae	Mexico State	Corn	Hernández (1965) and Becerra (1978)
H. multicinctus	Veracruz	Banana	Lara-Posadas et al. (2016)
Hoplolaimus galeatus	Mexico State	Corn	Hernández (1965) and Becerra (1978)
H. igualaensis	Guerrero	Okra	Cid del Prado (1994)
H. maggentii	Chiapas	Plantain	Cid del Prado (1994)
Globodera rostochiensis	Nuevo León, Coahuila, Tlaxcala, Veracruz, Puebla, Hidalgo, Mexico State, Guanajuato, Mexico City	Potato	Brodie (1998), Montes-Belmont (1988), and SENASICA (2013a)
Meloidogyne sp.	Veracruz	Pineapple	Domínguez (2001) and Rebolledo et al. (2002a, b)
	Michoacán	Guava	Franco-Navarro et al. (2000)
	Tabasco	Pineapple	Montes-Belmont (1988)
	Veracruz	Citrus	Gándara (1920)
	Durango	Apple	Cepeda et al. (1987)
	Chihuahua	Cotton	Del Valle (1948)

(continued)

Table 2.2 (continued)

Nematode	State	Crop	Reference
M. arenaria	Sonora	Peach	Jiménez and Martínez (1989)
	Aguascalientes, Zacatecas	Guava	Cid del Prado et al. (2001)
	Morelos	Papaya	Cid del Prado et al. (2001)
	Oaxaca	Pineapple, watermelon	Cid del Prado et al. (2001)
	Puebla	Carrot	Medina-Canales (2009)
	Tlaxcala	Potato	Tovar (1994) and Cid del Prado et al. (2001)
	Morelos	Tomato	Guzmán-Plazola et al. (2006)
	Durango	Tomato	Cid del Prado et al. (2001)
	Sonora	Grapevine	Cid del Prado et al. (2001)
	Tabasco	Banana	Cid del Prado et al. (2001)
	Veracruz	Banana	Lara-Posadas et al. (2016)
M. chitwoodi	Puebla	Potato	Tovar (1994)
	Puebla	Carrot	Medina-Canales (2009)
M. enterolobii	Sinaloa	Tomato	Ramirez-Suárez et al. (2014)
	Veracruz	Watermelon	Ramirez-Suárez et al. (2014)
M. hapla	Tlaxcala	Potato	Tovar (1994)
	Puebla	Carrot	Montes-Belmont (1988) and Medina-Canales (2009)
	Michoacán, Guanajuato	Strawberry	García (1967) and Montes-Belmont (1988)
	Mexico State	Chrysanthemum	Cid del Prado et al. (2001)

M. incognita	Guanajuato	Strawberry	Cid del Prado et al. (2001)
	Aguascalientes, San Luis Potosí	Chili, onion, garlic, Zucchini	Velásquez-Valle (2001)
	Sinaloa, Oaxaca	Chili	Cid del Prado et al. (2001)
	Veracruz	Pineapple	Cid del Prado et al. (2001)
	Morelos	Cucumber	Cid del Prado et al. (2001)
	Mexico State	Corn	Hernández (1965) and Becerra (1978)
	Puebla, Michoacán, Nuevo León, Baja California, Mexico State, Guanajuato	Potato	Tovar (1994)
	Tlaxcala	Potato	Tovar (1994) and Cid del Prado et al. (2001)
	Morelos	Bean	Cid del Prado et al. (2001)
	Zacatecas	Bean	Velásquez-Valle (2001)
	Sinaloa, Hidalgo, Michoacán, Oaxaca, Puebla	Tomato	Cid del Prado et al. (2001)
	Morelos	Tomato	Guzmán-Plazola et al. (2006)
	San Luis Potosí	Tomato	Martínez-Gallardo et al. (2015)
	Hidalgo	Guava	Borys and Alcalde (1992)
	Zacatecas, Aguascalientes	Guava	Avelar (1997) and Cid del Prado et al. (2001)
	Michoacán, Morelos	Papaya	Cid del Prado et al. (2001)
	Colima, San Luis Potosí	Papaya	Martínez-Gallardo et al. (2014)
	Baja California, Coahuila, Aguascalientes	Vine	Martínez (1980), Montes-Belmont (1988), and Ramirez (1989a, b, 1991)
	Veracruz, Chiapas	Coffee	Gándara (1906), Neri (1981), Hernández et al. (1991), Téliz et al. (1991), Cid del Prado et al. (2001), and García (1997)
	Tabasco, Morelos, Michoacán	Banana	Montes-Belmont (1988)
	Veracruz	Banana	Lara-Posadas et al. (2016)
	Chiapas	Banana	Adriano-Anaya et al. (2008)

(continued)

Table 2.2 (continued)

Nematode	State	Crop	Reference
M. javanica	Oaxaca	Tomato	Cid del Prado et al. (2001)
	Morelos	Tomato	Guzmán-Plazola et al. (2006)
	Aguascalientes, Zacatecas	Guava	Cid del Prado et al. (2001)
	Guanajuato	Strawberry	Cid del Prado et al. (2001)
	Sonora	Grapevine	Cid del Prado et al. (2001)
M. paranaensis	Veracruz	Coffee, banana	López-Lima et al. (2015)
Nacobbus aberrans	Oaxaca, Hidalgo, Morelos, Puebla, San Luis Potosí, Guanajuato, Tlaxcala, Coahuila, Mexico State, Michoacán	Tomato	Montes-Belmont (1986), Cid del Prado and García (1991), Cid del Prado et al. (2001), and Cabrera-Hidalgo et al. (2014)
	Mexico State, Puebla	Chili	Brunner (1967) and Cid del Prado and García (1991)
	Michoacán	Cucumber, zuchini	Cabrera-Hidalgo et al. (2014)
	Zacatecas	Bean	Cid del Prado and García (1991) and Velásquez-Valle (2001)
	Puebla	Red beet	Tovar-Soto et al. (2012)
Paratylenchus nannus	Mexico State	Corn	Hernández (1965) and Becerra (1978)
Pratylenchus spp.	Veracruz	Pineapple	Domínguez (2001) and Rebolledo et al. (2002a, b)
	Chiapas	Coffee	Montes-Belmont (1988)
	Durango	Apple	Cepeda et al. (1987)
P. coffeae	Veracruz	Coffee	Neri (1981) and Téliz et al. 1991
P. brachyurus	Coahuila	Apple	Cepeda and Hernández (1991)
	Veracruz	Banana	Montes-Belmont (1988)
	Michoacán, Guanajuato	Strawberry	García (1967) and Montes-Belmont (1988)
P. hexincisus	Mexico State	Corn	Hernández (1965) and Becerra (1978)
P. neglectus	Michoacán, Guanajuato	Strawberry	García (1967) and Montes-Belmont (1988)
P. penetrans	Mexico State	Corn	Hernández (1965) and Becerra (1978)
	Coahuila	Grapevine	Villalobos (1980)

P. pratensis	Mexico State	Corn	Hernández (1965), Becerra (1978), and Revelo (1991)
	Michoacán, Guanajuato	Strawberry	García (1967) and Montes-Belmont (1988)
	Veracruz	Banana	Montes-Belmont (1988)
P. thornei	Mexico State	Corn	Hernández (1965) and Becerra (1978)
	Guanajuato, Sonora	Wheat	Robles-Hernández and Pérez-Moreno (2011), Van Gundy et al. (1974), and Nicol and Ortiz-Monasterio 2004
P. vulnus	Coahuila	Grapevine	Villalobos (1980)
Punctodera chalcoensis	Mexico State, Puebla, Tlaxcala, Veracruz, Michoacán, Jalisco	Corn	Stone et al. (1976), Hernández (1965), Montes-Belmont (1988), Becerra (1978), Santacruz and Pedroza (1983), Sosa-Moss (1987), and Mundo-Ocampo et al. (1987)
Radopholus similis	Chiapas, Tabasco, Veracruz	Banana	Marbán and Marroquín (1984), Montes-Belmont (1988), and Lara-Posadas et al. (2016)
Bursaphelenchus cocophilus	Campeche, Tabasco, Veracruz, Colima, Guerrero, Sinaloa, Michoacán, Yucatán	Coconut	Alcocer (1955), Santos et al. (1997), and Montes-Belmont (1988)
Rotylenchulus sp.	Colima	Papaya	Martínez-Gallardo et al. (2014)
Scutellonema brachyurus	Veracruz	Banana	Montes-Belmont (1988)
Tylenchorhynchus acti	Mexico State	Corn	Hernández (1965) and Becerra (1978)
T. brevicaudatus	Mexico State	Corn	Hernández (1965) and Becerra (1978)
T. capitatus	Mexico State	Corn	Hernández (1965) and Becerra (1978)
T. cylindricus	Mexico State	Corn	Hernández (1965) and Becerra (1978)
T. mexicanus	Mexico State	Corn	Knobloch and Laughlin (1973)
Tylenchulus semipenetrans	Yucatán, Nuevo León, Baja California, Sonora, Veracruz, Colima, Jalisco, Tamaulipas, San Luis Potosí, Tabasco, Campeche, Morelos	Citrus	Sau (1970), González (1970), Rodríguez (1980), and Montes-Belmont (1988)
Xiphinema americanum	Sonora, Durango, Baja California, Aguascalientes, Coahuila	Grapevine	Ramírez and Jiménez (1987), Martínez (1980), Guevara and Mundo (1991), Villalobos (1980), Ramírez (1989a, b), and Cepeda et al. (1992)
X. index	Coahuila	Grapevine	Téliz and Goheen (1968)

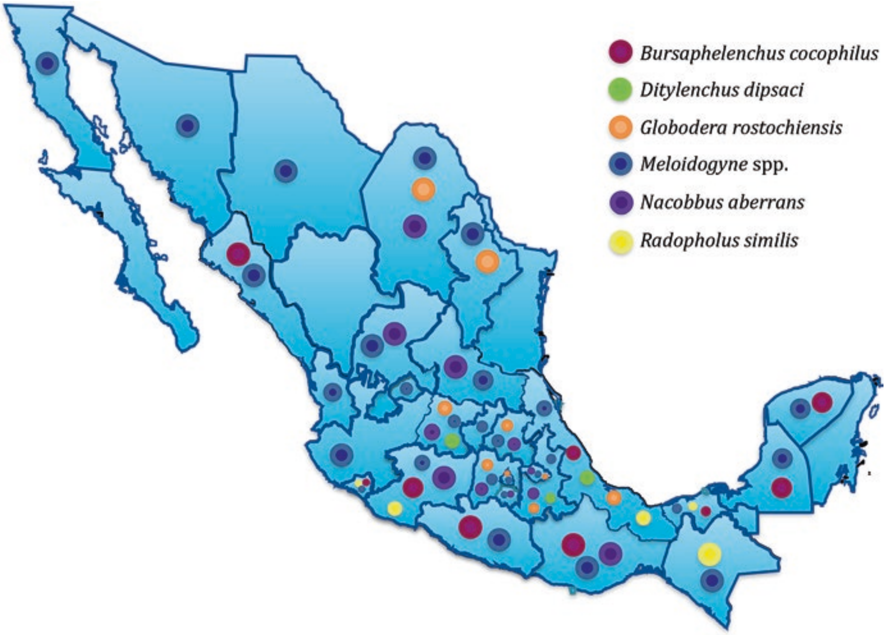

Fig. 2.1 Distribution of the main plant parasitic nematode species of in Mexico

temperate, semi-temperate and tropical areas causing damages and losses to a variety of crops such as grains, vegetables, fruits, ornamental, and even forest plants (Table 2.2). Species of this genus are highly pathogenic and induce hypertrophy and hyperplasia of roots cells resulting in the production of typical galls (Fig. 2.2a–g). They not only cause direct damage to plants and reduce their yields, but also predispose them to infection by other pathogens such as bacteria and fungi. The most common and/or important species that have been reported for Mexico are *M. incognita*, *M. arenaria*, *M. javanica*, *M. hapla*, *M. chitwoodi*, *M. enterolobii* and *M. paranaensis*. The last two species were most recently reported from Veracruz, Mexico, infecting watermelon cv. Sunsugar (Ramirez-Suárez et al. 2014) and coffee plants respectively (López-Lima et al. 2015). Both species have also been detected in tomato (Guzmán-Plazola et al. 2006; Martínez-Gallardo et al. 2015; Ramirez-Suárez et al. 2014), potato (Tovar 1994), pineapple (Domínguez 2001; Rebolledo et al. 2002a, b), grapevine (Ramírez 1989a, b; Ramírez et al. 1991), guava (Borys and Alcalde 1992; Avelar 1997; Franco-Navarro 2000), banana (Adriano-Anaya et al. 2008; Lara-Posadas et al. 2016), coffee plants (García 1997; Neri 1981; Téliz et al. 1991) and others (Table 2.2).

One of the most extensive samplings for determining the geographical distribution of *Meloidogyne* spp. in Mexico was conducted by Cid del Prado et al. (2001). They sampled different crops such as basic grains, vegetables, fruit trees and ornamentals from 47 localities in 18 states. A total of 56 populations of root knot nematode species were obtained of which 61% belonged to *M. incognita*, 21% to *M.*

Fig. 2.2 Symptoms caused by *Meloidogyne* spp. in roots of different crops. (**a**) Cork roots in coffee; (**b**) *Hibiscus* sp.; (**c**) Chili; (**d**) Pineapple; (**e**) Tomato under field conditions; (**f**) Tomato under greenhouse conditions; (**g**) Dissected root galls of tomato showing typical rounded females of *Meloidogyne* in high number

arenaria, 13% to *M. javanica* and 5% to *M. hapla*. From the total localities sampled, eight presented a mixture of species, three localities had *M. incognita, M. arenaria* and *M. javanica*, three had *M. incognita* and *M. arenaria*, one had *M. incognita*, *M. arenaria* and *M. hapla* and one locality had *M. incognita* and *M. javanica*. The races identified during the study were race 1 and 2 for *M. incognita* and race 2 for *M. arenaria* (Cid del Prado et al. 2001). Other important contributions to the geographical distribution of this genus was achieved in the state of Sinaloa by Carrillo Fasio et al. (2000); where tomato, chili pepper and egg plant are affected severely by different species of root knot nematode. They obtained 40 *Meloidogyne* populations from tomato, bell pepper, cucumber and eggplant in 24 localities sampled. The frequency of distribution of *M. incognita* was 83%, 13% for *M. arenaria* and 5% for *M. javanica*. A mixture of species was found in four sample sites: *M. incognita, M. arenaria,* and *M. javanica* were present in two, while in the other two, only *M. incognita* and *M. arenaria* were reported. There were no reports with yield losses and damages (Carrillo Fasio et al. 2000).

2.4.1.1 Management Strategies for Root Knot Nematodes

2.4.1.1.1 Chemical Control

Chemical control has usually been used against the root knot nematodes. Villalobos (1980) reported that applications of fenamifos and carbofuran granulated, reduced populations of root knot nematodes in grapevine and increased the yield of two grapevine varieties of interest. Santos et al. (1990) controlled *M. incognita* populations in a naturally infested potato field by combining mulch and nematicide (aldicarb), thus reducing the nematode population and increasing yield per hectare of the crop.

2.4.1.1.2 Host Resistance

Studies with a genetical focus have generated information on potato varieties with different resistance levels to *M. chitwoodi* race 1 (Tovar 1994) or coffee plants resistant to *M. incognita* race 2 (García 1997).

2.4.1.1.3 Biological Control

The fungus, *Purpureocillium lilacinus,* has been used to control populations of root knot nematodes in Mexico. One of the few studies has been made by Díaz (1986), who found that higher inoculum levels of the fungus resulted in a lower gall index induced by the nematodes. The fungus *Myrothecium verrucaria* has been used to control the root knot nematodes in guava; 16 applications were applied at 0.75 and 1.5 kg/ha, and after 30 months the population of *Meloidogyne incognita* was reduced significally at 1.5 kg/ha (Cepeda et al. 2004).

2.4.1.1.4 Amendments

The use of plants with antimicrobial properties have been studied by Castro et al. (1990), Gómez et al. (1992), Zavaleta-Mejía and Ochoa (1992), Zavaleta-Mejía et al. (1993), Zavaleta-Mejía and Gómez (1995). *Tagetes erecta* ("cempazúchil" o "flor de muerto") cultivated with chili pepper or tomato, or rotated and their residues incorporated into soil, can reduce significantly root galling induced by root knot nematodes. Aguirre et al. (1989) found that incorporation of cempazúchitl residues and application of aldicarb at a dose of 8 kg/ha can reduce the number of eggs masses and juveniles in a field naturally infested with *M. incognita*. Other plants such as *Crotalaria longirostrata* and *C. espectabilis,* reduce root galling and numbers of females of root knot nematodes when planted before, and in association with, tomato, and increase its effect when its foliage is incorporated into soil (Gutiérrez et al. 1990; Villar and Zavaleta-Mejía 1990). According to Torres-Barragán et al. (1995), when *Canavalia ensiformis* 1% or a mixture of *C. ensiformis* + *Stizolobium pruriens* 2% are incorporated in the soil, it is possible to reduce the gall index in plants infected with *M. incognita*. Likewise, with the incorporation of broccoli and cabbage, root galling in tomato caused by *M. incognita* can be reduced significantly (Zavaleta-Mejía et al. 1990). In greenhouse studies carried out by Zavaleta-Mejía and Rojas (1988), the incorporation of cabbage fragments in a proportion of 0.5–2.0% (w/v) reduced root galling by *M. incognita* on tomato, moreover, root rot caused by secondary invaders was greatly reduced. They also observed that as the amount of cabbage incorporated increased to a maximum of 2.0%, a consequential phytotoxic effect was manifested by necrosis at the apex of the folioles and reduction in plant growth.

In more recent years, the extracts from plants with antimicrobial properties has been used to evaluate their toxicity on the infective stages of some species of gall nematodes, for example, extracts of roots and leaves of *Calea urticifolia* reduced the number of galls of *M. incognita* on tomato cv Rio Grande grown in pots (Herrera-Parra et al. 2009). On the other hand, extracts derived from hickory *Carya illinoinensis*, were tested against the root knot nematode *M. incognita*. Of the extracts tested, those with higher nematicidal activity were FIM8 (aqueous husk) with 89.16%, FIM6 (etanolítico husk) with 69.22%, and FIM7 (aqueous shell) with 60.77% nematode reduction. All these extracts were at a concentration of 2% and nematodes were observed after 72 h of exposure to the extract (Garrido-Cruz et al. 2014).

The combination of soil solarization and chicken manure (10 ton/ha) 5 weeks before sowing, followed by the application of aldicarb to one side of the plants, and the incorporation of chicken manure between furrows at the time of sowing reduced root galling by *M. incognita* on bean var. Negro Puebla (Salgado 1989).

The Lower Basin of Papaloapan is the main region cultivated to pineapple in Mexico and comprises the south of Veracruz State and the north of Oaxaca State. This region is characterized by extremely acid soils with an average pH 4 and high nematode populations, both factors which reduce the yield of pineapple fruit (Domínguez 2001; Rebolledo et al. 2002a, b). The nematode management strategies usually followed by small and large pineapple producers in that region, include initial land preparation by gentle fallow using chisels instead of moldboard plows; this practice helps maintain the stability of soil aggregates and reduces nematode populations, since less soil remotion reduces washing exchangeable bases and makes the soil less acidic (Rebolledo et al. 2011). In addition to fallow, the fields are kept free of all weed vegetation over a period of 4–6 months before transplanting pineapple plants. These activities are done during the dry season when temperatures are high resulting in the death of soil-borne pathogens including nematodes, by starvation and desiccation (Rebolledo et al. 1998). Another practice that is used as part of the preparation of the field is the liming of soil, which can reduce nematode populations by up to 50% and increases the levels of calcium, magnesium as well as soil fertility (Rebolledo et al. 2002c). These activities are complemented by the preventive treatment of the land having sufficient and not excessive humidity, of granulated fenamiphos or etoprophos at doses of 50–100 kg/ha, or liquid etoprophos at doses of 8 l/ha in total spray, with the help of a high-volume sprinkler. During the production cycle, additionally etoprophos, oxamyl or fenamiphos are usually applied in doses of 5, 8 and 6 l/ha, respectively. Whatever the nematicide selected, it must be dissolved in water, applied at 50 mL of solution to the base of the plant and repeated according to the level of damage detected in previous samplings (Rebolledo et al. 1998; Domínguez 2001). The interval between applications including pre-planting, is usually 2–3 months, and is suspended 50–70 days before the floral induction treatment (Rebolledo et al. 2011).

2.4.1.1.5 Biofumigation of Soil

The incorporation of green manure as sorghum and crucifer residual plants in combination with the application of the fungus *Pochonia chlamydosporia*, has reduced populations of *Meloidogyne* in plastic greenhouses (Cid del Prado et al. 2010). In that case, biofumigation was carried out by preparing a mixture composed of 80 ton/ha of sorghum (*Sorghum bicolor*) and 40 ton/ha chicken manure, which was incorporated into the soil at a depth of 30 cm, watered to field capacity, covered with a black plastic sheet, and left for 4 weeks. After the organic matter had decomposed, the plastic sheet was removed and the soil left to aerate and eliminate toxic compounds for 3 weeks (Cid del Prado et al. 2010). The combination of *P. chlamydosporia* at 5×10^8 chlamydospores/g colonised rice, mixed with chicken manure, vermicompost or ground lucerne (*Medicago sativa*) has been used to control *M. arenaria* in guava (Torres-López et al. 2013).

2.4.2 *False Root Knot Nematode,* Nacobbus aberrans

The false root knot nematode, *Nacobbus aberrans*, is a species that seriously affects several crops, mainly vegetables of the Solanaceae family in Mexico (Cid del Prado et al. 1995). This nematode represents a serious danger to their host crops due to its great aggressiveness. *Nacobbus aberrans* is able to compete and displace different species of *Meloidogyne* when they are mixed in the same production system (Cruz et al. 1987).

Since the detection and reporting of *N. aberrans* in Mexico by Bruner in 1967, this nematode has been recorded several times for parasitizing crops of economic importance in the country including tomato, chili pepper and beans (Cid del Prado and García 1991) (Table 2.2). The damages caused mainly in tomato, bean and chili pepper crops are significant because their production can be greatly reduced. To this nematode, which induces the disease known as "jicamilla" (Fig. 2.3e) is attributed the abandonment of the tomato crop in Hidalgo State; and the most important disease infestation in tomato and chili in the municipality of Tecamachalco, Puebla, with losses at the field level of 50–70% (Cid del Prado et al. 1997a). According to Cristóbal-Alejo et al. (2001), in this municipality *N. aberrans* usually is distributed in approximately 300 ha, causing losses in production close to 83%.

Given its wide host range and distribution, *N. aberrans* has been considered as one of the potentially more aggressive nematodes in crops such as tomato, beans and chili. In Mexico, this nematode has been reported in at least ten states including Oaxaca (Montes-Belmont 1986), Hidalgo, Puebla, Mexico, San Luis Potosí, Guanajuato, Morelos, Tlaxcala, Coahuila and Zacatecas (Cid del Prado and García 1991; Cid del Prado et al. 1995), Michoacan State (Cabrera-Hidalgo et al. 2014), Coahuila State (García-Camargo and Sandoval 1995) (Fig. 2.1). *Nacobbus aberrans* affects a significant number of crops, inducing the formation of root galls (Fig. 2.3e) very similar to those produced by species of *Meloidogyne*, moreover, plants infected by *N. aberrans* usually show 7–68% reduction of N, P, K, and Ca in roots and foliage. Levels of B, Cu, Fe, Mn and Zn are decreased in foliage by up to 60% (Franco-Navarro et al. 2002).

The host range of *N. aberrans* includes economically important plants such as tomato, chili pepper (jalapeño or poblano type criollo), potato, eggplant, bean, pea, cucumber, squash, tobacco, red beet, spinach, amaranth, and bean (Aparicio et al. 1989, Cid del Prado 1985, Cid del Prado and Manzanilla 1992; Cid del Prado et al. 1993, 1997b; Carrillo 1988; Cornejo-Quiroz 1977b; Cruz et al. 1987; Santacruz and Marbán 1983; Tovar-Soto et al. 2012). This nematode does not only attack cultivated plants, but also other plants such as *Chenopodium murale*, *Portulaca oleracea*, *Datura estramonium*, *Malva parviflora*, *Solanum nigrum*, *Cestrum roseum* and *Amaranthus hybridus* (Hidalgo State) (Cruz et al. 1987), *S. elaeagnifolium*, *M. parviflora*, *A. hybridus*, *Marrobium vulgare*, *Verbecina encelioides*, *C. album*, *Salsola iberica* and *Kochia scoparia* (Coahuila State) (García-Camargo and Sandoval 1995).

Fig. 2.3 Symptoms caused by different plant parasitic nematodes. (**a**) Garlic infected by *Ditylenchus dipsaci*; (**b**) Destructed pineapple roots by *Pratylenchus* sp.; (**c**) Cysts of *Punctodera chalcoensis* on maize roots; (**d**) Red ring of coconut caused by *Bursaphelenchus cocophilus*; (**e**) Root galls on tomato induced by *Nacobbus aberrans*; (**f**) Citrus tree declined by *T. semipenetrans*

2.4.2.1 Management Strategies for False Root Knot Nematode, *Nacobbus aberrans*

2.4.2.1.1 Cultural

One important recommendation for growers is to remove carefully the infected plants and remaining galls that are in the soil in order to reduce the initial inoculum and avoid early infestation of plants, and at the entrance of greenhouses apply lime to clean shoes so to minimize risk of entrance of the nematodes and clean cultivation tools with sodium hypochloride (NaOCl) solution (Cid del Prado pers. comm.). Cultural management strategies such as the use of clear and black plastic over soil, reduced significantly infections of *Nacobbus aberrans* and *Phytophthora capsici* on tomato (Yañez 1997).

2.4.2.1.2 Host Resistance

Studies using resistant tomato plants to control *N. aberrans* were not conclusive (Sosa-Moss and González 1973b; Sosa-Moss and Muñoz 1973). In some cases, on few resistant varieties small and scarce galls were developed (Brunner 1967). In other studies, like those conducted by Zamudio (1987), 3 of 60 tomato varieties tested were highly resistant to the false root knot nematode. On the other hand, Castillo (1988) found native varieties of *Capsicum baccatum* to be tolerant to *N. aberrans*, allowing nematode reproduction without affecting the development of the plants. Recently, Gómez-Rodríguez et al. (2017) evaluated the resistance of 15 pepper lines to different *Phytophthora capsici* isolates, *M. incognita* and *N. aberrans.* Twelve pepper lines were resistant to *M. incognita*, five to *N. aberrans* and three to all pathogens evaluated.

2.4.2.1.3 Chemical Control

Several nematicides, namely fenamiphos, aldicarb and carbofuran have been used successfully to reduce populations of the false root knot nematode and increase yields in chili pepper, spinach and other crops (Cornejo-Quiroz 1977a; Equihua 1977; Santacruz and Marbán 1983). Marbán and Zamudio (1982) found that aldicarb (at 7 and 15 kg/ha), fenamiphos (at 40 and 20 kg/ha) and carbofuran (at 40 and 20 kg/ha) controlled *N. aberrans* and increased tomato production from 52% to 79%. Aparicio et al. (1989) tested the effect of urea and ammonium sulfate on second stage infective juveniles of *N. aberrans* under laboratory conditions and found that a higher urea dose led to higher numbers of dead juveniles, particularly at a dose of 120 kg/ha.

2.4.2.1.4 Amendments

The use of plants with nematicidal or nemastatic properties has increased, due to the recent restrictions on use of nematicides. The effective way of use of such plants is its application together with addition of organic amendments to the soil, which can induce considerable reductions levels nematode populations. Montes-Belmont (1973) found that the incorporation of corn and barley straws to the soil avoided stunting, reduction in foliage weight and galling of tomato roots induced by *N. aberrans*. In treatments with the amendments of corn straw and high levels of nitrogen, the number of juveniles of *N. aberrans* was reduced, as well as when barley straw was incorporated to the soil but in combination with low levels of potassium.

It is possible to increase crop yield with the use of manure and cempasuchil (*Tagetes erecta*) and plastic covering (Yánez-Juárez et al. 2001). Cid del Prado et al. (1995), under field conditions, found that the numbers of females and eggs of *N. aberrans* per gram of roots were lower and crop yield were higher with combined treatments of cempazúchil, chicken manure and nematicide. Franco-Navarro et al. (2002) also reported that the incorporation of cabbage amendments significantly reduced root galling by *N. aberrans* on tomato plants and increased the content of N, P, K, Ca, and Mg.

2.4.2.1.5 Biocontrol: Fungal Antagonists

The nematophagous fungus *Pochonia chlamydosporia*, is a highly efficient facultative parasite with the ability to colonize the rhizosphere of several economically important crops and thereby, control cyst nematode (Kerry et al. 1984) and *Meloidogyne* spp. (Atkins et al. 2003a, b; de Leij et al. 1992; Kerry and Hidalgo-Diaz 2004). Favourable results have also been achieved against *N. aberrans* in Mexico (Flores-Camacho et al. 2007; Franco-Navarro et al. 2009, 2013; Pérez-Rodríguez et al. 2007, 2011) using this fungus.

Pérez-Rodríguez et al. (2007) evaluated five Mexican isolates of *Pochonia chlamydosporia,* previously obtained by Flores-Camacho (2003), for the control of *N. aberrans* in tomato *cv.* Rio Grande under greenhouse conditions. These authors found that plants inoculated with a specific isolate (labeled SC1) at a dose of 15×10^3 chlamydospores/g of soil had a higher biomass than the other treatments. Moreover, these plants had the lowest level of nematode populations and showed least damage to roots. In addition, the fungus could be isolated again from soil, roots and eggs masses of the false root knot nematode, thereby, providing evidence of the parasitism of *P. chlamydosporia* on the nematode.

2.4.2.1.6 Other Integrated Management Strategies

Few studies have been made from a more comprehensive perspective and with a sustainable management approach of the false root knot nematode. Yánez-Juárez et al. (2001) tested different strategies combined to manage simultaneously *N. aberrans*, *Phytophthora capsici* and viruses in chili pepper under a field condition. Those treatments combining soil solarization with polyethylene (black or clear) and chicken manure incorporation in soil significantly reduced the nematode and fungus populations.

Cristóbal-Alejo et al. (2006) integrated several strategies for the management of the false root knot nematode in tomato. When plants were fertilized with an optimum dose of etoprofos and chicken manure, higher plant biomass was achieved and yield was increased by 20% when compared to the common commercial practices (use of fumigants and nematicides).

In an experiment under field conditions, the combination of vermicompost (15 ton/ha), cabbage residues (11.3-ton/ha) and the nematophagous fungus (15×10^3 chlamydospores/g of soil), *Pochonia chlamydosporia var. chlamydosporia*, reduced populations of *Nacobbus aberrans* and root galling and increased fruit yield of chili pepper (Pérez-Rodríguez et al. 2011).

2.4.3 Cyst Nematodes

2.4.3.1 Potato Cyst Nematode, *Globodera rostochiensis*

The first record of the golden cyst nematode, *Globodera rostochiensis* in Mexico was in 1953 from soil samples collected from potato in León, Guanajuato (Brodie 1998). Later samplings in several areas of potato production showed that the golden nematode was present in 46 localities within 9 states of the country (Table 2.2; Fig. 2.1), and Puebla, Tlaxcala and Mexico States had highest numbers of localities infested with this nematode. In a survey across nine potato-growing areas in Saltillo, Coahuila by Rueda-Puente et al. (2006), *G. rostochiensis* was found in only one locality, San Juan Vaqueria, Coahuila State at a density of 2–21 cysts per kg soil.

There are several reports of *Globodera* species detected in Mexico, mainly, *G. rostochiensis* and *G. tabacum virginiae*, although Sosa-Moss (1985) reported the presence of *G. tabacum tabacum* and *G. tabacum solanacearum*. According to Baldwin and Mundo-Ocampo (1991), some Mexican populations of *Globodera* obtained from weeds, but not infecting potato, are morphologically similar or almost identical to *Globodera pallida*, however, they belong to other species. Most reports of *Globodera* species are from the states of Michoacan, Tlaxcala and Mexico State, and include, *G. rostochiensis* in potato (variety Alpha mainly) and tomato, and *G. tabacum virginiae* in tomato, tobacco, eggplant, chili, shell tomato and several solanaceous weeds such as *Solanum dulcamara*, *S. quitoense* and *S. rostratum*. To this list can be added a Mexican species, *G. bravoae*, associated with roots of a wild Solanaceae, *Jaltomata procumbens* described fromn a national park at southwest of Mexico City (Franco-Navarro et al. 2000) and *Globodera mexicana* associated with roots of a wild Solanaceae *Solanum rostratum* (Bufalo bur) from a Tecoac town, Huamantla Valley in the State of Tlaxcala (Campos Vela 1967).

Damages caused by the golden nematode are related to the level of soil infestation. Potato plants infected with the nematode are present in patches and sometimes can be confused with damages caused by excessive use of herbicides, phytotoxicity or lack of fertilization. Nematode-infected plants can show poor or retarded growth, especially under dry conditions, chlorotic leaves and small and inefficient root systems, wilting of plants, inability to absorb efficiently nutrients like N, P, K, Mg, and increase in total plant content Ca content (SENASICA 2013a). On the other hand, tubers are small and reduced in number, and yield can be decreased. Some studies in Mexico have shown that the high level of nematode infestations can reduce potato production by up to 70% (Santamaría and Teliz 1985), and that, under experimental conditions, a density of 1000 cysts per kg of soil can reduce yields by more than 50% (Rodríguez 1973). The golden nematode is considered a quarantine pest in Mexico and is present in certain production areas under official control by Mexican Official Norms (012, 025, 040 and 041), in order to avoid introduction and movement of seed potato, and to determine those areas free of the nematode and available for production and vegetative reproduction of potato.

2.4.3.1.1 Integrated Control Methods

In Zinacatepec, Mexico State, different control methods were applied: integrated control, (Bionema™, chemical fertilization) traditional control (application of nematicides and fungicides) and only fertilization. The numbers of cysts per 1 kg of soil in the end of the vegetation season were 5505 in the variant with fertilization; 3726 after application of integrated control and 4308 after using traditional method (Salgado 2004).

2.4.3.1.2 Chemical Control

The main approach to control the golden nematode in Mexico is applications of non-fumigant, granular nematicides such as oxamyl, carbofuran or phenamiphos. Camacho (1977) reported that the application of nematicides increases the weight of the tubers up to 49%, even when there is infestation of the nematode. Camacho (1980) found some potato varieties with different resistance level to *G. rostochiensis* associated with *Pseudomonas solanacearum* race 3. According to López-Lima et al. (2013) *G. rostochiensis* can be controlled by *Purpureocillium lilacinum* and rotation with leguminous crops like *Pisum sativum* and *Vicia faba,* which can lead to 90% reduction of the nematode population. Estañol-Botello et al. (2005) combined application of carbofuran with foliar and soil fertilization and achieved increased tuber yield between 4 and 5 ton per ha and reduction in the number of cysts in soil.

2.4.3.2 Carrot Cyst Nematode, *Heterodera carotae*

Heterodera carotae was found in carrot fields (carrot cv. Mexicana) in the Tepeaca Valley, Puebla State, with wide distribution across 28 counties. Cristo, Acatzingo County was the locality where high number of cysts (1391 cysts per 200 cm^3 of soil) was found. Escobar-Avila et al. (2016) also studed the life cycle of the nematode under greenhouse conditions, which was completed in 73 days at 20–25 °C. Recently, the identity of this nematode was confirmed by molecular methods (Escobar-Avila et al. 2018).

2.4.3.3 Corn Cyst Nematode, *Punctodera chalcoensis*

The corn cyst nematode, *Punctodera chalcoensis* is the second most important cyst nematode after the golden nematode in Mexico (Sosa-Moss 1987). It has been suggested that *P. chalcoensis* was indigenous to Central Mexico and has co-evolved with corn (Stone et al. 1976). This nematode was originally identified as a *Heterodera punctata* Mexican race in a corn-producing area of Huamantla, Tlaxcala (Hernández 1965; Vásquez 1971, 1976; Sosa-Moss and Gonzalez 1973a), but later formally described as *P. chalcoensis* (Stone et al. 1976). This species is distributed in temperate corn-growing areas and causes significant damages in the Central Highlands of Mexico, mainly in the states of Puebla, Mexico State and Tlaxcala as well as in other states such as Veracruz, Michoacán and Jalisco, where corn (*Zea mays*) and the ancestral teocintle (*Zea mays* ssp. subsp. *mexicana*) have been grown (Becerra 1978; Mundo-Ocampo et al. 1987; Santacruz and Pedroza 1983; Sosa-Moss 1987; Montes-Belmont 1988) (Table 2.2; Fig. 2.3c).

Symptoms caused by *Punctodera chalcoensis* are similar to those caused by *Heterodera zeae*. Plants are stunted and yellowing, with reduction in stem width; leaves are chlorotic and exhibit pale color stripes. High population densities of the nematode can reduce the quality of the corn and the yield up to 90% (Vásquez 1976). According to Nicol et al. (2011), damages by *P. chalcoensis* can be severe and are dependent on cultivar susceptibility, density of the nematode population and adequate soil moisture levels in the last phase of the growing season. Although yield loss in field is expected to be high, experimental data are still lacking.

The control methods of this nematode basically include the rotation with oat crop and the use of criollo varieties (corn hybrids), most of them with tolerance to the nematode. Although use of nematicides is effective, it is not the best economical solution because of the relatively low value of the crop. According to Sosa-Moss and González (1973a) and Sosa-Moss (1987), early sowing dates and adequate fertilization can reduce damages caused by the nematode.

2.4.3.4 Cyst Nematodes of the Genus *Cactodera*

Cactodera cacti was the first species of this genus that was described from cacti plants in the Netherlands. This species has been also found in Milpa Alta, the southeast of Mexico City, a location, which is the main producing area of nopal (*Opuntia ficus-indica*), in Durango state, where it was associated with roots of sour tuna *Opuntia matudae* (xoconostle) and also in the state of Hidalgo (Baldwin and Mundo-Ocampo 1991), Mexico State and some rural localities surrounding Mexico City (Palomares-Pérez et al. 2015).

The genus *Cactodera* is considered to be endemic to Mexico and has a host range that includes plants from the families Cactaceae, Amaranthaceae, Poaceae and Chenopodiaceae. Several species were found in Mexico: *C. evansi* (Cid del Prado and Rowe 2000) in carnation (*Dianthus caryophyllus*) from Predio Las Parvas, Villa Guerrero, Mexico State, *C. galinsogae* (Tovar-Soto et al. 2003) in *Galinsoga parviflora* from La Raya, Singuilucan municipality, State of Hidalgo, *C. rosae* (Cid del Prado and Miranda 2008) in *Hordeum vulgare* from San Juan Ixtilmaco, Apan municipality, state of Hidalgo and *C. torreyanae* (Cid del Prado and Subbotin 2013) in the natural habitat of the host plant, *Suaeda torreyana*, in the experimental fields of Colegio de Posgraduados-Campus Montecillo, Mexico State (Table 2.2). *Cactodera* spp. does not cause significant economic crop loss in Mexico.

2.4.4 Root Lesion Nematodes, **Pratylenchus** *spp.*

Pratylenchus is the second most important group of plant parasitic nematodes after root knot nematodes and has a worldwide distribution. The genus contains numerous species, with most of its important species being highly pathogenic to a wide range of plant hosts. In Mexico, *Pratylenchus* is present in approximately 21 states in temperate and tropical zones. Their hosts are varied and species have been found associated with roots of many crops including grains such as corn, wheat, oat and sorghum; vegetables such as tomato, chili, potato, cucumber, zuchini or carrot; fruit such as peach, apple, banana, avocado, strawberry, pineapple, grapevine, mango, coffee, cocoa, coconut, citrus; forest tree species of the genus *Pinus* and *Juglans*, agave, sugar cane and ornamental such as rose, gardenia and gerbera (García 1967; Hernández 1965; Becerra 1978; Villalobos 1980; Neri 1981; Vazquez 1984; Cepeda et al. 1987; Montes-Belmont 1988; Cepeda and Hernández 1991; Domínguez 2001; Rebolledo et al. 2002a, b) (Table 2.2; Fig. 2.3b).

Pratylenchus thornei is the most well-known species in Mexico and has received most attention especially in the northwest region of the country (Van Gundy et al. 1974). This lesion nematode is a migratory polyphagous endoparasitic species that causes necrotic lesions on the root systems of host crops. It is reported to be a pathogen of wheat (*Triticum aestivum*) throughout the world and also in Mexico (Nicol and Ortiz-Monasterio 2004), causing stunted plants and reducing yield in susceptible wheat plants by much as 32%, under the natural environmental conditions in Sonora, Mexico (Van Gundy et al. 1974). The nematode is widely distributed throughout the wheat-growing region, and may be a problem during each crop-growing season.

With optimum irrigation the nematode does not affect wheat yield but, with limited irrigation where plants are under water-stress, yield loss of several resistant cultivars is comparable to that of intolerant and susceptible varieties (Warigal). Studies have demonstrated that there is a significant negative linear relationship between initial nematode density and grain yield under limited irrigation (Nicol and Ortiz-Monasterio 2004). Symptoms of wheat decline in Mexican soils usually appear within the first 20 days as patchy, usually yellowish areas. Seldom is an entire field uniformly affected. Foliar symptoms consist of stunting, chlorosis, occasional necrosis of leaf tips and flagging of young plants. Young plants may die and crop stand is reduced, but more often tillering is reduced and only one head is produced instead of two-to-four per plant. Head size is occasionally reduced. Nematode attack usually starts in the primary root, causing the plant to be stunted and vulnerable to attack by soil fungi (Van Gundy et al. 1974).

Pratylenchus thornei as well as other species of this genus usually are controlled by nematicides (oxamyl, carbofuran or fenamiphos), but this is not the best economical approach. On the other hand, since irrigated wheat in Mexico is a relatively low value crop, chemical soil fumigation as a commercial control procedure appeared to be neither practical nor economical. Efforts to control *P. thornei* using resistance cultivars have been made but without success. In fact, the International Wheat and Maize Improvement Center (CIMMYT) has bred wheat germplasm on infested sites for more than 50 years, but little is known about the resistance or tolerance of CIMMYT wheats to *P. thornei*. There is a strong need for sources of resistance to be identified and incorporated into the germplasm (Nicol and Ortiz-Monasterio 2004). A pest management approach using variety selection, nitrogen fertilizer, planting in cool soil (15 °C) and a crop rotation avoiding wheat after wheat is the most practical solution to the problems caused by this nematode on a commercial scale (Van Gundy et al. 1974).

2.4.5 Stem and Bulb Nematode, Ditylenchus dipsaci

The stem and bulb nematode, *Ditylenchus dipsaci* has become a serious problem in the cultivation of garlic (*Allium sativum*) in Mexico. The highest incidence of this nematode is reported in the main garlic and onion producing regions in the States of Guanajuato, Puebla, and Veracruz (SENASICA 2013b) (Fig. 2.1), with so-called garlic race present in Guanajuato state (Aguilera 1994). All garlic varieties cultivated in Mexico are susceptible to *D. dipsaci*.

In Mexico, stem and bulbs nematode affects crops belonging to the plant family Alliaceae (garlic and onion) (Table 2.2). The garlic yield losses due to this nematode can be between 30% and 100% (Zavala 1984). The nematode species is regulated for potato crop used for human consumption, as seed-tuber, microtuber and botanical seed and for other ornamental hosts used as propagative materials (tulip, hyacinth, iris, and others) (SENASICA 2013b).

Symptoms in field consist of a patchy distribution pattern where plants are yellow with poor growth. These patches can expand over time until they cover an entire field, and may be confused with damages caused by excessive use of herbicides, phytotoxicity, lack of fertilization, waterlogging, etc. (SENASICA 2013b). In garlic, *D. dipsaci* feeds on the parenchymatous tissue of stems and bulbs, injecting enzymes that dissolve the middle lamella resulting in size reduction, deformation or other damages to the bulbs (become soft, split or cloves become distorted) (Fig. 2.3a). Above ground, stems, petioles and leaves are deformed, distorted, and swollen (SENASICA 2013b). Under high levels of infestation, nematodes form and inhabit small and large cavities in leaf tissues, causing rickets with large losses of starches and other compounds. Consequently, garlic plants show size reduction, yellowing of the tissues starting at the base of the plant and detachment of both very small bulbs and the roots system (Cepeda 1995); sometimes plants do not emerge or die once they emerge. The increased presence of this nematode has become a serious problem in areas where garlic is grown mainly due to the use of infested seed (cloves/bulbs), and this, in turn, plays an important role in the spread of the nematode.

Main alternatives to control or manage the disease caused by this nematode consist of the use of certified seeds that are free of nematodes, and the applications of non-fumigant nematicides to the infested fields (Guerrero 2011).

2.4.6 *Burrowing Nematode,* Radopholus similis

The main species of the genus *Radopholus* reported in Mexico is *R. similis* infecting banana. This nematode causes the disease known as "black head" or "banana fall", since the destruction of the anchorage system of plants causes them to fall suddenly, just before harvest. *Radopholus similis* is one of the main pathogens of banana worldwide, causing large losses with population levels of only ten individuals per g of soil in poorly fertile soils. This nematode has been widely distributed in the States of Tabasco, Chiapas and Veracruz in association with *Musa* spp. (Adriano-Anaya et al. 2008; Lara-Posadas et al. 2016; Montes-Belmont 1988). According to Montes-Belmont (1988), this nematode was found in Michoacán (banana), Tabasco (cacao), Baja California Sur, Colima, Veracruz and San Luis Potosí (Table 2.2; Fig. 2.1).

Of the few studies reported on this nematode and its control, there is that of Marbán and Marroquín (1984) who obtained 36% increases in banana production in the States of Tabasco, and Chiapas respectively, by applying non-fumigant nematicides (carbofuran and fenamiphos). In fact, the widespread recommendation for the control of this nematode in already established plantations includes applications of granular or liquid nematicides every 4–5 months, in the patches where the disease is present. In areas of replanting the recommendations are: (1) rotating with non-host crops during 2–3 years or leaving the ground at rest for 10–12 months (avoiding growth of alternative host plants), (2) planting healthy materials (previously treated with hot water, produced in vitro, or without the infected parts), and (3) applying nematicides (2–3 g a. i. per plant) directly to the hole where the plants will be placed or mixed with the soil that will cover them.

2.4.7 *Citrus Nematode,* Tylenchulus semipenetrans

Tylenchulus semipenetrans was reported for the first time in Mexico in 1963, in samples of citrus roots from Oxqutzcab, Yucatán. By 1966, the citrus nematode was detected by the Plant Pathology Laboratory at Sonora University in samples collected from orchards off the coast of Hermosillo. Since that time, this nematode has been considered, as a potential pathogenic species in citrus (Sau 1970). González (1970) performed nematological surveys in lemon orchards and made morphological and morphometric descriptions of the populations of *T. semipenetrans*. This nematode, the causal agent of the "slow decline of citrus", has been observed in several citrus production areas of the Gulf of Mexico and has caused gradual reduction and losses in yield that lead to the abandonment of the orchards in some cases (Fig. 2.3f) (Montes-Belmont 1988; Rodríguez 1980).

In Mexico, citrus nematode has been reported in the states of Nuevo Leon, Colima, Yucatán, Tamaulipas, Baja California, Campeche, Jalisco, Morelos, San Luis Potosí, Sonora, Veracruz, Tabasco and Michoacán. Among its hosts are: *Citrus paradisi*, *C. sinensis*, *C. nobilis*, *C. grandis*, *C. limon* and *T. musicola*. (Table 2.2). In infested orchards, the common practice is the application of non-fumigant nematicides, which currently are oxamyl, carbofuran and fenamiphos.

2.4.8 Foliar Nematodes, **Aphelenchoides** *spp.*

The first report of *Aphelenchoides fragariae,* the causal agent of wrinkling leaves in strawberry plants, was made by García (1967) from Guanajuato and Michoacán. Later, Cid del Prado and Sosa-Moss (1978a, b) reported *A. ritzemabosi* on *Chrysanthemum máximum* from the locality of San José Villa Guerrero in Mexico State (Table 2.2). Nematode-infested *C. maximum* showed reddish-yellow lesions occurring on the lower leaves of young plants and, in older plants, these leaves showing marked chlorosis and more than 50% necrosis of the leaf surface. The foliage was usually scanty and flowers were few and deformed. Similar sympthoms were reproduced in clean plants 15–30 days after inoculation with *A. ritzemabosi*. The control treatment proposed for the nematode consisted of Parathion metilico at doses of 0.001% every 15 days (Cid del Prado and Sosa-Moss 1978a, b).

In 1981, during a survey of 21 fields in strawberry growing areas of Zamora, Michoacán and Irapuato, Guanajuato, Szczygiel and Cid del Prado (1981) found strawberry plants infested with *A. ritzemabosi* and *A. fragariae*. Symptoms included distortion, deformation and dwarfing of leaves, and angular blotches delimited by principal vein of stems and leaves. Later, another study was conducted on strawberry, both in Michoacán and Guanajuato States, to identify and estimate the population density of associated nematodes. For *Aphelenchoides* spp. the numbers were 20 and 30 nematodes per 200 g of soil, 10 and 15 nematodes per 5 g of roots, and 53 and 15 nematodes per 5 g of leaves in Irapuato and Zamora, respectively (Sandoval 1984).

2.4.9 *Red Ring Nematode,* Bursaphelenchus cocophilus

The "red ring of coconut" disease caused by *Bursaphelenchus cocophilus*, was first reported in Mexico by Alcocer (1955), but at that time was attributed to the species *Aphelenchus cocophilus.* The disease was present in both littorals of the country. In the Gulf of Mexico, Alcocer demonstrated the presence of the disease in Ciudad del Carmen (670 ha) and Palizado (225 ha), both in Campeche State. In Tabasco State, the disease was partially reported in 1953 covering about 137 ha, although according to Alcocer (1955) that distribution likely was not correct, since apparently, the disease has been spread at an alarming rate from this state. A high incidence of the disease was also reported in Veracruz State. On the Pacific coast, the highest incidence of the disease was in Colima, mainly in the municipalities of Tecomán (325 ha) and Manzanillo (150 ha). In Guerrero State, the reports of the disease corresponded to localities in the municipalities of Atoyac and Tecpan de Galeana covering an extension of approximately 200 ha (Santos 1993). The disease caused by the nematode is characterized by symptoms of yellowing, atrophied leaves and the fast death of infested palms. The major internal symptom of the infection is the typical red ring for which the disease has been named (Fig. 2.3d).

Bursaphelenchus cocophilus, whose vector is the curculionid weevil, *Rhynchonphorus palmarum*, causes important losses in coconut palm plantations, between 3.6% and 12.6% (Tabasco) or 10–45% (Guerrero), mainly in plantations of 3–10 years of age (Santos et al. 1996). Presently, this nematode has been reported in several states including Colima, Guerrero, Oaxaca, Tabasco, Veracruz, Campeche, Sinaloa, Michoacán and Yucatán (Landero-Torres et al. 2015a; Marbán 1973; Montes-Belmont 1988) (Fig. 2.1). The main host of *B. cocophilus* is *Cocos nucifera* (Table 2.2), although it can also parasitize and multiply in at least 15 other species of palms.

The best management of the disease is to control the vector using traps of 6–11 L placed at 1 trap per 5 ha, hung at 1.60 m from the soil and containing aggregation pheromone (500 μl of 2-methyl-5-(E) hepten-4-ol or rhinophorol), food attractant (1 kg mature banana, green coconut or fragments tissue of ornamental palm *Washingtonia robusta*), and 2 g methomyl (Santos et al. 1997; Segura-León and Cibrián-Tovar 1998; García-Ramírez et al. 1998; Pérez-Márquez et al. 1999; Camino et al. 2000; Osorio-Osorio et al. 2003; Landero-Torres et al. 2015b; Sumano-López et al. 2012). Experiments on the biological control of the vector using entomophatogenic fungi species, *Metarhizium* sp. and *Cordiceps bassiana* gave promising results (González et al. 1999).

2.4.10 *Dagger Nematodes,* Xiphinema *spp.*

According to de Bauer (1987), some species of *Xiphinema* have been found associated with corn, banana and alfalfa in several localities in Mexico. Jiménez (1986) reported the detection of *Grapevine fanleaf virus* (GFLV) in common weeds of infected vineyards in the region of Torreón, Coahuila. He found that weeds like *Brassica geniculata* and *Sonchus oleraceus* showed the highest levels of absorbance and therefore, had positive reaction to GFLV. In spite of the apparent presence of the virus, no any association with *Xiphinema* species were found.

De la Garza and Salinas (1986) sampled several localities of citrus trees in Tamaulipas State, and found specimens of the genus *Xiphinema* in two localities: one in Güemez Municipality and the other in Hidalgo Municipality. However, they did not identify these specimens. Ramírez (1989a) reported plant parasitic nematodes associated with grapevine in Hermosillo, Sonora and the Comarca Lagunera (Coahuila) and found high densities of *Xiphinema* populations, together with *Meloidogyne* in most of the vineyards. *Xiphinema index* had been reported from that region by Ramírez and Jiménez (1987), and by Téliz and Goheen (1968). Guevara and Mundo (1991) found species of *Xiphinema* in 87% of the vineyards within the Valley of Guadalupe, Baja California but *X. index* was not detected. Cepeda et al. (1992) conducted studies to determine nematode genera associated with grapevine varieties in the experimental field "El Bajío" in Buenavista, Municipality of Saltillo, Coahuila. One of the most frequent genera found was *Xiphinema* (between 82% and 94% of samples taken from approximately 35 varieties). These nematodes were identified to the species level. Other hosts of *Xiphinema* spp. reported in Mexico included *Pinus* sp., *Juglans regia*, *Casuarina* sp., *Acacia retinodes*, *Agave atrovirens*, *Annona* spp., *Carica papaya*, *Persea americana*, *Pyrus communis*, *Manguifera indica*, *Tamarindus indica*, *Musa* spp., *Malus* sp., *Prunus persicae*, *Citrus* sp. and *Theobroma cacao* (Montes-Belmont 1988). The genus *Xiphinema* has been reported in Mexico in almost all the states of the country, in association with the different hosts mentioned above (Table 2.2).

Because these nematodes are not considered to be a problem in the crop production regions in which they are found, producers do not pay attention to them. However, they usually continue to fumigate the soil or apply non-fumigant nematicides (oxamyl or carbofuran) to control nematodes.

2.5 Plant Parasitic Nematodes in Mexico: Reality and Perspectives

Agriculture in Mexico is abundant, diverse and extremely important for the country's trade market. There are certain crops whose production practices in some regions are still ancestral while other crops require modern technology. High levels of crop production make Mexico a leader in the export market. Crop production is not exempt from the damages and losses caused by several abiotic and biotic factors, which include plant parasitic nematodes.

There are several important and urgent tasks that would allow improvement of nematode management practices in Mexican agriculture. This includes, (i) conducting more nematological expeditions and national exploratory surveys to increase our knowledge of these organisms and their true impact in open field and protected agricultural environments (greenhouses), (ii) conduct studies to estimate the economic thresholds of various nematode species in different crops, (unfortunately, there are very few studies on this subject and the need for knowledge is paramount), (iii) develop more alternatives not only for the control of plant parasitic nematodes, but also for their management mainly through a sustainable approach (iv) incorporate and communicate actions taken by government agencies with those made by specialists in different centers of teaching and research in agricultural sciences, in order to promote and optimize work and research studies on plant parasitic nematodes.

Certainly, this is not a task for a few scientists alone, but also requires the coordination and participation of specialists, technicians, government officials, students and other stakeholders. Plant parasitic nematodes like other plant pathogens and pests do not know frontiers, types or models of agricultural production, and the damages and losses they cause affect small and large producers. Developing the best management practices are fundamental to coexist with them and maintain abundant and healthy agricultural production.

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Chapter 3
Plant Parasitic Nematodes of Montana and Wyoming

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3.1 Agricultural Crop Production in Montana and Wyoming

Montana is the second leading state in agricultural production in the United States accounting for 24.2 million hectares of agricultural land including farms and ranches (NASS 2016). Crops provide one third of the estimated agricultural income in Montana (MAS 2016). Wheat (*Triticum aestivum*) is the major field crop in Montana, followed by barley (*Hordeum vulgare*), dry edible pea (*Pisum sativum*), canola (*Brassica napus*), sugar beet (*Beta vulgaris*) and potato (*Solanum tuberosum*), and the total planted areas for these crops in 2016 were 2.11, 0.41, 0.25, 0.025, 0.018, 0.0046 million hectares, respectively. In recent years, due to a heightened attraction of Montana growers to pulse crops, the production area for pea (*P. sativum*), lentil (*Lens culinaris*) and chickpea (*Cicer arietinum*) combined have increased from 0.24 to 0.49 million hectares.

About 82% of the wheat acreage produced in Montana is non-irrigated, and each year over 1.62 million hectares of non-irrigated farmland are planted with spring and winter wheat varieties (MAS 2016). The leading wheat production areas are largely located in the northeastern portion of the state for spring wheat, and the northcentral portion for winter wheat. Even though majority of the wheat crop in the state is still grown following fallow, continuous cropping has become a common practice because of the emergence of no-till production systems (McVay et al. 2010).

Concerning Wyoming agricultural production, alfalfa (*Medicago sativa*) is the leading hay crop, followed by wheat (*T. aestivum*), corn (*Zea mays*) (for grain), sugar beet (*B. vulgaris*), dry edible bean (*Phaseolus vulgaris*) and oat (*Avena sativa*) and the total planted areas in 2016 were 202.4, 56.7, 28.0, 12.5, 13.4 and 8.9 thou-

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sand hectares, respectively (WAS 2016). Although, alfalfa production in the state varies over the years, on an average 70–80% alfalfa acreage is irrigated, while the remaining is non-irrigated. The leading alfalfa production areas are located in the northeastern, northwestern and southeastern regions, winter wheat in the southeastern region and sugarbeet mainly in the northwest and southeastern regions of the state.

3.2 Plant Parasitic Nematode Problems of the Economically Important Crops in Montana and Wyoming

A list of economically important plant-parasitic nematodes reported in Montana and Wyoming is provided in Table 3.1. Root lesion nematode *Pratylenchus neglectus*, sugar beet cyst nematode *Heterodera schachtii* and stem nematode *Ditylenchus dipsaci* are the plant parasitic nematode species that are currently inflicting significant economic damage to wheat, sugarbeet and alfalfa production respectively, in Montana and Wyoming combined. In addition, cereal cyst nematodes, have been recently reported in Montana (Smiley and Yan 2010; Dyer et al. 2015). According

Table 3.1 Occurrence reports of plant parasitic nematodes in Montana and Wyoming

Species	States	Damaging threshold	Crop	References
Pratylenchus neglectus	Montana	2500/kg dry soil	Wheat, barley	Johnson (2007) and May et al. (2016)
Heterodera schachtii	Montana, Wyoming	2.8 cyst/cm^3	Sugar beet	Gray (1995)
Ditylenchus dipsaci	Montana, Wyoming	-	Alfalfa	Gray et al. (1984, 1994)
Aphelenchoides ritzemabosi	Wyoming	-	Alfalfa, beans	Franc et al. (1993, 1996), Gray et al. (1994a, b) and Williams-Woodward and Gray (1999)
Heterodera avenae and *H. filipjevi*	Montana	5000 J^2/kg dry soil	Wheat	Smiley and Yan (2010) and Dyer et al. (2015)
Meloidogyne hapla and *M. chitwoodi*	Montana, Wyoming	-	Legumes	Gray et al. (1986), Griffin and Rumbaugh (1996) and Griffin and Jensen (1997)
Nacobbus aberrans	Montana, Wyoming	-	Sugar beet	Gray et al. (1997)
Tylenchorhynchus sp.	Montana	-	Wheat	Johnson (2007) and May et al. (2016)

to Hafez et al. (1992) and Smiley (2009a), cereal cyst nematodes are widespread problem on wheat production in the neighboring Pacific Northwestern states, including Washington, Oregon and Idaho.

Two species of root knot nematode including northern root knot *Meloidogyne hapla* from sainfoin (*Onobrychus viciifolia*) (Gray et al. 1986), Columbia root knot *M. chitwoodi* and *M. hapla* from legumes including alfalfa (Griffin et al. 1990, 1995; Griffin and Rumbaugh 1996; Griffin and Jensen 1997) and foliar nematode *Aphelenchoides ritzemabosi* from alfalfa (Gray et al. 1994a, b; Williams-Woodward and Gray 1999) and dry beans (*Phaseolus vulgaris*) (Franc et al. 1993, 1996) were reported from Wyoming. In Montana, stunt nematodes *Tylenchorhynchus* spp. (May et al. 2016) and seed gall nematode *Anguina agropyronifloris* (Norton 1965) were reported from wheat and western wheat grass (*Agropyron smithii*), respectively. False root knot nematode *Nacobbus aberrans*, was reported on sugarbeets from both Montana and Wyoming (Gray et al. 1997; Barry Jacobsen, Montana State University, pers. comm.). To the best of our knowledge, however, no wide spread occurrence and significant damage to the crops from these nematode species have been reported in either state.

The purpose of this chapter is to provide detailed information on the occurrence and management of major plant parasitic nematodes (root lesion, stem, foliar and sugarbeet cyst nematodes) that are reported to cause economic damages in Montana and Wyoming agricultural crop production systems. Although root knot and false root knot nematodes are not reported for causing significant losses to the crops cultivated in either state, they are considered as serious pests due to their potential for significant yield reductions when infections occur under field conditions. This chapter will therefore, present information on the occurrence of root knot and false root knot nematodes, and their management efforts pertaining to both states. In addition, the status of the emerging problem of cereal cyst nematode prevalence in Montana and its possibility for spreading further to the neighboring states (e.g. Wyoming) will be briefly discussed. The ecology and recommended management strategies for cereal cyst nematodes pertinent to the Pacific Northwestern states neighboring Montana and Wyoming are well discussed elsewhere in this book.

3.3 Root Lesion Nematodes, *Pratylenchus* spp.

Root lesion nematodes are migratory endoparasites capable of completing their life cycle within the host root system (Agrios 2005). Root lesion nematodes secrete cell wall degrading enzymes, through their stylet, which facilitates their entry and feeding inside the root system. At maturity, nematodes become reproductive and lay eggs inside root tissue, and may complete up to five generations within one growing season. After egg-hatch, young nematodes usually move back into the soil in search of new hosts. Since the nematodes are protected inside host roots, they normally do not rely on soil moisture for their survival (Duncan and Moens 2006; Moens and Perry 2009). Because of their ability to reproduce within roots, *Pratylenchus* spp.

are likely to thrive in semiarid wheat-growing regions (May et al. 2016). During dry field conditions and the unavailability of a host plant, these nematodes may enter a resting stage and later, revive under favorable conditions to continue their life cycle. In general, *Pratylenchus* spp. have a wide host range that includes legumes, oilseeds and other broad leaf and grass weed species (Vanstone and Russ 2001a, b). Therefore, *Pratylenchus* spp. have the potential to parasitize dryland rotation crops, including legumes and oilseeds in addition to cereals, in Montana and Wyoming.

Root lesion nematode infestations on wheat roots causes reduction in lateral root growth, and the formation of extensive dark, necrotic lesions, thereby, predisposing the root system to secondary fungal root pathogens such as *Fusarium oxysporum*, *Gaeumannomyces graminis* and *Rhizocotonia solani* (Taheri et al. 1994; Smiley 2009b; Smiley 2010). Aboveground symptoms usually include stunted plant growth, chlorosis and lower leaves premature death, which could be confused with lack of nutrients or soil moisture stress in the field. Cereal crops grown in root lesion nematode-infested fields, in conjunction with moisture stress conditions, may manifest even higher crop yield losses (Smiley et al. 2005a). In addition, reduction grains test weights (grain quality parameter) were also observed in an infested field (D. Wichman, Montana State University, pers. comm.).

Pratylenchus thornei and *P. neglectus* are the two major species that are reported to pose a serious threat to dry land cereal production worldwide (Smiley et al. 2004; Thompson et al. 2008; Vanstone et al. 2008; Smiley and Nicol 2009). *Pratylenchus thornei* is considered more destructive than *P. neglectus* and often causes higher wheat yield losses (Nicol and Ortiz-Monasterio 2004; Smiley et al. 2005a, b). In the Pacific Northwest United States, the threshold levels determined for *P. thornei* and *P. neglectus* populations in wheat crop are estimated to be 2000 and 2500 nematodes per kg^{-1} dry soil, respectively (Smiley et al. 2005b). Mixed populations of *P. thornei* and *P. neglectus* are common in cereal fields of the neighboring Pacific Northwest states (Smiley et al. 2004; Smiley 2015). This may present a management challenge for growers as resistance to root lesion nematodes in wheat is reported to be species specific (Farsi et al. 1995). *Pratylenchus neglectus* is the only species reported on the cereals within Montana (Johnson 2007; May et al. 2016) while there is no report of damaging population or crop losses caused by any of the root lesion nematode species from Wyoming. A population level of 2000 kg^{-1} dry soil of *P. thornei* was estimated to cause 7.6% and 6.8% average yield loss in winter and spring wheat, respectively (May et al. 2016).

3.3.1 Management

The first step in developing integrated management strategies for plant parasitic nematodes, including root lesion nematodes, is to estimate the population levels and distribution in infested area for management consideration. Johnson (2007) conducted a large-scale statewide survey covering more than 80% of the Montana total wheat acreage revealing *P. neglectus* as the prevalent root lesion nematode species.

The threshold level of *P. neglectus* population (2500 kg^{-1} dry soil) was detected in more than 13% of the surveyed fields and the damaging population levels were predominant in the northcentral counties of Montana. Wheat crop management practices have shown substantial impact on root lesion nematode population levels. In general, no-tilled fields experienced significantly higher nematode infestations compared to conventionally-tilled fields, but without any effect on annually cropped versus wheat-fallowed system (May et al. 2016). This study further revealed that winter wheat fields harbored significantly higher population levels of *P. neglectus* in contrast to the spring wheat fields. This appeared to be result of longer winter wheat growing season that may support increases in nematode population in Montana. Furthermore, a higher yield loss was observed in winter wheat (15%) than spring wheat (6.5%) in Montana (May et al. 2016). Based on these findings, research efforts to develop management strategies for root lesion nematodes should focus more on winter wheat crop than on spring wheat.

Several chemical nematicides are effectively and widely used for the management of plant parasitic nematodes (Kimpinski et al. 1987, 2005; Taylor et al. 1999; Smiley et al. 2005b). In the Pacific Northwest, Aldicarb (Temik® 15G) has shown some efficacy in the early protection of root development against root lesion nematodes. However, its use in large-scale dry land wheat production fields may not be economically feasible, since it will further increase production costs. In addition, Temik® 15G is currently not labeled for use in commercial cereal production in the United States due to its persistence, toxicity and higher application cost (Smiley et al. 2005a, b).

Development of resistant crop cultivars usually remains a principal goal in managing crop nematode pests. Currently, there are no known cereal varieties adapted to Montana that exhibit resistance to root lesion nematode *P. neglectus* (May et al. 2016). Recently, researchers from the Montana State University conducted resistance screenings test against *P. neglectus* in barley and wheat (spring and winter) cultivars or isogenic lines (May 2015; May et al. 2016). Greenhouse screening tests revealed tolerance to *P. neglectus* in two commercially available spring wheat (McNeal and Outlook) and barley cultivars (Harrington and Baronesse) that maintained normal yield levels even under high infestation of *P. neglectus* (May et al. 2016). For winter wheat, seven resistant lines possessing competitive agronomic traits were identified and efforts are underway to identify genomic regions associated with resistance to *P. neglectus* for use in marker-assisted breeding for cultivars suitable for Montana. Wheat germplasm exhibiting tolerances to *P. neglectus* have been effectively screened in Australia (Vanstone et al. 1998; Thompson et al. 2008) and similar efforts are underway in the Pacific Northwest (Smiley and Nicol 2009).

Because of the lack of currently available *Pratylenchus neglectus* resistance wheat cultivars, rotation with non-host crops may be the best recommended control strategy for this nematode in Montana. Smiley et al. (2014) stated safflower (*Carthamus tinctorius*), flax (*Linum usitatissimum*), triticale (*Triticosecale*) and field pea (*P. sativum*) to be poor or minor hosts for both *P. neglectus* and *P. thornei* prevalent in the Pacific Northwest. However, the feasibility of rotating all these non-host crops with small grains appears to be low in Montana, with the exception of field pea that is widely grown in this State. Other crops such as lentil, chickpea, canola (*Brassica napus*) and camelina (*Camelina sativa*) are best used in rotation with small grains in continuous cropping systems of Montana (McVay et al. 2010). Recently, May et al. (2016) conducted field studies regarding crops that can potentially be integrated in rotation with wheat for managing root lesion nematodes in Montana. Lentil was the best rotational crop since it reduced soil populations of *P. neglectus* by 96% in the following year. Camelina was the second preferred rotational crop, which reduced almost 50% of *P. neglectus* populations in the following year. In contrast, canola appeared to be the preferred host, as high populations of *P. neglectus* were observed following winter wheat. However, the authors also observed that the overwintering population of *P. neglectus* declined sharply before the seeding of a subsequent wheat crop. This could be due to the decomposition of canola stubbles releasing glucosinolates lethal to root lesion nematodes, as observed in other studies (Potter et al. 1998; Kirkegaard and Sarwar 1999). However, until further investigations of its interaction with RLNs populations are carried out in Montana dry land farming systems, canola may be a least recommended non-host crop for the management of root lesion nematode.

Weed host plants may influence the management of root lesion nematodes in cultivated lands. For example downy brome, (*Bromus tectorum*) and jointed goatgrass (*Aegilops cylindrica*), are reported as hosts for *P. neglectus* (Smiley et al. 2014). Although, host range studies on weeds have not been conducted in Montana, certain weed species such as downy brome and jointed goatgrass are widespread in the wheat fields of Montana and commonly infest other crops in the rotation (McVay et al. 2010). Therefore, this may be a significantly important factor while devising cultural practices and crop rotation strategies for host-free fallow periods (May et al. 2016). The growth of susceptible weeds allows increase and persistence of nematodes, compromising the use of resistant or tolerant crops in rotations for long-term management of *P. neglectus*. In addition to weed hosts, volunteers and wheat root tissues also continue to provide food and refuge for *P. neglectus* even after harvest in no-till systems, thereby, sustaining nematode populations even in the fallow periods (May et al. 2016). Therefore, susceptible weed hosts and volunteer wheat must be controlled during the rotation with non-host to keep *P. neglectus* population below the threshold level.

Management of *P. neglectus* could be best approached by integrating crop rotation with non-host crops and planting tolerant cereal cultivars that may have higher yield and possess resistance to other prevalent fungal root diseases (Smiley et al. 2005b). Biological control agents are not commercially available for the economical and practical management of *Pratylenchus* spp. on wheat (Smiley et al. 2014).

3.4 Stem and Foliar Nematodes

Stem nematode belonging to *Ditylenchus* and foliar nematode *Aphelenchoides* are one of the relatively few species that feed on above ground plant parts and rarely on the root system. Among these two species, stem nematode, *Ditylenchus dipsaci,* is reported as a common species parasitizing alfalfa shoots and known to cause significant damage in Wyoming (Gray and Koch 1998). The nematode's life cycle includes egg, four larval and adult stages. Larval and adult stages are capable of attacking alfalfa plants. Although, adults and eggs can overwinter in succulent tissues of alfalfa crown or in soil, fourth stage larvae are most likely to survive in a cryptobiotic state under unfavorable conditions and re-infect plant tissue when conditions become favorable. Fourth stage larvae can withstand dehydration for a long period and spread to un-infested fields through infested seed or other plant tissue, contaminated manure and irrigation water, and harvesting equipment (Hooper 1972; Vrain and Lalik 1983). Stem nematode damage symptoms observed in Wyoming alfalfa fields include white-flagging, swelling and stunting of plants (Gray 1995). In addition, *D. dipsaci* interferes with carbohydrate storage, resulting in winterkill and contributing further to reductions in alfalfa forage yield (Boelter et al. 1985).

Gray et al. (1984) reported widespread occurrence of the stem nematode in irrigated alfalfa fields of Wyoming. On an average, about 88% of the fields had infected plants exhibiting white-flagging symptoms. Among the major diseases responsible for alfalfa stand decline in Wyoming, disease inflicted by stem nematode is listed as the most important (Gray and Koch 1998). Gray et al. (1994a, b) reported limited occurrence of the stem nematode from Montana in their surveys that focused on the Western United States. Since then, there have been no other published reports on the occurrence of the stem nematode on alfalfa in the state.

Foliar nematode species *Aphelenchoides ritzemabosi,* commonly known as the chrysanthemum foliar nematode, feeds endoparasitically on leaves, and ectoparasitically on buds and growing points of plants (Agrios 2005). Foliar nematodes move in the water film over plants and free water like rain splashes contribute to its spread and re-infestation (Wallace 1959). *Aphelenchoides ritzembosi* is reported as a pest of several plant species, but the occurrence of foliar nematode in Wyoming has been mainly reported as a pest of significance on alfalfa cohabiting with stem nematode *D. dipsaci* (Gray et al. 1994a, b; Williams-Woodward and Gray 1999). Gray et al. (1994a, b) observed that the damage symptoms caused by foliar nematode *A. ritzembosi* on alfalfa plants were similar to that of stem nematode *D. dipsacii*, with the exception of no swelling of alfalfa tissues. Foliar nematode *A. ritzembosi* on dry bean (*Phaseolus vulgaris*) exhibiting angular leaf spots and lesions, was also reported during a survey of a field with the crop rotation history of alfalfa production (Franc et al. 1993, 1996).

3.4.1 Management

Preventive management methods such as sanitation and exclusion are the most appropriate management strategies for alfalfa stem nematode. Alfalfa growers should consider using clean and nematode-free seed, avoid moving contaminated farm machinery from an infested field to a clean field and reusing contaminated irrigation water (Gray et al. 1984; Griffin 1994; Simmons et al. 2008). Re-use of irrigation water appeared to be common in Wyoming and possibly lead to the rapid dispersal of stem nematode to other un-infested fields (Gray et al. 1984). Therefore, minimum applications of irrigation water to the alfalfa fields are often recommended since it keeps the soil surfaces dry, eventually reducing the spread of nematode to the later cuttings after the first cutting.

Crop rotation with non-host crops such as sorghum, small grains, beans and corn on a 2–4 year basis can be another strategy for successful management of alfalfa stem nematode populations (Gray et al. 1984). Cutting alfalfa fields only when the top 5–7.5 cm of soil is dry is another way to reduce reinfection. Moderate to high stem nematode resistant certified alfalfa cultivars, adapted to Wyoming growing conditions, are commercially available and are listed in the University of Wyoming Extension Bulletin (Gray and Koch 1998). A majority of these cultivars listed in this bulletin are also claimed to be resistant to other stand-decline diseases such as bacterial wilt, *Phytophthora* root rot and *Verticillium* wilt, commonly occurring in the alfalfa fields of Wyoming.

Gray and Soh (1989) tested three nematicides including carbofuran, phenamiphos and oxamyl as seed treatments to control the stem nematode on seedling alfalfa planted in stem nematode-infested soil. These chemical treatments were effective in decreasing stem nematode damage and increasing survival of alfalfa plants in Wyoming. Currently, there is no post-application chemical nematicide registered for controlling stem nematode in the U.S.

Due to identical soil moisture and temperature conditions favoring the concomitant occurrence of *D. dipsaci* and *A. ritzemabosi*, similar management strategies are recommended for foliar nematode as that of stem nematode (Gray et al. 1994a, b). Effective management of both stem and foliar nematodes seems to be best addressed by a combination of methods including irrigation management, crop rotation and planting of certified resistant cultivars. These management tactics may help in reduction of parasitism of even susceptible cultivars and ensure better yields from the resistant cultivars.

3.5 Sugar Beet Cyst Nematode, *Heterodera schachtii*

The sugar beet cyst nematode is one of the destructive pests of sugar beet worldwide and reported to occur in 17 states in the U.S. including Wyoming (Gray and Koch 1997) and Montana (Barry Jacobsen, Montana State University, pers. comm.). *Heterodera schachtii* attacks and destroys feeder roots of plants causing severe stunting. In an infested field, symptoms usually appear in circular or oval patches and over time these areas may enlarge and spread out. Although *H. schachtii* can parasitize mature plant roots, young plant roots (seedlings) are more susceptible. Above ground symptoms on young plants attacked by *H. schachtii* may develop elongated petioles and remain stunted until harvest. In addition, *H. schachtii* affected plants develop small storage roots that are severely branched with excess fibrous roots.

Heterodera schachtii is also known to inflict damage on other host crops such as turnip (*Brassica rapa*), kale (*Brassica oleracea*), radish (*Raphanus raphanistrum* subsp. *sativus*), spinach (*Spinacia oleracea*), broccoli (*Brassica oleracea*), cabbage (*Brassica oleracea*), cauliflower (*Brassica oleracea*), tomato (*Solanum lycopersicum*), brussel sprouts (*Brassica oleracea*), kohlrabi (*Brassica oleracea*), rhubarb (*Rheum rhabarbarum*) and other closely related crops. However, the damage level on these crops appeared to be low and insignificant in Wyoming (Gray and Koch 1997). In addition, weed species such as mustard (*Sinapis arvensis*), pigweed (*Amaranthus retroflexus*), lambsquarter (*Chenopodium album*), shepherds purse (*Capsella bursa-pastoris*), purslane (*Portulaca oleracea*), and other closely related weeds are also known to be the hosts of the sugarbeet cyst nematode.

Gray (1995) reported 57% sugarbeet fields infested with *Heterodera schachtii* in Northwestern Wyoming. Particularly severe damage was observed in fields located in close proximity to sugar processing plants where sugarbeets have been grown for several years. Due to continuous sugarbeet production in sugarbeet growing regions of Wyoming, it is not uncommon to find fields with high counts of sugarbeet cyst nematodes above the damage threshold level. Other factors such as soil temperature at the time of planting, plant growth stage and soil type affect parasitism of *H. schachtii* and crop yield reduction under field conditions (Griffin 1981a).

3.5.1 Management

Sugarbeet root yield reduction due to *Heterodera schachtii* is correlated primarily to a high initial nematode population density in the soil (Griffin 1980, 1981b). The sugarbeet cyst nematode can be managed by long-term rotation (3–5 years) with non-host crops such as barley or corn. However, due to high cash value of sugarbeet crop and lack of other crops with similar value adapted to Wyoming, crop rotation is not a widely adapted management option in the state (Griffin 1981a). In Wyoming, non-host crops include wheat, barley, corn, beans and alfalfa. However, weed hosts must also be controlled during rotation. The number of years of rotation out of sugarbeets to reduce the soil population of *H. schachtii* below a damaging level will depend primarily on the initial density of viable cysts in the soil. The number of years a non-host crop must be grown in order to reduce the nematode population below the threshold level can be estimated by using the annual decline rate of 40–60% (Gray 1995; Gray and Koch 1997).

Nematicides such as Telon® (1,3 dichloropropene) and Temik® are commonly recommended in Wyoming to control *H. schachtii*, particularly in short rotations and when the cyst population is above the damage threshold level prior to sugar beet planting (Koch et al. 1999a). Temik® is the most widely used chemical, notably because of its dual activity on both nematodes and insects. Application of Temik®, at the recommended rate of 30 kg/ha, inhibits the egg hatching and disorients juveniles and adult males in soil. In addition, Temik® suppresses the development of *H. schachtii* after penetration into the sugar beet root. Counter® (15G and 20CR) is another chemical nematicide registered for sugar beet cyst nematode management, but only recommended for use in fields with low to moderate nematode populations. Based on the University of Wyoming sugar beet cyst nematode management guidelines, soil fumigant nematicides must be applied either in fall or pre-plant, during the early spring (Gray and Koch 1997). The effectiveness of fumigant nematicide often depends on other factors such as depth of application, soil temperature and moisture, soil type, compaction, and organic matter content. It is further recommended that the soil surface be sealed, especially if the fumigant is applied by using moldboard type plow applicators.

Trap crops such as oil radish and yellow mustard, have been used to control the sugar beet cyst nematode in Wyoming (Koch and Gray 1998; Smith et al. 2004). Roots of the trap crops mimic those of sugarbeet and other host crops by stimulating egg-hatch and attraction of nematode juveniles to the roots (Smith et al. 2004). However, after entry into the roots, juveniles fail to develop into adults and reproduction does not occur. In Wyoming, field research trials conducted by Koch and Gray (1998) using the nematode resistant trap crop radish, planted in late July and early August, showed an average reduction of 63% in number of *Heterodera schachtii* eggs in soil. The sugar yield response to the nematode resistant trap crop radish was greater than the response to the nematicide aldicarb. Trap crops, when used in conjunction with a non-host rotation crop, further lowered the soil population of *H. schachtii* and reduced the need for nematicide in the following sugarbeet crop. Oil radish and the white mustard cultivars were found to be effective in suppressing nematode population levels compared to the susceptible sugarbeet cultivars (Koch and Gray 1998; Smith et al. 2004). Among the trap crops, radish cultivars were found to be superior to mustard cultivars relative to their potential in reducing Wyoming sugar beet cyst nematode population levels (Smith et al. 2004). Trap crops are recommended to be planted in late summer or early fall following harvest of a rotation crop (Koch et al. 1999b). Based on the results of these studies using trap crops in general and nematode resistant radish appears to be a promising substitute to nematicide for the management of sugar beet cyst nematode in Wyoming.

Sugarbeet varieties with a tolerance-type resistance to *H. schachtii* are able to produce high yields even in the presence of high nematode populations. However, fields where tolerant cultivars are planted will not have lower populations of the cyst nematode at the end of a production season, whereas, varieties with immunity have lower populations since the cyst nematode is unable to reproduce on them (Barry Jacobsen, pers. comm.). While unknown at this time, the development of new races of cyst nematodes could be a problem with immunity-type resistance. Therefore, it is critical that growers and pest control advisors monitor varieties carefully for resistance failure. The tolerance-type resistance of sugarbeet cultivars has been quite stable in Montana and it is likely that its use will enhance increases in levels of natural predators and parasites of *H. schachtii* (Barry Jacobsen, pers. comm.).

Heterodera schachtii population numbers of less than three viable eggs and larvae per cubic centimeter of soil, may present little or no yield loss to sugarbeet in Wyoming (Gray and Koch 1997). Based on this threshold level, Montana State

University recommends that Montana growers plant cyst nematode susceptible varieties, with high yielding capacity and resistance to other diseases, in fields having cyst nematode populations less than three viable eggs and larvae per cc of soil (Barry Jacobsen, pers. comm.). A soil analysis for determining *H. schachtii* numbers in a field is worthwhile to sugarbeet growers prior to any decision for nematicide application. Precision based methods such as grid sampling and GPS-based applications, are suggested to minimize nematicide use under field conditions (Opp 2001). While Telone® is still available, the use of cyst nematode resistant varieties is the best economic alternative for SBCN management (Barry Jacobsen, pers. comm.).

3.6 Root Knot Nematodes and Their Management

For detailed information on the occurrence of root knot nematode species, worldwide crop losses and management options for general crop production, see Perry et al. (2009). The most widespread and economically important species are *Meloidogyne incognita*, *M. javanica, M. arenaria, M. hapla, M. chitwoodi* and *M. graminicola.* Root knot nematode females are globose and sedentary at maturity, establish a feeding site within the plant root system and form giant-cells. Cells neighboring the giant-cells also enlarge and divide rapidly and result in gall formation on the root system. As the female root knot nematode enlarges, its posterior region break the epidermis of the root, and the eggs are deposited into a gelatinous egg mass. Galling on the roots, upon which the common name is derived is quite variable among the different species and the plant hosts. Limited occurrence of root knot nematodes species including the northern root knot nematode *M. hapla* on sainfoin (*Onobrychus viciifolia*) (Gray et al. 1986, 2006); and both *M. hapla* and *M. chitwoodi* (Columbia root knot) on legumes including alfalfa (Griffin et al. 1990; Griffin and Rumbaugh 1996; Griffin and Jensen 1997) are reported from Wyoming. Worldwide and regional estimates of crop losses due to both *M. hapla* and *M. chitwoodi* are reported by various authors, but no data is available pertaining to Wyoming. No root knot nematode species is reported from Montana.

Studies conducted by the University of Wyoming researchers primarily focused on host screening and, temperature effects on the pathogenicity against root knot nematodes (*Meloidogyne hapla* and *M. chitwoodi*) on leguminous species common in Wyoming rangelands (Griffin and Jensen 1996; Griffin and Rumbaugh 1996). Based on the root knot nematode galling index (number of galls) on the root system, authors concluded that northern root knot species, *M. hapla*, was more pathogenic and caused heavy galling as compared to *M. chitwoodi*. All legume species regardless of the species, were moderately to heavily galled except for pea vine, where little or no galling occurred. In general, alfalfa and yellow sweet clover were more susceptible to both the nematode populations collected from different geographical regions. The greatest galling however, occurred on yellow sweet clover exposed to the *M. hapla* Wyoming population and was most pathogenic at 25 °C compared to other high and low temperature exposures.

From the above discussion it is clear that the root knot nematode species *M. hapla* followed by *M. chitwoodi*, appears to be a problem on legume plant species common to the Wyoming rangelands. Host screening studies discussed above in the late 1900s were an important step in the selection of poor or non-host legumes to the prevalent root knot nematode species in the state and may have important management implications. However, since majority of the root knot nematode species are known to have a wide host range (Perry et al. 2009), recent surveys should consider the current status of root knot nematode on other crops and prevalent species in both Wyoming and Montana. For instance most discoveries of plant parasitic nematodes including root knot nematode species occur several years after the introduction into a new region. By the time they are discovered, they have typically already spread to other areas but are still at low enough numbers that they will not be discovered in the newly infested fields for many more years, if not decades.

3.7 False Root Knot Nematode, *Nacobbus aberrans*, and Its Management

The biology, ecology and general management of the false root knot nematode (*Nacobbus* sp.) is reviewed in detail by Manzanilla-López et al. (2002). As the external symptoms on the root system due to *N. aberrans* infestation are similar to those produced by the root knot nematode, *N. aberrans* is commonly referred to as the false root knot nematode. It is a sedentary endoparasite of the host root system and is considered a species complex with many pathotypes having different host preferences (Inserra et al. 2005; Manzanilla-López 2010). *N. aberrans* is observed throughout the Great Plains region of the United States, including Montana and Wyoming (Inserra et al. 1996; Gray et al. 1997). Although, *N. aberrans* is primarily an economic problem on sugarbeet in the United States, this pathogen can affect numerous other vegetable hosts such as carrot, pea, lettuce, tomato and numerous species in the mustard and cucurbit families (Manzanilla-López et al. 2002). Detailed information on the management of *N. aberrans* is limited in regards to Wyoming and Montana. Crop rotation with non-host crops was considered to be an effective strategy for the management of *N. aberrans* under field condition in Wyoming (Gray et al. 1997).

3.8 Cereal Cyst Nematode: A Potential Threat to Wheat Production in Montana and Wyoming

Cereal cyst nematodes are sedentary endoparasites. Second stage juveniles are mobile and invade and embed themselves in young host plant root tissues by forming specialized feeding sites called syncytia (Agrios 2005). Mature females become sedentary and embedded in the root. The presence of the white swollen female body (about the size of a pin head) can be seen around the flowering time of wheat. One or more females are generally visible at the point of abnormal root proliferation. Males fertilize the females, and each mature female retains several hundreds of eggs. Cereal cyst nematodes undergo one reproductive cycle per growing season. Upon the death of the host roots, the female body dies, dislodges, and forms a hardened dark-brown cyst, which serves as a protective structure for eggs and juveniles during host-free periods. Eggs within cysts can remain viable for several years. Juveniles require a period of dormancy prior to their emergence from the cyst structure. The dormancy period varies, depending on the nematode species and environmental conditions.

Two species *Heterodera avenae* and *H. filipjevi*, have been reported to parasitize cereal crops in the Pacific Northwestern region of the United States (Smiley 2009a; Smiley et al. 2013). *H. avenae* can reduce yields of winter wheat and barley by as much as 50%, and total crop failures for spring wheat stands have been reported in severely infested commercial fields in Oregon. First report of cereal cyst nematode *H. avenae* in Montana is documented in the year 2006 (Smiley and Yan 2010). Dyer et al. (2015) confirmed cereal cyst nematode species *H. filipjevi* in Chouteau County, Montana, on the roots of stunted winter wheat plants by performing molecular analysis of internal transcribed spacer (ITS1 and 2) and 28S rRNA gene. Information related to economic damage and statewide distribution of *H. avenae* and *H. filipjevi* in Montana remains unknown as no surveys have been conducted in the state. Presently, there have not been any report of the occurrence of any of the species of cereal cyst nematodes in Wyoming and to our knowledge, no survey has been conducted in that state.

3.9 Conclusions and Future Research Directions

Major plant parasitic nematodes causing significant crop yield losses are root lesion (*Pratylenchus neglectus*), stem (*Ditylenchus dipsaci*) and sugar beet cyst (*Heterodera schachtii*) nematodes. In addition, other nematode species such as cereal cyst and root knot nematodes that have been considered as minor pests, could have a larger economic impact in the near future in this region.

The extent of damage caused by root lesion nematode *P. neglectus* was recently reported from Montana in 2007. Since then, research on the management practices are underway including screening of winter wheat germplasm against *P. neglectus* and non-host crop studies for developing favorable management options applicable to Montana field conditions. Future research efforts should continue to focus on the development of commercially available resistant wheat cultivars suitable for Montana. Due to a lack of availability, economic feasibility and environmental concerns over the use of nematicides, more applied research efforts are needed on sustainable and cultural management methods. Furthermore, a survey to assess the occurrence and prevalence of root lesion nematodes in particular from Wyoming, should be conducted.

Concerning the stem and bulb nematode *Ditylenchus dipsaci* and foliar nematode *Aphelenchoides ritzemabosi*, no information is available on crop loss estimates in Montana, although an incidence was reported in the year 1994. In Wyoming, it is considered an economical pest in irrigated alfalfa fields based on available research reports. Practices such as irrigation management, crop rotation and planting of certified resistant cultivars seem to be helpful in reduction of nematode parasitism and improved forage yield. Nearly 50% of alfalfa production in Montana is also irrigated (MAS 2016), therefore, statewide surveys of alfalfa fields should be conducted to assess the current status and geographical distribution of stem and bulb and foliar nematodes.

In Montana, sugar beet cyst nematode *Heterodera schachtii*, is reported from sugarbeet fields, but current research studies are lacking. In contrast, it has been considered a significant pest of sugarbeet from Wyoming since the early 1980s. Management strategies including precision-based nematicide application, trap crops, long-term rotation (3–5 years) with non-host crops (if economically feasible), are recommended for both states, based on research conducted in Wyoming.

It is worthwhile to state here that cereal cyst nematode species *Heterodera avenae* and *H. filipjevi* were detected in Montana in 2006 and 2015, respectively. Generally, cyst nematode species have a high ability to spread with soil to uninfested regions. For instance, cereal cyst nematode species, *H. avenae,* is now reported in seven different US states. Therefore, further spread of these nematodes may pose a serious threat to cereal production in Montana and Wyoming in the near future. The current distribution of cereal cyst nematode species (*H. avenae* and *H. filipjevi*) in Montana and Wyoming is unknown. Therefore, assessment of the geographical distribution of both species in Montana and Wyoming must be conducted to reduce further spread to unifested cereal growing regions.

3.10 Perspective of Nematode Management Practices in the Sustainable Agriculture in Montana and Wyoming

Nematode problems are gradually increasing in crop production systems in Montana and Wyoming. From the sections above it appears that the current available management practices focus primarily on short term strategies. Agronomic challenges cannot be ignored while considering management options in Montana and Wyoming. These may include large fields dominated by a mono-cropping system with limited crop rotation options and mainly rainfed-based cropping systems. In Montana, particularly, soils are shallow, prone to nutrient leaching, and heavy nitrogen applications are gradually contributing to soil acidification in some cropping areas.

Henceforth, development of sustainable nematode management practices (e.g., biological control, crop rotation, resistance and soil biological conservation) is much needed in this region for agricultural sustainability. In addition, there is need of science-based knowledge for devising multiple-approach, integrated nematode management tools. Presently, it appears that if plant parasitic nematode populations reach threshold levels, management will rely on strategies focused on short-term goals. This short-term approach probably demands a shift to long-term sustainable integrated approaches.

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Chapter 4
Plant Parasitic Nematodes and Their Economic Relevance in Utah and Nevada

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4.1 Introduction

Crop damage induced by plant parasitic nematodes has been known in Utah since the beginning of the development of plant nematology in the United States (USA), under the leadership of N.A. Cobb. Observations of nematode damage on sugar beet were recorded in Utah in 1907 (Thorne 1961). At that time, E. G. Titus, a professor of zoology and entomology at Utah State University, observed nematode infestation in a declining sugar beet stand in Lehi, Utah. Titus reported his finding to the United States Department of Agriculture (USDA), where N. A. Cobb was initiating a nematology research program. This report resulted in the identification of the nematode causing the decline as *Heterodera schachtii*, a damaging nematode previously reported in Europe. A survey of this parasite was soon after conducted in 1915, by

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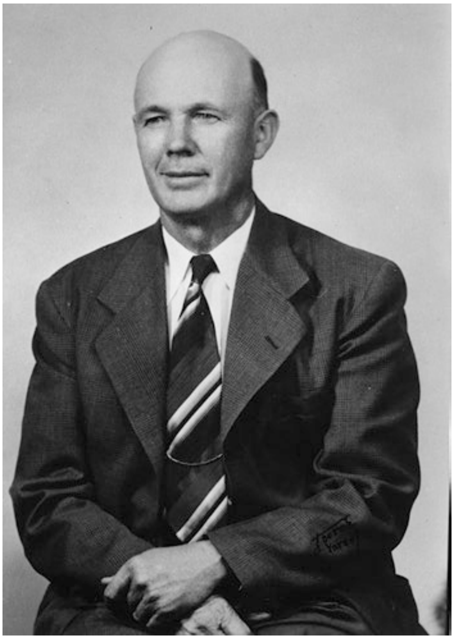

Fig. 4.1 Gerald Thorne. (Courtesy of J. Eisenback)

H. B. Shaw in many states of the USA. The great economic importance of the sugar beet industry, at that time, and the managerial skill of E. G. Titus made possible the initiation of a sugar beet nematode project at the USDA. In those years, Gerald Thorne (1890–1975) (Fig. 4.1) was working in Beltsville, Maryland, under the guidance of Cobb who facilitated the transfer of Thorne from Beltsville to Salt Lake City, Utah, where he led this project, and in time, assumed the position of senior nematologist with the USDA, Division of Nematology. Thorne held this position from 1918 to 1956. During those years, he worked on the damaging effects and taxonomy of nematode parasites of sugar beet and other crops before he moved, in 1956, to the University of Wisconsin, Madison in the capacity of professor of Plant Pathology and Zoology (Webster and Van Gundy 2008). This new teaching and research position allowed Thorne to train many distinguished nematologists, including Gerald Griffin (1927–2011) who joined the USDA, Agricultural Research Service (ARS) and transferred to the USDA-ARS, Crops Research Laboratory, in Logan, Utah, in 1963. Griffin maintained this USDA-ARS position in Logan from 1963 until his retirement in 1997. During those years, Griffin continued Thorne's nematological work on agronomic crops and expanded his studies on nematodes damaging leguminous forage and grasses in pastures and rangelands. The work conducted by Thorne and Griffin remains the most valuable source of information about nematodes damaging agricultural crops in Utah and Nevada. The authors of this chapter would like to point out that in the last 20 years little is known of applied nematological research that has been conducted in Utah and Nevada. Information on recent nematode problems on crops of these two states can be obtained from recent studies conducted in Idaho by one of the authors of this chapter, Saad Hafez, since the State of Idaho shares many crops and associated nematological problems with Utah and Nevada. Although Nevada and Utah are the two driest states in the US (NOAA National Climatic Data Center 2018), agricultural crops are very successful where irrigated. Livestock and livestock products are the major components of agriculture in Utah and Nevada (USDA Statistics 2006). Thus, forage legumes and grasses are the largest crops grown in the two states. Cereals including barley, corn and wheat are also important agricultural commodities. The most common vegetable crops are dry beans, onions and potatoes. Smaller acreages of fruit trees, nuts and berries are also grown throughout much of Utah and Nevada. The nematode parasites of these crops and fruit trees in Utah and Nevada are also common in Idaho and other states in the Intermountain Region. In this chapter, nematodes are divided into groups according to their type of parasitism (Jenkins and Taylor 1967).

4.2 Problems Caused by Nematode Parasites of Above Ground Parts of Plants

The most common nematode parasites of above ground plant parts occurring in Utah and Nevada are the seed gall nematodes of the genera *Anguina* and *Mesoanguina* and the stem and bulb nematode, *Ditylenchus dipsaci*. These nematodes are present in temperate areas of many countries.

4.2.1 Seed Gall Nematodes

Seed gall nematodes induce the formation of galls on the flower structures, stems and leaves of their hosts. The nematodes develop, mate and reproduce inside the galls. The females are obese and sluggish. Although their economic importance is less relevant than in the past, we mention the following three species reported in Utah and the Intermountain Region. They are: the bent grass nematode, *Anguina agrostis*, the wheat cockle nematode, *A. tritici* and the arrowleaf balsamroot leaf gall nematode, *Mesoanguina balsamophila*.

4.2.2 Bent Grass Nematode, **Anguina agrostis**

The bent grass nematode has been reported in the Intermountain Region and Pacific Northwest as a damaging parasite of pasture grasses such as alpine bluegrass (*Poa alpina*), annual bluegrass (*P. annua*), colonial bent grass (*Agrostis tenuis*), Kentucky bluegrass (*P. pratensis*) and sheep fescue (*Festuca ovina*), which are stunted and show deformed inflorescences caused by the cigar-shaped galls induced by the nematode in the florets (Thorne 1961; Griffin 1984). The second-stage juveniles (J2) are enclosed in the galls that are sown with seeds and burst when in contact with water in moist soil, releasing the J2. They initiate the infestation and invade the seedlings feeding at first ectoparasitically on young leaves, which become distorted and twisted. In time, the J2 colonize the inflorescence and enter the ovules where they develop into adult males and obese females. Nematode feeding induces hypertrophy and hyperplasia of ovarian tissues and the formation of spindle-shaped galls containing nematode life stages and eggs (up to 1000). These galls are harvested with seeds and sown, perpetuating the nematode infestation. The life-cycle is completed in three to four weeks. The nematode spreads by infested seeds, plant debris, water and machinery. Growth suppression of bent grass can be severe (50–75%) in some cases (Jensen 1961). Toxicity resulting in nervous disorders has been reported after cattle and sheep were feeding on *Festuca* spp. infested by *A. agrostis*. Other species of *Anguina* may be involved in these reports (Stynes et al. 1979). Appropriate crop systems which should exclude host crops are effective. However, volunteer host grasses may hamper the effect of these crop rotation systems (Griffin 1984). Burning of the stubble provides good results in mitigating the nematode damage. Phytosanitary practices which include the use of certified seeds free from galls, which contain the nematodes, are the best approach to avoid the infestation of this parasite (Jensen et al. 1958).

4.2.3 Ear Cockle Nematode, **Anguina tritici**

The ear cockle or wheat cockle nematode is a species occurring in many geographical areas. In the past, this species had economic relevance for the cereal industry in Utah and other states in the Intermountain Region (Griffin 1984). The biology of this foliar nematode does not differ from that of *A. agrostis*. The J2 invade the shoot of wheat (*Triticum* spp.) seedlings causing leaf distortion and stunting. They then colonize the inflorescence where they develop into the adult stage. These nematodes feed on the floret primordia causing cell hypertrophy and hyperplasia, which results in the formation of a gall (ear cockle) containing the nematode colony and the eggs. The galls become brown-dark in color and replace the kernel. The infested ears are smaller and distorted compared to health ears (Fig. 4.2a). At ear maturation, the cockles are harvested with the healthy kernels, if they do not fall to the ground. Ear cockles can persist for many years in the soil protecting viable nematodes that start new infestations of wheat seedlings. Adoption of appropriate phytosanitary measures and use of certified seeds free from ear cockles have eliminated this nematode from most commercial wheat production areas in the United States and developed countries (Griffin 1984; Duncan and Moens 2013). It is worthy to mention that *A. tritici* is on the quarantine lists of regulated organisms in many countries.

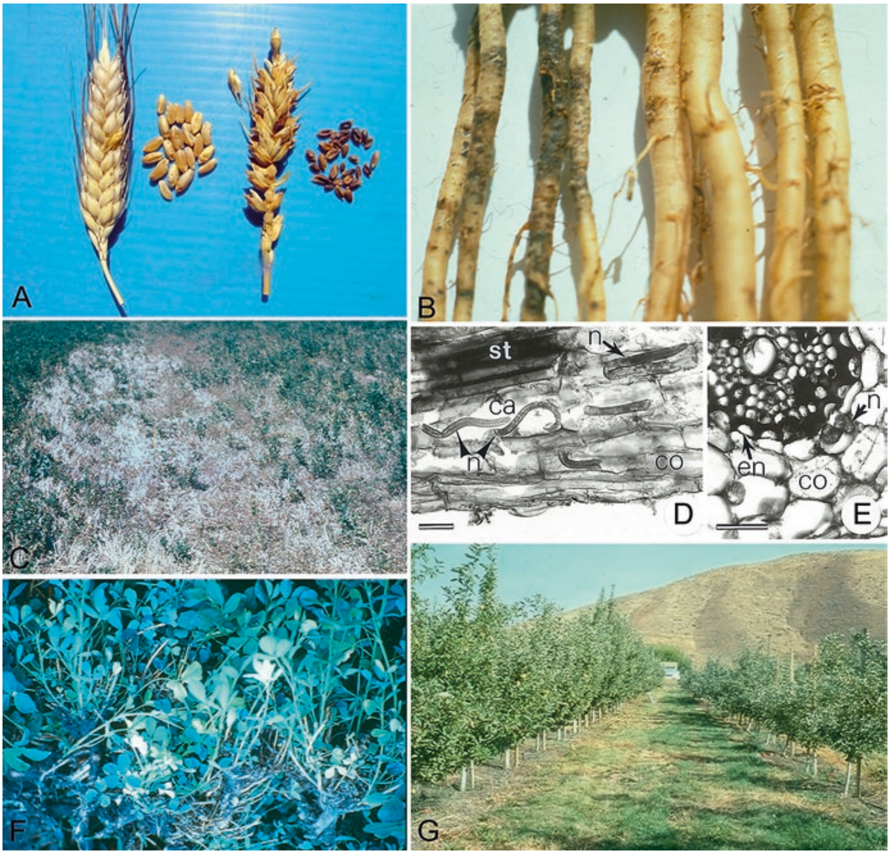

Fig. 4.2 Damaging effect of plant parasitic nematodes on alfalfa, apple, range grass and wheat. (**a**) Symptoms induced by *Anguina* tritici parasitism on wheat cv. 'Creso'. Note a parasitized head and dark seed galls (cockles) (right) and a healthy head and kernels (left); (**b**) Symptoms induced by *Pratylenchus penetrans* on alfalfa cv. 'Vernal' roots. Right: Healthy roots. Left: Nematode infested roots showing dark necrotic lesions that affect a small portion or the entire root. (**c**, **f**) Symptoms induced by *Ditylenchus dipsaci* on susceptible alfalfa cv. 'Vernal'; (**c**) Field with dead stands. F: White flagging of second cutting; (**d**, **e**) Anatomical alterations induced by *Pratylenchus neglectus* in rangeland grass roots; (**d**) Longitudinal section of *Agropyron cristatum* cv. 'Fairway' with a cavity (ca) in the cortex (co) induced by nematode (n) feeding and migration. (**e**) Cross section of *Pascopyrum smithii* cv. 'Rosana' showing crossed nematodes (n) in a cortical cell adjacent to the endodermis (en). (Scale bars = 100 μm); (**g**) Declining apple cv 'Rome Beauty' resets after replanting in Idaho. Vigorous apple resets growing in soil treated with a fumigant nematicide (left). Smaller and stunted apple resets growing in non-fumigated soil infested with *Pratylenchus vulnus* and other plant parasitic nematodes (right)

4.2.4 *Arrowleaf Balsamroot Leaf Gall Nematode,* Mesoanguina balsamophila

The arrowleaf balsamroot leaf gall nematode is a species described by Thorne (1926) who detected it on arrowleaf balsamroot (*Balsamorhiza sagittata*), a flowering plant related to sunflower in the Asteraceae family. This species was found in Utah, the type locality, as well as Colorado, Idaho and Washington. The fourth stage juveniles (J4) of *M. balsamophila* overwinter in the soil and enter the tender young leaves of this flowering plant in the spring and feed in the mesophyll. Here, they develop into females and males and induce hypertrophy and hyperplasia of the mesophyll, resulting in the formation of galls underneath the blade of the leaves, which become distorted, small and may die if severely infested. Nematodes reproduce in the galls and remain protected in the gall tissues until the death of the leaves, which fall to the ground. During the winter, the J4 become quiescent into the dead leaf tissues until the spring. The damage caused by the nematode to this fodder has not yet been assessed. However, *M. balsamophila* has mainly environmental and ecological importance because it infests plants such as *B. sagittata* and the related *Wyethia amplexicaulis* (Mule-ears), which thrive in natural areas and range lands in Utah and the Intermountain Region where they provide forage to mule deer, domestic sheep and other animals.

4.2.5 *Stem and Bulb Nematode,* Ditylenchus dipsaci

Ditylenchus dipsaci has a wide host range and many biological races (*sensu* Perry and Moens 2013) specialized to feed on selected host plants including alfalfa (*Medicago sativa*). The race of *D. dipsaci* that parasitizes alfalfa is commonly called the alfalfa stem nematode. This race parasitizes alfalfa and sainfoin (*Onobrychis viciaefolia*) and does not reproduce in other plants (Griffin et al. 1975; Griffin 1984). However, this race can invade and induce high seedling mortality of onion (*Allium cepa* 'Sweet Spanish'), sweet clover (*Melilotus indica*), and to a lesser extent, sugarbeet (*Beta vulgaris*), tomato (*Lycopersicon esculentum* 'Stone Improved') and wheat (*Triticum durum*), despite the fact that it does not reproduce in these crops (Griffin 1968, 1975).

The alfalfa stem nematodes congregate under the developing leaflets of alfalfa at or near the soil surface. They penetrate succulent stem and buds and feed in parenchymatic tissues. The nematode feeding activity results in swollen, distorted, blackened and malformed stems, which have swollen nodes and shortened internodes, making the plant more brittle. Nematode colonization of the stem causes cell necrosis, which can involve the crown of alfalfa resulting in a reduction of the number of stems and an increase in plant mortality (Fig. 4.2c). Nematodes can invade leaf tissue in heavily infested plants and can destroy chloroplasts in the leaves which become white and very noticeable in infested stands (O'Bannon and Esser 1988). These symptoms are commonly known as "white flagging" (Fig. 4.2f). Serious infestations of *D. dipsaci* can lead to severely depleted alfalfa stands. The developmental stages of *D. dipsaci* include eggs, four juvenile stages and adult females and males. These stages develop inside the plant tissues and are abundant in spring and fall. Optimum temperatures for invasion and reproduction in alfalfa are 15–20 °C, which facilitate the completion of the nematode life-cycle in 10–15 days (Griffin 1984). The fourth-stage juvenile (J4) can withstand adverse environmental conditions such as drying and very low temperatures, and perpetuates the nematode infestation in the field by overwintering in the alfalfa crown, plant debris and soil. Under cool and moist conditions J4 and other motile life stages reach and invade the buds by moving in a film of water adhering to the surface of the stem. Dry and hot conditions are unfavorable for movement and infestation of the nematode. Damaging additive effects of concomitant infestations of *D. dipsaci* with infections of the fungus *Fusarium oxysporum* f. sp. *medicaginis* have been observed on old alfalfa cultivars such as 'Lahontan', 'Moapa 69' and 'Ranger' in greenhouse experiments conducted by Griffin (1990). Concomitant infestations of *D. dipsaci* and the chrysanthemum foliar nematode, *Aphelenchoides ritzemabosi* have been observed on alfalfa stands growing in the western states of the United States. However, no chrysanthemum foliar nematodes were detected during a survey conducted in five sites close to Heber, Logan, Smithfield, St. George and West Jordan and located in Wasatch, Cache, Washington and Salt Lake Counties in Utah (Grey et al. 1994). In greenhouse experiments conducted by these authors, 'Moapa' and 'Ranger' alfalfa cultivars were the most susceptible, whereas 'Vernema', 'Caliverde 65' and 'W2S2' were resistant to concomitant infestations of the two nematodes.

The use of resistant alfalfa cultivars, crop rotations, appropriate irrigation procedures and certified seeds not contaminated with nematodes are the most effective agronomic practices to manage the infestations of the stem and bud nematode. 'Lahontan', 'Washoe' and other new cultivars have been used successfully to minimize nematode damage in many areas where these common cultivars are adapted (Griffin and Waite 1971; Griffin 1984). Additional cultivars, having moderate to high resistance to the nematode, have also been selected by seed companies. Burning crop residues in the field is effective specifically in the fall. However, burning in the spring can increase nematode populations because it stimulates early plant sprouting and nematode activity by warming the soil. The use of alfalfa seed from nematode infested field can spread the nematode in many areas if the seed is not cleaned. Spread of the nematode can be prevented by avoiding the use of irrigation water from ditches containing waste water contaminated with the nematode. Presently, the nematode is causing less damage than in the past because of the adoption of resistant cultivars and improved phytosanitary practices such as the use of certified and dry-cleaned alfalfa seed that is free of contaminating nematodes.

4.3 Problems Induced by Root Feeder Nematodes

The root feeder nematodes are the most economically important species in the states of the Intermountain Region. No less than 81 root feeder plant parasitic nematodes have been reported in a recent survey conducted in Idaho, a state that shares environmental, edaphic and ecological conditions like those of Utah and Nevada (Hafez et al. 1992, 2010). Many of the species found in Idaho have also been reported in Utah and/or Nevada (Thorne 1961; Griffin 1984; Griffin and Thomson 1988). The damage that root feeder nematodes cause to cultivated crops depends on many factors such as parasitic habits, adaptation to the cool environment of the Intermountain Region, ability to withstand antagonistic biological agents and competition with other plant parasitic species. Root feeder nematodes can either be ectoparasitic (feeding and development occur outside the root) or endoparasitic (feeding and development occur inside the root tissues). The adult females can be migratory, if they are mobile and acquire nutrients from different parts of the root system, or sedentary, if they are not motile (usually obese) and acquire nutrients from specialized feeding sites that they induce in selected root tissues. Semi-endoparasitic species have sedentary and obese adult females that induce and feed on specialized feeding sites. These life stages remain attached to the roots by the anterior portion of their body. Their swollen posterior portion of the body protrudes from the root surface.

4.3.1 Ectoparasitic Migratory Nematodes

Several species of ectoparasitic migratory nematodes have been reported by Thorne (1949, 1955, 1961) in Utah (*Tylenchorhynchus maximus, Hemicycliophora aberrans, H. obesa, H. obtusa, H. similis, H. tenuis, Geocenamus productus, Tylenchorhynchus cylindricus* and *Xiphinema americanum*). An additional species *Quinisulcius acutoides* was found on 'Thiokol' crested wheat grass *Agropyron intermedium*, during surveys conducted, in May 1983, by G. D. Griffin, R.N. Inserra and N. Vovlas (unpublished) in Northern Utah rangelands. The economic importance of many of the listed species does not appear to be relevant. However, among those listed, the dagger nematodes of the *X. americanum* group are the most damaging because of their ability to induce fruit trees decline directly by feeding on their roots and because of their ability to vector viruses. Studies conducted by Lamberti and Morgan Golden (1986) using the specimens of *X. americanum* group collected by Thorne in the 1920s in Utah indicated that they contained representatives of the species *X. utahense* described by Lamberti and Bleve-Zacheo in 1979 from specimens collected by S. Sher from *Rhus trilobata* in Coal Creek Canyon, Jefferson Co., Utah. This species seems to be widespread in Utah since Thorne collected populations of this species from cedar (*Cedrus* sp.) in Cove Fort, Millard Co., oats (*Avena sativa*) in Holladay and Red Butte Canyon, Salt Lake Co. and sugar beet in

Ogden, Weber, Co., in Utah. *Xiphinema brevicolle* is another dagger nematode reported by Lamberti and Morgan Golden (1986) in Nephi, Juab Co., Utah and Wells, Elko Co., Nevada. The occurrence of these dagger nematodes together with the ring nematode *Mesocriconema xenoplax* in Idaho (Hafez et al. 2010), on fruit trees such as *Prunus* spp., confirms their wide distribution in fruit orchards in the Intermountain Region. *Mesocriconema xenoplax* is one of the causal agents of a disease complex called peach tree short life (PTSL). Cold injury and the bacterial canker (*Pseudomonas syringae*) are other major contributing factors or causal agents of PTSL. Hafez et al. (2010) report presence of dagger and ring nematodes in peach orchards in Idaho, these nematodes may also be a potential threat to the stone fruit industry in Utah and Nevada. The use of nematode free peach rootstocks and those resistant to PTSL such as 'Lovell' and 'Guardian' rootstocks, is the best and sustainable practice to manage this peach disease. Use of Metam Sodium as pre-plant treatment has been effective in Idaho.

4.3.2 Endoparasitic Migratory Nematodes

The most reported endoparasitic migratory nematodes in Utah and Nevada are root lesion nematodes of the genus *Pratylenchus*. Three species, *P. neglectus*, *P. thornei* and *P. vulnus* have major economic importance (Thorne 1961; Griffin 1991). These species have also been reported in Idaho and other states of the Intermountain Region. Other species such as *P. crenatus*, *P. penetrans* and *P. scribneri* reported in Idaho by Hafez et al. (2010), may occur in Utah and Nevada. The listed species share similar developmental stages, feeding and reproductive habits. The juveniles (J2, J3 and J4) as well as the adult stages are all motile and penetrate feeder or secondary roots, where they complete development before depositing eggs. Nematode feeding and tunneling cause cell necrosis and large cavities in the cortical parenchyma and stele. Small necrotic spots are visible on the root surface of infested roots. Damaged root tissues are abandoned by the nematodes in exchange for healthy tissues thereby, debilitating the root system further and compromising the transfer of water and nutrients from the roots to the plant canopy. Serious infestations of these nematodes can suppress the growth and yield of many crops (Thorne 1961; Inserra and Vovlas 1977; Duncan and Moens 2013).

4.3.2.1 Root Lesion Nematode, *Pratylenchus neglectus*

This root lesion nematode is the most common species in Utah and the Intermountain Region. It is a temperate nematode that is commonly reported from many continents and countries. Its wide host range includes cereals, crucifers, flowering ornamentals, forage, legumes, strawberry and fruit trees. Alfalfa, cereals and grasses are the most common hosts of this nematode in Utah. Population levels of up to 14,000 specimens per root system have been recorded under field conditions on alfalfa and wheat

(*Triticum* sp.) by Griffin and Grey (1990). The damaging effect of this root lesion nematode to alfalfa was demonstrated under controlled environment by these authors, who observed growth suppression of alfalfa cultivars 'Ranger', 'Lahontan' and 'Nevada Synthetic XX' by 16–40% at initial population levels of 1000 and 10,000 nematodes per plant, respectively. Different virulence among the Utah populations of *P. neglectus* has also been ascertained in experiments conducted by Griffin (1991). Populations from Northern Utah were more damaging to 'Lahontan' alfalfa cultivar than other populations from Central and Southern Utah or Wyoming. Lesions and necrosis induced by *P. penetrans*, alone or in association with *P. neglectus*, have been observed in roots of alfalfa in Idaho by Hafez et al. (2010) (Fig. 4.2b) suggesting that *P. penetrans* may occur on alfalfa also in Utah and Nevada. Many forage grasses are often infested by *P. neglectus* in Northern Utah rangelands. Unpublished results of nematode surveys conducted in 1983 by G. D. Griffin, R.N. Inserra and N. Vovlas in Northern Utah rangelands indicated that 16 native grasses were hosts of this root lesion nematode. Nematode root population densities were variable with up to 1000 specimens per gram of fresh roots in the cultivars of some species such as 'Fairway' crested wheatgrass and 'Rosana' western wheatgrass. Nematode migration and feeding induced large cavities in the cortical parenchyma of the host's feeder roots (Fig. 4.2d). Occasionally, nematodes were observed in cortical cells adjacent to the endodermis (Fig. 4.2e). However, no evidence of stelar invasion was detected. High population densities of *P. neglectus* may inhibit the resistance of these grasses to drought (Griffin 1984).

4.3.2.2 Root Lesion Nematode, *Pratylenchus thornei*

This species was reported for the first time in Utah by Sher and Allen (1953) from wheat (*Triticum* sp.) samples collected in Holladay, Salt Lake Co. Later, Thorne (1961) observed damage induced by *P. thorne*i to wheat and corn (*Zea mays*) in some areas of the same county. Thorne also noticed growth suppression and stunting of oats in nematode infested fields. Nematode invasion and damage of root tissue resulted in small inflorescences with a few shrunken seeds. No nematode infestations on alfalfa, or sugar beet were noticed during his field studies. However, this species was found on cereals and other crops such as beans (*Phaseolus* sp.), hops (*Humulus* sp.), potato and sugar beet in Idaho cropping systems (Hafez et al. 2010).

4.3.2.3 Root Lesion Nematode, *Pratylenchus vulnus*

Thorne (1961) detected this nematode on raspberries (*Rubus* sp.) in unspecified localities throughout Utah. However, other cultivated plants such as apple (*Malus sativus*) and other fruit trees, are very probably infested by *P. vulnus* in Utah and Nevada since Hafez and Fallahi (1994) and Hafez et al. (2010) have reported it alone or in association with *P. penetrans* and other plant parasitic nematodes in declining apple resets used for transplanting old apple orchards in Idaho (Fig. 4.2g).

The use of clean rootstocks free of root lesion nematodes is the best agronomic practice to prevent the damage of these parasites.

4.3.3 Endoparasitic Sedentary Cyst Forming Nematodes

The species belonging to this group of nematodes have significant economic relevance because of the damage they cause to agricultural crops in Utah, Nevada and other states in the Intermountain Region. Cyst-forming nematodes of the genus *Heterodera* have been well known in Utah since 1907. This is because of the serious damage that *H. schachtii* caused to sugar beet in many areas of the state. This nematode has become a major limiting factor of sugar beet production throughout the Intermountain Region. The cereal cyst nematode, *H. avenae*, is another cyst-forming nematode that is present in the Intermountain Region and reported in Colorado, Idaho, Oregon, Montana and Washington. This species was detected in Utah, in 2006 (Smiley 2009; Subbotin et al. 2010). There is no evidence, so far, that the Filipjev's cereal cyst nematode *H. filipjevi* is present in Utah. This species, which resembles *H. avenae* morphologically, may arrive from Eastern Oregon where it was reported in 2008. Other cyst-forming nematodes that are reported in the Pacific Northwest and may be accidentally introduced in Utah and Nevada are two representatives of the genus *Globodera* that parasitize potato: *G. ellingtonae*, found in Oregon in 2008 (Subbotin et al. 2010; Handoo et al. 2012) and *G. pallida* detected in Idaho in 2006 (Hafez et al. 2007). Surveys for potato cyst nematodes (PCN) conducted in 2006 by the USDA-APHIS-PPQ-CAPS did not detect these parasites in Utah and Nevada. However, the potato industry in Utah and Nevada should adopt rigorous phytosanitary measures to prevent the arrival of these two damaging PCN into their states because of the potato crop losses and, also, serious regulatory implication that they cause to the trade not only of potatoes, but also other crops. The use of certified potato seeds free from nematodes and the exclusion of machineries from the areas infested with PCN in Idaho and Oregon are imperative agronomic practices that potato growers should implement. Periodic surveys of PCN in potato fields of Utah and Nevada should be conducted routinely to confirm the absence of PCN in the two states. The detection in Idaho since 2006 of the clover cyst nematode *H. trifolii*, the hop cyst nematode, *H. humuli* and the rye grass cyst nematode, *H. mani*, a parasite of ryegrass, should be of concern for forage grass industry in Utah and Nevada (Hafez et al. 2010). *Heterodera trifolii* and *H. mani* are known parasites of forage legumes and grasses, respectively, whereas *H. humuli* has the ability to infest forage legumes such as vetch (*Vicia sativa* L.) in addition to hop (Subbotin et al. 2010). These nematodes may already be present or arrive with contaminated seeds and machinery from Idaho. In this chapter, more detailed information is provided on *H. avenae* and *H. schachtii* because of the emerging economic relevance of the former and the historical importance of the latter species.

4.3.3.1 Cereal Cyst Nematode, *Heterodera avenae*

The cereal cyst nematode has been known in Europe, for more than a century, as a distinct population of *H. schachtii* capable of parasitizing cereals (Kühn 1874). After its description (Wollenweber 1923), this species was found outside Europe in distant geographical continents such as Asia and Australia. In the USA, *H. avenae* was detected in Western Oregon in 1974 (Jensen et al. 1975) and subsequently in other parts of the state including the eastern region where it was found associated with the morphologically related species *H. filipjevi*. Outside Oregon, *H. avenae* occurs in Idaho, Utah and Washington (Hafez and Golden 1984, 1985; Smiley 2009). However, no data are available on its distribution and biology in Utah and its potential occurrence in Nevada. We report information on this nematode from geographical areas with climatic conditions similar to those of North Utah. Although the cumulative yield losses of cereals caused by this nematode in Europe average about 3 million Euros annually, losses vary in different countries because of the presence of pathotypes and cryptic species which differ in their virulence, suggesting that *H. avenae* is a species complex (Subbotin et al. 2003, 2010).

Mature females of *H. avenae* retain the eggs inside the body. At the completion of the life cycle, they die and become brown cysts containing the embryonated eggs. Temperatures in the range of 5–15 °C are suitable for hatching of J2. In North Europe, seedling roots are penetrated by J2 soon after germination in autumn-sown cereals. Nematode development in the root is suspended during winter months and is completed in the spring with formation of white females, and subsequently, cysts. In spring-sown cereals, the J2 soil populations peak in April and decline sharply in June. Females can be found 90 days after J2 penetration in the roots (Decker 1972). The nematode completes one generation per year. Nematode infested wheat fields show large areas with stunted, chlorotic plants as well as reduced tillering and small heads. Similar nematode biology and symptoms on wheat have been observed in Idaho and occur in Utah (Fig. 4.3a). Wheat root systems are reduced in size, knotted, and show the females (or cysts) protruding from the root surface exposing the posterior portion of their bodies (Fig. 4.3c). As in the case of other cyst-forming nematodes, *H. avenae* induces formation of syncytia that can expand into more than 40% of the stele. The disorganization of the vascular system compromises the normal transfer of water and nutrients from the roots to the above ground part of the plants. The damage caused by the cereal cyst nematode in the USA has not been assessed for decades since its detection. Studies conducted in the Pacific Northwest in the last 25 years have provided evidence of the detrimental effect of *H. avenae* infestations on the yield of both autumn-sown and spring-sown cereals (Smiley et al. 2005). Yield suppressions of 25% and 50% were recorded in spring and winter wheat plots, respectively, during field studies conducted in Oregon (Smiley 2009). This author estimates average crop loss for the entire Pacific Northwest to be 10%. Taking into consideration the fact that two thirds of the wheat fields in Utah are not

Fig. 4.3 Damaging effect of cereal and sugar beet cyst nematodes on sugar beet and alfalfa. (**a**, **c**) Symptoms induced by *Heterodera avenae* on winter wheat cv. 'Brundage' in Idaho. A: A nematode infested field showing large patches of stunted plants; (**c**) A white female attached to a root segment. (Scale bar = 292 μm). (**b**, **d**) Symptoms induced by *Heterodera schachtii* on sugar beet cv. 'Betaseed'; (**b**) Healthy plants growing in soil treated with a fumigant nematicide (left) compared with stunted and small plants growing in non-fumigated soil infested by the nematode (right); (**d**) Females of *Heterodera schactii* attached to a root segment of sugar beet cv. 'Tasco AH 14'. (Scale bar = 754 μm)

irrigated and potentially more damaged by the nematode, the wheat crop losses in nematode infested fields likely surpass 10%.

Appropriate agronomic practices are the most economically effective methods to manage the cereal cyst nematode. Cropping systems including the rotation of fallow land-small grain-legumes, have been effective in suppressing nematode populations (Smiley 2009). However, broad leaf crops in rotation with wheat do not grow well in non-irrigated fields. Breeding programs have made available new selections of wheat with the *Cre 1* and barley with *Rha2* genes, which confer resistance against *H. avenae*. These resistant varieties can be used in breeding programs to introduce these genes in local varieties adapted to the environment of Utah and Nevada. At least 28 wheat varieties used by Utah growers do not possess any resistant traits against the cereal cyst nematodes. Resistant cereal varieties have been successfully used in many countries in rotation with susceptible cultivars to manage *H. avenae* infestations (Smiley 2009). In Utah and Nevada, cereal field surveys of the nematode are necessary to delimit the nematode infestations and protect the areas not infested by the spread of this parasite. The characterization of Utah and Nevada populations for presence of new pathotypes or cryptic species is imperative for the implementation of appropriate management practices of the cereal cyst nematode.

4.3.3.2 Sugar Beet Cyst Nematode, *Heterodera schachtii*

At the beginning of the last century, the sugar beet industry flourished in Utah. Sugar beet yields were at a high for more than 25 years after the establishment of this new crop in the western states of the USA. These record-breaking yields declined in the 1920s when the sugar beet cyst nematode, which very probably arrived from Europe, increased in population levels in the fields. Population increases were due to continuous monoculture of sugar beets and the use of nematode infested tare soil that was returned to the farmers from the beet-unloading sites at the processing plants. The implementation of appropriate agronomic practices aiming to suppress the nematode populations such as rotations of sugar beet with non-host crops, appropriate fertilization and the use of sugar beet cultivars resistant to bacterial and fungal diseases, improved yields (Thorne 1961). Once again, the cultivation of sugar beet became profitable in fields infested with the sugar beet cyst nematode in nine Central and Northern Utah counties (Box Elder, Cache, Davis, Millard, Salt Lake, Sanpete, Sevier, Utah and Weber) where the nematode was detected during a survey conducted by Caveness (1958). However, the sugar beet nematode remained a limiting factor of sugar beet production (Fig. 4.3b) in Utah and has contributed to the decline of the sugar beet industry in the state in recent years. The life cycle of *H. schachtii* does not differ from that outlined previously for cyst forming nematodes. Females deposit some eggs in a gelatinous matrix outside their body. However, the majority of the eggs are retained inside their body. The number of eggs per female in Utah populations can reach up to 500. As with the other cyst nematodes discussed, white females protrude with the posterior portion of their body from the root surface (Fig. 4.3d). They acquire nutrients for egg production from specialized cells, syncytia, which expand into the central cylinder of the root disrupting the vascular system and preventing normal uptake of water and nutrients of the infested plants. Seedling mortality and suppression of plant growth and yield are common symptoms induced by nematode colonization of the roots. Nematode-infested fields show large spots without or with small chlorotic plants that are covered by weeds. The effect of initial population levels, soil temperature and age of plants on the damage induced by *H. schachtii* was studied in Utah by Griffin (1981a, b). In these studies, a population from Utah was more damaging to sugar beet than other populations from Idaho or Oregon (Griffin 1981c). Results of field trials conducted in Northern Utah indicate a soil damage threshold level of 200 eggs/100 cm^3. However, crop damage induced by higher initial population levels was influenced by the length of exposure of the plants to the nematode generations. Sugar beet growth suppression of 87% occurred when plants were exposed to initial soil population densities of 1200 eggs/100 cm^3 for five generations of the nematode, compared to a growth suppression of 47% after two generations of exposure (Griffin 1988). The wide host range of this nematode includes species in the families Amaranthaceae and Brassicaceae. However, some species in families Caryophillaceae, Polygonaceae, Scrophulariaceae and Solanaceae are also hosts. A population of *H. schachtii* parasitizing tomato (*Solanum* *esculentum*) has been reported in Northern Utah by Griffin and Waite (1982). Under greenhouse conditions this population suppressed growth of tomato plants exposed for 80 days to initial densities of 1000 J2 per pot of unspecified size. However, the number of eggs per cyst on tomato roots was 40% less than that on sugar beet roots.

The best approach for the management of sugar beet cyst nematode is the combination of non-chemical and chemical practices. Cropping systems which include non-host crops such as alfalfa, corn, cereals, potato and fallow under weed control are effective in suppressing nematode populations. One-year rotation with non-host crops such as barley, corn and wheat suppressed soil population levels in field plots by 50–60% (Griffin 1980, 1988). However, the rotation period to reduce nematode soil populations to non-damaging levels (200 eggs/100 cm^3) is influenced by the initial soil population levels. A 5-year rotation period is required at soil initial population levels of 3300 eggs/100 cm^3 compared to a 2-year rotation period at initial population levels of 800 eggs/100 cm^3 (Griffin 1988). Implementation of rigorous phytosanitary practices such as the use of clean seeds free from cysts and sanitized machinery not contaminated with soil particles containing nematode cysts and soil amendments with organic matter free from nematode parasites of sugar beet should be important components of the management of this nematode. When it is economically feasible, soil treatments with fumigant and non-fumigant nematicides provides excellent results and yield increase (Griffin 1980).

4.3.4 Endoparasitic Sedentary Non-cyst and Non-gall Forming Nematodes

The life cycle of these species is like that of cyst forming species. The swollen females of these non-cyst forming and sedentary nematodes protrude from the root surface similar to those of cyst forming nematodes (Subbotin et al. 2010).

A species of this group was found in Utah and initially described as *Cryphodera utahensis* by Baldwin et al. (1983). Subsequently, the results of phylogenetic analyses conducted by Wouts (1985) indicated that this species belongs to the genus *Bellodera*.

4.3.4.1 *Bellodera utahensis*

This species was found infesting the roots of wild rose (*Rosa* sp. L.) growing in Clear Creek Canyon and Gates Creek in Sevier County, in Central Utah. *Bellodera utahensis* differs from cyst-forming nematodes in inducing in wild rose roots the formation of a specialized feeding site, which consists of a single uninucleate giant cell rather than a syncytium induced by cyst-forming nematodes (Mundo-Ocampo and Baldwin 1984). The damage caused by this nematode to wild roses is not known.

4.3.5 Endoparasitic Sedentary Nematodes Having Swollen Juvenile and Adult Females and Inducing Root Galls (Root Knot Nematodes)

These species are included in the genus *Meloidogyne*. They are polyphagous, widespread and very damaging plant parasitic nematodes that induce small or large root swellings called root knots or galls. *Meloidogyne* species can reproduce by amphimixis or parthenogenesis and are adapted to different environmental conditions. Some species of *Meloidogyne* sp. are cryophils and are adapted to temperate climates while others are thermophils and thrive in warm environments (Karssen et al. 2013). The species that infest agricultural crops in Utah and Nevada are likely cryophils and are represented by the Columbia root knot nematode, *M. chitwoodi* and the northern root knot nematode, *M. hapla*. However, we cannot exclude the occurrence of thermophils species on crops growing in enclosed or more temperate environments in the two states.

4.3.5.1 Columbia Root Knot Nematode, *Meloidogyne chitwoodi*

Meloidogyne chitwoodi, is widespread in the Pacific Northwest, where it was initially confused with *M. hapla* for many years. This species was differentiated from *M. hapla* and described as a separated taxon in the State of Washington, using specimens collected from potato (*Solanum tuberosum*) (Golden et al. 1980). The nematode was found soon after in Idaho, Oregon, and later in Iron County, Utah (Griffin and Thomson 1988). The biology of the Columbia root knot nematode does not differ from that of other *Meloidogyne* species. *Meloidogyne chitwoodi* is a polyphagous parasite of many crops including dicots and monocots. The most economically important crops damaged by this root knot nematode in Utah are alfalfa, cereals, forage grasses and potatoes. A population of *M. chitwoodi,* which parasitizes alfalfa, was detected in Beryl, Iron County, Utah by Griffin and Thomson (1988). This population belongs to a physiological race distinct from other populations that do not reproduce on this forage legume. These authors observed for this population three to sevenfold reproduction rates on alfalfa cultivars ‘Rangers’ and ‘Synthetic XX’, respectively. The damage induced on potato by this Utah population was more serious than that caused by two populations from Idaho. More tubers (64%) were galled by the Utah population compared to those galled by two Idaho populations (24% and 32%) (Griffin and Thomson 1988). Wheat and barley were also damaged by *M. chitwoodi* in Utah. Wheat roots infested by an Idaho population of *M. chitwoodi* showed egg masses attached to small galls that contained clusters of swollen females (Fig. 4.4a, c) (Inserra et al. 1985). Yield suppression caused by the Utah population from Beryl differed among the cultivars of these two cereals. Winter wheat cultivars ‘Nugaines’ and ‘Wanser’ allowed greater nematode reproduction rate than the cultivars ‘Daws’, ‘Dusty’ and ‘Manning’ (Griffin 1993). In this study, the Utah population from Beryl and another from Ft. Hall, Idaho

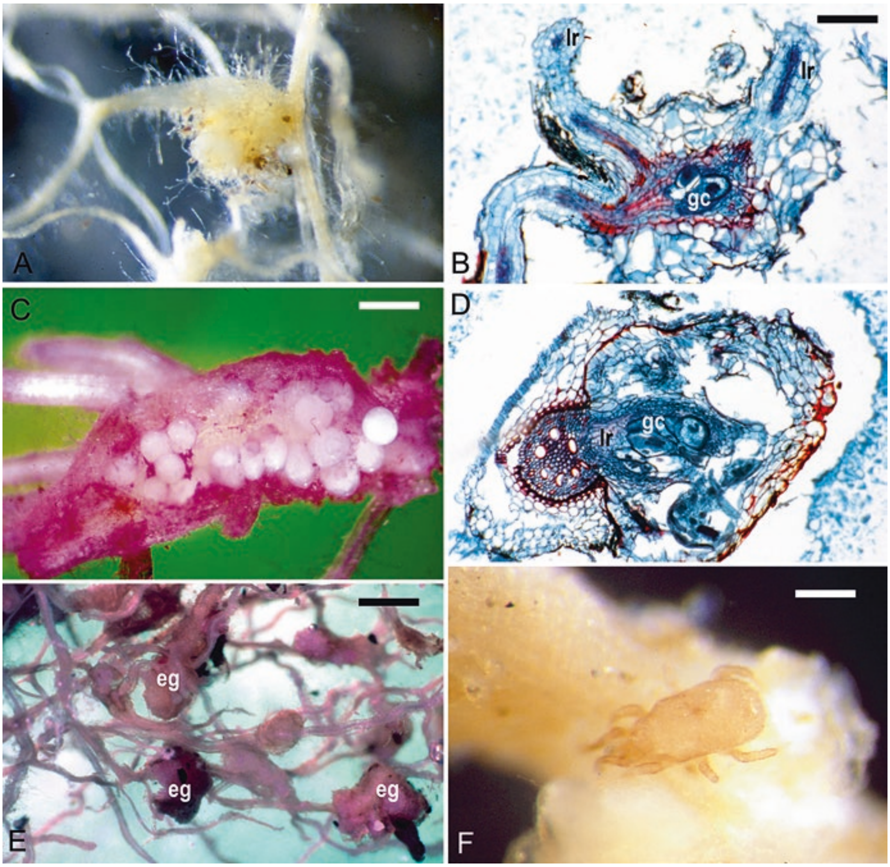

Fig. 4.4 Roots colonized by the Columbia root knot nematode and a predatory mite. (**a**, **c**) 'Nugaines' wheat roots infested by *Meloidogyne chitwoodi*; (**a**): Egg masses; (**c**) A colony of packed females in a small gall. (Scale bar for both figures = 644 μm). (Adapted from Inserra et al. 1985); (**b**, **d**) Anatomical changes induced by *Meloidogyne chitwoodi* on rangeland grass roots; (**b**) Cross section of orchardgrass *Dactylis glomerata* showing lateral roots (lr) proliferation induced by nematode feeding on giant cells (gc)in the stele; (**d**) Cross section of *Agropyron desertorum* cv. 'Nordan' showing giant cells (gc) in the stele of a primordium of a lateral root (lr) (Scale bar = 137 μm). (Adapted from Griffin et al. 1984); (**e**) Orchardgrass, *Dactylis glomerata,* roots infested by *Meloidogyne chitwoodi* egg masses (eg) (Scale bar = 327 μm); (**f**) A predator laelapid mite, *Hypoaspis aculeifer,* feeding on *Meloidogyne chitwoodi* egg masses attached to a tomato root. (Scale bar = 396 μm). (Adapted from Inserra and Davis 1983)

reproduced at high rates on winter and spring barley. However, reproduction rates on barley were 54% less than those on wheat. In contrast with these findings, the winter wheat cultivar 'Nugaines' was less infested by other populations of *M. chitwoodi* from Washington (Nyczepir et al. 1984). Yield suppression of wheat induced by Utah populations of *M. chitwoodi* was greater than that of Idaho populations, suggesting variability on the aggressiveness of populations of the

Columbia root knot nematode (Griffin 1992). At any case, wheat and barley maintain or increase *M. chitwoodi* populations in the soil, further complicating the selection of appropriate cropping systems in potato operations, which are severely affected by the infestations of this nematode. The results of greenhouse studies conducted in Logan, Utah, using an Idaho population of *M. chitwoodi* indicate that many range grasses are also potential hosts of the Columbia root knot nematode. These potential host grasses include 'Barton' western wheat grass, 'Nordan' standard crested wheat grass, orchardgrass (*Dactylis glomerata*) and smooth bromegrass (*Bromus inermis*) (Griffin et al. 1984). Of the grasses, orchardgrass was the most susceptible to the nematode (100% of the plants infested), followed by smooth bromegrass (82%), 'Barton' western wheatgrass (70%), 'Nordan' standard crested wheatgrass (47%) and Great Basin wild grass (14%). Roots of orchard grass were severely galled (Fig. 4.4e). Histological examination of these galls revealed fragmentation, obliteration and asymmetry of the stele caused by the formation of large giant cells (Fig. 4.4b). Similar anatomical alterations were observed in galls induced by the nematode in roots of 'Nordan' standard crested wheatgrass (Fig. 4.4d) (Griffin et al. 1984). The results of subsequent greenhouse experiments conducted in Utah, using the *M. chitwoodi* population from Beryl, indicated that this population suppressed also the growth of the alfalfa cultivars 'Lahontan', 'Moapa' and 'Nevada Syn XX' at 15, 20 and 25 °C, attaining final population densities that were significantly greater than those of *M. chitwoodi* from Idaho and Washington (Griffin et al. 1986). In subsequent field plot experiments a population of *M. chitwoodi* was able to reproduce on both alfalfa and grasses suppressing the growth of 'Hycrest' crested wheatgrass grown alone or in association with alfalfa (Griffin et al. 1992).

Potato is not a crop of great economic relevance in Utah and Nevada. However, this crop is damaged by *M. chitwoodi* in limited areas of Iron County, Utah (Griffin and Thomson 1988). Nematode infestation affects mainly the quality of potato tubers that are not marketable for the potato chip industry. In Utah, the amount of damage caused by *M. chitwoodi* to potato should be comparable to that reported in field plot studies conducted by Griffin (1985) in Idaho. These studies show that nematode damage is directly correlated to the temperatures occurring during the potato growing season. In warm seasons, more than 2000 degree-days accumulate during the potato growing cycle resulting in approximately three nematode generations, allowing a high percentage of tubers to be parasitized, exceeding the 5% tolerance level established by processing companies. In warm years a chemical control approach is imperative to produce salable potato tubers. In cool growing seasons, 979 or fewer degree-days, the percentage of damaged tubers is negligible because the nematode completes only one generation per growing season (Griffin 1985). The wide host range of *M. chitwoodi* among dicots and monocots complicates the non-chemical management of this parasite on economically valuable crops, such as potato, because no effective cropping systems can be adopted to suppress its population levels. The inclusion of resistant crops such as alfalfa cultivars in rotation with potato, is not effective in Utah because cultivars resistant to *M. hapla* such as 'Nevada Syn XX', are not resistant to Utah populations of *M. chitwoodi* (Griffin et al. 1986). These nematode management difficulties, along with limited water irrigation sources and other agronomic factors may prevent the expansion of potato industry in the state. The use of biological control agents has not been included in management studies of this nematode in the past. A laelipid predator mite, *Hypoaspis* nr. *aculeifer* (Canestrini) feeding on *H. schachtii* and *M. chitwoodi* egg masses was found in soil collected in Logan and used as a growing medium in greenhouses (Fig. 4.4f). However, the impact of this predator in suppressing nematode population levels is still not known (Inserra and Davis 1983).

4.3.5.2 Northern Root Knot Nematode, *Meloidogyne hapla*

The northern root knot nematode is a cosmopolitan and temperate root knot nematode species. A report of a root knot nematode female found overwintering on dandelion (*Taraxacum officinale*), in Nevada in 1939 by M. W. Allen, may be considered as the first record of *M. hapla* in that state (Thorne 1961). Nevertheless, we can speculate that the description of *M. chitwoodi*, 40 years later, along with the confusion of the morphology of this new species with that of *M. hapla*, and the lack of biochemical analyses at that time, may cast doubt about the validity of this record. The northern root knot nematode and the Columbia root knot nematode share similar biology, but differ in their host range. *Meloidogyne hapla* parasitizes mainly dicots and rarely monocots, which, as discussed previously, are good hosts for *M. chitwoodi*. In Utah and Nevada, the northern root knot nematode is a damaging parasite of alfalfa (Fig. 4.5a). A population of *M. hapla* from Ogden, Utah, suppressed the growth and reproduced on susceptible alfalfa cultivars 'Lahontan' and 'Moapa' at 15–25 °C, but did not reproduce on and neither damaged the resistant 'Nevada Syn XX' cultivar. However, the nematode overcame the resistant traits of 'Nevada Syn XX' at 30 °C by reproducing and suppressing the growth of the infested plants kept at this temperature. This Utah population of *M. hapla* colonized 'Moapa' nodulated roots including *Rhizoboum meliloti* nodules, which showed egg masses on their surface. The nematode also established permanent feeding sites in their vascular bundles (Griffin et al. 1986).

The reaction of *Lathyrus* species to *M. hapla* was also evaluated in these studies. *Lathyrus hirsutus*, *L. latifolius* and *L. sylvestris* were resistant to the northern root knot nematode compared to *L. ochrus* and *L. tingitanus* that were susceptible (Rumbaugh and Griffin 1992). These results are relevant for the selection of species used as forage legume and soil conservation.

Potato is a vegetable crop damaged by the northern root knot nematode in Utah. Tubers are infested by the egg-laying females, which induce brownish lesions caused by the lignification of cortical cell walls in contact with the egg masses, as reported for *M. chitwoodi* (Finley 1981). These brownish lesions and blisters make the tubers unmarketable. However, it is reasonable to assume that *M. hapla* in Utah should be less damaging to potato than *M. chitwoodi* because it requires higher temperatures for root invasion and its development (Inserra et al. 1983).

Sugar beet is an industrial crop infested by *M. hapla* in the Pacific Northwest. The nematode was found in sugar beet fields in three counties (Cache, Davis and

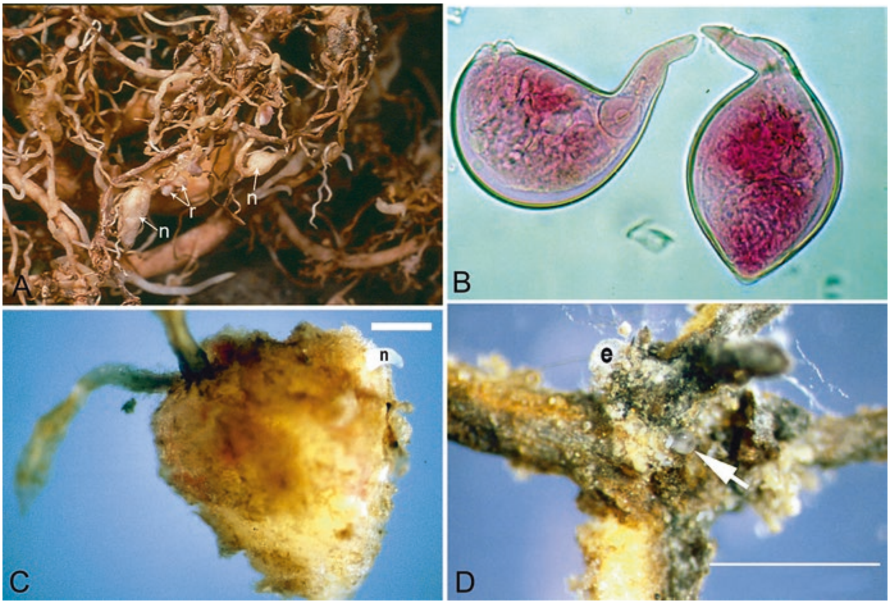

Fig. 4.5 Root alterations induced by the false root knot, the northern root knot and tylenchuloid nematodes; (**a**) Symptoms induced by *Meloidogyne hapla* on alfafla cv.'Vernal' roots in Idaho. Note root galls (n) induced by the nematode and *Rhizobium* sp. nodules (r). (**b**, **d**) Photomicrographs of *Sphaeronema rumicis*; (**b**) Fixed swollen females detached from cottonwood root tissues; (**d**) Cottonwood root segment with attached a swollen female (arrowed) and egg masses (**e**). (Scale bar = 196 μm in **b** and 891 μm in **d**). (Adapted from Vovlas and Inserra 1986); (**c**) Large gall induced by a Nebraska population of *Nacobbus aberrans* in a sugar beet cv. TASCO AH 14 root during host-parasite relationship studies conducted by some of the authors in Logan, Utah. Note a portion of the nematode (n) posterior body protruding from the surface of the gall (Scale bar = 325 μm)

Millard) in Northern Utah (Caveness 1958). The result of greenhouse tests indicates that sugar beet cv 'AH-14' is a better host for *M. hapla* than *M. chitwoodi* from Idaho even if both nematodes suppress sugar beet growth (Griffin et al. 1982). Initial population of 12 J2/cm^3 of soil of a Northern Utah population from lettuce induced the same amount of growth suppression of sugar beet cv. 'Tasco AH14'seedlings as that caused by *H. schachtii* at the same initial density (Inserra et al. 1984). The results of these tests indicate that the northern root knot nematode in Utah is a parasite that can constrain sugar beet production as observed in other states of the Pacific Northwest (Jatala and Jensen 1976).

Non-chemical management of *M. hapla* can be successfully implemented using cropping systems that include monocots, since they are not susceptible to *M. hapla*. Alfalfa cultivars resistant to the northern root knot nematode have been selected. 'Nevada Syn XX' is one such cultivar, which can be used successfully in rotation with other crops. It is known that *M. hapla* can break the resistance of this cultivar at temperatures of 30 °C or above, however, soil temperatures this high rarely occur in Utah or Nevada.

4.3.6 Endoparasitic Nematodes with Vermiform and Swollen Females That Induce Root Galls (False Root Knot Nematodes)

The false root knot nematodes are species native to the western regions of North America and South America. They are included in the small genus *Nacobbus*. Mature females of the false root knot nematodes are sedentary, swollen and induce root galls as do *Meloidogyne* species. However, in contrast to *Meloidogyne* species they induce a permanent feeding site consisting of a syncytium rather than of giant cells. The juvenile stages of the false root knot nematodes do not induce formation of galls in the roots. They are not swollen and induce cavities and lesions in the root tissues comparable to those of root lesion nematodes. Some of the false root knot nematode species are damaging parasites of potato, sugar beet, tomato and other vegetable crops. The most economically important species of this genus is *N. aberrans*.

4.3.6.1 False Root Knot Nematode, *Nacobbus aberrans*

This species was discovered by Thorne (1935), on shadscale (*Atriplex confertifolia*) in the foothills west of Utah Lake, Utah. After its detection and description in Utah, the false root knot nematodes were found infesting sugar beet in Colorado where they were considered a different taxon from *N. aberrans* and named *Nacobbus batatiformis* by Thorne and Schuster (1956). However, this new species was not considered valid and different from *N. aberrans* in subsequent revisions of the genus *Nacobbus* (Sher 1970; Siddiqi 2000; Manzanilla-López et al. 2002). It seems that the native populations of *N. aberrans* found on shadscale, a bush native to the Intermountain region, became adapted to infest sugar beet, which is botanically related to shadscale and also a representative of the Chenopodiaceae family. The nematode suppresses sugar beet growth and yield by deforming the roots with swellings and large galls (Fig. 4.5c). The biology and parasitic habits of this species do not differ from those discussed previously for the *Nacobbus* species. In addition to Colorado, *N. aberrans* has been detected on sugar beet in Kansas, Montana, Nebraska, South Dakota and Wyoming (Caveness 1958). Association of this species with the sugar beet cyst nematode was often observed in these detections. There are no records of infestations of this parasite on cultivated crops in both Utah and Nevada. The economic impact of the false root knot nematode on sugar beet production in the United States is negligible. This is probably because this nematode is a weak competitor when it is associated with the sugar beet cyst or the northern root knot nematodes (Inserra et al. 1984). Outside the USA, this species occurs in Mexico and many Andean countries of South America, where it seriously damages potatoes and other major crops. Unlike the populations in South America, the populations of the Pacific Northwest do not parasitize potatoes. Molecular, morphological and host range studies conducted throughout the Americas (North and South) have disagreements on host preferences, aggressiveness and genetic traits of the false root knot nematode, suggesting that *N. aberrans* is a species complex having different host preferences (Manzanilla-López et al. 2002; Manzanilla-López 2010). Phytosanitary measures implemented in the USA have prevented the arrival from Latin American Countries of the populations able to parasitize potatoes, which may escape detection at the port of entry by remaining hidden under the skin of potato tubers colonized by the quiescent juveniles of *N. aberrans*.

4.3.7 Semi-endoparasitic Sedentary Nematodes

Reports of these nematodes are not common in Utah or Nevada. A representative of the genus *Sphaeronema* was found on narrowleaf cotton wood (*Populus angustifolia*) in a canyon, in the vicinity of Salt Lake City, Utah. This species was identified morphologically as *Sphaeronema rumicis* by Vovlas and Inserra (1986). The J2 of *S. rumicis* penetrate the feeder roots of narrowleaf cotton wood with the anterior portion of their body and induce a specialized feeding site (syncytium) in the stele. Juvenile females develop into swollen and sub-spherical females that produce eggs embedded in a gelatinous matrix that protects the eggs and the posterior portion of the body (Fig. 4.5b). Egg masses are covered with soil particles and encrust the infested roots (Fig. 4.5d). Males are vermiform and are not parasitic. The damage caused by this nematode is not known (Vovlas and Inserra 1986).

4.4 Concluding Remarks

The largest crops grown in Utah and Nevada consist mainly of forage legumes, grasses and cereals. Nematode chemical management measures on these crops are not economically feasible. Agronomic practices such as rotations and the adoption of nematode resistant varieties are the most appropriate and economically profitable management strategies to protect these crops from nematode damage. The search for nematode resistant crop varieties and effective crop rotation systems has been the major objective of the applied research conducted by nematologists for decades in these two states. The results of these studies have provided growers with nematode management practices that are economically profitable and sustainable. These studies have also shown that resistant crop varieties that have been selected for nematode populations in these two states may be not effective for different populations in other states. These findings emphasize the importance of testing the effectiveness of resistant crop varieties on local nematode populations before providing nematode management recommendations to the growers. The search of resistant crop varieties and appropriate crop systems are a persistent necessity since the appearance of nematode populations able to overcome the resistant traits of selected resistant crops occurs often under field conditions. Chemical management is another option for the growers if the chemical applications are limited to the seeds before sowing. Seed treatments have resulted on yield increase of wheat in Australia (Brown 1987). This practice should be effective also in Utah and Nevada.

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Chapter 5
Plant Parasitic Nematodes of New Mexico and Arizona

Stephen H. Thomas and Claudia Nischwitz

5.1 Introduction

New Mexico and Arizona share topographic and climatic similarities that greatly influence crop production and plant parasitic nematodes in both states. The region is comprised of mountainous terrain interspersed with semi-arid, hot deserts, river valleys and plains. Crops are irrigated and grown mainly in the southern half of both states – within the northern reaches of the Sonoran (AZ) and Chihuahuan (NM) deserts. An exception is 29,160 ha of cropland in northwest NM operated by the Navajo Nation's Navajo Agricultural Products Industry. Eastern New Mexico derives water from the western edge of the Ogallala Aquifer, but most cropland in both states relies on snow melt-derived water associated with river valleys. Mountain ranges and the Grand Canyon, in conjunction with numerous Native American homelands, US National Forests and Federal Bureau of Land Management holdings afford a certain level of geographic isolation to many crop-producing areas. This isolation and the semi-arid environment have somewhat reduced the prevalence and introduction of some agricultural pests – undoubtedly including plant parasitic nematodes. Limited private arable acreage and irrigation water greatly affect grower decisions involving crop selection and sustainable nematode management. Southern root knot nematode (*Meloidogyne incognita*) is the most widely distributed and damaging plant parasite in the region, affecting most annual and some perennial crops. Other root knot nematodes including *M. hapla, M. chitwoodi, M. graminis,*

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M. marylandi and *M. partityla* damage some annual crops, turf and pecan. *Ditylenchus dipsaci* and *Tylenchulus semipenetrans* are pathogenic to alfalfa and citrus, respectively in Arizona, while criconematids have recently been associated with turf injury in New Mexico. Lesion nematodes (*Pratylenchus* spp.) affect cotton, corn and bean production in both states. This chapter focuses on the sustainable management practices for these nematodes within the context of cropping constraints associated with the region.

5.2 New Mexico Agriculture

Western European crop production methods in the state date to the early 1600s. Spanish settlers brought acequia irrigation technology from Spain and Northern Africa to produce crops along the Rio Grande Valley from Colorado to what is now, El Paso, Texas. Beginning with Elephant Butte Dam in 1916, this technology was modified and enhanced through the construction of numerous reservoirs that retain spring runoff from snow melt in the mountains. This availability of more dependable irrigation along the river systems and improvements in well drilling technology in other parts of the state allowed further expansion of crop production. Approximately 344,250 ha of irrigated crops were planted in 1922, with hectarage peaking at ~359,000 ha in 1961 (Sutherland et al. 1962). Since the 1970s, competing demand for water, that has accompanied regional urban expansion coupled with declining reserves in the Ogallala Aquifer, saw a decline to less than 338,600 irrigated ha in 2008 (Bustillos and Hoel 2015). By 2013, this hectarage had declined further to under 281,500 due to these continuing pressures and the added effects of a 14-year drought. The New Mexico annual crop profile has always been dominated by grain production that made up 49%, 56%, 41% of total irrigated hectares in 1922, 1961 and 2015, respectively (Sutherland et al. 1962; Bustillos and Hoel 2016). The remaining hectares have changed dramatically over the past century from sugar beet (24%) and hay (21%) in 1922 to cotton (23%), hay (18%) and specialty crops (vegetables and peanut; 3%) in 1961 to today's hay (36%), silage (15%), cotton (4%), specialty crop (pecan, onion, chili pepper, peanut; 4%) profile, in which specialty crops accounted for 45% of the $702 million total crop receipts in 2105. High economic dependence by many producers on the return received from only 4% of crop hectarage heavily influences management decisions for the principal nematodes described below.

5.3 Plant Parasitic Nematodes of New Mexico

5.3.1 Southern Root Knot Nematode, Meloidogyne incognita

Meloidogyne incognita (SRKN) is the predominant nematode pathogen of crops in New Mexico. Left unmanaged, it can result in yield reductions that exceed 50% in chili pepper (*Capsicum annuum*) (Thomas 1994; Thomas et al. 1995) and cotton

(Thomas and Smith 1993) and complete crop failure in melons and watermelon. This nematode occurs in irrigated fields throughout the state, but has not been observed on known host vegetation in native surroundings adjacent to cultivated land, thereby, suggesting that perhaps the pest was introduced and disseminated through agricultural activities. Nearly all annual crops produced in New Mexico and many weeds are hosts for *M. incognita*, greatly reducing the option for producers to use crop rotation as an effective management tool (Fig. 5.1; Schroeder et al. 2004; Vezzani et al. 1993). In addition, most grains grown for forage or in rotation with dicotyledonous crops such as chili pepper, cotton, lettuce or melon to suppress soil-borne fungal diseases, are good hosts that further increase southern root knot nematode populations. Despite known losses in yield and/or quality that occur in grains and some specialty crops, the absence of *M. incognita*-resistant crop varieties or economically feasible nematicides leaves producers with no viable management alternatives for most crops. Extreme market price volatility and uncertainty of commodity prices at harvest for crops such as onion and lettuce, typically prevent growers from committing the needed additional costs for nematode suppression when making their preplant management decisions (Fig. 5.1b, d; personal communication from numerous growers and crop consultants).

The lack of economically-feasible sustainable southern root knot nematode management options forces most growers who produce stably-priced high value specialty crops such as chili pepper, melon and watermelon, to fumigate with 1,3-dichloropropene (1,3-D). Although a limited number of root knot resistant *Capsicum annuum* cultivars are available for some bell and cayenne pepper genotypes produced in other parts of North America, none are available for the New Mexican (also known as 'long green' or 'Anaheim'), paprika, or New Mexico cayenne pod types grown in the Southwest (Bosland et al. 1996; Fery et al. 1986; Thies et al. 2008). Fallowing is rarely considered due to a shortage of irrigated land that forces producers to intensively farm all available hectares. In addition, absence of adequate soil moisture slows *M. incognita* egg development and hatch, requiring producers to either 'dry fallow' fields for multiple years or incur the added expense of irrigating fallow fields and then controlling weeds that support nematode reproduction, which would negate the benefit of fallowing. Crop rotation is seldom considered for reasons previously discussed, with one exception – when fields are co-infested with *M. incognita* and nutsedges that create a pest complex which reduces efficacy of 1,3-D (Thomas et al. 2004).

Yellow nutsedge (*Cyperus esculentus*) and purple nutsedge (*C. rotundus*) are creeping perennial weeds that host southern root knot nematode and are major problems in chili pepper and in vegetable and cotton rotation crops due to limited nutsedge control alternatives (Schroeder et al. 1993). Both are good hosts for the nematode and are undamaged by high nematode populations, which also induce the nutsedges to produce more and larger tubers that are the primary propagative units for these weeds (Schroeder et al. 1999, 2004). In turn, infected nutsedge tubers protect southern root knot nematode from 1,3-D fumigation and unfavorable biotic and abiotic soil conditions (Thomas et al. 2004; Trojan et al. 2005). Nematode infection also reduces the efficacy of herbicides used to control nutsedges (Norsworthy et al. 2005; Schroeder et al. 1994, 2004). Resurgence of southern root

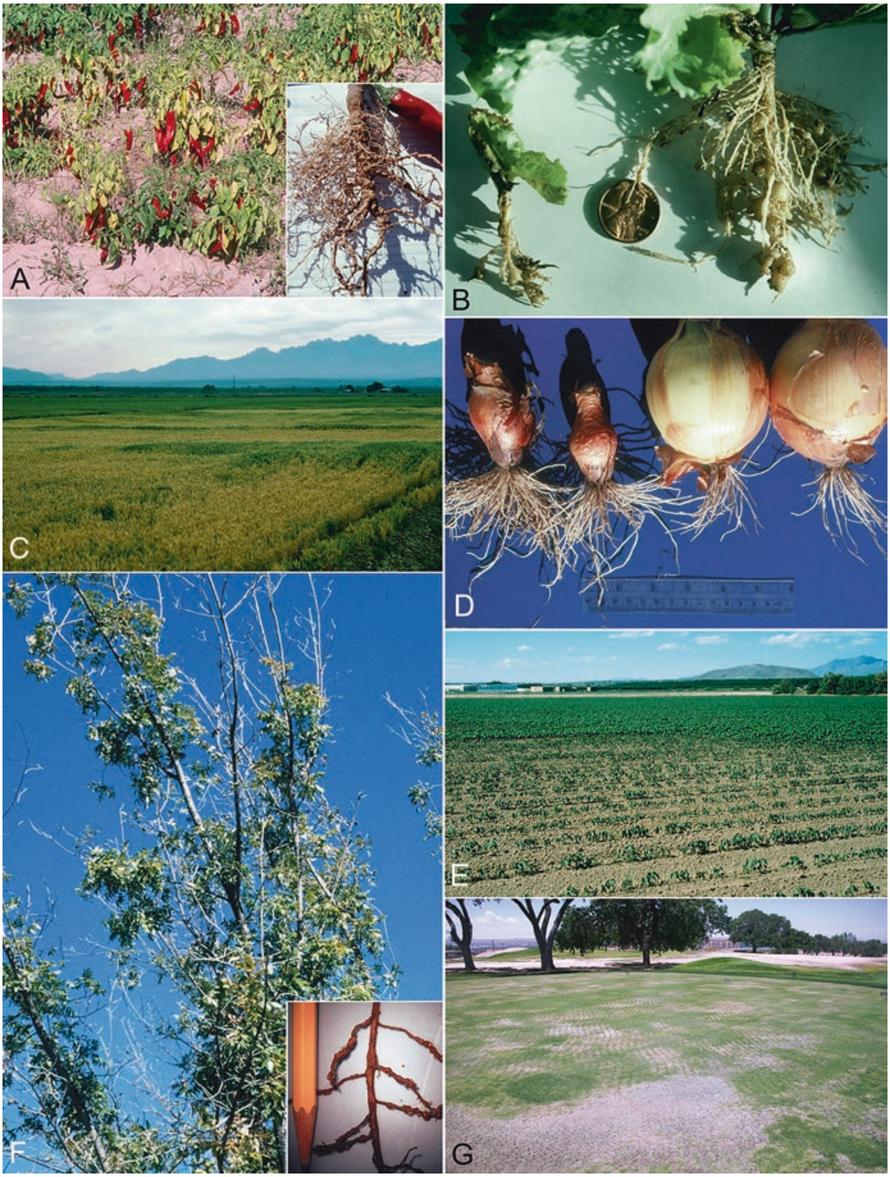

Fig. 5.1 Plant parasitic nematode damage symptoms in New Mexico; (**a**). *Meloidogyne incognita*-induced stunting, chlorosis and root galling in chili pepper; (**b**) Galling on lettuce infected with *M. incognita*; (**c**) Stunting and early senescence in *M. incognita*-infected wheat; (**d**) Root proliferation and reduced bulb development in onion infected with *M. incognita* (left) compared to uninfected bulbs (right); (**e**) Early season stunting of Acala 1517-75 cotton infected with *M. incognita*; (**f**) Pecan dieback and root galling from *M. partityla*; (**g**) Injury to bentgrass golf green from *Mesocriconema nebraskense*

knot nematode on nutsedge roots that emerge from infected tubers following spring irrigation results in substantial nematode population increases 2–3 months earlier than would be expected after 1,3-D fumigation (Schroeder et al. 2007). This mutually beneficial coexistence sustains and enhances the pest complex by reducing the efficacy of recommended pesticides and increasing pest densities and injury to chili pepper and rotation crops. Successful management, which requires simultaneous suppression of all three pests, has been achieved using a 3-year rotation with *M. incognita*-resistant, nondormant alfalfa (Fig. 5.2) (Fiore et al. 2009). Both nutsedges are sensitive to the effects of shading, which reduces photosynthetically-active radiation and depresses vegetative growth. High plant populations of resistant alfalfa, which regrows rapidly after cutting, creates the necessary shading to suppress nutsedge tuber production and simultaneously prevents *M. incognita* reproduction. Chili pepper yields, without the use of 1,3-D fumigation following 3 years of *M. incognita*-resistant alfalfa, were significantly greater than those achieved with 1,3-D treatment following a 3-year rotation of conventionally- managed cotton (Fig. 5.2a, b) (Fiore et al. 2009). Although this sustainable practice has been adopted by some producers, its use is not as widespread as might be expected due to grower concerns about future water availability (alfalfa is a high water- use crop and shortening to a 2-year rotation has not effectively managed the pest complex) and pest resurgence the 2nd year following production of susceptible crops such as chili pepper.

The incidence of *M. incognita* injury to cotton in New Mexico remained relatively constant at 5% statewide for many years, similar to losses observed in Arizona (National Cotton Council of America, n.d.-b). The 1517-type or 'New Mexico Acala' varieties grown exclusively until the late 1990s are characterized by greater fiber length and strength than other Acala and upland cotton varieties, having heritage that can be traced back to the late 1920s (Smith et al. 1999). These varieties were selected over time for maximum yield and disease tolerance under New Mexico and upper Chihuahuan Desert growing conditions. Though not specifically screened for resistance to *M. incognita*, these Acala 1517 cultivars produced smaller galls and fewer eggs per plant than susceptible upland or California Acala cultivars, often leading producers to grow cotton in the season prior to planting more susceptible crops like chili pepper (Klump and Thomas 1987). In these situations, producers routinely applied aldicarb at planting to manage southern root knot nematode and early season thrips until registration of this pesticide was cancelled in 2010. Seeds for *M. incognita*-resistant Acala NemX varieties that perform well and reduce nematode populations in California are difficult to obtain and cultivars do not perform well under New Mexico growing conditions (Ogallo et al. 1999). A brief increase in southern root knot nematode injury occurred shortly after the turn of the century as growers adopted more susceptible transgenic varieties that offered advantages in controlling bollworms and weeds. However, shortly thereafter the combined effects of low cotton prices and water shortages triggered a steady decline in cotton hectares to 12,500 ha harvested in 2015, as growers prioritized water use for crops with greater net profit per hectare (Bustillos and Hoel 2016). Nematode damage has declined to <1% loss statewide during the same period as growers increasingly

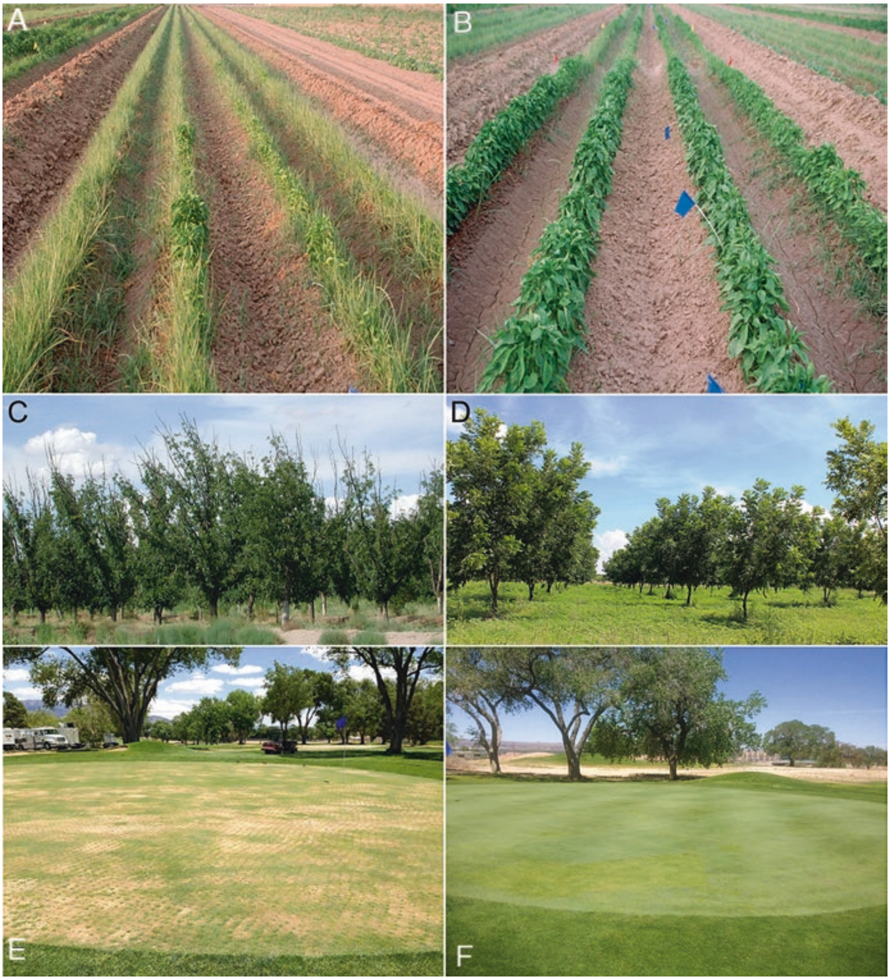

Fig. 5.2 Host response to plant parasitic nematode management in New Mexico; (**a**, **b**) Nonfumigated chili pepper response to suppression of the *Meloidogyne incognita*/yellow nutsedge/purple nutsedge pest complex by a 3-year rotation with nondormant alfalfa cultivar Magna 8 (**b**), compared to chili pepper fumigated with 1,3-D following 3-year rotation with cotton (**a**); (**c**, **d**) Healthy replanted pecan orchard after removal of *Meloidogyne partityla*-infected trees and 5-year alfalfa rotation (**d**) and prior to tree removal (**c**); (**e**, **f**) Response of *Mesocriconema nebraskense*-infested bentgrass golf green to consecutive fall and spring abamectin treatments (**f**) *vs*. prior to treatment (**e**)

restrict cotton production to heavier textured soils where southern root knot nematode problems are uncommon (National Cotton Council of America n.d.-a).

Perennial crops such as alfalfa and wine grapes, also experience damage from *M. incognita*. Stand establishment problems including complete crop failure, are known to occur in fall-planted alfalfa following silage corn or sorghum in sandy, root knot infested fields. Growers are learning that absence of gall symptoms on roots of these forages does not necessarily indicate low M. *incognita* populations in fields with a history of root knot nematode problems in other crops and that preplant soil testing is essential to avoid potential stand failure. Once established, alfalfa is usually tolerant of Southern root knot nematode, but higher populations have been observed in portions of older fields experiencing stand decline. The use of nondormant varieties (dormancy class of 8 or higher) with a high proportion of African alfalfa parentage that are resistant to *M. incognita* is recommended in root knot infested fields in Southern New Mexico (Lauriault et al. 2011; Reynolds and O'Bannon 1960). Nematode-suppressive benefits from such varieties aide in production of alfalfa and subsequent susceptible crops, as previously discussed (Fiore et al. 2009). Vineyards planted in *M. incognita*-infested fields that were previously cropped to cotton or specialty crops, can experience sustained yield losses of 50% or more beginning 6–10 years after establishment. Root knot densities exceeding 1400 J2 per 100 cm^3 soil are frequently encountered under such circumstances. Winter injury and vine death can be more prevalent under such conditions. Following the loss of fenamiphos in 2007, few available nematicides have shown high efficacy against southern root knot nematode in vineyards, although new chemistries and new formulations of current nematicides are being evaluated. Growers confronted by southern root knot nematode injury in vineyards presently have two management options available – both of which are sustainable: (1) enhance growing conditions for infected vines by adjusting irrigation and nutrient application, reducing soil compaction and improving root penetration through incorporation of compost and use of cover crops that are poor or non-hosts for *M. incognita*; (2) remove infected vines and replant using vines grafted to *M. incognita*-resistant rootstocks (McKenry and Bettiga 2013). The first option is more widely used and has enhanced berry quality but has not reversed yield losses.

5.3.2 Northern Root Knot Nematode, **Meloidogyne hapla**

Meloidogyne hapla currently occurs only in Eddy, Chaves, Lea, Roosevelt and Curry Counties in Southeastern New Mexico and is considered the second most damaging plant parasitic nematode in the state. Prior to 1990, this nematode was an uncommon pest occasionally found parasitizing peanut in Roosevelt and Lea Counties. Growers have long recognized the need to use a 4-year rotation with corn, cotton, small grains, or sorghum between peanut crops to control soilborne diseases (Marsalis et al. 2009). These rotation crops, none of which are hosts for *M. hapla*, likely account for the past lack of root knot injury to peanut. Increased irrigation pumping costs, brought about by declining water levels in the Ogallala Aquifer during the 1980s, caused Eastern New Mexico growers to reduce hectarages of less profitable non-host crops and increase the hectares of higher value vegetables such as green bean and chili pepper, both of which are good hosts for *M. hapla*. The 2002 US Farm Bill's cancellation of the peanut price support program resulted in a shift of many peanut hectares to vegetables – primarily chili pepper – within the region. Northern root knot nematode is the predominant nematode pest of chili pepper produced in fields formerly or still cropped to peanut where *M. incognita* does not occur. Growers have the opportunity to sustainably manage both root knot species using crop rotation practices (peanut as a nonhost in *M. incognita*-infested fields and cotton and sorghum in *M. hapla*-infested locations), but few opt to do so, due to economic uncertainty and the diversity of farm equipment and cropping knowledge required with complex rotation schemes.

5.3.3 Pecan Root Knot Nematode, Meloidogyne partityla

Economic returns from 16,200 ha of pecan (*Carya illinoinensis*) totaled nearly $183 million in 2015, making it the most valuable crop in the state (Bustillos and Hoel 2016). New Mexico ranks second only to Georgia in revenue from pecan production in North America. *Meloidogyne partityla* (PRKN) is a severe pathogen of pecan that affects an estimated 3.2% of the state acreage and, at least, one orchard in Eastern Arizona (Thomas 2008; Whiteakar 2001). In addition to characteristic galls on roots, infected trees experience die-back of new growth, substantial reduction in yield and progressive decline (Fig. 5.1f; Heerema et al. 2010; Thomas et al. 2001; Nyczepir et al. 2006). The first orchard exhibiting severe symptoms was encountered in Doña Ana County in 1995, but was not diagnosed until this nematode was reported from Texas the following year (Starr et al. 1996). The nematode has a very narrow host range of plants in Juglandaceae and a few *Quercus* species, making it highly likely that it was introduced on pecan rootstock, since New Mexico's only native member of Juglandaceae is uncommon and restricted to alpine regions far removed from cultivated orchards (Brito et al. 2016; Starr et al. 1996; Little 1950). Most nematode reproduction occurs during the spring and fall, coinciding with major flushes in pecan root growth (Thomas unpublished data). Prior to cancellation of its use in pecan, maximum rates of aldicarb applied to soil within the drip zone for insect control, had no effect on *M. partityla* populations on roots (Whiteakar 2001).

With no viable pesticide alternatives and no known resistant rootstocks available, regional pecan producers must rely completely on other sustainable management alternatives (Nyczepir 2013). First and foremost, growers must only plant container-grown nursery stock or material otherwise known to be free of plant parasitic nematodes. To avoid introduction of pecan root knot nematode from infested orchards, no pruning or harvesting equipment from infested orchards is permitted to enter uninfested orchards for fear of accidental contamination from adhering soil or root debris. The extremely narrow host range of *M. partityla*, which cannot reproduce on any crops or weeds in the state, greatly reduces the possibility of pest persistence outside infested orchards or accidental pest introduction. Some producers whose orchards are infested have successfully reversed tree decline and returned their orchards to profitability by: (1) refraining from mechanical practices to disrupt hardpans that result in root pruning and soil movement such as deep-chiseling; (2)

modifying pruning of mature trees to maintain heights at 7.3–8.5 m to reduce plant stress; (3) carefully using irrigation and fertilization practices to minimize tree stress and permit trees to tolerate the parasite. The third and least desirable option, but one that has proven effective, is removal and destruction of infected trees including removal of as many infected roots as possible, followed by a 5-year rotation with alfalfa (Fig. 5.2c, d). Pecan root knot nematode has not been detected in re-established orchards at previously-infested sites following a 5-year rotation.

5.3.4 *Ring nematode,* Mesocriconema nebraskense

Ring nematode injury to creeping bentgrass (*Agrostis stolonifera*) golf course greens in New Mexico is an emerging problem. Turf samples received in 2011 from declining greens at an Albuquerque golf course contained high populations of *M. nebraskense* (Thomas et al. 2017), some of which exceeded 9500 individuals per 100 cm^3 soil. Heavily infested greens failed to respond to supplemental irrigation and fertilization, eventually becoming unsuitable for play (Fig 5.1g). Due to close proximity of the golf course to high public use areas, initial efforts to manage nematode numbers utilized the Organic Materials Review Institute (OMRI)-certified *Bacillus firmus*, which reduced nematode populations but not to sufficient levels for greens to recover. Subsequent application of abamectin reduced *M. nebraskense* populations to 140/100 cm^3 soil and the bentgrass recovered (Fig 5.2e, f; Thomas et al. 2017). Similar injury has recently been observed at other Albuquerque golf courses as well as courses in Roswell and Carlsbad in southeastern New Mexico. Unlike golf courses in Arizona and many other western states, no *Meloidogyne* species have been detected at any of these New Mexico courses, all of which were established by direct seeding of bentgrass greens following augmentation of native sites with additional sand. *Mesocriconema nebraskense* is known to occur in native prairies in the North American Great Plains (Olson et al. 2017).

5.3.5 *Lesion Nematodes,* Pratylenchus *spp.*

Lesion nematodes have been associated with damage to corn and pinto bean in New Mexico and may be emerging as a potential pathogen of vineyards and of creeping bentgrass on golf courses. Crop injury from *Pratylenchus* spp. has yet to be observed in fields that are co-infested with *M. incognita*, but does occur in fields where corn is planted following repeated crops of small grains, corn, or sorghum in the absence of root knot nematodes. Similarly, injury to pinto bean can occur in fields previously cropped to gramineaceous hosts that increased *Pratylenchus* populations While the impact of crop rotation on enhancing lesion nematode injury to subsequent crops is well known, there is little information on the use of rotation to reduce *Pratylenchus* populations in New Mexico crops. Lesion nematode populations in turf are being closely watched on golf courses where bentgrass is recovering from *M. nebraskense* injury. *Pratylenchus* numbers recovered from soil at some of these sites have increased tenfold to 390/100 cm^3 soil as ring nematode numbers decline and turf recovers. No information is available on damage thresholds for *Pratylenchus* spp. in turf in New Mexico, but the observed numbers exceed thresholds established on turf elsewhere (Dickerson et al. 2000). Recently *Pratylenchus* populations were discovered to be associated with declining Riesling grapes in a vineyard in North Central New Mexico. Nematode numbers were 15–30 times greater than what is considered a high population in vineyards in California (Bettiga 2013).

5.4 Arizona Agriculture

Agriculture acreage in Arizona was highest between 1940 and 1980 (Ottman 2002), however, it has been declining ever since. The largest acreages today are 113,000 ha of alfalfa, 81,000 ha of cotton, 53,000 ha of vegetables (mostly lettuce, spinach, melons, broccoli, squash, potatoes and watermelon), 40,000 ha of wheat and 7200 ha of citrus (USDA Census of Agriculture 2016). There are smaller hectarages of peppers and other vegetables, pecans, apples, date palms and sudan grass. Plant parasitic nematodes have always been a problem for Arizona growers. Root knot nematodes caused significant yield losses in vegetables in the 1940s. At that time, there were very few regulations with regard to the movement of infected plant material and root knot nematodes were inadvertently spread and introduced to new fields in the state (Brown 1948). Even today root knot nematodes (*Meloidogyne* spp.) cause high yield losses, if fields are left untreated. The following is a description of the major plant parasitic nematodes in Arizona and methods used to manage them.

5.5 Plant Parasitic Nematodes of Arizona

5.5.1 Stem and Bulb Nematode, Ditylenchus dipsaci

Alfalfa stem nematode was reported in Arizona for the first time in 1935 (George 1936). A survey of alfalfa fields in the 1980s showed that *Ditylenchus dipsaci* was present in fields in Graham, Maricopa and Yuma Counties (Nigh 1987). Of the 344 fields sampled 31% were infested with stem nematodes. Today, stem nematodes in Arizona affect alfalfa only in Maricopa County (Mike Ottman, University of Arizona; personal communication). It has not been detected in other alfalfa producing counties. Stem nematodes can be easily spread through soil attached to equipment, contaminated seed or shared irrigation canals. The nematodes prefer residing in plant tissue rather than soil. They migrate up a plant stem in a film of water and infect developing buds after entering the plant through stomates. Once inside the bud the nematodes release enzymes that affect plant growth resulting in swollen nodes and stunted plants. With a crop value of over $360 million (USDA Census of Agriculture 2016), an estimated yield loss of 1–10% in susceptible alfalfa varieties due to stunted plants would translate into $3.6–36 million of lost economic revenue in Arizona. Alfalfa stem nematodes are very host specific and can only reproduce on alfalfa, sainfoin or sweet clover. If no suitable host is found the nematodes can go into an anhydrobiotic state, which means they completely desiccate and survive for several years waiting for a suitable host (Skantar 2015). Management options have been studied for years. In the 1950s, Henderson and Williams (1955) evaluated the application of broadcast aldrin and parathion dust incorporated in the soil. The aldrin treatment was more effective than the parathion treatment. Alfalfa seedlings grew vigorously compared to seedlings in untreated control plots. In the 1980s research was conducted on the efficacy of nematicides/insecticides in reducing populations of stem nematodes. Many of the tested pesticides were effective (Nigh 1983, 1988). All tested insecticides/nematicides tested were highly effective in the trials. Nigh showed that applications in the fall often eliminated the need for additional applications in the spring but spring applications frequently required additional applications in the fall. None of the insecticides/nematicides still on the market that were registered for alfalfa in the 1980s is registered for use today. The main management option is crop rotation for about 3–4 years to reduce the number of nematodes in the field to levels that allow alfalfa production. There are resistant alfalfa varieties but even the highly resistant ones have only about 50% resistant plants. A combination of crop rotation and resistant varieties would be the best option for managing alfalfa stem nematode. To prevent the spread and introduction into uninfested fields, cleaning equipment and purchasing certified nematode-free seed are also important. It is unknown how widespread the implementation of equipment cleaning and certified seed use is in Arizona.

5.5.2 Root Knot Nematode, Meloidogyne incognita *in Vegetables and Cotton*

Meloidogyne incognita is widespread in Arizona and is present in most vegetable and cotton growing counties. Vegetables most commonly affected are melon, watermelon, carrots, potatoes and peppers. On cotton, galls on roots are small, but vegetable roots can be severely deformed and unable to take up enough nutrients and water to sustain the plant. On average, the yield loss in cotton due to root knot nematodes alone is 5% in Arizona (National Cotton Council of America n.d.-b). There are a few cotton varieties that are resistant to root knot nematodes that can be used in sustainable production. Research was conducted in the 1970s by McClure et al. (1974) on determining factors that influence resistance to root knot nematodes in cotton. The study showed that nematodes can still colonize the roots but that there were fewer females per gall and fewer eggs per egg-mass. In addition, galls were often void of nematodes when dissected and stained. Root knot nematodes do not only cause yield losses they in cotton but they can also exacerbate cotton seedling disease caused by *Rhizoctonia solani*. A study conducted by Reynolds and Hanson (1957) demonstrated that even though seedling emergence was not affected, the percentage of seedlings infected with *Rhizoctonia* increased by 16% in treatments containing both nematodes and the fungus compared to *Rhizoctonia* treatments alone. Stand loss in treatments containing both nematode and *Rhizoctonia* was nearly 50% compared to plots that had been fumigated and had 5–8% stand loss. In contrast, there are no sustainable management options for *M. incognita* in vegetables that could be used in large scale agricultural production. To manage root knot nematodes in vegetables in Arizona, 90% of growers fumigate with 1,3-dichloropropene. When fumigation is used, yield losses are zero, however, if no fumigation is conducted in a yield the losses can easily reach 100% as fields are being abandoned and not harvested (Mike Arbogast, PCA, personal communication). To prevent their spread and introduction into uninfested fields, cleaning equipment is important, but it is unknown if this management option is being implemented.

5.5.3 Root Knot Nematodes in Turf, **M. graminis** *and* **M. marylandi**

Root knot nematodes had been associated with yellowing of golf course greens but no attempts had been made until 2008 to determine the species present in golf course greens in the Western United States and their association with turf grass types. From 2008 to 2012, research was conducted at the University of Arizona on golf courses in the Western United States to determine the presence of root knot nematodes on golf course greens. Overall 60% of sampled golf courses had root knot nematodes in their greens. In Arizona, *Meloidogyne graminis* and *M. marylandi* were the two species identified in golf courses with *M. marylandi* being the most common species (McClure et al. 2012). Both *M. graminis* and *M. marylandi* prefer warmer climates. The higher percentage of root knot infested golf courses in the Western United States compared to reports from other states may be due more to golf courses following standards set by the United States Golf Association for golf course greens. The greens have to consist of at least 92% sand, which is very conducive for root knot nematode establishment and development. Sustainable management options for root knot nematodes in golf course greens are limited to cultural options and sanitation. Cleaning equipment before moving from one golf course to the next to prevent the spread of nematodes on soil attached to the equipment is very beneficial. In established turf, maintaining vigorous plants with a good root system will allow infected turf to cope with the nematodes and minimize symptoms (Moseley et al. 2017).

5.5.4 *Citrus Nematode,* Tylenchulus semipenetrans

The citrus nematode was first found in Arizona in 1926 (Olsen et al. 2011). *Tylenchulus semipenetrans* is the only nematode species affecting citrus in Arizona where up to 90% of the citrus hectarage is affected. The nematodes feed on the roots and cause the trees to decline over time. The rate of decline depends on the overall health of infected trees. Vigorous trees that become infected may not show any signs for many years while heavily infected, stressed trees may show dieback in the upper canopy, yellowing of leaves, defoliation and reduced yield and fruit quality after 3–5 years. There are four known races of citrus nematodes. In Arizona, the race “Citrus” is found that can, in addition to reproducing on citrus, also reproduce on persimmon and olive (Inserra et al. 1980). The main management options are the use of resistant rootstock and certified nematode-free planting material. Chemical control was studied by Reynolds and O’Bannon (1958). 1,2-Dibromo-3chloropropane (DBCP) was found to be very effective as a treatment in established citrus orchards. Testing different rates (3.12, 6.24 and 9.36 kg per hectare), low to medium rates were found to be 99% effective. In combination with hedging or selective pruning resulted in rejuvenation of severely infected trees and increased fruit size. The product was used by Arizona citrus growers until 1977 when it was taken of the market. Other control products, aldicarb and fenamiphos, were not popular with growers. Fenamiphos was ineffective for nematode control in the desert (Van Gundy et al. 1981) and aldicarb had a very high mammalian toxicity and was very mobile in water (McClure and Schmitt 1996). In the 1990s, McClure and Schmitt (1996) tested cadusafos for control of citrus nematodes under desert conditions. At the time cadusafos had been registered in South Africa to manage citrus nematodes there. In two trials in Yuma, AZ citrus orchards two products containing cadusafos were very effective in reducing nematode populations on many trees below detection levels. Citrus yield was increased by 29–45%. In addition, the trials showed the products were so effective that treatment would only have to be done every other year. There is currently no research on citrus nematodes in Arizona.

5.5.5 *Root Lesion Nematodes,* Pratylenchus *spp. on Cotton*

Lesion nematodes are the second most important plant parasitic nematode species found on cotton in Arizona. *Pratylenchus* spp. are found in all cotton growing counties (Husman et al. 2001). The nematodes feed on the roots causing wounding that allows other pathogens such as bacteria and fungi, to colonize roots and maximize the damage caused to the plant. For example, *Verticillium dahliae*, a soilborne pathogen common in cotton fields in Arizona, has been shown to have a synergistic relationship with lesion nematodes. Mountain and McKeen (1962) found that *V. dahliae* increased reproduction rates of lesion nematodes in eggplant and tomato roots. The number of *P. penetrans* per pound of soil doubled in tomato and eggplant plots when *Verticillium* was added to the soil in contrast to plots without the fungus. In addition, the authors saw an increase in *Verticillium* wilt with increasing population sizes of *P. penetrans*. This could indicate that feeding on the roots by the nematodes provides additional entrance wounds for the fungus to enter the host plant. None of the cotton varieties grown in Arizona have resistance to lesion nematodes and there are no other sustainable management options available.

5.5.6 Other Nematodes

There are several nematode species that can potentially cause serious losses in minor crop in Arizona. The dagger nematode was found in high numbers in a survey in 1995 in Arizona vineyards. The populations in some of the vineyards reached levels that were considered damaging to the plants (McClure 1999). Dagger nematodes can transmit several viruses to host plants. No viruses were found in the surveyed grapes. To manage dagger nematodes that can cause a slow decline in grapes a few resistant rootstocks are available (Bettiga et al. 2016).

Meloidodera charis was found in Arizona in the 1970s in association with honey mesquite roots. The distribution in the state was mainly in the regions where honey mesquite had been planted. To date no damage to plants by the nematode has been reported by a host range test showed that the nematode can infect other plants besides honey mesquite including tomato, melon, saguaro and golden barrel cactus. The experimental host plants are important crops and landscape plants in Arizona (Hartman 1978).

Two species of needle nematodes, *Longidorus africanus* and *L. orientalis* have been discovered in a survey of date palms in Yuma County, Arizona and in Florida on inspected date palms produced in Arizona (Subbotin et al. 2015). Both needle nematode species are native to the Middle East and may have been introduced to California on date palm offshoots as early as the first half of the 1900s. The presence of *L. orientalis* is mostly in areas of date palm production. The host range of *L. orientalis* includes date palms, citrus, fig trees and grapevines in Middle East, Spain and Greece (Loof 1982; Palomares-Rius et al. 2010; Tzortzakakis et al. 2014). No *Longidorus* species were discovered in the survey of Arizona vineyards (McClure 1999).

5.6 Conclusions

Major factors that contribute to limited use of sustainable plant parasitic nematode management practices in New Mexico and Arizona include a lack of regionally-adapted nematode-resistant or tolerant cultivars and perhaps, more importantly, competition for available water and arable land. Much of the land mass in both states is publicly owned and not suitable for crop production due to inherent physical characteristics and/or a lack of access to water and irrigation infrastructure.

Existing farmland must compete with urban demands for limited water resources and land use requirements, driving up both the cost of irrigation and land value. As a result, producers are less likely to adopt nematode management strategies that limit their ability to respond to market opportunities or reduce land use profitability. A recent survey of chili pepper producers in New Mexico confirmed that the majority are aware of sustainable and integrated pest management strategies and are willing to utilize such techniques as long as profitability is maintained (Martinez 2017). Above all else, sustainable nematode management practices must not pose economic risk to producers, if these practices are to be implemented.

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Chapter 6
Plant Parasitic Nematodes in California Agriculture

John J. Chitambar, Becky B. Westerdahl, and Sergei A. Subbotin

6.1 Introduction

California continues to lead the United States in agricultural production and is a main provider of food for the nation and much of the world. As the nation's third largest state by land area comprising of distinct topographical contrasts, California produces numerous agricultural crops primarily within its valley regions. Plant parasitic nematodes are associated with these crops and can be a significant threat to the state's agricultural production. An overview of California's agricultural crop production and associated plant parasitic nematode problems and management strategies are provided in this chapter.

6.2 California's Major Agricultural Crops

California's climate and geography allows the production of the largest diversity of agricultural crops in the U.S. (Table 6.1; Fig. 6.1). In 2016, fruits, nuts and vegetables continued as the state's leading crops and accounted for 56% of the nation's non-citrus fruit and nut production and over 46% of the nation's citrus production. The total value of all fruits and nuts produced in California was $19.7 billion. California is the number one producer of grapes in the nation, producing 88% of the

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Table 6.1 Selected economically important crops of California for 2016 (California Agricultural Statistics Review 2016–2017)

Crops[a]	Area harvested 1000 ha	U.S. rank	CA share of U. S. receipts percent	Total value $1000	Five leading counties by gross value of production
Fruit and nut crops					
Almonds	376.0	1	100.0	5,158,160	Kern, Fresno, Stanislaus, Merced, Madera
Apples	5	6	1.6	54,013	El Dorado, San Joaquin, Santa Cruz, Fresno, Sonoma
Apricots	3.4	1	85.2	48,929	Stanislaus, Fresno, Kings, Tulare, San Joaquin
Avocados	20.8	1	93.6	412,050	San Diego, Ventura, Santa Barbara, San Luis Obispo, Riverside
Blueberries	2.5	2	14.5	108,765	Tulare, Kern, San Joaquin, Ventura, Fresno
Cherries, Sweet	13.2	2	21.4	184,490	Kern, San Joaquin, Fresno, Tulare, Kings
Dates	4.0	1	68.9	46,650	Riverside, Imperial
Figs	2.4	1	100.0	29,230	n/a[b]
Grapefruit, all	3.8	2	26.6	67,664	Riverside, San Diego, Tulare, Kern, Imperial
Grapes, all	336.4	1	89.2	5,581,410	Kern, Napa, Fresno, Tulare, Sonoma
Kiwifruit	1.4	1	100.0	44,431	Tulare, Yuba, Butte, Fresno, Sutter
Lemons	18.8	1	78.6	(Withheld)	Ventura, Riverside, Tulare, Kern, San Diego
Nectarines	7.6	1	92.6	137,418	Fresno, Tulare, Kings, Kern, Contra Costa
Olives	14.0	1	100.00	138,090	Tehama, Tulare, Glenn, San Joaquin, Yolo
Oranges, all	62.8	2	42.9	826,294	Tulare, Kern, Fresno, San Diego, Madera
Peaches, all	16.0	1	55.7	350,285	Fresno, Tulare, Stanislaus, Sutter, Kings
Pears, all	1.7	3	19.7	93,585	Sacramento, Fresno, Lake, Mendocino, Tulare
Pecans	n/a	6	2.1	14,656	n/a

(continued)

Table 6.1 (continued)

Crops[a]	Area harvested 1000 ha	U.S. rank	CA share of U. S. receipts percent	Total value $1000	Five leading counties by gross value of production
Pistachios	95.6	1	100.0	1,506,120	Kern, Tulare, Fresno, Madera, Kings
Plums and Prunes	25.4	1	100.0	195,754	Fresno, Tulare, Kings, Kern, Madera[c]
Raspberries	4.1	1	83.1	380,447	Ventura, Santa Cruz, Monterey, Santa Barbara
Strawberries, all	15.1	1	78.5	1,834,783	Monterey, Ventura, Santa Barbara, San Luis, Obispo, Santa Cruz
Tangerines, Mandarins, Tangelos and Tangors	22.8	1	93.3	(Withheld)	Kern, Tulare, Fresno, Madera, Riverside
Walnuts	126.0	1	100.0	1,241,660	San Joaquin, Butte, Glenn, Tulare, Stanislaus
Vegetable and melon crops					
Artichokes	2.7	1	100.0	69,119	n/a
Asparagus	3.2	1	35.5	26,624	Fresno, Monterey, San Joaquin, Kern, Imperial
Beans, fresh	2.8	2	20.3	55,020	n/a
Broccoli	49.2	1	91.5	779,186	Monterey, Santa Barbara, Imperial, San Luis Obispo, Fresno
Cabbage, fresh market	5.7	1	39.5	158,976	Monterey, Ventura, Imperial, Santa Barbara, Kern
Carrots, fresh	26.9	1	89.8	702,030	Kern, Imperial, Monterey, Riverside, Fresno
Cauliflower	12.9	1	82.7	322,154	Monterey, Santa Barbara, Imperial, San Luis Obispo, Riverside
Celery	10.8	1	94.8	340,035	Ventura, Monterey, Santa Barbara, Imperial, San Benito
Corn, fresh sweet	13.9	1	18.3	163,751	Imperial, Contra Costa, Fresno, Riverside, Santa Clara
Cucumber, fresh market	3.7	2	20.9	36,285	n/a

(continued)

Table 6.1 (continued)

Crops[a]	Area harvested 1000 ha	U.S. rank	CA share of U. S. receipts percent	Total value $1000	Five leading counties by gross value of production
Garlic	11.0	1	100.0	268,665	Fresno, Kern, Riverside, Santa Clara, Madera
Lettuce, all	83.6	1	68.0	1,960,266	Monterey, Imperial, Santa Barbara, San Benito, Fresno
Melons, cantaloupe	10.2	1	43.9	91,035	Fresno, Imperial, Merced, Riverside, Kern
Melons, honeydew	4.4	1	100.0	67,584	Fresno, Riverside, Imperial, Sutter
Melons, watermelon	5.0	2	21.2	122,850	San Joaquin, Kern, Riverside, Fresno, Imperial
Onions, all	17.7	1	24.6	183,386	Imperial, Fresno, Kern, Monterey, San Benito
Peppers, all	10.6	1	55.3	496,770	Riverside, Ventura, Kern, San Benito, Santa Clara[d]
Pumpkin	2.0	5	7.3	15,255	n/a
Spinach, fresh market	11.4	1	57.7	174,406	Monterey, Imperial, San Benito, Santa Clara, Santa Barbara
Squash	2.5	1	21.9	35,925	n/a
Tomatoes, all	116.6	1	64.7	1,329,523	Fresno, Merced, San Diego, Kern, Santa Clara[e]
Field and seed crops					
Beans, dry	19.6	5	9.5	70,286	Stanislaus, Tulare, San Joaquin, Fresno, Sutter
Cotton lint, all	86.4	3	7.5	(Withheld)	Kings, Fresno, Merced, Kern, Tulare
Cottonseed	n/a	3	6.7	75,175	Kings, Fresno, Kern, Tulare, Merced
Hay, alfalfa and others	480.0	1	12.5	966,192	Imperial, Kern, Merced, Tulare, Riverside[f]
Potatoes (excl. sweet)	13.2	5	6.8	265,305	Kern, San Joaquin, Imperial, Siskiyou, Riverside
Potatoes, sweet	8.0	2	21.4	151,280	Merced, Stanislaus, Kern

(continued)

Table 6.1 (continued)

Crops[a]	Area harvested 1000 ha	U.S. rank	CA share of U. S. receipts percent	Total value $1000	Five leading counties by gross value of production
Rice	214.4	1	29.1	649,289	Colusa, Butte, Sutter, Glenn, Yolo
Sugar beets	10.0	7	3.0	n/a	Imperial

[a]Crops in bold are included in California's top 20 commodities for 2016, by value and rank
[b]*n/a* Not available
[c]Five leading counties for plums; five leading counties for dried plums (prunes) in 2016 were Tulare, Butte, Yuba, Sutter and Tehama
[d]Leading counties for bell peppers
[e]Leading counties for fresh market tomatoes only
[f]Leading counties for alfalfa hay only

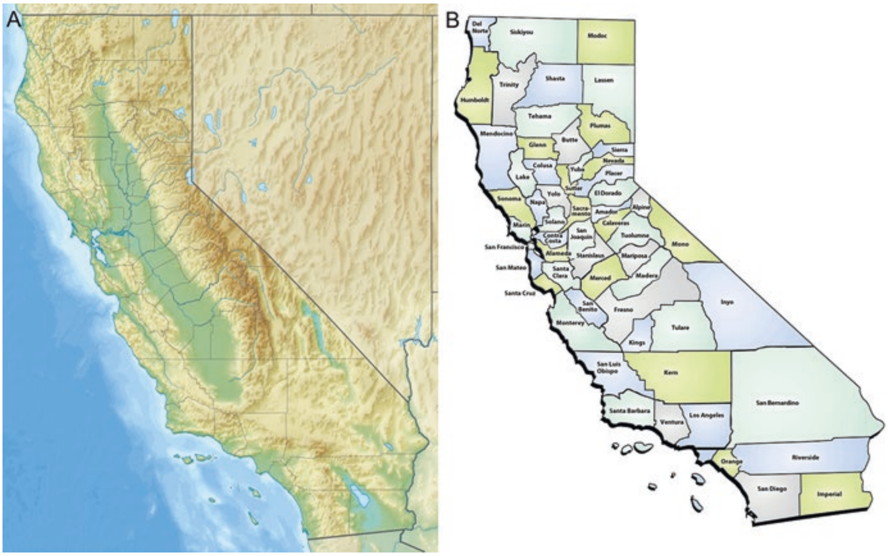

Fig. 6.1 (**a**) California physical map; (**b**) California county map. (Source **a** quazoo.com; **b** picquery)

nation's total tonnage. The state also produces 80% of worldwide almond production. The total value of fresh and processing vegetables and melon production was $7.4 billion with lettuce as the leading vegetable crop, in value of production ($2.0 billion), followed by tomatoes ($1.3 billion). Furthermore, California is the nation's sole producer of 99% or more of almonds, artichokes, dates, figs, garlic, grapes (raisins), kiwifruit, Honeydew melons, olives, peaches (clingstone), pistachios, rice (sweet), seed (Ladino clover) and walnuts (CDFAa 2016–2017). California is the largest producer of almonds in the world, with approximately 80% in global production, and the second largest producer of walnuts in the world. Almonds continue to be the state's top valued agricultural export commodity, with $4.50 billion in foreign sales in 2016. California is, also, the nation's largest agricultural exporter of 14.9% of total U.S. agricultural exports in 2016, and the sole exporter of 99% or more of almonds, artichokes, dates, dried plums, figs, garlic, kiwifruit, olives and olive oil, pistachios, raisins, table grapes and walnuts (CDFAb 2016–2017). California's nursery, greenhouse and floriculture crop production, which includes cut flowers, potted plants, foliage plants, bedding plants and indoor decorative, was valued at $947 million in 2015. California's numerous public and private golf courses are major users of turfgrasses and represent 3.5% of total turf grass cultivated in the state. The golf industry ($6.3 billion in 2011), is comparable in size to other important state industries including greenhouse/nursery crops, and therefore, the use and importance of turf grass management cannot be under rated (SRI International 2013).

6.3 California's Major Agricultural Regions

The Central Valley, which includes all or part of 18 Northern California counties and extends through the center of the state from Shasta County in the north to Kern County in the south, is the state's agricultural heartland that produces more than 250 different crops with an estimated value of $17 billion per year. The Valley alone accounts for one-fourth of the nation's food including 40% of the nation's fruit, nut and other agricultural crops, on less than 1% of the nation's total farmland and is marked by a hot Mediterranean climate in the north, and a dry, desert-like climate in the southernmost regions (USGS 2017). The top four agricultural counties namely Kern, Tulare, Fresno and Monterey Counties, that lead in total value of production and leading commodities are in the Central Valley and experience a growing season of 9–10 months (CDFAa 2016–2017; Morgan and McNamee 2017). The Central Valley is subdivided into (1) the Sacramento Valley which encompasses the region north of the Sacramento-San Joaquin River Delta and comprises all or part of ten Northern California counties, and (2) the San Joaquin Valley which extends from the Delta to the Tehachapi Mountains in the south and includes seven northern counties as well as most of Kern County in Southern California.

The Salinas Valley lies within Monterey County, west of the San Joaquin Valley and south of San Francisco Bay, with cool summers and relatively mild winters in the northern region and warmer summers and colder winters in the southern region. The Salinas Valley is the State's major producer of salad and vegetable crops as well as strawberries and wine grapes.

The Coachella Valley is part of the Colorado Desert extending from the Salton Sea through Riverside County to the San Gorgonio Pass in Southern California, with warm climates through the year and generally, extremely arid climate with most precipitation occurring during the winter months. Irrigation and warm climates have resulted in production of varied vegetables, fruits including date palms, citrus and mangoes, cotton and alfalfa (Britannica 2018).

The Imperial Valley, lying within Southern California's Imperial County and extending south of the Coachella Valley to the Gulf of California, has desert climate and extreme daily temperatures. Summer temperatures are usually greater than

38 °C, whereas, temperatures from late October to mid-April are relatively mild. The Imperial Valley comprises thousands of hectares of irrigated farmland and is a major producer of winter fruits that cannot endure cool temperatures, and vegetables, cotton and grain crops.

The Napa and Sonoma Valleys lie adjacently north of San Francisco along the coastal mountain ranges. These regions have a Mediterranean climate of warm and dry days and cool nights during summers and wet and cool winters, well-suited for the cultivation of premium wine grapes.

Several small valleys lie within California's Central Coast which includes parts of San Luis Obispo, Santa Barbara and Ventura Counties and provide unique climate niches and soil types ideal for year-round production of fruits, wine grapes, cool and warm season vegetables and seed crops (UCCE 2005).

6.4 Nematology in California: Early Discoveries

Nematode problems in agriculture were not fully recognized in the USA until the early 1900s. The early development of Nematology was mainly limited to reports on root knot nematodes and initial work was concentrated on the US east coastal region. This recognition soon led to initial nematode surveys in California during 1907 and a first report by E. A. Bessey in 1911 of the presence of root knot nematodes (*Meloidogyne* spp.) and sugar beet cyst nematodes (*Heterodera schachtii*) in several regions of the State. With growing awareness of nematode problems in California, in 1912, the citrus nematode was discovered by a Los Angeles County Agricultural Inspector, J. R. Hodges., and in 1928, was shown to cause serious damage to citrus seedlings, by E. E. Thomas at the Citrus Experiment Station in Riverside. Initial surveys in the early 1920s also detected the stem and bulb nematode, *Ditylenchus dipsaci*, and in 1927 the root lesion nematodes, *Pratylenchus* spp., were first reported on fig. In the decade that followed, root lesion nematode damage to fig, walnut and cherry trees was found to be widespread in California. Critical to the initial detections, research and management of plant parasitic nematodes in California agriculture, was the development of the Department of Nematology at the University of California and the Nematology Regulatory Program at the California Department of Agriculture. At that time, the State Department of Agriculture estimated the value of nursery stock rejected due to root knot nematode infestation, during the December 1922 to April 1923 planting season, to be $100,000 (Siddiqui et al. 1973; Raski et al. 2002). Losses caused by nematodes were difficult to assess then as several species of ectoparasitic nematodes were being discovered to feed on plant roots without causing distinct symptoms other than restricted root growth. Much about their damage potential and distribution was unknown and their impact on crop growth was recognized only when nematicides were applied to areas where poor plant growth occurred by unknown cause. With the advent of fumigant nematicides, several ectoparasitic nematodes were soon recognized to cause more damage to crops than that caused by endoparasites. In 1959, the Department of

Nematology estimated annual crop losses due to nematodes at \$89,442,000–\$141,721,000 (Allen and Maggenti 1959). In 1951, after review of the nematode situation at that time, the Department of Agriculture and the University of California produced the first distribution record of plant parasitic nematodes in California (Raski et al. 2002). Since then, several in-state surveys have been conducted collaboratively or individually by federal, state, county and University of California agencies, for targeted plant parasitic nematodes such as the burrowing nematode, sugar beet cyst nematode, golden nematode, potato pale cyst nematode, Columbia root knot nematode, sting nematode, strawberry foliar nematode, reniform nematode and other exotic and non-exotic species associated with host plants in cultivated and non-cultivated crop fields, orchards, nurseries and golf greens.

6.5 Economically Important Plant Parasitic Nematodes of Major Crops in California

Plant parasitic nematodes can significantly impact crop production in California. While several species have been found to be associated with different plants grown in the state (Table 6.2), in this chapter, only certain main, economically important plant parasitic nematode species associated with major crops of the state are discussed. These species include the root knot, lesion, stem and bulb, citrus, dagger, ring, pin and sting nematodes and a few others.

6.5.1 Root Knot Nematodes, Meloidogyne *spp.*

Since first being reported in California by E. A. Bessey in 1911, root knot nematodes (*Meloidogyne* spp.) have become the most extensively studied genus in the state. Six species are of significant economic concern: *M. incognita, M. javanica, M. arenaria, M. hapla, M. chitwoodi* and *M. naasi*. Another three species have been reported: *M. graminis, M. marylandi* and *M. fallax* (Table 6.2; Fig. 6.2).

The host ranges of the various species are highly varied (Table 6.2), but as a whole encompass most of the economically important annual perennial, and ornamental crops grown in California (Table 6.1). Species are distributed throughout California's agricultural areas but show some regional and crop distribution preferences. For example, *M. chitwoodi* is found on potatoes and small grains in the northern part of the state in Modoc and Siskiyou Counties. In this same area, *M. naasi* parasitizes barley, wheat and grasses. An isolated occurrence of *M. naasi* has also been found on a bowling green in the Los Angeles area. The northern root knot nematode *M. hapla* is found statewide, particularly in fields cropped to alfalfa where it can reduce alfalfa stand densities by 62% (Noling and Ferris 1985). As the only species that parasitizes cotton, *M. incognita* may be more common on land regularly cropped with cotton (McKenry and Roberts 1985).

Table 6.2 Plant parasitic nematodes associated with various crops in California

Species	Crop	References
Anguna agrostis	Creeping bentgrass	Siddiqui et al. (1973)
A. pacificae	Bluegrass	Cid Del Prado Vera and Maggenti (1984) and McClure et al. (2008)
Aphelenchoides fragariae	Strawberry, ornamentals	Siddiqui et al. (1973) and McKenry and Roberts (1985)
A. ritzemabosi	Strawberry, alfalfa, ornamentals	Siddiqui et al. (1973) and McKenry and Roberts (1985)
Atalodera gracililanceae	*Festuca* sp.	Robbins (1978a)
Belonolaimus longicaudatus	Grasses	Mundo-Ocampo et al. (1994)
Cacopaurus pestis	Walnut	Thorne (1943)
Criconemoides annulatus	Plum, beet, barley, citrus, apple, cotton, strawberry, alfalfa, tomato, tobacco, sorghum, clover, corn, walnut	Raski (1952a) and Siddiqui et al. (1973)
Criconema permistum	Grape	Siddiqui et al. (1973)
Ditylenchus dipsaci	Alfalfa, garlic, onion, sugar beet, alfalfa, phlox, pea, clover, barley	Siddiqui et al. (1973) and McKenry and Roberts (1985)
D. destructor	Potato	Ayoub (1970)
Gracilacus anceps	Tomato	Siddiqui et al. (1973)
G. idalimus	Grape	Dong et al. (2007)
G. mirus	Grape	Raski (1962)
Helicotylenchus digonicus	Oat, beet, citrus, fig, barley, tomato, bean, wheat, grape, corn, nectarine	Siddiqui et al. (1973) and Dong et al. (2007)
H. dihystera	Grape, bermudagrass, onion, beet, citrus, cotton, barley, tomato, rice, almond potato, sorghum, grape, corn, apricot, cherry, peach, plum	Siddiqui et al. (1973), McKenry and Roberts (1985), Subbotin et al. (2015b), and Dong et al. (2007)
H. erythrinae	Beet, cotton, apple, grape	Siddiqui et al. (1973)
H. microlobus	Corn	Subbotin et al. (2015b)
H. paragiris	Apricot, cherry, nectarine, plum	Dong et al. (2007)
H. paxilli	Grasses	Subbotin et al. (2015b)
H. pseudorobustus	Grasses, rice, grape, beet, apricot, cherry, nectarine, plum	Siddiqui et al. (1973), Subbotin et al. (2015b), and Dong et al. (2007)
Hemicriconemoides californianus	Grape	Pinochet and Raski (1975)
Hemicycliophora arenaria	Citrus, tomato	Siddiqui et al. (1973) and Dong et al. (2007)
H. biosphaera	Citrus	Dong et al. (2007)
H. sheri	Prune	Dong et al. (2007)
H. striatula	Nectarine	Dong et al. (2007)

(continued)

Table 6.2 (continued)

Species	Crop	References
Heterodera cruciferae	Table beets, cabbage, Brussels sprouts, broccoli, cauliflower	Siddiqui et al. (1973) and McKenry and Roberts (1985)
H. fici	Fig	Sher and Raski (1956)
H. schachtii	Sugar beet, table beet, cabbage, Brussels sprouts, broccoli, cauliflower, radish, spinach, turnips	Siddiqui et al. (1973) and McKenry and Roberts (1985)
H. trifolii	Clover	McKenry and Roberts (1985)
Hirschmanniella belli	Rice	Siddiqui et al. (1973) and McKenry and Roberts (1985)
Longidorus africanus	Bermudagrass, lettuce, cotton, orange	McKenry and Roberts (1985), Ploeg (1998), and Dong et al. (2007)
L. elongatus	Grape	Siddiqui et al. (1973) and Robbins and Brown (1991)
L. ferrisi	Citrus	Robbins et al. (2009)
L. orientalis	Date palm	Subbotin et al. (2015a)
Meloidogyne arenaria	Alfalfa, apple, grape, nectarine, peach, plum, prune, beans (dry), broccoli, cabbage, cauliflower, carrots, lettuce, cucurbits, sugar beet, wheat, barley, potato	Siddiqui et al. (1973)
M. chitwoodi	Barley, oat, potato	McKenry and Roberts (1985)
M. hapla	Strawberry, sugar beet, carrot, table beets, cabbage, Brussels sprouts, broccoli, cauliflower, celery, lettuce, garlic, onion, tomato, alfalfa, clover, tomato, potato, grape	Raski (1957), Siddiqui et al. (1973), McKenry and Roberts (1985), and Dong et al. (2007)
M. incognita	Beet, cucumber, onion, soybean, olive, alfalfa, bean, tomato, hop, potato, nectarine, grape	Siddiqui et al. (1973) and Dong et al. (2007)
M. graminis	Grasses	McClure et al. (2012)
M. fallax	Grasses	Nischwitz et al. (2013)
Meloidogyne floridensis	Almond	Westphal et al. (unpublished) and Chitambar (2018)
M. marylandi	Grasses	McClure et al. (2012)
M. naasi	Grasses, barley, oat, rye, wheat, turfgrass	Radewald et al. (1970), Siddiqui et al. (1973), McKenry and Roberts (1985), and McClure et al. (2012)
M. javanica	Beet, citrus, tomato, olive, potato, grape, peach	Siddiqui et al. (1973) and Dong et al. (2007)
Merlinius brevidens	Grasses, artichoke, corn, lettuce, alfalfa, cereals, cabbage, carrot, cotton, rice, pea, almond, grape, prune, corn, wheat, potato	Allen (1955), McKenry and Roberts (1985), and Dong et al. (2007)
Mesocriconema rusticum	Grape	Siddiqui et al. (1973)

(continued)

Table 6.2 (continued)

Species	Crop	References
M. xenoplax	Grape, citrus, tomato, apple, plum, walnut, rice, apricot, cherry, peach	Raski (1952a), Siddiqui et al. (1973), and Dong et al. (2007)
Nacobbus dorsalis	Barley, corn	Siddiqui et al. (1973)
Nanidorus minor	Alfalfa, almond, cabbage, barley, bean, carrot, cotton, corn, peppers, sugar beet, onion, tomato, olive, plum	Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Kumari and Subbotin (2012)
Paralongidorus microlaimus	Walnut	Robbins (1978b)
Paratrichodorus allius	Onion	Norton et al. (1984)
P. porosus	Fig, tomato, apple, alfalfa, olive, plum, peach	Siddiqui et al. (1973)
Paratylenchus baldacci	Prune, citrus	Dong et al. (2007)
P. bukowinensis	Apricot, cherry, citrus, nectarine, plum, prune	Dong et al. (2007)
P. dianthus	Citrus	Dong et al. (2007)
P. hamatus	Fig, peach, plum, apricot, beet, carrot, cabbage, barley, alfalfa, apple, potato, grape, peach, almond, cherry, nectarine, plum, prune, citrus	Thorne and Allen (1950), Siddiqui et al. (1973), Raski (1975), Dong et al. (2007), and Van den Berg et al. (2014)
P. holdemani	Citrus	Dong et al. (2007)
P. lepidus	Apricot, cherry	Dong et al. (2007)
P. nanus	Grasses, walnut, alfalfa, cabbage	Siddiqui et al. (1973), Raski (1975), and Van den Berg et al. (2014)
P. neoamblycephalus	Plum, apricot	McKenry and Roberts (1985) and Dong et al. (2007)
P. projectus	Bean, plum	Siddiqui et al. (1973)
P. similis	Citrus	Dong et al. (2007)
P. straeleni	Prune	Van den Berg et al. (2014)
Pratylenchus brachyurus	Cotton, barley, alfalfa, grape, corn, prune	Siddiqui et al. (1973), McKenry and Roberts (1985), and Dong et al. (2007)
P. crenatus	Beet, carrot, barley, olive, tomato, peach, potato, corn	Siddiqui et al. (1973)
P. hexincisus	Grape	Dong et al. (2007)
P. penetrans	Cowpea, cherry, strawberry, oat, cabbage, barley, tomato, alfalfa, pea, potato, wheat, almond, corn, apricot, cherry, plum, grape	Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Subbotin et al. (2008)
P. scribneri	Sudan grass, beans, alfalfa, corn, grape, apple, beet	Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Subbotin et al. (2008)

(continued)

Table 6.2 (continued)

Species	Crop	References
P. thornei	Grasses, sorghum, wheat, onion, sugar beet, cabbage, alfalfa, beans, sorghum, corn, apricot, cherry, grape	Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Subbotin et al. (2008)
P. neglectus	Onion, sugar beet, oat, cabbage, citrus, carrot, alfalfa, barley, soybean, peach, bean, tomato, apple, potato, bean, wheat, corn, clover, grape, apricot, cherry, nectarine, plum, prune, barley	Siddiqui et al. (1973), Dong et al. (2007), and Subbotin et al. (2008)
P. vulnus	Walnut, grape, fig, citrus, apricot, avocado, cherry, olive, peach, almond, plum, raspberry, boysenberry, apple, strawberry, pear, pistachio, nectarine	Allen and Jensen (1951), Hart (1951), Lownsbery (1956), Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Subbotin et al. (2008)
Quinisulcius acutus	Apple, sorghum, peach, grape	Siddiqui et al. (1973)
Rotylenchulus parvus	Alfalfa, cotton, olive, sugar beet, sorghum	Siddiqui et al. (1973) and Dong et al. (2007)
Rotylenchus robustus	Apple, potato, olive, grape, grasses	Siddiqui et al. (1973), Dong et al. (2007), and Cantalapiedra-Navarrete et al. (2013)
Scutellonema brachyurus	Peach, plum	Dong et al. (2007)
S. clathricaudatum	Apricot	Dong et al. (2007)
S. conicephalum	Apricot, cherry, plum	Dong et al. (2007)
Trichodorus californicus	Rose	Siddiqui et al. (1973)
Tylenchulus semipenetrans	Persimmon, citrus, grape, olive	Baines and Thorne (1952), McKenry and Roberts (1985), Dong et al. (2007), and Tanha Maafi et al. (2012)
Tylenchorhynchus agri	Cherry	Dong et al. (2007)
T. aspericutis	Nectarine	Dong et al. (2007)
T. annulatus	Plum	Dong et al. (2007) and Handoo et al. (2014)
T. capitatus	Pear, cabbage, carrot, barley, apple, rye, corn, plum	Allen (1955) and Siddiqui et al. (1973)
T. claytoni	Citrus, tomato, apple, peach, grape, corn	Siddiqui et al. (1973)
T. clarus	Citrus, alfalfa, barley, beans, bermudagrass, cotton, carrot, barley, olive, rice, plum, peach, potato, corn, grape, clover, wheat	Allen (1955), Siddiqui et al. (1973), McKenry and Roberts (1985), and Handoo et al. (2014)

(continued)

Table 6.2 (continued)

Species	Crop	References
T. cylindricus	Cotton, apple, olive, almond, potato, grape, corn, bean	Allen (1955) and Siddiqui et al. (1973)
T. ebriensis	Peach	Dong et al. (2007)
T. elegans	Cherry, plum, grape	Dong et al. (2007)
T. mashhoodi	Apricot, cherry peach, plum, grape	Dong et al. (2007)
T. microconus	Cherry	Dong et al. (2007)
T. nudus	Apricot	Dong et al. (2007)
Xiphinema americanum sensu lato	Plum, apricot, grape, grasses, orange, pecan, walnut, cherry, peach, cherry, alfalfa, apricot, apple, citrus pear, pistachio, raspberry, strawberry, tomato, rice, sorghum, bean	Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Orlando et al. (2016)
X. californicum	Orange, grape, grapefruit, lemon, peach, cherry, plum, lemon, walnut, olive, alfalfa,	Lamberti and Bleve-Zacheo (1979), Lamberti and Golden (1984), Robbins (1993), and Orlando et al. (2016)
X. pachtaicum	Plum, lemon	Robbins (1993) and Orlando et al. (2016)
X. rivesi	Grasses	Orlando et al. (2016)
X. index	Fig, grape	Thorne and Allen (1950) and Siddiqui et al. (1973)
X. insigne	Plum, grasses	Luc and Southey (1980) and Cai et al. (2018)
X. vuittenezi	Grape, fig, citrus, carrot	Luc et al. (1964) and Siddiqui et al. (1973)

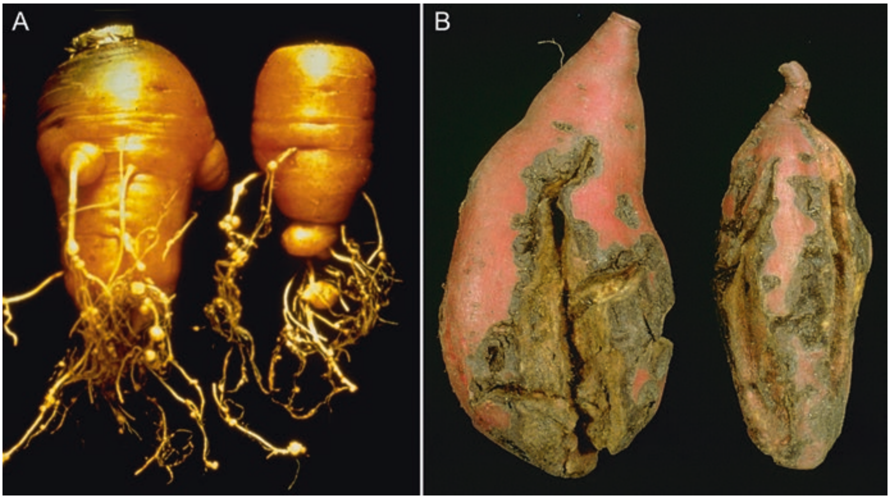

Fig. 6.2 *Meloidogyne* spp. damage (**a**) Carrot; (**b**) Sweet potato. (Credit: J. Radewald and University of California, Riverside)

Characteristic aboveground symptoms of *Meloidogyne* infestation include stunting, loss of quantity and quality of yield, wilting during hot periods of the day, and increased susceptibility to foliage diseases and vascular wilts. In contrast, mild infections can actually stimulate an increase in growth and yield. Belowground, *Meloidogyne* infection causes both a decrease in the size of the root system and the development of root galls. Depending upon the nematode-host combination and the number of nematodes present, galls vary in size from minute to extremely large. Galls on trees and vines, are typically smaller than those on annual crops. In some cases, infections may cause an aesthetic problem rather than growth reduction. In carrots, for example, an early attack on the developing tap root can cause disfiguration through galling and splitting of the tap root, rendering the plant unmarketable (McKenry and Roberts 1985).

Heavily infected roots are often badly discolored and rotted due to the invasion of roots by fungi such as *Rhizoctonia*, *Fusarium* and *Pythium* which cause rotting and breakdown of galled tissue, and by bacteria. A severe root rot of tomato caused by *M. incognita* and *R. solani* was associated with nutrient mobilization into gall tissue and root exudations, but root decay did not develop when root exudates were continuously removed by leaching (Van Gundy et al. 1977).

Second-stage juveniles (J2) of this sedentary endoparasitic nematode that hatch from eggs and move within the film of water that lines soil pores, are the infective stage. Photoperiod influences the migration of *M. incognita* juveniles toward tomato root (Prot and Van Gundy 1981b). The stylet is used to penetrate root tips at the zone of elongation. After penetrating the plant root, J2 migrate towards the vascular cylinder where they establish a feeding site and initiate feeding using their stylets. Gall formation may be influenced by secretion of plant-growth regulators by the nematode (Viglierchio and Yu 1965). Once feeding is initiated, J2s become sedentary and undergo three additional moults to become pear or nearly spherical-shaped adults. The adult female lays 150–250 eggs in a gelatinous matrix on or below the surface of the root. From the eggs new infective J2s hatch and start a new cycle (Atamian et al. 2012). The number of males in a population are typically low, but larger numbers may be found toward the end of the growing season, when populations are dense and host plants are under stress (McClure and Viglierchio 1966).

Distinguishing between the species of *Meloidogyne* can be a difficult problem. The female cuticle is finely striated and assumes patterns in the perineal region which are characteristic of the species. Variations of the perineal patterns within a given species are wide, so identification is often difficult and must be based upon examination of many specimens. Cultural management techniques such as crop rotation and trap cropping, rely on knowing the species present in a field. The ability to analyze DNA has progressively led to more advanced and accurate methods of species identification (Hyman et al. 1990) including the ability to distinguish mixed populations of single juveniles (Williamson et al. 1997), and juveniles extracted directly from soil (Qiu et al. 2006). Host races occur within root knot nematode species. Four host races within *M. incognita* can be differentiated by a host differential test. M. *incognita* races 3 and 4 will reproduce on cotton, whereas races 1 and 2 will not (McKenry and Roberts 1966).

Meloidogyne species occur in a wide range of soil textures, but they appear to predominate in coarse textured sandy and sandy loam soils where plant damage is often accentuated in sandy patches or streaks within a field. However, clay particles may aid in the migration of root knot juveniles to plant roots by absorbing and holding root exudates or bacterial by-products which form a concentration gradient enabling nematodes to locate roots (Prot and Van Gundy 1981a). Soil oxygen concentrations below 3.5% reduced root growth, size of developing females, production of nematode eggs and root galls of *M. javanica* (Van Gundy and Stolzy 1961).

6.5.1.1 Management

Resistant cultivars of some *Meloidogyne* susceptible crops are available including tomato, cotton, cowpea, lima bean and sweet potato (Roberts 1993). Nemaguard rootstock is resistant to root knot nematodes and is widely used in California for perennial crops including almonds and peaches. Processing tomatoes are a major California crop (Table 6.1). Tomato cultivars are available with the *Mi* gene located on chromosome 6 that are resistant to *M. incognita, M. javanica* and *M. arenaria* but not to *M. hapla* (Ho et al. 1992). *Mi*-mediated resistance is characterized by a localized necrosis of host cells near the invading nematode that begins about 12 h after infestation occurs. Resistance mediated by *Mi* is lost above 30 °C (Williamson and Hussey 1996). The use of resistant varieties became increasingly popular following field trials demonstrating the effectiveness of the resistance (Roberts and May 1986). The selection of resistance breaking populations in fields cropped to resistant varieties for multiple years began to be seen in 1995 (Kaloshian et al. 1996).

Another resistance gene, *Mi-3*, identified in *Lycopersicon peruvianum* on the short arm of chromosome 12 confers resistance to nematodes that are virulent on tomato lines that carry *Mi-1*, and is effective at temperatures at which *Mi-1* is not effective (Ammati et al. 1986; Williamson 1998; Yaghoobi et al. 1995, 2005). A heat-stable resistance gene, *Mi-9* from *Lycopersicon peruvianum* has been found that is localized on the short arm of chromosome 6 (Ammiraju et al. 2003).

Following a field observation that nematode resistant tomatoes were also resistant to the potato aphid, *Macrosiphum euphorbiae*, it was determined these traits are tightly linked (Kaloshian et al. 1995; Martinez De Ilarduya and Kaloshian 2001). Subsequently, it was determined that on the short arm of tomato chromosome 6, a cluster of disease resistance genes have evolved harboring the *Mi-1* and *Cf* genes. The *Mi-1* gene confers resistance to root knot nematodes, aphids, and the sweet potato whitefly (*Bemisia tabaci*) (Nombela et al. 2003). Ol-4 and Ol-6 that confer resistance to tomato powdery mildew are also in this cluster (Seifi et al. 2011). Changes in expression of jasmonic acid (JA)- and salicylic acid (SA)- dependent defense genes in response to potato and green peach aphids suggest that aphid feeding involves both SA and JA/ethylene plant defense signaling pathways and that *Mi-1*-mediated resistance might involve a SA-dependent signaling pathway (Martinez De Ilarduya et al. 2003).

Genetic material is being developed to transfer root knot (*M. incognita, M. javanica, M. arenaria)* resistance from 'Brasilia' carrot germplasm into California fresh market carrots via two resistance genes found on chromosome 8 (Roberts 1993; Ali et al. 2014). In fields with medium or high levels of nematode infestation, root galling in NemX, an Acala-type upland cotton, resistant to *M. incognita* was reduced and lint yields were increased compared to those on a susceptible variety (Ogallo et al. 1997). The variety was also highly effective in protecting plants from race 1 of *Fusarium* wilt as a disease complex (Wang and Roberts 2006). In resistant cowpea, the induction of resistance is relatively late compared to that in tomato. Nematodes were able to develop normal feeding sites similar to those in susceptible roots up to 9–14 days post inoculation. Following this, giant cell deterioration was observed and the female nematodes showed arrested development, failed to reach maturity and did not initiate egg laying in resistant roots (Das et al. 2008).

Optimum temperatures for *Meloidogyne* vary among different species and even among the different life stages (Ploeg and Maris 1999). The *M. incognita* life cycle is completed in 4–6 weeks at 26–28 °C (Atamian et al. 2012). Nematode reproduction was directly proportional to temperature between 14 and 30 °C for *M. incognita* and between 18 and 26 °C for *M. javanica* (Roberts and Van Gundy 1981). The migration of *M. incognita* juveniles begins at about 18 °C and reaches its maximum at 22 °C. Juveniles of *M. hapla* are able to migrate at a lower temperature than those of *M. incognita* (Prot and Van Gundy 1981b). For *M. incognita*, delay of planting date for a host crop until soil temperature is below 18 °C can be used to minimize damage because the plants will not be infected, and therefore, nematode development and reproduction will not occur (Roberts et al. 1981a). If plantings are made at temperatures above this threshold, nematode development and reproduction may occur during winter. Planting at cool soil temperatures will mean that nematode activity is low and young root systems can establish before nematode activity increases as soil temperature rises during the spring. Certain crops may be planted during the winter months and harvested before injury occurs in the spring. The potato industry of the San Joaquin Valley has utilized this method. Plantings can be made during cool months and harvested before June without visible infestation. If allowed to remain a month or two longer, the entire crop would be unsalable. For crops due for harvest that are infested with nematodes, growers should schedule the infested crop for an early harvest to prevent additional nematode reproduction and buildup (McKenry and Roberts 1985).

Determination and use of economic thresholds is an important consideration in nematode pest management programs, but their development has been limited by reliability of nematode population assessment techniques (Ferris 1978). A computer-simulation model of a *Meloidogyne*-grapevine system (Ferris 1976) developed in conjunction with extensive field sampling, greenhouse and laboratory research has contributed to our knowledge of the biology and management of nematodes in vineyards (Ferris and McKenry 1974, 1975, 1976; Melakeberhan et al. 1989). The economic importance of grapes statewide (Table 6.1), and their status as hosts to multiple genera of plant parasitic nematodes has led to extensive host range testing and breeding to develop rootstocks resistant not only to multiple genera of nematodes, but to virus and insect pests as well (Chitambar and Raski 1984; Anwar and McKenry 2002; McKenry et al. 2004). After a 15-year screening process, 13 selections emerged with either almost complete or complete combined resistance to *M. incognita* Race 3, *M. incognita* pathotype Harmony C, *M. arenaria* pathotype Harmony A, and *X. index*. After a total of 204 separate trials, the rootstocks were released to the grape industry as UCD GRN1, UCD GRN2, UCD GRN3, UCD GRN4, and UCD GRN5 (Ferris et al. 2012, 2013).

A number of studies in California have increased our knowledge of the potential for using biological control to manage *Meloidogyne* spp. Second stage juveniles of *Meloidogyne* spp. were readily infected with the endoparasite *Pasteuria penetrans* (Mankau and Prasad 1977). Hyphae of *Dactylella oviparasitica* proliferated rapidly through *MeIoidogyne* egg masses, and appressoria formed when they contacted eggs (Stirling and Mankau 1979). The nematophagous fungi, *Paecilomyces lilacinus* and *Verticillium chlamydosporium*, were found in a high proportion of Northern California tomato fields but were determined to not be effectively suppressing populations of *M. incognita* (Gaspard et al. 1990). The nematophagous fungus *Hirsutella rhossiliensis* infested *M. javanica* but did not provide effective control (Tedford et al. 1993). Three species of the nematode-trapping fungi *Arthrobotrys* and two of *Nematoctonus* were detected in both organic and conventional field plots but did not suppress *M. javanica* in a laboratory bioassay (Jaffee et al. 1998). Three *Pochonia chlamydosporia* var. c*hlamydosporia* strains isolated from a *M. incognita*-suppressive soil showed potential as biological control agents against root knot nematodes in greenhouse trials (Bent et al. 2008; Yang et al. 2012). Chitinolytic microflora may contribute to biological control of *Meloidogyne* by causing decreased egg viability through degradation of egg shells as shown by laboratory trials with *Lysobacter enzymogenes* strain C3 (Chen et al. 2006) and field trials with a chitin-urea soil amendment (Westerdahl et al. 1992). Various formulations of four entomopathogenic nematode (EPN) species and the supernatants of their mutualistic bacteria were found to suppress *M. incognita* and *M. arenaria* in tomato roots (Kepenekci et al. 2016).

Crop rotation and related techniques are seeing increasing use. Greenhouse and field trials found cultivars of alfalfa, amaranth, oilseed radish, oilseed rape, and safflower that were suitable rotation crops for *M. chitwoodi* (Ferris et al. 1993). *Crotalaria juncea* and *Sesamum indicum* have potential as cover crops to reduce *M. javanica* numbers (Araya and Caswell-Chen 1994). All cultivars of oilseed radish, white mustard, buckwheat, and phacelia tested were hosts to *M. incognita* and *M. javanica* (Gardner and Caswell-Chen 1994). Grafting susceptible melons on *Cucumus metuliferus* rootstocks reduced levels of root galling, prevented shoot weight losses, and resulted in significantly lower levels of *M. incognita* at harvest (Sigüenza et al. 2005). Aguiar et al. (2014) found resistant bell pepper cultivars to be effective in reducing damage by *M. incognita.* Weed hosts of *Meloidogyne* such as the solanaceous nightshade plants, need to be controlled if rotation crops are to be used successfully (McKenry and Roberts 1985).

Field corn and wheat are hosts for root knot nematodes but are tolerant to damage and can yield well under moderate-to-heavy infection. They will maintain or even build up root knot nematode populations in the soil, but they have been grown on infested land without significant yield reduction (McKenry and Roberts 1985). The wheat cultivar Lassik with the *Rkn3* gene is resistant to several isolates of *M. incognita* and *M. javanica* including those that can reproduce on tomato with the resistance gene *Mi-1* (Williamson et al. 2013). Wheat varieties resistant to *M. chitwoodi* have also been found (Kaloshian et al. 1989). Mixed populations of two or more species of *Meloidogyne* are possible in a field, as are the presence of other nematode genera complicating the use of crop rotation and resistant varieties. For example, five plant-parasitic species were found in an alfalfa field: *M. arenaria, Pratylenchus minyus, Merlinius brevidens, Helicotylenchus digonicus,* and *Nanidorus minor* (Goodell and Ferris 1980). Root systems of perennial crops are commonly fed upon simultaneously by multiple nematode species (McKenry and Anwar 2007).

Biofumigation is a technique investigated for management of weeds and fungi as well as nematodes. Brassica species such as broccoli produce glucosinolates, and when these degrade in the soil they release isothiocyanates that are similar to the active ingredient in metam sodium which is one of the more widely used nematicides (Westerdahl 2011; Zasada and Ferris 2003; Edwards and Ploeg 2014; López-Pérez et al. 2010). Marigolds have also been found to reduce damage by *Meloidogyne* on subsequent crops (Ploeg 1999; Huang and Ploeg 1999). Trap cropping can be utilized for sedentary endoparasitic nematodes such as root knot (Westerdahl 2011). A susceptible host is planted and larvae of a sedentary parasitic nematode are induced to enter and establish a feeding site within the roots. Once this has occurred, and the female nematode begins to mature, it is unable to leave the plant root. The plants are then destroyed before the life cycle of the nematode can be completed, trapping nematodes within the root. Soil solarization has shown mixed results, but in some field experiments *M. incognita* J2 were significantly reduced and yield of carrot and survival of cotton seedlings was increased (Stapleton et al. 1987). Goodell et al. (1983) showed that *M. incognita* populations were reduced by approximately 40% (within the tilled zone) for each plowing, following destruction of a cotton crop.

A number of chemicals have been shown to be effective against *Meloidogyne* spp. including aldicarb (Hough and Thomason 1975), phenamiphos (Greco and Thomason 1980), avermectins (Garabedian and Van Gundy 1983), ozone gas (Qiu et al. 2009), DMDS (Cabrera et al. 2014), and fluensulfone (Westerdahl et al. 2014). Sublethal effects of aldicarb stimulated hatch of *M. javanica* (Hough and Thomason 1975).

6.5.2 Citrus Nematode, Tylenchulus semipenetrans

Tylenchulus semipenetrans is commonly referred to as the "citrus nematode" because of its historical association with citrus. Yield losses to citrus due to *T. semipenetrans* are in the range of 10–30% depending on the level of infestation

(Verdejo-Lucas and McKenry 2004). *Tylenchulus semipenetrans* was discovered on citrus roots in Los Angeles County in 1912, and subsequently described by Cobb (1913, 1914). Within a few months of its discovery, it was found to also be present in other citrus growing areas around the world, probably due to distribution on infested nursery stock (Cobb 1914). E. E. Thomas of the Riverside Citrus Experiment Station (predecessor to the Riverside campus of the University of California) conducted the early research on pathogenicity and management of this nematode (Cobb 1914). In 1939, J. C Johnston and G. Thorne examined more than 100 samples from citrus orchards in various parts of the state and found all but one to be infested with *T. semipenetrans* (Thorne 1961).

Van Gundy (1958) conducted a detailed study on the life history and morphology of citrus nematode. Juveniles penetrate the root 2–3 weeks after hatching. A juvenile burrows its anterior end deep inside the root cortex while the posterior end remains outside in the soil. Young females become embedded in the cortex with their anterior regions retaining the ability to move about in a cavity formed from a single plant cell. Feeding occurs on six to ten so-called "nurse cells," which are cortical parenchyma cells about the nematode anterior regions. Eggs are laid in a gelatinous matrix deposited by the female nematode on the root surface. The life cycle from egg to egg takes 6–8 weeks. Reproduction occurs over a wide range of temperatures, soil types, and pH values (Kirkpatrick et al. 1965b). Maximum population growth occurs between 28 and 31 °C, although some reproduction occurs as low as 21 °C, but not above 31 °C. Van Gundy and Martin (1961) found a correlation between nematode injury and plant nutrition. The greatest retardation in growth of citrus was caused by *T. semipenetrans* in soils that were deficient or nearly deficient in calcium, sodium, and potassium. The leaf content of calcium and zinc was less in plants grown in these soils. Higher population densities of *T. semipenetrans* were found in alkaline than in acid soils. Soil moisture affects reproduction with a dry soil being more favorable than a wet one, probably due to an oxygen deficiency when soil moisture is high (Van Gundy and Tsao 1963; Van Gundy et al. 1964).

R. C. Baines conducted extensive host range studies (Baines 1950; Baines et al. 1948). In addition to citrus, *T. semipenetrans* parasitizes grape, lilac, olive, and persimmon. It is common in table grape vineyards in the Coachella Valley (Riverside County). It has also been found in peach and almond orchards on "Lovell" rootstock in the San Joaquin Valley (Duncan et al. 1992), and on ponderosa pine (Viglierchio 1979). Baines et al. (1974) found four citrus nematode biotypes in California that could be differentiated by means of a host range test utilizing four citrus rootstocks.

Baines identified *Poncirus trifoliata* rootstock as having resistance to *T. semipenetrans*. In resistant plants, juveniles penetrate epidermal and hypodermal cells. These cells and the first row of cortical parenchyma cells then collapse and often become necrotic. A wound periderm forms in the parenchyma, effectively isolating the area of penetration. Penetration does not progress, and nematodes neither mature nor reproduce. In addition to this mechanical resistance, there appears to be a toxic chemical associated with nonhost plants (Verdejo-Lucas and McKenry 2004).

6.5.2.1 Management

Of 15 grape rootstocks tested, McKenry and Anwar (2006) found Ramsey and SO4 to be resistant to *T. semipenetrans*, Thompson seedless to be highly susceptible, and the others to be susceptible. Ferris et al. (2012) reported that of 13 grape rootstocks tested, 8 were susceptible, three were resistant, 1 was moderately resistant, and 1 was moderately susceptible. Two newly released grape rootstocks GRN-1 and GRN-3 were resistant, and a third GRN-2 was susceptible.

Mature citrus trees can tolerate a considerable number of citrus nematode before showing lack of vigor and decline symptoms. Susceptible trees planted in lightly infested soil may grow for many years without apparent damage and then suffer a "slow decline". Typical above ground signs consist of reduced vigor, the death of terminal buds, chlorosis and dying of leaves, early wilting under moisture stress, and twig dieback. Fruit is reduced in size, quantity and quality. Damage is greater when trees are predisposed by other factors such as *Phytophthora* root rot and water stress. Infested root systems are smaller than noninfested ones and have a dirty appearance because of the adhesion of soil particles to the gelatinous matrix deposited by the female nematode on the root surface during laying of eggs.

Baines researched and recommended use of soil fumigants for pre-plant management (Baines et al. 1957). Post-plant nematicide treatments are warranted if more than 400 nematode females/g root are found in samples collected in February to April or 700 females/g root in May and June. The same is true for populations of juveniles greater than 5000 per 500 g of soil in February to April, or greater than 8000 in May to July (Becker and Westerdahl 2009). Little effect of treatment on yield and fruit quality may be obtained the 1st year after a post-plant application, but with continued treatment, efficacy can often be demonstrated in the 2nd year (Verdejo-Lucas and McKenry 2004). Duncan et al. (1992) found that placement of a 3-m-wide, black, polyethylene film mulch down rows of peach (*Prunus persica* 'Red Haven' on 'Lovell' rootstock) and almond (*Prunus dulcis* 'Nonpareil' on 'Lovell') trees in the San Joaquin Valley for water conservation, also resulted in reductions of levels of citrus nematode. It is common to be able to recover several thousand citrus nematode juveniles from just 50 g of soil. This has led to use of citrus nematode infested soil as a model system for bioassaying the efficacy of potential new nematicides as alternatives to methyl bromide (Wang et al. 2004; Westerdahl et al. 1992). Such studies have shown toxicity of nematicides to citrus nematode to be similar to that for root knot nematode (Roberts and Thomason 1988; Zasada and Ferris 2003).

6.5.3 *Stem and Bulb Nematode,* **Ditylenchus dipsaci**

One of the earliest nematode problems recognized in California was the impact of the stem and bulb nematode on garlic and narcissus production. In 1925, D. G. Milbrath of the California Department of Agriculture, reported 5% losses of garlic due to *Ditylenchus dipsaci* (Siddiqui et al. 1973). Soon afterward, the use of hot water treatments, first developed by the Europeans, proved most successful in controlling *D. dipsaci*-infested narcissus bulbs in the northern coastal counties (Allen and Maggenti 1959; Siddiqui et al. 1973). Presently, *D. dipsaci* is a major nematode pest mainly of garlic, onion and alfalfa in California and, if not managed, can impact all regions of production. California is the largest producing state in the U.S. for garlic and onion with major production regions for garlic located within the Western San Joaquin Valley and minor production regions within few southeast desert counties, northern and central coastal counties (CGORAB 2007). Onions are grown throughout the state and alfalfa is mostly produced in Southern California and the San Joaquin Valley (Table 6.1; CDFAa 2016–2017; Geisseler and Horwath 2016). By 1959, host-specific biological races of *D. dipsaci* on alfalfa, narcissus, onion and garlic were found to be generally distributed whereas, other races were not (Allen and Maggenti 1959). Subsequently, in 1960, at the request of seed garlic growers, the California Seed Certification Program was established by the California Department of Agriculture and continues to date. In this Program, garlic plants are approved as propagative stock when tested by laboratory examination and found free from the stem and bulb nematode and the white rot fungal pathogen, *Sclerotium cepivorum*, and when found to meet certain minimum requirements. The program has proven successful, and from 1983 to 2017 a total of 16,637 garlic seed samples examined by the CDFA, have resulted in issuance of certified commercial planting stock free of the stem and bulb nematode. Brendler et al. (1971), reported a serious problem of tulip root disease incited by *D. dipsaci* in oat varieties cultivated in the coastal areas of Southern California.

Ditylenchus dipsaci, the stem and bulb nematode, is an obligate migratory endoparasite of more than 500 host plants (Fig. 6.3). *Ditylenchus dipsaci* has been documented in early reports as a complex containing several species (Sturhan and Brzeski 1991). However, *D. dipsaci sensu stricto* can now be distinguished from other related species by host plant range, chromosome number, morphometric values and gene sequences (Subbotin et al. 2005). The nematode feeds mainly on aerial parts of plants, within parenchymatous tissue of stems, bulbs, leaves, inflorescences and buds, but is also found within bulbs, tubers, rhizomes, stolons and rarely in roots (Sturhan and Brzeski 1991). A single female can lay 200–500 eggs within garlic and onion tissue and with a life cycle of about 21 days at 15 °C, several generations can occur in one crop season causing substantial damage. All postembryonic stages of *D. dipsaci* can infect plants, but fourth stage larvae are the most important infective stage as they have the unique capability of withstanding desiccation by undergoing anabiosis and surviving for long periods within stems, leaves, bulbs and seeds. Plants are invaded through stomates or tissue are directly penetrated at the base of stems and leaf axils (Becker and Westerdahl 2018). The nematodes may invade seedlings below the soil surface causing their retarded emergence and malformation or migrate upwards to apices of shoots.

As a result of nematode feeding, general symptoms develop that include swelling, distortion, discoloration and stunting of aerial plant parts and necrosis and rotting of bulbs and tubers (Anon 2008). Germinating onion and garlic cloves are

Fig. 6.3 Stem and bulb nematode, *Ditylenchus dipsaci.* (**a**) Alfalfa normal stem on left and ones with shortened internodes infected with *D. dipsaci* on right; (**b**) Daffodil bulb infected with nematodes; (**c**, **d**) Raised spikkels on leaves of daffodil. (Credit: W. Hart and J. Radewald; University of California, Davis and Riverside)

penetrated by *D. dipsaci* and surviving plants are stunted with distorted and bloated tissue appearing spongy; leaves are thickened and shortened, often with yellowish or brown lesions; softening of bulb tissue initiates at the stem and neck and proceeds downward into the scales which become soft, loose and pale gray or brown in concentric circles when observed in transverse section, and bulbs split at the base under dry conditions, or become malformed. Under moist conditions, bulbs rot due to the presence of secondary invading fungi, bacteria and onion maggots (Becker and Westerdahl 2018; Sturhan and Brzeski 1991). Infected alfalfa plants are stunted with few shoots and deformed buds. Infected stems are enlarged and discolored and, when nematode population numbers are high, lower stems may turn black, especially under moderate temperatures and high humidity. 'White flags' are formed when the nematodes move into leaf tissue and destroy chloroplast (Westerdahl et al. 2017a, b). Damage to alfalfa is most severe in moist, cool weather in cooler, sprinkler-irrigated inland valley and foggy coastal areas of California. Damage is usually seen in the first and second cuttings of alfalfa under cool and optimum conditions (15–20 °C) for nematode development, and less often later in the season under hot and dry conditions when nematode activity diminishes. The species may be found as far south in the Central Valley as Madera County (Westerdahl 2007).

6.5.3.1 Management

The development of control strategies for *D. dipsaci* in bulbous plants and alfalfa gained much attention particularly during the 1960s through 1990s with increased problems in garlic, narcissus and alfalfa crop production and loss of registration of pesticides. With the establishment of the California Seed Certification Program in 1960, authorized by the California Food and Agriculture Code, California growers continue to be provided with a strong preventive measure to guard against the stem and bulb nematode. This measure has resulted in far less problems in production fields (CGORAB-CSCC 2007). The use of clean nematode-free seeds is the primary preventative step against nematode infestation. The Program allows for seed garlic to be approved as propagative stock when tested by laboratory examination and found free from the stem and bulb nematode, *Ditylenchus dipsaci*, and certified when inspected and found free of the white rot fungus, *Sclerotium cepivorum*, in fulfilment of minimum requirements as specified by regulation. Grower participation is voluntary, but strongly encouraged. Essential elements of the Program include (1) use of clean "foundation" or "registered" or stock with an equivalent history for planting, (2) geographic areas for planting are protected by county ordinances and where contamination by the stem and bulb nematode and white rot fungus is not likely to occur, on which no *Allium* sp. has grown for 5 years prior to planting, no white rot has been detected and located at least 152 m from *Allium* sp. not entered in the program, (3) sanitation measures to protect seed garlic from contamination by the nematode and fungus, (4) sampling and laboratory testing for the stem and bulb nematode and (5) inspection by the CDFA and county personnel. In support of the above requirements it would be necessary to obtain information on the potential presence and identity of the nematode species and its population density in the target field as well as the cropping history of the field.

Hot water-formalin treatment of bulbs has been used historically in California against the stem and bulb nematode in narcissus bulbs. Lear and Johnson (1962) and Johnson and Lear (1965) refined the treatments to handle small volumes of garlic cloves. However, during the late 1980s, this technique decreased mainly due to uncertainty in registration of formalin, grower perception that hot water treatment resulted in deformed flowers, length of time required for dipping, safety concerns over handling of formalin-treated bulbs and disposing of large volume of formalin. This lead to evaluative studies of hot water treatment against *D. dipsaci* in daffodil bulbs and Qiu et al. (1993) determined that hot water treatment with 0.37% formaldehyde at 44 °C for 150 min controlled the nematode without detrimental effects on plant growth and flower production. Alternatively, nematode control was also obtained with hot water treatment at 44 °C for 240 min without chemicals. Roberts and Mathews (1995) reported the use of abamectin and sodium hypochlorite as effective alternatives to replace formalin. Abamectin at 10–20 ppm as a 20-min cool dip (18 °C) following a 20-min hot water dip and sodium hypochlorite at 1.052–1.313% aqueous solution as the 20-min hot dip were highly effective in controlling *D. dipsaci*, although neither treatment was effective as a hot water-formalin treatment and did not eradicate the nematode. Hot water treatment can reduce stem and bulb nematode in garlic cloves but is not completely eradicative (Becker and Westerdahl 2018).

The standard management of *D. dipsaci* in daffodils in California was hot water-formalin treatment of bulbs and preplant chemical treatment of soil. In addition, growers used preplant fumigation with 1,3-dichloropropene (1,3-D) and 1,2-dichloropropane (1,2-D) and/or at-planting application of aldicarb. However, after 1,2-D and aldicarb were found in groundwater and subsequently removed from the market, the latter was replaced with fenamiphos (Nemacur) which met the same fate in 1986. Since then, 1,3-D and phorate (Rampart) were used as preplant control treatments. Several non-fumigant nematicides applied directly onto garlic seed cloves in seed furrows in different types of soil gave differing results in suppressing *D. dipsaci* infection (Roberts and Greathead 1986). Westerdahl et al. (1991) found that foliar applications of oxamyl reduced nematode infestation in daffodil bulbs without phytotoxicity but not as well as hot water-formalin dipping. Currently, nematicides registered in California for use in garlic and onion are preplant fumigants, 1.3-Dichloropropene/chloropicrin (inline), 1,3-Dichloropropene (Telone EC), metam sodium (Vapam HL) and metam potassium (K-Pam HL). Oxamyl (Vydate L) is applied at or after planting (Becker and Westerdahl 2018).

There are no nematicides presently registered for use against the alfalfa stem nematode in California (Westerdahl et al. 2017a).

Planting resistant varieties is regarded the most effective control measure against *D. dipsaci* in alfalfa. Currently, greater than 50% resistance to *D. dipsaci* is available in several resistant varieties (Alfalfa Variety Ratings 2018).

Rotation with non-host crops provides some reduction of alfalfa stem nematode populations, which has a very limited host range. Rotating with non-host crops such as tomato, small grains, beans and corn for 2–4 years has resulted in reduced nematode numbers, whereas, growing no-hosts or poor hosts such as corn for 3–4 years can reduce stem and bulb nematode in garlic and onion (Westerdahl et al. 2017a; Becker and Westerdahl 2018).

6.5.4 Cyst Nematodes, Heterodera *spp.*

6.5.4.1 Sugar Beet Cyst Nematode, *Heterodera schachtii*

In California, *Heterodera schachtii* was first detected in 1907 in Alameda, Los Angeles and Salinas Counties (Caswell and Thomason 1985) (Fig. 6.4). In 1920, an intra-state survey revealed more than 1000 ha to be infected by this nematode (Thorne and Gidding 1922). Since then, *H. schachtii* has been detected in 23 countries (Siddiqui et al. 1973) and is widespread in all former and present California sugar beet growing areas, especially the Imperial Valley, central regions of the

Fig. 6.4 (**a**) Sugar beets – healthy and infected with *Heterodera schachtii*; (**b**) Sugar beet field infected by *H. schachtii.* (Credit: I. Thomason and J. K. Clark, University of California)

Central Valley, the Salinas Valley, and Monterey, Santa Barbara and Ventura Counties where sugar beet production is most concentrated (Caveness 1958; Cooke and Thomason 1978; Caswell and Thomason 1985). Sugar beet nematode has been recovered from all soil types. In the Imperial Valley 11% of the total cultivated acreage were infected. It is assumed that this cyst nematode was introduced to the Central Coast Valley during the time when sugar beet production was a primary crop in this area. Estimates of yield loss can reach 25 t/ha in untreated fields. Damage threshold levels vary with soil temperature, type and moisture and are characteristic for different sugar beet growing areas. The damage threshold in the Imperial Valley, California, is attained with 1–2 eggs/g soil (Cooke and Thomason 1979). In California, beside sugar beet, *Heterodera schachtii* was also found in Brussels sprouts, broccoli or cauliflower and cabbage (*Brassica oleracea*).

The life history and morphology of the sugar beet nematode was studied in detail by Raski (1949). In the laboratory, plant host tests conducted by Raski (1952c) with infested field soil collected near Salinas, California, resulted in detection of some cysts from roots of Golden Queen and Jubilee tomatoes, annual lupin, Golden Wax bush bean, Iron cowpea, garden pea, sweet pea (*Lathyrus odoratus*) and purple vetch. Steele (1965) also provided a list of plant hosts among weeds and agricultural plants belonging to seven families for California populations of *H. schachtii. Heterodera schachtii* females were also collected from the roots of *Amaranthus retroflexus*, *A. graecizans*, *Chenopodium murale* and *Solanum nigrum,* but only rarely (Raski 1952c). The penetration, development, and reproduction of a California population of the sugar beet cyst nematode were observed on phacelia (*Phacelia tanacetifolia*), buckwheat (*Fagopyrum esculentum*), oilseed radish (*Raphanus sativus*), and white mustard (*Sinapis alba*) (Gardner and Caswell-Chen 1993).

6.5.4.1.1 Management

Crop rotation and nematicidal application minimized yield losses (Cooke and Thomason 1978). However, high cost of treatment in relation to sugar prices often restricts nematicide use. To reduce crop damage caused by *H. schachtii*, representatives of the local sugar beet factory, growers, the County Agricultural Commissioner and nematologists from the University of California designed a cropping scheme based on a cyst nematode dump-sample survey (Roberts and Thomason 1981). A dump sample is a 500-cm^3 representative soil sample collected from sugar beets harvested from an approximately 2-ha area. Fields are considered infested if three or more cysts are found in a sample. Sugar beets cannot be planted in non-infested fields more than two consecutive years and not more than 4 out of 10 years. Sugar beets can be grown only once every 4 years in infested fields. The success of this program is due to the natural decline of *H. schachtii* in the absence of host plants. For example, in the Imperial Valley, annual population decline rates of more than 50% have been reported. In addition, egg densities in four different fields dropped below the detection level during the 4th year under continuous non-host alfalfa (Roberts et al. 1981b).

It has been shown that egg parasitism by *Fusarium oxysporum*, *Acremonium strictum, Hirsutella rhossiliensis, Dactylella oviparasitica* and other fungi (Nigh et al. 1980; Jaffee et al. 1991; Westphal and Becker 1999; Becker et al. 2013) play a major role in *H. schachtii* egg destruction and consequently contribute to the decline of the nematode population. Soil moisture in relation to type of cropping sequence apparently influenced egg hatch and activity of fungal parasites (Roberts et al. 1981a).

Westphal et al. (2011) studied soil suppressiveness against the sugar beet cyst nematode, *Heterodera schachtii*, using 11 soils from Southern California locations. The study illustrated that the comparison of population development of *H. schachtii* in non-treated and fumigated portions of field soils had the potential to detect suppressiveness in multiple soil texture classes. It has been shown that soil suppressiveness existed in various soil texture classes, suggesting the broad potential for directly exploiting the natural mechanisms that reduce population densities of nematodes for sustainable agricultural production.

6.5.4.2 Cabbage Cyst Nematode, *Heterodera cruciferae*

In the USA, *Heterodera cruciferae* is only known to occur in California (Raski 1952b; Raski and Sciaroni 1954). This nematode species is known from Yolo, San Mateo, Santa Cruz, Monterey and Santa Barbara Countries (Siddiqui et al. 1973) and recognized as economically important (Lear et al. 1965).

6.5.4.3 Clover Cyst Nematode, *Heterodera trifolii*

In California, *H. trifolii* was reported by Raski and Hart (1953) from white clover in the lawn of a private residence in Camarillo, California. The nematode also developed on carnation (*Dianthus caryophyllus),* Golden Wax bush bean (*Phaseolus vulgaris*) *and Sesbania macrocarpa*. Later, this nematode was collected from other places in California, but its pathogenicity was not reported.

6.5.4.4 Fig Cyst Nematode, *Heterodera fici*

In California, *Heterodera fici* was first detected in *Ficus elastica* showing poor growth in a nursery at San Bernardino and in field-grown commercial fig*, Ficus carica*, in Yolo County. Later, this nematode was also found in other counties. Infection of plants under greenhouse conditions has been successful only in the genus *Ficus*. Fig cyst nematode pathogenicity in commercial cultivars of fig has not been determined (Sher and Raski 1956).

6.5.5 Ring Nematode, Mesocriconema xenoplax

The ring nematode, *Mesocriconema xenoplax*, was first discovered and described by Raski (1952a) as *Criconemoides xenoplax* (= *Macroposthonia xenoplax*, *Criconemella xenoplax*) from specimens collected from a California vineyard. At that time, the species was also commonly encountered in walnut and prune orchards and vineyards (Raski 1952a; Siddiqui et al. 1973; Lownsbery et al. 1974). In 1968, the species was detected in 26 of 29 walnut orchards in San Joaquin County and by 1974, *M. xenoplax* was found in all four, main prune-cultivation regions of the state, namely Santa Clara, Napa-Sonoma, Sacramento and San Joaquin Valleys (Lownsbery et al. 1974). During a survey of 14 out of 17 almond-producing counties of California, McKenry and Kretsch (1987) found *Mesocriconema xenoplax* to be the most damaging nematode of almond production in the Northern San Joaquin region (San Joaquin, Stanislaus and Merced Counties), in sandy soils in the Southern San Joaquin region (Fresno, Kings, Tulare and Kern Counties), and occasionally in the Sacramento Valley and a coastal region of non-irrigated hillside near Paso Robles. The species is widely distributed in vineyards and several other perennial crops planted throughout the state (Ferris et al. 2012). Currently, *M. xenoplax* is becoming more prevalent and increasing in population levels in California. This increase is probably associated with the advent of drip irrigation plus soil additives that increase size of pore spaces (McKenry, UCR pers. comm.). During statewide detection surveys for the presence or absence of 22 economically important nematode species in major agricultural crops and nursery production areas within California, the CDFA reported higher frequencies of detection of *M. xenoplax* in rhizosphere soils of apricot, cherry, plum, prune, grape, peach, walnut and alfalfa, and relatively few detections in soils of cotton, long bean, oats, orange and tomato, from 16 counties (Dong et al. 2007).

Mesocriconema xenoplax is a sedentary ectoparasitic nematode that inhabits the rhizosphere soil of host plants and feeds on root tissue through an elongate stylet inserted into a root while the body remains outside. Feeding is completed in 1–2 weeks resulting in the death of fine roots. During the 1st year after transplanting, up to 85% of fine roots can be absent (Westerdahl and Duncan 2015). Seshadari (1964) determined that *M. xenoplax* reproduced best in very sandy soils than in loam or silty loam, and at the highest soil moisture level (sticky point = 15.5%). The nematode had a life cycle of 25–34 days at 22–26 °C (Seshadari 1964). High populations are attained on stone fruit and grape and the nematode is associated with orchards with a replant history (McKenry and Kretsch 1987; Ferris et al. 2004). In studies conducted during the mid-1970s, *M. xenoplax* was experimentally shown to adversely affect growth of stone fruit including peach, Myrobalan and Marianna 2624 plum (Braun et al. 1975; Lownsbery et al. 1977; Mojtahedi et al. 1975), almond (McKenry and Kretsch 1987), and walnut (Lownsbery et al. 1978). Damage caused by *M. xenoplax* alone in a walnut orchard was difficult to assess due to the combined presence of *Pratylenchus vulnus*, as both species were found to retard plant growth by causing lesions and longitudinal cracks in plant roots, however, Lownsbery et al. (1978) gave experimental evidence that initial non-coalesced lesions caused by *M. xenoplax* were smaller than those caused by *P. vulnus*. Ring nematode reduced number and volume of feeder roots, destroyed cortical root tissue, darkened roots, altered water stress, lowered nutrient levels in leaves, reduced fresh and dry weight, and caused stunted growth in Myrobalan and Marianna 2624 plum, Nemaguard and Lovell peach and French prune (Braun et al. 1975; English et al. 1982; Lownsbery et al. 1977; Mojtahedi and Lownsbery 1975; Mojtahedi et al. 1975). Ring nematode also damages young grape vines and while it may be difficult to assess damage and crop loss in older grape vines, both symptoms are highly probable given the high ring nematode population levels often encountered in California vineyards (Ferris et al. 2012). McKenry (1992) reported reduction of 10–25% in grapevine yield with more than 500 *M. xenoplax* kg^{-1} soil (0.5 nematodes/g^{-1} soil). However, the greater economic damage caused by *M. xenoplax* is its ability to predispose *Prunus* spp. and *Malus* spp. to bacterial canker caused by *Pseudomonas syringae* pv. *syringae*, contributing to peach decline and mortality in the San Joaquin Valley of California (Lownsbery et al, 1973; English et al. 1980) and *Cytospora* canker of prune caused by *Cytospora leucostoma* (English et al. 1982). Bacterial canker was severe when associated with *M. xenoplax* (Lownsbery et al. 1977) and higher densities of the nematode resulted in higher incidence of bacterial canker (Underwood et al. 1994). *Mesocriconema xenoplax* was the most damaging nematode of almonds because of the associated bacterial canker complex in the San Joaquin Valley where about half the orchards had both pathogens (McKenry and Kretsch 1987). In the Southeastern United States *M. xenoplax* is a major contributor to a similar association with *P. syringae* pv. *syringae* and cold injury resulting in Peach tree short life disease complex (Nyczepir et al. 1983).

While earlier reported studies on *M. xenoplax* in California largely involved container experiments, through the years experimental evidence obtained under field conditions have furthered our knowledge on ring nematode, host and environment interactions over time with relevance to appropriate management choices. Seasonal effects on ring nematode population under field conditions have been reported. In a 3-year study on population fluctuations of ring nematode in five prune orchards in California, Westerdahl et al. (2013) found highest number of ring nematodes at depths of 0–30 cm in the summer months and 30–60 cm in the fall and winter, with nematode numbers being lowest before irrigation and sharply increased after irrigation. The type of sampling tool had no effect on nematode recovery. An optimum sampling strategy to detect the presence of ring nematodes in a prune orchard would therefore, incorporate those determined results. On the other hand, Ferris et al. (2012) found all life stages of *M. xenoplax* to be present through the year but with lower ratios of juveniles to adults and lower proportions of nematode populations in the upper 30 cm than at 30–90 cm depths in the summer months in California *Prunus* orchards where trees were irrigated by flooding of large basins when the soil became dry thereby, resulting in root zone soil being subject to extreme wet and dry cycles, particularly in the upper 30 cm. They determined that two samplings, one in spring and the other in fall, are needed to determine the annual trajectory of ring nematode dosage in *Prunus* orchards.

The initial management measure to prevent spread of *Mesocriconema xenoplax* to non-infested fields includes the use of certified planting stock, removal of soil from equipment prior to moving between orchards and avoidance of recycling irrigation water (McKenry and Westerdahl 2009).

6.5.5.1 Management

In 1960, the development of the 'Approved Treatment and Handling Procedures for the Control of Nematodes in Deciduous Fruit and Nut Tree, Grapevine, Berry and Vegetable Plant Growing Ground Inspection Program' based on acre-by-acre composite sampling and laboratory examination for nematodes, soon resulted in significant improvement in nematode cleanliness of California-grown nursery stock. Sampling was waived if the land had been pre-fumigated at high rates. This program is continued to date under the CDFA's Nursery Stock Nematode Control Program (NIPM #7) that specifies soil treatment and handling procedures to ensure field and container grown nematode-free nursery stock for farm planting (Raski et al. 2002).

Most *Prunus* rootstocks support populations of *M. xenoplax* but differ in response to other plant parasitic nematodes. Nemaguard rootstock is planted to 90% of the peach industry in California. In earlier studies, Lownsbery et al. (1977) found scions on Nemaguard and Lovell rootstocks to be highly susceptible to bacterial canker and *M. xenoplax* in container experiments and indicated the need for comparison of the rootstocks under field conditions. Although Nemaguard rootstock is resistant to root knot nematodes, it is damaged by *M. xenoplax* and is a better host to the ring nematode than Lovell rootstock, which is more tolerant to bacterial canker and resistant to root knot nematode. Furthermore, Nemaguard is among the most difficult to successfully replant because of the 'rejection component' of the replant problem. Marianna 2624 and Myrobalan 29C rootstocks also commonly used in California, although resistant to root knot nematodes, are highly susceptible to *M. xenoplax*. Viking rootstock is reported to offer some tolerance to ring nematode similar to Lovell rootstock with comparable protection against bacterial canker (McKenry and Westerdahl 2009).

Over a 15-year period, Ferris et al. (2012) tested five new grape rootstocks with broad and durable nematode resistance at four general grape-growing regions of the state: north coast, Northern San Joaquin Valley, central coast region and the Central and Southern San Joaquin Valley. They reported UCD GRNI, UCD GRN5 and VR 039-16 to be resistant to ring nematode. UCD GRN1 has broad nematode resistance and these studies resulted in the patenting and release of the five rootstocks to the grape industry. Furthermore, populations of *M. xenoplax* from the five locations differed in virulence – as indicated by their reproduction on susceptible rootstock. Resistance to *M. xenoplax* was not compromised at high soil temperature, even at 30 °C where the nematode was still biologically active (Ferris et al. 2013).

Preplant and postplant nematicides have been important in the chemical control of ring nematodes and bacterial canker. The earliest choice of postplant nematicide was dibromochloropropane (DBCP). However, with its removal from the market as well as the removal of other nematicides, the choice got narrower. Ferris et al. (2012) reported that applications of phenamiphos in spring and summer were most effective for controlling ring nematode and reducing annual tree mortality due to bacterial canker in California *Prunus* orchards. Currently, preplant nematicides registered for use in California are methyl bromide (under Critical Use Exemption), metam sodium (Vapam^{R}) and 1, 3-Dichloropropene (Telone II^{R}).

Among postplant products, Ditera^{R} (a toxin produced by *Myrothecium verrucaria*), Nema-Q^{R} (an extract of Quillaja, the soapbark tree) (Westerdahl et al. 2013), Enzone^{R} (sodium tetrathiocarbonate) and Movento^{R} (Spirotetramat) are available for use against nematodes infesting fruit and nut crops (Bettiga et al. 2016; McKenry and Westerdahl 2009).

Preplant applications of different rates of lime ($CaCO_3$) in peach and almond orchards (0, 13.2, 18.2, 27.3 or 54.2 kg lime/peach tree and 0, 6.4, 12.8, or 25.0 kg lime/almond tree) altered soil pH but did not affect numbers of *C. xenoplax* in peach and almond, nor did it reduce incidence of bacterial canker in peach (Underwood et al. 1994).

The nematophagous fungus *Hirsutella rhossiliensis* naturally parasitizes *Mesocriconema xenoplax* in a density-dependent manner in many stone fruit orchards in California (Jaffee et al. 1989) and there have been several studies aimed at its exploitative use as a biocontrol agent against the ring nematode under field conditions in California. However, *H. rhossiliensis* was found to be a weak regulator of *M. xenoplax* population density (Jaffee et al. 1989) and did not regulate ring nematode populations in a newly planted *Prunus* orchard in California (Ferris et al. 2004). Efforts to enhance parasitism of nematodes by *H. rhossiliensis* through the addition of organic matter have been unsuccessful. In a related study, Jaffee et al. (1994) determined that parasitism of *M. xenoplax* by *H. rhossiliensis* was only slightly suppressed and numbers of nematodes were not affected by the addition of 73 mt of composted chicken manure/ha to a peach orchard in California.

6.5.6 *Root Lesion Nematodes,* Pratylenchus *spp.*

Pratylenchus spp. were first discovered in California in 1927, however their importance as plant pathogens was not realized until investigations held from 1930 to 1943 revealed damages caused by root lesion nematodes to walnut, fig and cherry trees. At that time, confusion over species identities, distribution and host range made it difficult for state and county regulatory agencies to restrict the spread of root lesion nematodes until the group was revised by Sher and Allen (1953). By 1959, *P. brachyurus, P. penetrans, P. vulnus, P. scribneri* and *P. hexincisus* were recognized as root lesion nematodes of economic importance in California, while *P. pratensis, P. thornei, P. minyus* and *P. coffeae* were also present in the state, but their importance was not known (Allen and Maggenti 1959). In the early 1960s, a nematode survey of pear orchards was conducted in response to the occurrence of pear decline in California. Of the several different *Pratylenchus* species found in pear orchards, only *P. vulnus* and *P. penetrans* were recovered from pear roots. *Pratylenchus zeae*, a species not generally distributed in California, was discovered in 10 or 20 pear orchards in Placer County (French et al. 1964). *Pratylenchus penetrans*, *P. vulnus, P. neglectus* and *P. thornei* are discussed in this section in further detail.

In general, *Pratylenchus* spp. are migratory endoparasitic nematodes that feed within root cortical tissue and are also found in the surrounding soil. Infected plants have roots with black lesions and fewer feeder roots than non-infected plants thereby resulting in stunted root growth. Top growth may exhibit general symptoms of an impaired root system including lack of vigor, dieback, chlorotic and small leaves and reduction of yield.

6.5.6.1 *Pratylenchus vulnus*

Pratylenchus vulnus was first reported in 1951 in California as a new species and important plant parasite of various trees and vines, namely walnut, grape, fig, citrus, apricot, avocado, weeping willow, cherry, olive, peach, almond, plum, raspberry and boysenberry (Allen and Jensen 1951). *Pratylenchus vulnus* is the most common root lesion nematode found associated with almonds in the Sacramento Valley (McKenry and Kretsch 1987) and is commonly distributed in California vineyards seriously affecting grape yield (Lider 1960; Raski et al. 1973). Root systems of young grapevines may be restricted in growth with absence of major roots and dead feeder roots while root lesions at feeding sites may not be present. *Pratylenchus vulnus* is also the root lesion species most commonly found in walnut orchards in California (Westerdahl et al. 2017b). Walnut tree vigor and yields are reduced by the feeding activity of *P. vulnus* which places infected trees under stress (Lownsbery 1956). In California, as in many regions worldwide, this nematode is the primary cause of tree decline and replant problems in orchards (Nyczepir and Halbrendt 1993; McKenry 1999). Growth of young walnut trees can be arrested by *P. vulnus* and the replant problem, even at 1 nematode/250 cm^3, and established walnut orchards in California are able to support 500 *P. vulnus*/250 cm^3 soil (Buzo et al. 2009). *Pratylenchus vulnus* reduced plum yields by 16%, 16%, 10% and 6.4% in Lovell, Nemaguard, Myrobalan 29C and Marianna 2624 plum rootstocks, respectively, with reduced levels of calcium and magnesium in scion petioles. Monthly and annual fluctuations of *P. vulnus* populations were observed in a plum orchard, with the most stable levels occurring during fall months and at higher population levels in the top 30 cm than lower 30–60 cm depths (McKenry 1989). During the 1970s, *Pratylenchus vulnus* was also found to affect rose production in California (Lear et al. 1970) and was involved in a disease of Manetti rose rootstocks with optimum nematode reproduction in silt loam soil at 20 °C (Santo and Lear 1976).

6.5.6.1.1 Management

Non-chemical control of *Pratylenchus vulnus* begins with preventive measures taken by planting nematode-free planting stock. In California, the CDFA's Nursery Stock Nematode Control Program (NIPM #7) specifies soil treatment and handling procedures to ensure field and container grown nematode-free nursery stock for farm planting.

The loss and restriction of nematicides has resulted in reliance on alternate options, in particular use of resistant plants, for control of soil-borne nematodes. Over the years, the host status of fruit and nut and grape rootstock varieties to *Pratylenchus vulnus* and other important plant parasitic nematodes have been assessed for resistance, susceptibility, tolerance and intolerance in California. Screening and monitoring plant response to plant parasitic nematode and plant vigor over several years was found necessary as nematode reproductive values can differ after the 1st year of growth (Westphal et al. 2016a). Currently, no resistance to *P. vulnus* has been found in *Juglans* spp. English and black walnut are very susceptible to root lesion nematode, but their hybrid Paradox is more tolerant than either parent, when nematode population numbers are not too high. Of the presently available clonal Paradox walnut rootstocks in California, clonal Paradox VX211 is nematode-tolerant and was released to California growers in 2007 (Buzo et al. 2005, 2009; Hasey et al. 2018; Westerdahl et al. 2017b). Buzo et al. (2005) determined *P. vulnus* population increases about three times the initial inoculum density in fleshy root tips than within primary roots of four walnut cultivars including the more aggressively-growing Paradox hybrid. Hybrid vigor is a primary quality of VX211 (Buzo et al. 2009).

Studies on host status of grape rootstocks included interactions of 18 and 16 grape cultivars and *Pratylenchus vulnus* in microplots trials that revealed root lesion nematode resistance in cultivars Ramsey and K51–32 after 10 and 24-month periods (McKenry et al. 2001; McKenry and Anwar 2006). McKenry and Anwar found that certain cultivars selected for nematode resistance such as Dogridge, Freedom, Ramsey and 3309C, often stimulated vine growth when fed upon by the nematode, and regarded this growth-stimulating response as a form of tolerance associated with resistance. Ferris et al. (2012) found moderate resistance to *P vulnus* in five new grape rootstocks, UCD GRN1, UCD GRN2, UCD GRN3 UCD GRN 4 and UCD GRN 5, after a 15-year screening process in the Northern, Central and Southern San Joaquin Valley, and central and north coast regions, which resulted in their eventual release to the grape industry. Furthermore, they provided a compilation of current knowledge of host status of 27 other rootstock cultivars to plant parasitic nematodes including USDA-ARS rootstocks, USDA 10-17A, USDA 10-23B and USDA 6-19B which were evaluated as resistant to *P. vulnus* (Ferris et al. 2012; Gu and Ramming 2005a, b).

Pistachio is an expanding nut crop in California and the selection of rootstocks is critical to mitigate potential risk for increase of *Pratylenchus vulnus* populations in orchards. Westphal et al. (2016b) determined that an aggressive population of *P. vulnus* was more aggressive on the popular 'UCB1' pistachio rootstock which in turn, was less susceptible to the nematode than various *Prunus* rootstocks.

Experimental efforts to control root lesion through genetic engineering involving gene silencing and crown gall and nematode resistance gene stacking technologies resulted in simultaneous control of crown gall and *Pratylenchus vulnus* (Walawage et al. 2013).

6.5.6.2 *Pratylenchus penetrans*

Pratylenchus penetrans is another economically important root lesion nematode species found throughout the state on various host plants including apple, cherry, peach, apricot, plum, pear, strawberry, alfalfa, garlic, ornamentals and several other crops (French et al. 1964; Siddiqui et al. 1973; McKenry and Roberts 1985; Dong et al. 2007; Westerdahl et al. 2017b). Of particular economic importance is the species' detrimental impact to commercial productions of Easter lily and Oriental lily in Humboldt and Del Norte counties in California which, along with Curry County, Oregon, is the only area in the United States where Easter lily bulbs are grown commercially (Westerdahl et al. 1993, 1998). *Pratylenchus penetrans* has been found in Easter lilies since 1946 (Butterfield 1947) causing restricted root growth and retarded top growth as well as of non-emergence of shoots from bulbs. *Pratylenchus penetrans* is frequently found in apple orchards in Northern California and is occasionally associated with apple replant disease (Westerdahl 2015), whereas, in alfalfa, it is present only in localized areas of the state (Westerdahl et al. 2017a).

6.5.6.2.1 Management

In California, early studies on the control of *Pratylenchus penetrans* have mainly been on Easter lily (Maggenti et al. 1967, 1970; Hart et al. 1967). Chemical control of *P. penetrans* in Easter lily fields has traditionally consisted of a preplant fumigation with a mixture of 1,3-dichloropropene (1,3-D) and 1,2-dichloropropane (1,2-D) followed by at-planting applications of an organo-phosphate or carbamate, since the nematode infests both planting stock and soil. However, the withdrawal of 1,2-dichloropropane, aldicarb and fenamiphos (Nemacur) in the early and mid-1980s, following their discovery in groundwater, left the use of 1,3-dichloropropene (1,3-D, Telone II) which was suspended in California from April 1990 until early 1996. Consequently, growers used metam sodium or methyl bromide plus an at-planting application of an organophosphate, phorate (Rampart^{R}) (Westerdahl et al. 1998). Following the phase-out of methyl bromide, currently, effective preplant soil fumigation with chloropicrin or Telone II and metam sodium (Vapam^{R}) are available for use in strawberry and apple. Effective application methods of nematicides have been studied (Westerdahl et al. 1993), but subsequently, concerns over groundwater pollution through use of nematicides in sandy soils of Del Norte County led to investigations of alternative management strategies.

Due its very wide host range, non-chemical control of *P. penetrans* through crop rotation and resistant varieties have not been feasible. In California, lily bulbs are usually rotated with pasture grasses. Westerdahl et al. (1998) determined that *P. penetrans* populations fluctuated under pasture grass and continuous fallow following Easter lilies but generally increased on pasture grasses and decreased under fallow, although not completely. In alfalfa, a field left fallow and weed-free can reduce lesion nematode numbers but not sufficiently to prevent damage to newly-planted alfalfa. Currently, there are no commercially certified alfalfa varieties with resistance to root lesion nematodes (Westerdahl et al. 2017a). For apple, some nematode tolerance to *P. penetrans* has been observed in standard and certain dwarfing rootstocks, however, the latter are known to be susceptible to *P. vulnus* (Westerdahl 2015).

Hot water and ozone treatments of Easter lily for control of *P. penetrans* gave varying results in a 3-year field trial study. Giraud et al. (2001) found that several treatments performed better than the untreated control but not as well as commercial chemical standard treatment. Hot water treatment at 39 °C for 35 min or 46 °C for 90 min reduced nematode numbers but did not improve bulb growth, however, this was the reverse case for ozone.

New natural products are being tested against *P. penetrans* with some promising results. Nema-Q®, a bionematicide, has been tested in vitro, greenhouse and field environments against several important plant parasitic nematodes including lesion nematode *P. penetrans,* and was found effective in controlling them at a concentration of 10,00 ppm. Lesion nematodes were reduced from 1200 to 350 per 205-g soil in Cabernet wine grapes (Marais et al. 2010). During a 2-year field trial study, Giraud et al. (2011) tested meadowfoam seed meal, mustard bran, *Quillaja*, DiTera®, the fungi *Paecilomyces lilacinus* and *Muscodor albus* for management of lesion nematode and improvement of plant health. *Muscodor albus* applied with

Thimet at planting, and meadowfoam seed meal had lower numbers of lesion nematodes than the controls. Similar studies were conducted with essential oil products Dougard, EF400, EF300 and Cinnamite tested as preplant dips of bulblet planting stock and *Paecilomyces lilacinus* as a soil treatment showed varying levels of lesion nematode reduction within roots over the controls (Westerdahl and Giraud 2017).

6.5.6.3 *Pratylenchus neglectus*

Pratylenchus neglectus, reported earlier as *P. minyus*, is the most widely distributed root lesion nematode species in California (Allen and Maggenti 1959; McKenry and Roberts 1985).

Although particularly associated with grasses and cereal crops, *P. neglectus* has a very wide host range and in California is frequently found in annual crops such as barley, oats and potatoes as well as perennial crops such as alfalfa and other forage crops (Siddiqui et al. 1973; McKenry and Roberts 1985; Dong et al. 2007). In recent surveys conducted by the CDFA, *P. neglectus* was found more frequently in grape than in other commercial field-grown fruit and nut trees in California (Dong et al. 2007).

During the early 1980s, the discovery of *Pratylenchus neglectus* and the Columbia root knot nematode, *Meloidogyne chitwoodi,* in potato and barley fields in the Klamath basin in Northeastern California, led to further studies on the effects of temperature and host plant interaction of the lesion nematode and barley, a crop that was then being used in rotation with potato and alfalfa (Ferris et al. 1993). Umesh and Ferris (1992) determined a low threshold temperature of 7.75 °C required for the development of a Klamath basin population of *P. neglectus* in petridish trials, whereas the optimum temperature for development of this population was about 25 °C, which differed from higher optimal temperatures for reproduction and development of *P. neglectus* reported from other regions and hosts in the country. Temperatures above 25 °C did not favour the Klamath basin population on barley and total nematode numbers were greatest at 25 °C but lower above and below that temperature. Maximum nematode activity occurred at 20 °C through 2-cm sand in lab studies and corresponded to the cool spring soil temperatures of the Klamath basin. In further experimental trails, Umesh and Ferris (1994) showed that *P. neglectus* and *M. chitwoodi* interacted competitively and this interaction was affected by soil temperature and the host plants, barley and potato. The restrictive effect of *M. chitwoodi* on *P. neglectus* was greatest at 25 °C on barley and potato, while the restrictive effect of *P. neglectus* on *M. chitwoodi* was greatest at 15 °C in barley and at 25 °C in potato. They inferred that *P. neglectus* has the potential to suppress *M. chitwoodi* populations and reduce the damage it causes to potato and barley, but further studies in this area are needed.

Pratylenchus neglectus was found to be a weak pathogen of barley in pot experiments (Umesh and Ferris 1992) and a weak or non-pathogen of wheat and barley in field trials, as its rates of increase were highest in the highest yielding cereal varieties but could become important if it were to increase in prevelance (Ferris et al. 1993). Similar observations were made of *P. neglectus* inoculated into six alfalfa cultivars resulting in either absent or at low population levels after 4 years (McKenry and Buzo 1985). Although *P. neglectus* increases susceptibility of potato plants to *Verticillium*, the nematode has not been shown to damage potatoes in California (Westerdahl and Kodira 2012).

In studies conducted over a 7-year period in fields used for potato cultivation and infested with *M. chitwoodi* and *P. neglectus* in the Klamath basin of Northeast California, Ferris et al. (1994) determined nematode population changes under different crop rotation sequences and the impact of those changes on potato yield and quality. Season multiplication rates and overwinter survival rates of both species were related to populations measured in the previous fall, and spring, and in fall respectively. A positive relationship occurred between potato tuber blemish and population levels of *P. neglectus* measured in the previous fall and yields were associated with higher population levels of *P. neglectus*. By their analyses, potato yield and quality can be expected based on population levels of *P. neglectus* (or *M. chitwoodi*) measured either in the previous fall or in the spring before planting, whereas winter survival rates of both nematodes are a function of nematode population measured in the fall and increase or decrease in nematode population can occur on various crops or fallow conditions. These predictions of crop damage and nematode population changes had direct implications on nematode management decisions.

6.5.6.4 *Pratylenchus thornei*

Pratylenchus thornei is found in all climatic conditions throughout California, particularly in clay and loam soils such as those in the Imperial Valley, Sacramento Valley and eastern slopes of the San Joaquin Valley (McKenry and Roberts 1985). This lesion nematode has a wide host range comprising annual field, vegetable crops, fruit and nut trees and ornamentals (Siddiqui et al. 1973). It is also associated with small grains causing probable damage particularly in warm areas such as the Imperial Valley (Westerdahl and Kodira 2007). However, their effect on associated crops has not been studied in California. While *P. thornei* has been found mainly associated with small grains: sorghum, wheat, barley, oats in the state (McKenry and Roberts 1985; Westerdahl and Kodira 2007; Dong et al. 2007) during recent surveys, the CDFA also found it associated with alfalfa, grape, apricot, cherry, cotton, prune and walnut (Dong et al. 2007). Grain crops infested with *P. thornei* are stunted and yellow in patches in a field, with brown leaf tips, fewer tillers and smaller heads (Westerdahl and Kodira 2007).

6.5.7 Dagger Nematodes, Xiphinema *spp.*

6.5.7.1 California Dagger Nematode, *Xiphinema index*

Xiphinema index was first described by Thorne and Allen (1950) from specimens extracted from soil around fig trees showing leaf drop and poor growth in Madera Country. In California, *X. index* is found in approximately 10% of California vineyards (Feil et al. 1997; McKenry et al. 2004). Hewitt et al. (1958) showed that *X. index* is the natural vector of the *Grapevine fanleaf virus* (GFLV) which is soil-borne. This study was also the first to prove that nematodes are able to vector soil-borne viruses and that spread is typically slow and in a concentric pattern (Hewitt et al. 1958). Just as with GFLV, *X. index* almost certainly was introduced into California, because no evidence exists that suggests it is native to the state. Several plants in California were also identified by Weiner and Raski (1966) as hosts: *Pistacia vera, P. mutica, Ampelopsis aconitifolia* and *Parthenocissus tricuspidata.*

In California, *Xiphinema index* significantly reduced root and shoot growth of the grape cultivar French Colombard. Bud break was delayed and buds were less vigorous than in the control (Anwar and Van Gundy 1989). Grapevine plants grown at 16.6 °C and inoculated with 500 *X. index* had, in the 1st year, 23% increased abscission of oldest leaves, and in the 2nd year, 65% and 38% reduction in top and root weights, respectively. Inoculated plants also had 60% fewer inflorescences and 89% reduced fruit size (Kirkpatrick et al. 1965a).

The length of the life cycle of *X. index* is reported as 27 days in California (Radewald and Raski 1962). *Xiphinema index* counts were always highest in the winter months. Temperature likely limits *X. index* reproduction in California because the summers are hotter and the growing season is longer than in most other grape-growing regions of the world. The findings of the study by Radewald and Raski (1962) showed that *X. index* populations fluctuate throughout the year and can be correlated with soil temperature. The possibility of detecting *X. index* in a vineyard can be maximized by sampling within rows during the winter months (Feil et al. 1997). Raski and Hewitt (1960) noted that under starving conditions, *X. index* retained the ability to transmit *Grapevine fanleaf nepovirus* for up to 9 months. The virus did not affect the rate of reproduction of *X. index* but did improve its survival rate during starvation (Das and Raski 1969).

6.5.7.1.1 Management

Soil fumigation with methyl bromide or 1,3-dichloropropene was successful over a 3-year period in controlling *X. index.* Such treatments can also give 99.9% reduction of all nematode species in the top 1.5–2 m of soil when properly applied (Raski et al. 1971). However, in 1990, the use of 1,3-dichloropropene was halted in California.

Nematode-resistant rootstocks are a promising alternative to the ban of nematicides. Since the 1970s, the University of California, Davis has been developing rootstocks to resist fanleaf degeneration. During the development of this breeding program two *V. vinifera* x *M. rotundifolia* (VR) hybrids, O39-16 and O43-43 were found to be highly resistant to *X. index* and prevent fanleaf degeneration. These root-stocks were derived from crosses of *V. vinifera x Muscadinia rotundifolia* Small (VR hybrids) and eventually patented and released (Walker et al. 1985, 1989, 1991; McKenry et al. 2004). After a 15-year sequence of intensive studies involving 204 separate trials, the five rootstocks (UCD GRN1, UCD GRN2, UCD GRN3, UCD GRN4, and UCD GRN5) with broad and durable resistance to root knot and dagger nematodes were released to nurseries in California in 2009 and were available commercially in 2011 (Ferris et al. 2012). Based on nematode densities, Harmony and Freedom, commercially acceptable for their resistance to root knot nematode, were rated resistant to *X. index* (McKenry et al. 2004).

Crop rotation is also a possible management strategy in California dagger nematode control. Before vineyards are replanted with grapevines, the land can be cropped with cereals or grains to suppress nematodes. An early study by Raski (1955) suggested that 3 years is an adequate period for crop rotation. However, more recent studies suggested that *X. index* infested sites should be left fallow or rotated to crops other than grapes or figs for at least 10 years (McKenry 2000). In moist sterile soil without food, *X index* died after 9–10 months, but survived for 4–5 years in soil where grapevines were removed, but roots remained (Raski et al. 1965).

6.5.7.2 American Dagger Nematode, *Xiphinema americanum*

The *Xiphinema americanum*-group is a large species complex comprising 55 nominal taxa of dagger nematode. At present, five valid species of the *X. americanum*-group: *X. americanum s. str.*, *X. brevicolle*, *X. bricolense*, *X. californicum, X. pachtaicum* and *X. rivesi* have been reported in California (Robbins 1993; Orlando et al. 2016). At least two unidentified *Xiphinema* species were also reported using molecular methods (Orlando et al. 2016). Representatives of this group are very widely distributed in agricultural fields and orchards in California. For example, sampling from 126 orchards showed that *X. americanum* and *Paratylenchus hamatus* occurred in more than 90% of the orchards and in all pear-growing areas of the state (French et al. 1964). Although, there are no studies showing direct evidence of pathogenicity of *X. americanum* group species in California, it has been shown that they transmit viruses: *X. americanum sensu stricto – Cherry rasp leaf virus* (CRLV), *Tobacco ringspot virus* (TRSV), *Tomato ringspot virus* (ToRSV) (Teliz et al. 1966; Brown and Halbrendt 1992) and *X. californicum – Cherry Rasp leaf virus* (CRLV), *Tobacco ringspot virus* (TRSV), *Tomato ringspot virus* (ToRSV) (Hoy et al. 1984; Brown and Halbrendt 1992).

6.5.8 Pin Nematodes, Paratylenchus *spp.*

Paratylenchus hamatus and *P. neoamblycephalus* are the two most common species of pin nematode encountered in California. Because of their small size, all species of *Paratylenchus* have the common name of "pin nematode". Among other characteristics, these two species can be differentiated by lack of a stylet in the males of *P. neoamblycephalus*. *Paratylenchus hamatus* was first collected in 1944 from a fig orchard in Merced County, and identified by Thorne (Thorne and Allen 1950). In California, it has also been identified from Butte, El Dorado, Fresno, Kern, Marin, San Joaquin, San Mateo, Santa Barbara, Stanislaus, Sutter, Tehama and Tulare Counties by Raski (1975) from grape, peach, prune, oak, rose, plum, pear and walnut.

Paratylenchus neoamblycephalus was described by Geraert (1965). In California, Raski (1975) identified it from Alameda, Contra Costa, Kings, Monterey, San Francisco, San Joaquin, Solano and Yolo Counties associated with prune, apricot, plum on peach root, rose, walnut, fig, apple, pear, grape and peach.

Paratylenchus was found in 65 of 97 prune orchards sampled (Lownsbery et al. 1974). In this survey, *P. neoamblycephalus* was the most common species, and was found in all four of the important prune growing districts in the state. Braun et al. (1975) and Braun and Lownsbery (1975) demonstrated pathogenicity of *P. neoamblycephalus* to Myrobalan plum by several methods including comparison of plant growth in fumigated and nonfumigated soil and inoculating plants with suspensions of extracted nematodes. Roots of Myrobalan seedlings inoculated with surface-sterilized nematodes were smaller, darker and had fewer feeder roots than those of non-inoculated controls. Nematodes were observed feeding ectoparasitically, but with heads embedded in roots as deep as the cortex. They were associated with small lesions and dead lateral roots. Clusters of nematodes were common at ruptures in the epidermis and where lateral roots emerged.

Paratylenchus hamatus, on the other hand, is somewhat of a conundrum because it is not uncommon to find high numbers of nematodes occurring in perennial cropping systems without causing apparent harm. For example, Ferris and McKenry (1975) found that in a vineyard in which vine yield growth and vigor were negatively correlated with populations of *Xiphinema americanum*, there was a positive correlation of *P. hamatus* with the same factors. In contrast, trees in a fig orchard infested with *P. hamatus* had dieback of twigs, and chlorotic leaves that died and fell from the tree along with undersized fruit. Infested roots exhibited enlarged and spongy cells which caused a slight swelling of the entire root, and growth of the growing point was apparently blinded (Thorne 1961). Feeding of large numbers on grape roots produced shallow, localized lesions (Raski and Radewald 1958). Ferris and McKenry (1975) found densities of *P. hamatus* were greater in fine-textured soils.

Ferris et al. (2012) studied the susceptibility of five newly released UCD series grape rootstocks to *P. hamatus*. Four of the new rootstocks (GRN1, GRN2, GRN3, and GRN5) were moderately resistant and one (GRN4) was found to be moderately susceptible. In contrast, of 22 rootstocks tested in previous studies, 15 were susceptible, 4 were moderately susceptible, and 3 were moderately resistant to this nematode.

6.5.9 Needle Nematode, Longidorus africanus

During the fall of 1967, the nematode *Longidorus africanus* was found in soil around the roots of stunted lettuce seedlings in the Imperial Valley of Southern California (Fig. 6.5). Root tips of lettuce seedlings attacked by this nematode are

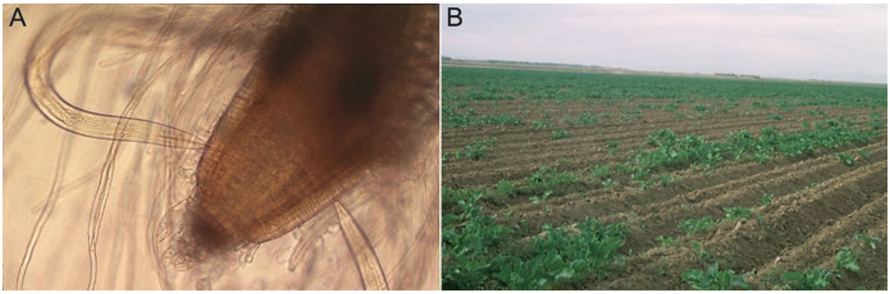

Fig. 6.5 (**a**) Needle nematode, *Longidorus africanus* feeding on root tip; (**b**) *Longidorus africanus* sugar beet field damage, Imperial Valley, California (A. Ploeg and University of California, Riverside)

swollen and usually have necrotic spots. Seedlings are severely stunted and because it feeds on root tips, plants are often severely stunted before the first true leaf develops (Radewald et al. 1969a). As infected plants mature, stunting continues, and they may never reach harvest-maturity. Root systems of older infected plants are greatly reduced in size. *Longidorus africanus* can cause a serious seedling disease at relatively low population levels in soil (Kolodge et al. 1986). This study showed that *L. africanus* can cause severe growth reductions in both carrot and lettuce, especially when nematode attack occurs within 10 days of seedling. Tolerance levels for carrot and lettuce exposed to *L. africanus* at seeding were less than 5 nematodes per 250 g soil (Huang and Ploeg 2001a).

The experimental work showed that this nematode has a wide host range including sorghum, barley, Bermuda grass, corn, wheat, cotton, okra, snap bean, lima bean, cucumber, cantaloupe, eggplant, and sugar beet. Most valley crops, with the exception of the crucifers, should be considered capable of supporting populations high enough to cause economic damage to fall-planted crops. In a state-wide survey for certain exotic and economically important plant parasitic nematodes in California, the CDFA detected *L. africanus* populations associated with commercial cotton and orange plants in the Imperial Valley (Dong et al. 2007).

The life cycle of *L. africanus* was completed in 7 weeks (Kolodge et al. 1986, 1987). *L. africanus* population densities increased with increasing depth. Chances for detecting this nematode were greatest in summer at depths of 60–90 cm (Ploeg 1998). Field studies in the Imperial Valley showed a strong correlation between the vertical distribution of *L. africanus* and soil temperature, with high populations occurring in the upper soil layers during the hot summer months (Ploeg 1998). Nematode multiplication is greatest at relatively high soil temperatures, ca. 28 °C. The results suggested that seeding of carrot or lettuce at soil temperatures less than 17 °C would significantly reduce damage by *L. africanus* (Huang and Ploeg 2001b). In the Imperial Valley, where *L. africanus* occurs, this would correspond to the period from November through March.

Longidorus africanus can be effectively controlled with nematicides (Radewald et al. 1969b), but because of increasing costs and restrictions on their use, alternative methods need to be developed.

6.5.10 Rice White Tip Nematode, Aphelenchoides besseyi

The first documentation of the possible presence of *Aphelenchoides besseyi* in California was in 1963 when the species was found in a culture of the fungus, *Sclerotium oryzae,* which had been isolated from a sample collected from a rice field in Butte County. The rice field was used by a research facility that exchanged seed with regions in Southeastern USA where *A. besseyi* was known to parasitize rice (Chitambar 1999). During 1997, in response to developing international trade agreements between Turkey and the USDA APHIS, the CDFA conducted intensive surveys of paddy rice seed in county driers of 13 rice-producing counties in California. *Aphelenchoides besseyi* was detected in few samples obtained from Butte and Sutter Counties. Subsequent detections were from paddy rice seed shipments intended for export in 1999, 2001, 2002, 2005 and 2008 in Sutter and Yolo Counties. This nematode species remains very limited in its distribution and infrequent occurrence within rice fields of Butte, Sutter and Yolo Counties and therefore, a 0% loss of rice yield due to *A. besseyi* was estimated for California in 1994 (Koenning et al. 1999). Based on international trade agreements, export shipments of paddy rice are handled on a per shipment basis and disqualify for phytosanitary certification if found contaminated with the white-tip of rice nematode (Chitambar 2008). The origin of the nematode species in California is not known. If it was introduced, then its low rate of detection and sporadic occurrence in cultivated field is an indication of its inability to fully establish to damaging levels within the state. Chitambar (2008) reasoned that certain biological, cultural and ecological factors, such as insufficient moisture, planting by airplane directly into flooded fields, presence of resistant varieties and high ambient temperatures, may be working against the nematode's ability to successfully establish and spread within California.

6.5.11 Sting Nematode, Belonolaimus longicaudatus

The sting nematode, *Belonolaimus longicaudatus* (Fig. 6.6) was discovered for the first time in 1992, associated with dying Bermuda turfgrass at a golf course near Rancho Mirage, Riverside County. Consequently, intensive delimiting surveys in the Coachella Valley were conducted by the CDFA and the Riverside County Department of Agriculture and by late 1993, the sting nematode was detected on Bermuda and rye turfgrass in eight golf courses (Chitambar 2008). The nematodes suppressed turfgrass root growth and caused stunting and chlorosis (Mundo-Ocampo et al. 1994). Based on its morphology, the nematode species was identified as *B. longicaudatus* and later confirmed by rDNA characterization (Cherry et al. 1997). Cherry et al. (1997) hypothesized that the California sting nematode was introduced from the Eastern United States. There had been earlier detections of the sting nematode in few interstate shipments of plant samples to California that were intercepted on entry and consequently, destroyed by state regulatory action. The current known distribution of the sting nematode is restricted to the original eight

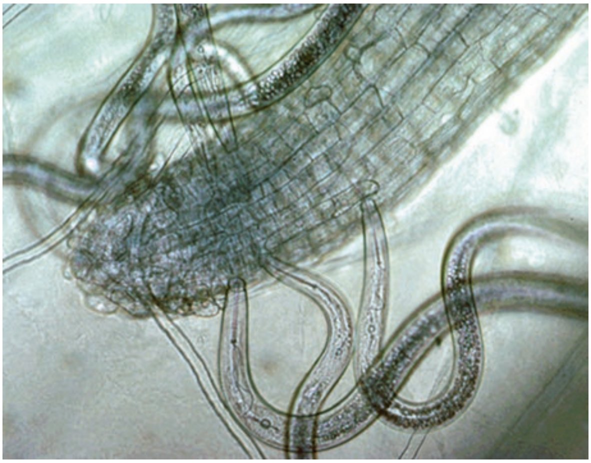

Fig. 6.6 Sting nematode, *Belonolaimus longicaudatus* feeding on root tip (O. Becker and University of California, Riverside)

golf courses in the Coachella Valley. This was confirmed by surveys of several major golf courses in California, conducted in 2012–2013 by the CDFA and sponsored by the USDA APHIS Cooperative Agricultural Pest Survey (CAPS) Program survey.

The Bermuda turfgrass in the Coachella Valley golf courses typically exhibited chlorosis at the beginning of April when the sting nematode populations began to increase. In a study on population dynamics of the sting nematode monitored at monthly intervals at three golf courses in Rancho Mirage, Coachella Valley, soil temperature and fluctuation of nematode densities were significantly correlated. At one golf course, population density peaked in October, with 1000 nematodes per 100 cm^3 of soil, but declined rapidly, with the lowest population density occurring in December with approximately 50 nematodes per 100 cm^3 of soil. Significant increases in nematode populations did not occur until temperature reached 20 °C or late spring. Nematode distribution was greatest in the top 15 cm of soil except during the hottest summer months, when the population was higher at depths of 15–30 cm (Bekal and Becker 2000b).

Belonolaimus longicaudatus is a major parasite of grasses and is also capable of parasitizing a wide range of crops including grapes, citrus, cantaloupes, lettuce tomatoes, cotton, ornamentals and weeds, however, its host range is not restricted to horticultural grasses or agricultural crops (Bekal and Becker 2000a). Many weeds, such as *Euphorbia glyptosperma*, *Sisymbrium irio*, *Paspalum dilatatum*, *Portulaca oleracea*, *Sorghum sudanense* and *Cyperus esculentus*, can serve as hosts for *B. longicaudatus* and only *Abelmoschus esculentus*, *Citrullus lanatus* and *Nicotiana tabacum* were non-hosts among the tested species. In the Coachella Valley, the sting nematode has not been found in grapes, citrus and other agricultural crops. *Belonolaimus longicaudatus* had a high reproductive fitness on a majority of species tested and is considered a major threat for most agricultural and horticultural crops grown in sandy soils (>80% sand) (Bekal and Becker 2000a).

Following its 1992–1993 detection, quarantine restrictions were imposed by State and County in order to contain or suppress the sting nematode within the Coachella Valley. Eradication was not deemed a practical alternative, due to high cost of operations, extensive sampling required and nature of dissemination of the nematode. Restrictions were placed on movement and disposal of mowed grass clippings from sting nematode-infested properties to non-infested properties or agricultural lands. Composting with sewer sludge was chosen as control of potentially infested grass clippings or thatch. Compliance agreements were established with golf course superintendents accordingly. Regulatory restrictions continue to keep *B. longicaudatus* under suppression in the Coachella Valley (Chitambar 2008).

6.5.12 Stubby Root Nematodes, **Trichodorus** *spp.,* **Paratrichodorus** *spp. and* **Nanidorus** *spp.*

Nematological surveys revealed that the stubby root nematodes are widely distributed in California. Presently, several valid species are reported: *Nanidorus minor, Paratrichodorus allius, P. grandis, P. porosus, Trichodorus aequalis, T. californicus, T. intermedius* and *T. dilatatus* (Allen 1957; Siddiqui et al. 1973; Rodriguez-M and Bell 1978). However, molecular analysis of trichodorid samples collected from non-agricultural areas revealed its high genetic diversity and indicated the presence of at least eight unidentified or putatively new species from the genus *Trichodorus* (Subbotin and Decraemer unpublished). *Nanidorus minor* and *P. porosus* are the mostly distributed species in agricultural fields and orchards. French et al. (1964) reported *N. minor* occurred in 12 pear orchards and *P. porosus* in 6 pear orchards in Placer County. Influence of the stubby-root nematode on growth of alfalfa was studied by Thomason and Sher (1957). Ayala and Allen (1968) tested four stubby root nematode species for their ability to transmit *Tobacco rattle virus* (TRV). *Paratrichodorus allius* was a good vector and was used in all experiments on nematode-virus interrelationships, whereas *N. minor* and *P. porosus* were moderately good vectors. The results showed that the populations of *P. allius* became infective after feeding on virus-infected tobacco for 1 h. Efficacy increased as the feeding time was increased up to 24 h. Populations remained infective for 20 weeks when kept at 20 °C without a host and 27 weeks when feeding on a virus immune host (Ayala and Allen 1968).

6.5.13 Citrus Sheath Nematode, **Hemicycliophora arenaria**

A brief account of the citrus sheath nematode, *Hemicycliophora arenaria*, is included here as this species has for long, only been reported from California, until more than 25 years later, when it was also reported from Australia and Southern

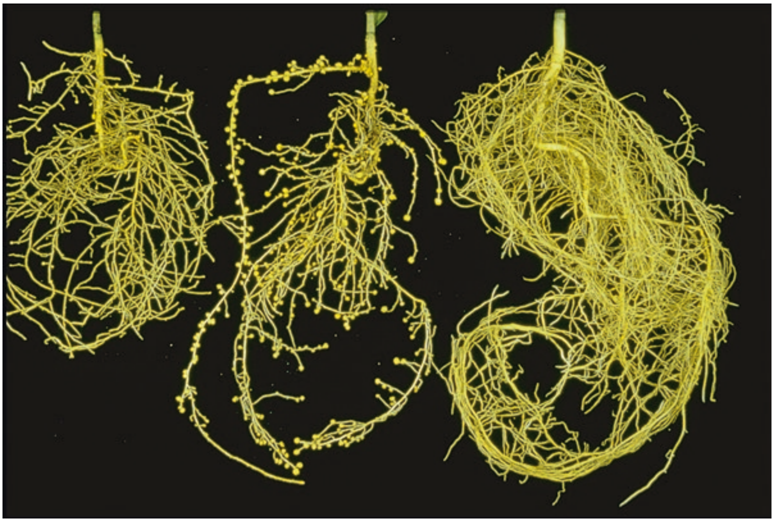

Fig. 6.7 Citrus root systems infected with *Hemicycliophora arenaria* (left and middle) and healthy root system (right). (Credit: F.D. McElroy and S.D. Van Gundy, University of California, Riverside)

Argentina (Reay 1984; Brugni and Chaves 1994; Chitambar and Subbotin 2014). The nematode was first reported by Van Gundy (1957) as an unknown species parasitizing rough lemon seedlings in a grower's nursery in the Coachella Valley, near Mecca, Southern California, causing 'peculiar galling' of infected roots quite unlike those caused by the root knot nematode (Fig. 6.7). A year later, the species was named and described by Raski (1958) as *H. arenaria.* By 1964, *H. arenaria* was found in a citrus ranch approximately 3.2 km from the original site in Riverside County and on citrus land in Imperial County. All properties were planted with citrus trees from a commercial nursery located near Niland in Imperial County, approximately 40 miles from the original site in Riverside County. This nursery had been planted on virgin desert soil and failed due to lack of moisture, and consequently, was abandoned in 1956. Surveys were conducted by the CDFA at that time to establish origin and extent of spread of the nematode species. In 1965, *H. arenaria* was found in a number of soil samples collected from cheese bush, a California native plant, growing in a virgin desert region about 1 mile north of the original abandoned nursery. At about the same time, the nematode species was also found on cheese bush in another native situation near Palm Springs, about 30 miles northwest from the infestation in Mecca. Additionally, another California native plant, coyote melon, was experimentally shown to be a host of the nematode species (McElroy and Van Gundy 1967). In 1971, *H. arenaria* was found in soil and root samples collected from roadside cheese bush plants near the entrance of a desert state park in San Diego County. These detections indicated that *H. arenaria* is indigenous to native plants in low and high elevation deserts within Imperial, Riverside and San Diego Counties of California and had been spread with citrus nursery stock from the abandoned nursery planting near Niland. Subsequent regulatory action taken by the

CDFA established the nematode as quarantine actionable and limited in distribution within California (Chitambar 2016). In 2006, CDFA once again detected this species in lemon and grapefruit soil in Imperial County (Chitambar 2008).

The preference of high temperature and sandy soils explains the very limited distribution of the citrus sheath nematode within desert regions of California, where it was discovered to be endemic on native desert plants (McElroy et al. 1966; McElroy and Van Gundy 1967). This ectoparasitic species reproduces at 30–32.5 °C, with 32.5 °C being the optimum, to complete a short life cycle of 15–18 days. Almost no reproduction occurs at 20 °C and is greatly reduced at 35 °C. Van Gundy and Rackham (1961) found reproduction to be greatest in sandy soil and gave experimental evidence of high reproduction in tomato plants. Subsequently, the citrus sheath nematode gained economic importance as a parasite of agricultural crops with the reclamation of Southern California deserts (Maggenti 1981). In California, citrus is the main host, while other agricultural crops have been experimentally shown to include tomato, blackeye bean, pepper, celery, squash and Tokay grape (Van Gundy 1959; Van Gundy and Rackham 1961; McElroy et al. 1966; McElroy and Van Gundy 1967, 1968; Van Gundy and McElroy 1969). Feeding of *H. arenaria* results in the production of galls at tips of lateral and terminal roots as well as a reduction in the number of feeder roots and top growth. Early studies established the damage potential of this species. The growth of rough lemon seedlings in *H. arenaria* infested soil at 30 °C for 5 months was reduced by 36% in comparison to seedlings in non-infested soil. Dry weight of tomato plants was reduced by 28%, and a 10–20% yield reduction in field-grown tomato and squash occurred at the original locality in Mecca, California. Growth of citrus and tomato was reduced from 12% at 25 °C to 37% at 30 °C (McElroy and Van Gundy 1967, 1968; Van Gundy and Rackham 1961).

6.5.14 Pacific Shoot-Gall Nematode, **Anguina pacificae**

Anguina pacificae was described by Cid del Prado Vera and Maggenti (1984) as a new species from the Northern Pacific Coast of California. This nematode causes stem galls at the base of tillers in annual bluegrass (*Poa annua*), resulting in yellow patches and irregular surfaces on North California golf course putting greens (Fig. 6.8). The disease has been found only along an approximately 20 to 30-mile-wide coastal corridor from Carmel to Mendocino (McClure et al. 2008). Over the years extensive research has been conducted to develop management strategies against *A. pacificae* (Westerdahl et al. 2005). Twenty-nine products were screened in a bioassay for efficacy against the nematode (McClure and Schmitt 2012). Of those, eight products showed some degree of control but only four were registered for use on golf course greens. McClure and Schmitt (2012) recommended biweekly application of products with the active ingredient azadirachtin that was derived from the Indian Neem tree (*Azadirachta indica*). Recently, Bayer CropScience developed fluopyram as a nematicide with excellent activity against several plant parasitic nematodes. Fluopyram significantly reduced the *A. pacificae* population and

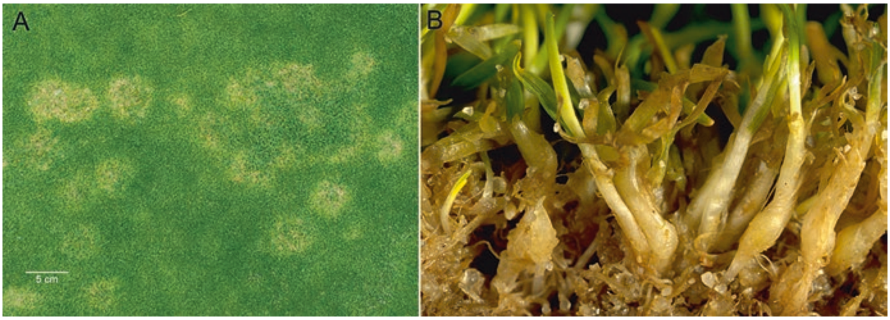

Fig. 6.8 *Anguina pacificae* on *Poa annua*. (**a**) Damaged putting green; (**b**) Galls on the crowns of infected plants. (Credit: M. McClure and L. Costello)

associated shoot galls compared to either Neemix[R] or the non-treated control by the end of the study. Two applications of fluopyram at either the low or high rate effectively restored turf health (Baird and Becker 2016).

6.5.15 Certain Plant Parasitic Nematodes of Common Occurrence in California

Plant parasitic nematodes in this category include species of genera such as *Helicotylenchus*, *Scutellonema* and *Tylenchorhynchus*, that are found frequently and distributed widely in cultivated and non-cultivated regions within California. In general, plant damage caused by high populations of these obligate migratory ectoparasitic root feeders may be more significant in small-area production sites and containerized crops in nursery, residential and local situations, than in larger areas and environments such as parks, pastures and cultivated fields. Furthermore, crop damage under field conditions is often difficult to assess since different genera and species are often present in mixed populations (Norton 1984).

6.5.15.1 Spiral Nematodes of the Genus *Helicotylenchus* spp.

In California, *Helicotylenchus* spp. are present in soil around the root zone of a wide range of plants including agricultural crops, fruit trees, ornamentals nursery stock forest trees and shrubs, desert shrubs, grasses and weeds, however, the host status of the associated plants is not always known. Feeding of spiral nematodes results in production of small discolored lesions in the root cortex and other underground parts, on which the nematode feed. Species reproduce mainly by parthenogenesis and high nematode population levels can severely damage roots causing them to become slightly swollen, spongy, discoloured with sloughed-off cortical tissue (Maggenti 1981). While species of *Helicotylenchus* may not be identified for nematode management in cultivated fields, certain species that have been reported in

California include *H. dihystera*, *H. digonicus, H. pseudorobustus, H. erythrinae* and other species (Siddiqui et al. 1973; Dong et al. 2007). Banana spiral nematode, *H. multicinctus*, is not distributed widely in California and was reported in the mid-1960s and 1970s from Riverside, Los Angeles and San Diego Counties (Sher 1966; Siddiqui et al. 1973). Pathogenicity of *Helicotylenchus* spp. has not been studied in California.

6.5.15.2 Spiral Nematodes of the Genus *Scutellonema*

In California, *Scutellonema* spp., also called spiral nematodes, are common associates of a wide range of agricultural crops, fruit trees, ornamentals, nursery stock, forest trees and shrubs, desert shrubs, grasses, and weeds. Agricultural crops include alfalfa, cotton, potato, corn and several other crops. The host status of associated plants is not always known. *Scutellonema brachyurus* has been reported as wide spread within the state (Siddiqui et al. 1973). General plant damage associated with *Scutellonema* spp. is commonly exhibited as numerous small, brown necrotic root lesion produced as a result of their feeding. Internally, isolated root cavities are produced by the nematodes while above ground symptoms may include leaf stunting and chlorosis, and reduced growth. The shallow root lesions become avenues for secondary invaders, namely bacteria, fungi and mites. Pathogenicity of *Scutellonema* spp. detected on agricultural and ornamental crops in California, has not been studied.

6.5.15.3 Stunt Nematodes, *Tylenchorhynchus* spp.

Tylenchorhynchus spp. are associated with the roots of a wide range of plants including cotton, oats, and corn as well as other agricultural crops, fruit trees, ornamentals, nursery stock, forest trees and shrubs, desert shrubs, grasses, and weeds. The host status of associated plants is not always known. General plant damage associated with *Tylenchorhynchus* spp. includes stunting of the root system which is expressed aboveground by yellowing of foliage, stunted top growth, and sometimes wilt and defoliation (Maggenti 1981). Generally, *Tylenchorhynchus* spp. are considered mild pathogens of plants and are common associates of several plants (Norton 1984; Table 6.2). Pathogenicity of several *Tylenchorhynchus* spp. detected on agricultural and ornamental crops in California has not been studied (McKenry and Roberts 1985).

6.6 Conclusion and Future Perspectives

California's multibillion dollar investment in the nation's largest diversity of agricultural crops, nursery and turf productions, and its role as a major provider of food for the nation and global communities, more than warrants the continued and future protection of the state's crop productions against damages and losses caused by plant parasitic nematodes. To reach this goal, the state continues to recognize and resolve challenges in nematode management and biological technologies. The future is promising.

Stimulated by the restricted availability of nematicides, California is looking ahead to the use of more sustainable management scenarios for managing plant parasitic nematodes. Recent developments offer new tools to fine tune the use of cultural and biological practices for local cropping systems. The commercial availability of several biological nematicides, of products with newer and safer modes of action, of the increasing availability of nematode resistant cultivars, of the development or selection of cover crop varieties for use against particular nematode species, and the use of green manures, biofumigation, and trap cropping are promising techniques. Combining these with a strong nematode control and certification program for nursery crops, the development of molecular techniques for identification of plant parasitic nematodes, online databases to rapidly search out nematode resistant crops, computerized soil temperature monitoring equipment plus computer models for calculating nematode degree days and modeling population cycling, and a greater understanding of nematode biology and population dynamics make it possible to develop promising scenarios to reduce damaging nematode populations and increase yields.

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Chapter 7
Plant Parasitic Nematodes in Hawaiian Agriculture

Brent Sipes and Roxana Myers

7.1 Introduction

Hawaii's diverse and mild climate allows for the cultivation of many crops. Different crops have been introduced and cultivated with each successive wave of immigrants to the islands. Many crop plants experienced an exponential growth in hectares only to face a decline in planted area as competition and economic factors drove production elsewhere. The introduction of each crop brought along associated nematode pests. These plant parasitic nematodes became established and are now endemic to the islands.

Hawaii is located on the Tropic of Cancer and has a subtropical climate. Hawaii is home to some of the tallest shield volcanoes in the world. The slopes of Mauna Kea at 4207 m, Mauna Loa at 4169 m and Haleakalā at 3055 m provide temperate climates that allow the cultivation of cool season crops such as carnation, strawberries, persimmon, blueberries and even short-chill peaches. Consequently, the range of plant parasitic nematodes found in Hawaii is not limited to solely tropical nematodes. Temperate species of plant parasitic nematodes can survive well in the higher elevations of the islands.

The Polynesians brought sugarcane, taro, banana, coconut, mountain apples, sweet potato and breadfruit to Hawaii (St. John and Jendrusch 1976). It is likely that these settlers to Hawaii brought not only the plants, but plant parasitic nematodes as

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well. Burrowing nematode, *Radopholus similis*, likely infected the banana corms that were transported from Tahiti to Hawaii. It is even possible that the reniform nematode, *Rotylenchulus reniformis*, was introduced on sweet potato as well.

Starting in the 1860s, Chinese immigrants began rice cultivation in Hawaii. Rice was ultimately grown on 4050 ha before being abandoned in the 1930s (Haraguchi 1987). A legacy of rice production in Hawaii, white tip of rice, caused by *Aphelenchoides besseyi*, was likely introduced during this time. *Aphelenchoides besseyi* is occasionally a problem in tuberose production (Holtzmann 1968) but generally of little importance. *Aphelenchoides fragariae* and *A. ritzemabosi* were also found in carnation and chrysanthemum but are less of a problem since the crops are not commercially grown in the state today. These nematodes are also sometimes found in anthurium and not uncommonly in orchids. The nematode causes abortion or deformation of the orchid flower spikes (Uchida and Sipes 1998). *Aphelenchoides* is now a legacy nematode in the state. As Hawaii is sometimes used as a winter nursery for seed, rice seed requires phytosanitary certification to be free of *A. besseyi* before it can be exported from the state.

A small number of fields are devoted to cole crops in Hawaii. At higher elevations on the islands of Maui and Hawaii, populations of *Heterodera schachtii* and *H. trifolii* were introduced and have established. Consequently, cabbage, broccoli, cauliflower and the Chinese mustard greens grown in these infested fields can suffer yield loss from the cyst nematodes. Interest in locally grown vegetables and increased production of cole crops could result in these cyst nematodes becoming a significant problem in Hawaii.

Plantation agriculture became the norm for Hawaii, with sugarcane and pineapple dominating agricultural production from the late 1880s to the 1980s (Melrose et al. 2016). Hawaii gained fame for its production of sugarcane and remains synonymous with pineapple. These crops were cultivated over large areas, using standard practices and equipment that moved from field to field. Plantation agriculture provided ample opportunities for the dispersal of nematodes across fields and even islands. Plantation agriculture determined the major nematode problems and approaches to nematode control in Hawaii. Consequently, root knot, reniform and burrowing nematodes have been the most widely studied plant parasitic nematodes in the state. By the 1990s, agriculture in Hawaii had begun a switch to diversified crops and ornamentals but the nematodes infesting the soil remained the same. Land formerly cropped with sugarcane or pineapple was planted to a variety of vegetable and fruit crops with the nematodes present continuing to cause yield loss (Table 7.1).

7.2 Root Knot Nematodes, *Meloidogyne* spp.

Many species of *Meloidogyne* are found in Hawaii. *Meloidogyne javanica* and *M. incognita* are most common in agricultural production. *Meloidogyne hapla* is found at higher elevations on the islands of Maui and Hawaii and, interestingly, on a low elevation planting of *Coffea arabica* cv. Mocha on Maui. *Meloidogyne arenaria* can

Table 7.1 Plant parasitic nematodes of common agricultural and ornamental crops in Hawaii

Nematode species	Crop and plant	References
Aphelenchoides besseyi	Orchids, hydrangea, tuberose, rice	Sher (1954), Holtzmann (1968), Raabe et al. (1981), and Uchida and Sipes (1998)
A. fragariae	Orchids, anthurium, ferns	Sher (1954), Raabe et al. (1981), and Uchida and Sipes (1998)
Helicotylenchus multicinctus	Banana, pineapple	Raabe et al. (1981), and Wang and Hooks (2009a)
Helicotylenchus sp.	Citrus, orchids, palms, tomato, beans	Raabe et al. (1981)
Heterodera schachtii	Sugarcane, brassicas	Oliveira (1940), and Raabe et al. (1981)
H. trifolii	Brassicas	Raabe et al. (1981)
Meloidogyne arenaria	Heliconia, tomato	Raabe et al. (1981)
M. graminis	Turf	McClure et al. (2012)
M. hapla	Lettuce, coffee, papaya	Sher (1954), Raabe et al. (1981), and Handoo et al. (2005)
M. incognita	Tomato, papaya, edible ginger, sweet potato, awa, pineapple, heliconia, protea, koa	Sher (1954), Trujillo (1964b), Raabe et al. (1981), and Nelson et al. (2001)
M. javanica	Papaya, pineapple, cordyline, tomato	Raabe et al. (1981) and Sipes et al. (2009)
M. konaensis	Coffee	Eisenback et al. (1994)
M. marylandi	Turfgrass	McClure et al. (2012)
Meloidogyne sp.	Taro, pineapple, sugarcane, banana, noni, ornamental ginger, brassicas, cucurbits, passion fruit, beans, poha	Parris (1941), Oliveira (1940), Raabe et al. (1981), Nelson (2005), and Wang and Hooks (2009a)
Pratylenchus brachyurus	Easter lily, pineapple, mango	Sher (1954), and Raabe et al. (1981)
P. coffeae	Breadfruit, banana	Raabe et al. (1981), and Lau et al. (2018)
Pratylenchus sp.	Sugarcane, papaya, dracaena, passion fruit, edible ginger	Sher (1954), and Raabe et al. (1981)
Radopholus similis	Anthurium, edible ginger, banana, bird of paradise, ornamental ginger	Sher (1954), Raabe et al. (1981), Aragaki et al. (1984), Nishina et al. (1992), and Wang and Hooks (2009a)
Rotylenchulus reniformis	Cowpea, pineapple, cucurbits, solanaceous crops, brassicas, sweet potato, papaya, cordyline, passion fruit, beans	Linford and Oliveira (1940), Linford and Yap (1940), Lange and Holtzmann (1958), Martin (1960), Raabe et al. (1981), and Robinson et al. (1997)
Tylenchulus semipenetrans	Citrus	Sher (1954)
Xiphinema americanum	Mango, ohia, sugarcane	Raabe et al. (1981)

be found in ornamental plants. Galling caused by root knot nematode can be observed on many agricultural crops, ornamental plants and native species. More often than not, the species is unidentified and attempts to identify the species result in data that does not match to any currently identified species. *Meloidogyne konaensis,* found on coffee on the island of Hawaii, presents an interesting story of an unknown species that was identified and characterized.

7.2.1 Coffee

Coffee is the most traded agricultural commodity in the world and *Coffea arabica* is an important specialty crop in Hawaii. Coffee was unsuccessfully introduced into Hawaii in the 1810s by Don Francisco de Paula Marin and then successfully established in 1825 by the Hawaiian Chief Kamauleule, the governor of Oahu. Chief Kamauleule imported coffee plants from Brazil (Kinro 2003). In 1892, Herman Weidemann introduced the Typica variety of coffee from Guatemala into the Kona region of Hawaii. Today, coffee is grown on all the major Hawaiian Islands. In Kona, most of the coffee orchards are less than 2 ha and managed by a single family (Bittenbender and Easton Smith 2008). Kona and Ka'u coffees from the island of Hawaii are among the highest valued coffee in the world. Historical records speak of these introductions as being seedlings or plants – either of which could easily have been infected with nematodes.

Root knot nematodes had been reported from *C. arabica* in the Kona region for many years but remained a misunderstood problem for the first century of coffee production (Raabe et al. 1981). The root knot nematode infecting coffee in Kona was initially identified as *M. incognita,* but upon closer examination determined to be a new species, *M. konaensis* (Eisenback et al. 1994). Initially, the problems now associated with root knot nematode were referred to as "transplanting decline," "replant problem," "nutritional stress," and "Kona wilt" (Zhang and Schmitt 1995). It was not until coffee trees began to die on a coffee research station and on commercial farms in the Kona area that root knot nematode was identified as the causal agent of "coffee nematode decline" (Zhang and Schmitt 1995). Coffee nematode decline severely stunts trees (Fig. 7.1a), causes extensive damage to the coffee root systems (Fig. 7.1b) and shortens tree life. The nematode infection can cause trees to flag or wilt under water stress and reduces coffee yield by 60%.

Morphological similarities exist between *M. konaensis* and the coffee-parasitizing *M. paranaensis* found in Central America and Brazil (Carneiro et al. 1996). Interestingly, *M. konaensis* does not parasitize coffee in Brazil (Monteiro et al. 2016) like the species does in Hawaii. Populations of *M. konaensis* collected from coffee roots can lose the ability to parasitize coffee when grown on alternative hosts for several generations (Sipes et al. 2005). The ability of *M. konaensis* to parasitize coffee may be a mutation, since this nematode has a wide host range (Zhang and Schmitt 1994) and easily loses the ability to develop on coffee when removed from coffee.

Fig. 7.1 (**a**) Infection by *Meloidogyne konaensis* causes significant stunting of *Coffea arabica*. Inoculated plants on the left and uninoculated plants are on the right; (**b**) Comparative root damage observed on *Coffea arabica* infected or uninfected with *Meloidogyne konaensis*. Infected coffee roots are on the right and uninfected coffee roots are on the left

Management of coffee nematode decline has followed several approaches. The common practice to establish new coffee plantings was to collect seedlings from under existing trees. These seedlings were termed "pula-pula" in the local pidgin. The seedlings germinated from berries that were not harvested and fell to the ground. These seedlings became infected with the root knot nematode, were pulled from the ground, transplanted into new orchards and subsequently the nematode infested new fields. Producing coffee seedlings in a nursery operation has limited nematode infestations into new fields. Grafting nematode tolerant rootstocks to *C. arabica* scions has also proven effective. *Coffea liberica* 'Dewevrei', *C. canephora* 'Nemaya', *C. canephora* 'Apoatã' and *C. arnoldiana* have better shoot growth, healthier root systems and less nematode reproduction compared to *C. arabica* (Cabos et al. 2010; Schmitt et al. 2001). *Coffea liberica* 'Dewevrei' is currently employed as a nematode tolerant rootstock for coffee in Hawaii (Serracin and Schmitt 2002).

7.2.2 Ginger

Edible ginger, *Zingiber officinale*, is grown for the fresh market in Hawaii and U.S. mainland, consequently the appearance of the rhizome is very important. Several nematodes infect the rhizome including *M. incognita* and *R. similis* (Nishina et al. 1992). *Meloidogyne incognita* is especially important to control because it acts synergistically with *Ralstonia solanacearum* resulting in entire rhizome loss (Trujillo 1964b). In ginger, root knot nematode does not form noticeable galling on the rhizomes (Fig. 7.2). Rather with heavy nematode infection, the rhizomes appear lumpy and cracked. These lumpy and cracked rhizomes are unmarketable.

Control of *M. incognita* in ginger is a challenge. Previously, methyl bromide fumigation served as the management practice. With the loss of methyl bromide, growers adopted a process of rotating to "virgin fields" or fields not having a history of ginger production. This approach worked well for several years until the availability of virgin fields was exhausted. Resistance and tolerance to *M. incognita* is found within *Z. officinale* germplasm (Eapen et al. 1999; Myers et al. 2017). Several germplasm lines had low yield differences between infected and uninfected plants suggesting tolerance (Myers et al. 2017). One *Z. officinale* germplasm accession had a Reproductive factor (Rf) half that of the highest Rf, suggesting partial resistance to *M. incognita* (Myers et al. 2017). These ginger germplasms hold promise for breeding work to incorporate genetic control into the crop.

Fig. 7.2 *Zingiber officinale* cultivars showing reduction in size of ginger hands and total amount of ginger harvested when infected with *Meloidogyne incognita*. Infected rhizomes are on the right and unifected rhizomes are on the left

7.3 Burrowing Nematode, *Radopholus similis*

Radopholus similis is a tropical nematode that is found on multiple crops of economic importance in Hawaii. *Radopholus similis* is often associated with toppling disease in banana, however, in Hawaii the nematode causes more damage to anthurium and the nematode is a quarantined pest. The populations of *R. similis* found on banana and anthurium appear to have different origins. B. G. Chitwood noted, while working in Hawaii, that burrowing nematode from banana differed slightly from those he found in anthurium. RAPD markers grouped banana populations together and separately from anthurium populations (B. Sipes, unpublished). These lines of evidence suggest that burrowing nematode may have been introduced into Hawaii on banana and separately on anthurium, crops that are both vegetatively propagated.

7.3.1 Anthuriums

Anthuriums, *Anthurium andraeanum*, are Hawaii's top selling cut flower (USDA NASS and HDOA 2016). Originally brought to the islands to decorate the estates of sugar plantation owners, farmers began to cultivate the plant for cut flower sales in the 1940s (Alvarez et al. 2006). By developing export markets to the U.S. mainland and Europe, production reached its peak in 1980 with 2.5 million dozen flowers sold (Kamemoto 1981). The decline in cultivation today is due to global competition and the high cost of disease management associated with bacterial blight and plant parasitic nematodes. Anthurium is an example of the boom and bust cycle common to many commercial crops in Hawaii.

Radopholus similis and, to a lesser extent, *Meloidogyne incognita* cause damage to anthurium plants in the field with limited control options for growers. Plants infected with *R. similis* become severely stunted resulting in yield reductions of up to 50% (Aragaki et al. 1984). Anthurium decline not only reduces the number of flower stems but also the size of harvested cut flowers (Fig. 7.3a) (Sipes et al. 2004). Below-ground symptoms of burrowing nematode infection start with dark lesions on the roots followed by a root rot and blackening of the root system.

In Hawaii, new fields of anthurium are planted using cuttings from old production sites. The anthurium cane, known locally as gobo (the Japanese word for burdock), can harbor *R. similis* without noticeable symptoms (Sipes et al. 2004). Replanting infected material is the most common method of dissemination of these nematodes followed by contaminated tools and water run-off. The nematode population at the time of planting greatly affects the severity of the decline (Sipes et al. 2004). Leaf production was reduced by 75% when small plants were inoculated with 1000 *R. similis* (Sipes and Lichty 2002). Overtime as nematode populations exponentially increase, reductions in plant growth become more evident.

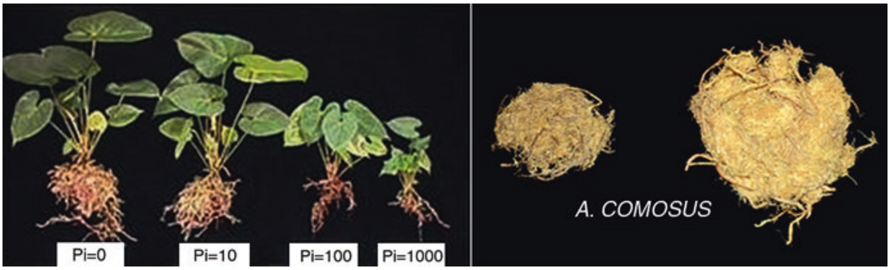

Fig. 7.3 (**a**) *Anthurium andraeanum* exhibiting effects on growth at different initial populations of *Radopholus similis*; (**b**) Root biomass of pineapple (*Ananas comosus*) infected with *Rotylenchulus reniformis* (left) compared to the biomass of an uninfected pineapple (right)

Historically metam-sodium was used as a pre-plant treatment with post-plant fenamiphos applications (Higaki et al. 1994). Growers would also commonly replace the volcanic cinder growing media at the establishment of new plantings. Propagative gobo can be treated with hot water at 50 °C for 10 min (Higaki et al. 1994) to eliminate *R. similis*. Nursery plants are grown on raised benches to avoid infested field conditions. With the phase-out of fenamiphos and the limited availability of volcanic cinder, commercial growers also have incorporated greater levels of sanitation and good agricultural production practices. These practices include starting new fields with tissue-cultured anthurium plantlets or disinfested cuttings planted into clean beds to manage burrowing nematode (Sipes et al. 2004).

7.3.2 Banana

Banana, *Musa* spp., is common in Hawaii as commercial orchards and backyard plantings. Banana is among the "canoe plants" introduced with the first Polynesian settlers. The first Hawaiians brought Iholenas, Maolis, Popoulus and Fei starchy bananas to the islands between 200 and 1350 CE (Kepler and Rust 2011). The dessert bananas, like Cavendish, were introduced later after European contact but constitute the majority of plantings today. The Hawaiians travelled with the bulb-like banana rhizomes as planting material (Pope 1926), that likely were infected with plant parasitic nematodes. Today, Cavendish and Brazilians (locally referred to as apple bananas) constitute the major cultivars grown in Hawaii (Chia 1981; Huggins et al. 1990).

In Hawaii, surveys of banana showed presence of *Radopholus similis*, *Meloidogyne* spp. and *Helicotylenchus multicinctus* (Wang and Hooks 2009b). *Radopholus similis* is a major pest of economic importance in the majority of banana growing regions throughout the world and the most common nematode recovered on the island of Hawaii (B. Bushe, University of Hawaii at Manoa College of Tropical Agriculture and Human Resources, personal communication; Gowen et al. 2005; Wang and Hooks 2009b). Toppling of plants is not common in Hawaii, rather nematode damage manifests in smaller bunches and fewer suckers being produced in the mat. Banana is often propagated by division of these suckers originating from the base of a mother plant. This propagation method can result in the movement and spread of nematodes with the planting material.

Management of nematodes in banana has evolved over time. Paring of the corm and subjecting the corm to elevated temperatures was an early recommendation (Trujillo 1964a). Current recommendations for disinfesting banana suckers are for a 10-min soak in a 50 °C bath (Wang and Hooks 2009a). The use of nematicides was common until concern grew for non-target effects and removal of products from the market. Carbofuran, ethoprop and fenamiphos have been used for management of nematodes in banana in Hawaii. However, propping fruiting plants with poles to prevent toppling, managing the numbers of suckers, mulching and fertilizer applications to increase plant vigor are preferred by growers over using nematicides. Tissue-cultured plantlets provide a clean banana that can be planted into soil and substantially reduce damage and lengthen tree life (Perez and Hooks 2008). Natural enemies of plant parasitic nematodes including omnivorous and predatory nematodes, nematode-trapping fungi and *Pasteuria penetrans* are commonly found in banana (Wang and Hooks 2009a). Given the perennial nature of banana, these organisms may provide control and limit losses due to nematodes when used in conjunction with cultural controls.

7.3.3 Quarantines

Differences among populations of *R. similis* in their parasitic behavior is well documented. In Florida, populations of *R. similis* infect citrus leading to slow decline. The infection of citrus by the Florida populations resulted in quarantine restrictions for *R. similis* around the world with particular impacts on Hawaii.

Quarantine restrictions to Hawaii's primary plant export destinations of Japan, California, Arizona and Texas prohibit entry of all plants contaminated with burrowing nematode (L. Wong, Hawaii Department of Agriculture, personal communication; Evans and Greczy 1995). Growers must follow strict protocols to receive certification to ship plants to these destinations including growing plants on benches above the ground, using soilless media such as peat, sphagnum, bark, charcoal, perlite, vermiculite, rockwool, pumice or volcanic cinder and having regular inspections and samplings for the nematode. Certification adds to the cost of production for growers and the loss of plants intercepted infected with burrowing nematodes can be economically devastating. Raised benches provide the best protection from nematode spread (Ko et al. 1997). Volcanic cinder provided a reasonably priced growing media until plant parasitic nematodes were detected in the cinder sources (Cabos et al. 2012a, b). Steam sterilization of cinder media effectively decontaminate media of *R. similis* and other nematodes and has been adopted throughout the foliage industry (Cabos et al. 2012a). Pre-shipment decontamination of plants with drenches or dips in abamectin effectively reduce the nematode population to non-detectable levels (Chinnasri et al. 2005). Post-plant decontamination of potted plants delivering a continuous stream of 50 °C water for 10 min directly to the media and roots of infected plants effectively reduced nematode populations but is not yet approved as a quarantine treatment (Cabos et al. 2012b).

7.4 Reniform Nematode, *Rotylenchulus reniformis*

Rotylenchulus reniformis was discovered on cowpea by researchers working at the Pineapple Research Institute of Hawaii (Linford and Oliveira 1940). The sedentary females swell upon establishing feeding sites and their swollen shape resembles a kidney, resulting in the nematode's common name. The reniform nematode has a unique lifecycle among plant parasitic nematodes. After hatching, all moults take place outside of the host yet only the adult females infect a root to feed (Rebois 1973). *Rotylenchulus reniformis* has an extensive host range that includes some of the canoe plants (Robinson et al. 1997). It is possible *R. reniformis* was introduced on plants like sweet potato. *Rotylenchulus reniformis* is widespread across the state occurring on the islands of Kauai, Oahu, Maui, Molokai, Lanai and Hawaii or cultivation of canoe plants by Hawaiians. This wide distribution may be a result of pineapple production on many of these islands. Whereas *R. reniformis* causes direct yield reduction, it is also a Class A quarantine pest in California resulting in the same quarantine restrictions as *R. similis*.

7.4.1 Pineapple

Pineapple, *Ananas comosus* var. *comosus* is a tropical perennial originating in South America (Coppens d'Eeckenbrugge and Leal 2003). The pineapple plant was introduced to Hawaii at the same time as coffee by Don Francisco de Paula y Marin, a Spanish advisor to King Kamehameha I. However, California migrants to Hawaii, most notably James D. Dole, did not began developing pineapple as an export crop until 1898 (Bartholomew et al. 2012). The pineapple industry expanded from then and by 1960 accounted for 80% of the world canned fruit production (Bartholomew et al. 2012). The industry aggressively marketed Hawaiian pineapple such that Hawaii became synonymous with the crop.

Within 20 years of widespread commercial cultivation of pineapple in Hawaii, nematodes were recognized as a serious production constraint (Caswell and Apt 1989). By the 1950s, *R. reniformis* had displaced root knot nematodes as the most serious nematode pest of pineapple (Rohrbach and Apt 1986). Pineapple infected with *R. reniformis* has leaves that are less erect than uninfected plants, are reddish in color and the plants show poor growth. *Rotylenchulus reniformis* allows the pineapple roots to elongate and provide good anchorage, but the nematode inhibits secondary root formation (Fig. 7.3b). Improper management of reniform nematodes typically leads to ratoon crop failures in pineapple. Interestingly, the reniform nematode population density does not increase immediately after pineapples are planted and begin rooting, but rather the densities remain static for up to 8 months (Sipes and Schmitt 1994a, b). After this period of relatively stable populations, *R. reniformis* enters a linear growth phase and increases to levels of up to 10,000 nematodes/250 cm^3 soil (Sipes and Schmitt 1994a, b). This delayed population development may be related to endogenous protease inhibitors found in the pineapple roots (Radovich et al. 2009). *Rotylenchulus reniformis* can tolerate extreme temperatures and survives extended periods without a host. The nematode survives fallow periods in the egg stage or as anhydrobiotic juvenile stages (Tsai and Apt 1979).

The severity of damage to pineapple from *R. reniformis,* as well as from *M. javanica*, resulted in substantial efforts to manage the nematode. Early research at the Pineapple Research Institute included screenings for host plant resistance and biological control (Caswell and Apt 1989). George H. Godfrey initiated seminal research "to pave the way for biological control" of nematodes but this avenue of research was cut short by the Great Depression (Caswell and Apt 1989). Work by scientists at the Pineapple Research Institute resulted in the discovery and development of fumigant nematicides. The nematicidal activity of D-D (1,2-dichloropropane, 1,3-dichloropropene) was uncovered by Walter Carter (1943). The discovery of this first fumigant nematicide allowed the full extent of nematode reductions to yield to be fully measured. A decade later, Carl T. Schmidt discovered and patented 1,2-dibromo-3-chloropropane (DBCP) for use as a nematicide while working at the Pineapple Research Institute. The use of post-plant nonfumigant nematicides for control of *R. reniformis* was pioneered by Walter J. Apt. Apt's extensive research demonstrated how nonfumigant nematicides like fenamiphos, metam sodium, or oxamyl could be successfully applied using drip irrigation systems (Apt and Caswell 1988). The application of nematicides, especially those with high mammalian toxicity, via drip irrigation provides greater protection to applicators and non-target organisms, allows for better distribution of the nematicide in the root zone and for lower effective rates to be used.

7.4.2 Sweet Potato

Sweet potato, *Ipomoea batatas*, was introduced to Hawaii by early Polynesian settlers (Valenzuela et al. 1994). With approximately 230 cultivars historically grown, sweet potato was an important staple food for Hawaii for many years (Nelson and Elevitch 2010). Today, sweet potato plays a crucial role in local consumption and as a valuable export commodity. Commercial production started in 1849 (Valenzuela et al. 1994) and has grown to 7575 metric tons annually (NASS 2012). Commercial sweet potato production primarily occurs on the Hamakua Coast of Hawaii Island with the Okinawan Purple the preferred cultivar for the export market (Miyasaka and Arakaki 2010).

Reniform nematode is widely distributed among farm lands on the Hamakua Coast. The first report of *I. batatas* as a host of reniform nematode occurred in 1960 in Louisiana (Martin 1960). Hawaiian wood rose, *I. tuberosa*, was documented as a host by Linford and Yap (1940) much earlier. *Rotylenchulus reniformis* incites necrosis and discoloration of roots as well as reduces the overall volume of the sweet potato root system (Martin 1960). The tuberous roots become cracked and distorted with infection by *R. reniformis* resulting in marketable yield losses (Clark and Wright 1983). Since cracking occurs early in the development of the tuberous root, damage occurs in fields with low populations of *R. reniformis*. Size differences in tuberous roots occur more commonly in heavily infested fields where nematodes have caused root pruning and stunting of the plants than in farm lands where nematodes are absent.

A common practice for commercial growers is to move to a new field after one cropping cycle and avoid replanting sweet potato for 3–4 years (Valenzuela et al. 1994). If this is not practical, fields are plowed to allow decomposition of debris for 2–3 months before fumigating with a nematicide. Crop rotation with non-hosts of *R. reniformis* can also reduce field populations. Differences in damage from reniform nematode were observed among sweet potato variety trials suggesting that planting nematode resistant or tolerant sweet potato cultivars may be a viable management strategy (Miyasaka and Arakaki 2010).

7.4.3 Papaya

Carica papaya, commonly called papaya, is a short-lived small tropical fruit tree. The fruit can be consumed as a vegetable when green but in Hawaii the fruit is harvested when ripe and consumed as a fresh fruit. Papaya, like many of the crops, was introduced to Hawaii from its native Central America by Don Francisco de Paula y Marin (Manshardt 2012). The cultivars grown today in Hawaii are derived from a gynodioecious Caribbean solo papaya introduced by Gerrit P. Wilder in 1911 (Manshardt 2012). With a farmgate value of $9.7 million in 2016, papaya is a significant agricultural commodity in Hawaii (USDA NASS 2017).

As the papaya industry grew in Hawaii, nematode problems were identified (Lange and Holtzmann 1958). Papaya planted into nematode-infested soil that was fumigated responded with increased yield (Lange 1960). However, chemical controls for reniform nematode, or root knot nematodes for that matter, never became a common commercial practice in Hawaii.

An underlying reason why nematode control is not considered important in papaya is because the plant has a high damage threshold for *R. renifomis* compared to other crops. A Paraguaná type papaya had a damage threshold of 4000 vermiform stages/250 cm^3 soil (Crozzoli et al. 2004). Soil fumigation in Florida did not increase papaya yields and fumigation was not recommended for initial populations below 195 *R. reniformis*/250 cm^3 soil (McSorley et al. 1983). The Solo type papaya behaves similarly (Alston et al. 2003). Initial population densities of *R.*

reniformis below 5000/250 cm^3 soil did not cause damage to the plant. The same is true for *M. javanica*.

Papaya is unique among crops in Hawaii for this tolerance to plant parasitic nematode infection. In a comparison of papaya cultivar susceptibility to *M. javanica*, the Hawaiian cultivars were all susceptible with Rf all greater than 1. The cultivar Sunrise had an Rf greater than 10 (Sipes et al. 2009). Indirect selection for tolerance to reniform nematode may have taken place by breeders.

7.5 Conclusions

As Hawaii adopts sustainable goals and looks for greater food resilience, plant parasitic nematodes will remain as a primary constraining factor. Often good agricultural practices would have prevented the introduction of a plant parasitic nematode or could have limited their spread. Since nematodes have been introduced and spread through the state, the need for effective, economic and environmentally friendly management options for plant parasitic nematodes has never been greater. Plant parasitic nematodes in the soil or cryptic habitats like plant tissue are challenging to control, detect and manage. Fundamental and applied research needs to be conducted that leads to the development of cost effective and sustainable approaches for controlling nematodes in high cost of production places such as Hawaii. Likely, the best management options will combine chemicals, biological control agents, cover crops and plants that have been bred or genetically engineered for tolerance or resistance. Original and innovative approaches will allow us to manage the diverse plant parasitic nematodes found in Hawaii's subtropical environment.

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Chapter 8
Plant Parasitic Nematodes of the Pacific Northwest: Idaho, Oregon and Washington

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8.1 Overview of Agriculture in the Pacific Northwest

Agriculture in the Pacific Northwest (PNW) of the United States is diverse. The states within this region, Washington, Idaho and Oregon, are ranked as the 11th, 20th and 21st respectively, in the U.S. for crop value, including nursery and ornamentals in 2012 (USDA NASS 2014). Combined, over 17 million ha of land were farmed within this region of the U.S. in 2015 (USDA NASS 2016a, b, c). The ability to produce a diversity of commodities is due to the range of eco-climates in the region. The PNW spans three ecoregions as defined by Omernik (1987) and outlined by the Commission for Environmental Cooperation (1997). Eco-regions are defined as areas where the type, quality and quantity of environmental resources are generally similar. The region closest to the Pacific Ocean in the PNW is defined as the Marine West Coast Forest. This region has precipitation evenly dispersed

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throughout the year and has a narrow temperature range with cool summers (temperatures below 22 °C) and mild winters (temperatures above 0 °C). The inland forested mountainous region found in the PNW is characterized by a transition from a moist, maritime climate in the west to a drier, continental climate in the east. The eastern part of the PNW, encompassing the middle portions of Washington and Oregon and southern portion Idaho is part of the North American Desert region. This arid region is characterized by an annual precipitation of approximately 230 mm.

Table 8.1 summarizes the most economically important commodities grown in the PNW in 2015 (USDA NASS 2016a, b, c). A commonality across the region is the large amount of area farmed with hay and wheat, with over 2 million ha dedicated to these crops and a combined income of US$3.3 billion. Other crops consistently grown across the PNW include onion and potato with approximately 233,000 ha farmed and a combined value of US$1.6 billion. Idaho is the number one producer of potato in the U.S. with an economic value close to US$1 billion (USDA NASS 2016a). The production of wheat and barley in Idaho is also economically important with a combined value of US$784 million. In Oregon, greenhouse and nursery production of ornamental plants is the leading contributor to the agriculture economy (USDA NASS 2016b). Oregon leads the nation in production

Table 8.1 Value and area of production of economically-important agricultural crops grown in the Pacific Northwest of the United States in 2015 (NASS 2016a, b, c)

	Idaho		Oregon		Washington	
Commodity	Value (US$1000)	Area (ha)	Value (US$1000)	Area (ha)	Value (US$1000)	Area (ha)
Apples	14,978	931			2,396,250	59,893
Barley	306,763	23,472				
Beans (dry)	70,011	4816				
Blueberry			104,307	4047	146,847	4452
Cherry (sweet)					436,918	14,164
Christmas trees			123,857	16,997		
Corn (grain)	68,103	2833				
Grass seed			383,972	151,757		
Greenhouse and nursery			894,833	Not available		
Grapes (wine)			147,550	7689	262,200	19,425
Hay (all)	836,640	53,823	604,062	428,967	499,140	303,514
Hazelnuts						
Hops	30,799	1983			280,025	13,031
Onion	49,803	3237	125,273	7487	177,698	8053
Pears			152,497	5908	145,880	4937
Peppermint	34,154	615				
Potato	912,800	130,309	176,450	15,742	772,310	68,797
Raspberries						
Wheat (all)	478,800	46,741	217,433	335,080	629,124	900,426

of other unique crops, including grass seed (many species) and Christmas trees and other specialty crops such as peppermint oil, hazelnuts, prunes and plum and blackberries. Washington is the leading producer of apples in the U.S.; apple out-earns the next highest value commodity, potato, by three times (USDA NASS 2016c). Washington is also the largest U.S. producer of hops, spearmint oil, concord grapes, sweet cherries, pears, green peas and blueberries.

8.2 Overview of Plant Parasitic Nematodes Commonly Encountered in the Pacific Northwest

Several surveys defining the distribution of plant parasitic nematodes in the PNW have been conducted. Commodity-specific surveys include those in wine and juice grapes in Idaho, Oregon and Washington (Pinkerton et al. 1999; Zasada et al. 2012), potato in all three states (Nyczepir et al. 1982), turfgrass in Washington and Oregon (Chastagner and McElroy 1984; McClure et al. 2012), grass seed in Oregon (Alderman 1991; Alderman et al. 2005), blueberry in Oregon and Washington (Zasada et al. 2010) and raspberry in Washington (Gigot et al. 2013). Broader surveys have also been conducted to consider the crops grown in rotation in the arid regions of the PNW (Hafez et al. 1992; Smiley et al. 2004). Additionally, data is available from diagnostic lab samples (Hafez et al. 2010). It is important to note that the diversity of plant parasitic nematodes associated with the economically-important ornamental industry in Oregon has received limited attention (Jensen 1961). This is mostly likely due to the tremendous diversity of this industry, with over >800 species cultivated in container and open ground production systems. The plant parasitic nematodes reported to be found in the PNW are presented in Table 8.2. At least 19 genera of plant parasitic nematodes have been reported. Within the most economically important groups of nematodes (Nicol et al. 2011), there are six species of *Heterodera*, two species of *Globodera*, four species of *Meloidogyne* and 11 species of *Pratylenchus* reported found in the PNW (Table 8.2).

A summary of the data from several diagnostic laboratories in the region from 2012 to 2016 (Zasada, unpublished data) provides a current view of the plant parasitic nematodes commonly encountered in the PNW (Table 8.3). The most frequently encountered plant parasitic nematode in the PNW is *Pratylenchus* spp.; when species identification was available, species commonly found were *P. penetrans*, *P. neglectus*, *P. thornei* and *P. crenatus*. In Idaho from 2012 to 2016, almost 90% of samples contained *Pratylenchus* spp. Hafez et al. (2010) reported *Pratylenchus* spp. as being commonly encountered in the state, but at a lower percentage occurrence of 30%. The second most commonly found genera in the PNW, with 34% occurrence, is *Meloidogyne* spp., comprised of *M. chitwoodi*, *M. hapla* and *M. naasi*. Other genera of lesser importance that were present in >20% of diagnostic lab samples were *Paratylenchus* and *Tylenchorhynchus*. The virus-vectoring nematode genera found in the PNW include *Paratrichodorus*, which was consistently present in approximately 25% of diagnostic samples and *Xiphinema* spp.

Table 8.2 Plant parasitic nematodes reported to be associated with agricultural crops in the Pacific Northwest of the United States

Nematode	Crop	References
Anguina agrostis	Bentgrass, fescue	Jensen (1961) and Alderman (1991)
A. funesta	Annual ryegrass	Meng et al. (2012)
Anguina sp.	Orchardgrass	Alderman et al. (2005)
Aphelenchoides fragariae	Lily, spearmint, strawberry	Jensen (1961) and Hafez et al. (2010)
A. ritzemabosi	Begonia, chrysanthemum, Gloxinia, Easter lily, pepperoni, African violet	Jensen (1961)
Criconema mutabile	Potato	Hafez et al. (2010)
Ditylenchus destructor	Potato, dahlia	Jensen (1961) and Hafez et al. (1992)
Ditylenchus dipsaci	Alfalfa, daffodil, garlic, onion, phlox, primrose, strawberry	Blodgett (1943), Jensen (1961), Hafez et al. (1992, 2010), Hafez (1998a)
Geocenamus brevidens	Wheat	Smiley et al. (2006)
Globodera pallida	Potato	Hafez et al. (2007)
G. ellingtonae	Potato	Skantar et al. (2011) and Handoo et al. (2012)
Helicotylenchus pseudorobustus	Annual bluegrass	Chastagner and McElroy (1984)
Helicotylenchus spp.	Beet, blueberry, sugar beet, hops, apple, alfalfa, peppermint, pear, potato, corn, wheat, onion, turnip, bean, grape, gardenia	Jensen (1961), Pinkerton et al. (1999), Hafez et al. (2010), and Zasada et al. (2010, 2012)
Hemicycliophora spp.	Apple, barley, blueberry, bluegrass, grape, potato, wheat	Hafez et al. (1992), Pinkerton et al. (1999), and Zasada et al. (2010)
Heterodera avenae	Barley, oats, wheat	Jensen et al. (1975), Hafez and Golden (1984, 1985), Hafez et al. (1992, 2010), and Smiley et al. (2005c)
H. filipjevi	Wheat	Smiley et al. (2008) and Smiley and Yan (2015)
H. goettingiana	Green pea, edible dry pea, faba bean	Tedford and Inglis (1999)
H. humuli	Hops	Hafez et al. (1992, 2010)
H. mani	Grasses	Hafez et al. (2010)
Heterodera schachtii	Sugar beet	Jensen (1961), Hafez et al. (1992, 2010), and Hafez 1998b
H. trifolii	Legumes	Jensen (1961) and Hafez et al. (1992)
H. urticae	Peach	Hafez et al. (2010)

(continued)

Table 8.2 (continued)

Nematode	Crop	References
Hoplolaimus spp.	Apple, beet, potato, wheat	Hafez et al. (1992 and 2010)
Longidorus elongatus	Bluegrass	Chastagner and McElroy (1984)
Longidorus spp.	Legume, peppermint	Jensen (1961)
Meloidogyne chitwoodi	Alfalfa, sugar beet, potato	Jensen (1961), Santo et al. (1980), Hafez (1998a, b), and Hafez et al. (2010)
M. hapla	Alfalfa, grape, sugar beet, potato, various vegetables (carrot, lettuce, onions, parsnips, cabbage, cucumber, tomato), clematis, coleus, cyclamen, snapdragon, African violet, strawberry, peppermint	Jensen (1961), Hafez (1998a), Pinkerton et al. (1999), and Zasada et al. (2012)
M. minor	Turfgrass	McClure et al. (2012)
M. naasi	Turfgrass	McClure et al. (2012)
M. incognita	Potato	Jensen (1961)
Meloidogyne spp.	Alfalfa, apple, bean, corn, peppermint, potato, wheat	Hafez et al. (1992)
Mesocriconema curvatum	Alfalfa, apple, clover, peppermint, potato, wheat	Hafez et al. (1992)
M. ornatum	Apple, bluegrass, spearmint	Chastagner and McElroy (1984) and Hafez et al. (1992)
M. rusticum	Potato	Hafez et al. (1992)
Mesocriconema spp.	Grape, corn, beet, apple, peppermint, bean, legumes, wheat, pear, blueberry	Pinkerton et al. (1999), Hafez et al. (2010), and Zasada et al. (2010, 2012)
Nanidorus minor	Beet, barley, apple, bean, pear, potato, clover, sugar beet, wheat	Hafez et al. (1992, 2010)
Paratrichodorus allius	Sugar beet, potato	Hafez 1998b and Hafez et al. (2010)
P. porosus	Beet, barley, potato	Hafez et al. (1992, 2010)
P. renifer	Blueberry	Forge et al. (2009)
P. teres	Potato	Riga and Neilson (2005)
Paratrichodorus spp.	Beet, bean potato, wheat, blueberry	Hafez et al. (1992, 2010) and Zasada et al. (2010)
Paratylenchus hamatus	Legumes	Riga et al. (2008)
P. nanus	Bluegrass	Chastagner and McElroy (1984)

(continued)

Table 8.2 (continued)

Nematode	Crop	References
Paratylenchus spp.	Apple, barley, bluegrass, onion, grape, bean, potato, spearmint, wheat, peppermint, sugar beet, alfalfa, bean, pea, pear, legumes, corn, blueberry, hops, hay, blueberry	Jensen (1961), Hafez et al. (1992, 2010), Pinkerton et al. (1999), and Zasada et al. (2010, 2012)
Pratylenchus agilis	Potato	Hafez et al. (2010)
P. brachyurus	NA	Hafez et al. (2010)
P. coffeae	Apple, peppermint, spearmint, wheat	Hafez et al. (1992, 2010)
P. crenatus	Blueberry, bluegrass, apple, alfalfa, wheat	Chastagner and McElroy (1984), Hafez et al. (1992, 2010), and Zasada et al. (2017)
P. hexincisus	Bean	Hafez et al. (2010)
P. neglectus	Alfalfa, apple, wheat, cresting wheat grass, legumes, onion, beet, sugar beet, brassicas, barley, hops, apple, peppermint, spearmint, bean, Kentucky bluegrass, pear, potato, corn, turnip	Hafez et al. (1992), Smiley et al. (2005b), and Hafez et al. (2010)
P. penetrans	Alfalfa, raspberry, peppermint, spearmint, legumes, potato, Easter lily, apple, cherry, peach, pear, strawberry, potato, wheat	Jensen (1961), Hafez et al. (1992), Hafez (1998a), Ingham et al. (2005), Hafez et al. (2010), and Gigot et al. (2013)
P. pratensis	Bulbs, strawberry	Jensen (1961)
P. scribneri	Potato, wheat, corn	Hafez et al. (1992, 2010)
P. thornei	Alfalfa, wheat, legumes, onion, beet, sugar beet, barley, hop, apple, peppermint, bean, potato, corn	Hafez et al. (1992, 2010), Smiley et al. (2005a), and Riga et al. (2008)
P. vulnus	Barley, apple	Jensen (1961) and Hafez et al. (1992, 2010)
Pratylenchus spp.	Barley, apple, alfalfa, pear, potato, grape, blueberry	Hafez et al. (1992, 2010), Pinkerton et al. (1999), and Zasada et al. (2010, 2012)
Subanguina radicicola	Bluegrass	Mitkowski (2007)
Trichodorus spp.	Sugar beet, legumes, onion, grape, peppermint	Jensen (1961), Hafez et al. (1992), Hafez (1998b), andZasada et al. (2012)
Tylenchorhynchus spp.	Legume, onion, beet, brassica, apple, alfalfa, potato, wheat, hay, peppermint, spearmint, pea, corn, grape, barley, corn, hop, bluegrass	Chastagner and McElroy (1984), Jensen (1961), Hafez et al. (1992, 2010), and Zasada et al. (2012)

(continued)

Table 8.2 (continued)

Nematode	Crop	References
Xiphinema americanum sensu lato	Apple, blueberry, grape, pear, potato, raspberry	Hafez et al. (1992, 2010), Pinkerton et al. (1999), and Zasada et al. (2010)
X. bakeri	Raspberry	McElroy (1970)
X. californica	Apple	Hafez et al. (1992)
X. rivesi	Cherry, potato	Hafez et al. (1992, 2010) and Akinbade et al. (2014)
Xiphinema spp.	Apple, alfalfa, blueberry, corn, grape, legume, potato, sugar beet, wheat	Jensen (1961), Hafez et al. (1992, 2010), and Zasada et al. (2010, 2012)

which was not normally found across the region. Two other economically important plant parasitic nematodes, *Ditylenchus* spp. and *Heterodera* spp. were more commonly found in samples from Idaho than Oregon or Washington.

8.3 Economically Important Plant Parasitic Nematodes in the Pacific Northwest

8.3.1 Columbia Root Knot Nematode, Meloidogyne chitwoodi

There is no tolerance for *Meloidogyne chitwoodi* in seed potato in international export markets. Its presence can result in the rejection of an entire shipment due to quality defects that can result in total crop loss (Ingham et al. 2000a; King and Taberna 2013). In the European Union, *M. chitwoodi* is a quarantine pathogen because of its potential to cause destruction to a wide range of important crops in the region. *Meloidogyne chitwoodi* is a temperate climate root knot nematode. It can overwinter in the egg stage and become active at relatively cool temperatures (6 °C) (Pinkerton et al. 1991). As the soil begins to warm in the spring, the nematode multiplies and can complete three or more generations in a long, warm growing season. A *M. chitwoodi* population that starts at just 1 nematode/250 g soil at the beginning of the growing season could grow exponentially to thousands of nematodes/250 g soil by harvest (Ingham et al. 2000a). As a result, there is potential for crop rejection even when there are low levels of nematodes present in the soil at the beginning of the growing season. In addition, this nematode can also continue to develop on tubers in storage, leaving the tubers with visible quality defects that may not have been detectable at harvest (Ingham et al. 2000a).

Meloidogyne chitwoodi was first identified in potatoes grown in the PNW in 1980 (Santo et al. 1980). Because it was first found in the Columbia River Basin of South Central Washington and North Central Oregon, this nematode was given the common name Columbia root knot nematode. Both *M. hapla* and *M. chitwoodi* are

Table 8.3 Occurrence of plant parasitic nematode genera detected in diagnostic laboratory samples in the Pacific Northwest (PNW; Oregon, Idaho and Washington) of the United States from 2010 to 2016

State/ Region	Criconematidae	*Ditylenchus*	*Helicotylenchus*	*Hemicycliophora*	*Heterodera*	*Meloidogyne*	*Paratrichodorus*	*Paratylenchus*	*Pratylenchus*	*Tylenchorynchus*	*Xiphinema*
	Percentage (%) of samples in which detected										
Oregon	1	1	1	<1	<1	22	26	25	61	21	1
Idaho	2	13	14	<1	13	27	26	30	89	67	2
Washington	4	1	1	1	<1	37	25	20	69	30	4
All PNW	3	1	1	1	1	34	25	21	68	30	3

Plant parasitic nematode genera found in less than 1% of samples: *Hoplolaimus, Aphelenchoides, Rotylenchus, Longidorus*
Oregon (N = 4022 samples), Idaho (N = 649 samples), Washington (N = 13,688 samples), PNW (N = 18,359 samples)

found in the PNW. Across the region, *M. chitwoodi* was more commonly detected in diagnostic samples from 2012 to 2016 with 22% occurrence compared to 14% for *M. hapla* (Zasada, unpublished data). When root and soil samples from potato were analyzed (Nyczepir et al. 1982), the dominant species in the region was *M. chitwoodi* (56–93% incidence) with *M. hapla* present in 0–39% of the samples. The greater incidence of *M. chitwoodi* was attributed to a cool growing season and increased acreage of small grain rotation crops, which are better hosts for *M. chitwoodi* than *M. hapla*.

Scientists first identified *M. chitwoodi* on potatoes, but this nematode is polyphagous and can infect both monocots and dicots. Tomato, potato and sunflower are good hosts (Ferris et al. 1993). Plants that are often used in rotation with potato such as oats, barley, corn and wheat, are also hosts for *M. chitwoodi* (O'Bannon 1982). Sugar beets, onion, carrot, beans and legumes such as common vetch, can maintain *M. chitwoodi* populations (Santo and Ponti 1985; Santo et al. 1988; Westerdahl et al. 1993). Various Poaceae (weeds and grasses) are susceptible to *M. chitwoodi,* and common weed species can serve as sources of inoculum if weed control is inadequate (Rich et al. 2009). Plants in the Brassicaceae, Cucurbitaceae, Fabaceae, Lamiaceae, Liliaceae and Vitaceae are moderate to poor hosts for the nematode (CABI 2015). However, it is important to keep in mind that cultivars within a genus can vary in their host suitability for *M. chitwoodi*. For example, certain cultivars of sundangrass are hosts to *M. chitwoodi*, while other cultivars are non-hosts (Mojtahedi et al. 1993). In general, yield losses of crops susceptible to *M. chitwoodi* have not been reported, rather, quality losses are of concern (Ingham et al. 2000a).

Across the potato growing regions of the Columbia Basin, *M. chitwoodi* is a severe nematode pest that infects both potato roots and tubers. On infected roots, *M. chitwoodi* causes galling, although the severity of galling is dependent on the potato variety and environmental conditions (Viaene et al. 2007). On infected tubers, small pimple-like blemishes appear on the surface, giving it a rough, bumpy appearance (Fig. 8.1a). These noticeable tuber galls are due to the large, globose females that reside just under the skin of the tuber, usually within 5 mm of the tuber surface (Viaene et al. 2007). Areas of necrosis also occur around the females, leading to small brown spots just below the peel to several mm deep into the tuber (Fig. 8.1b). The internal and external tuber blemishes make the tubers unacceptable for processing and the fresh market.

Originally, alfalfa was recommended as a rotation crop to suppress *M. chitwoodi* populations because it was thought to be a poor host for the nematode (Santo et al. 1980). However, it was later discovered that there is diversity in the *M. chitwoodi* populations and that there are at least two races of *M. chitwoodi* (race 1 and race 2) in the PNW. Differential host tests showed that race 1 and race 2 are distinguished by their ability to reproduce on carrot and alfalfa (Mojtahedi et al. 1988). Alfalfa is a poor host to race 1 and a good host to race 2, while 'Red Cored Chantenay' carrot is a good host to race 1 but a poor host to race 2 (Santo and Pinkerton 1985). In the potato growing regions of the PNW, race 1 is more common than race 2 (Brown et al. 2009).

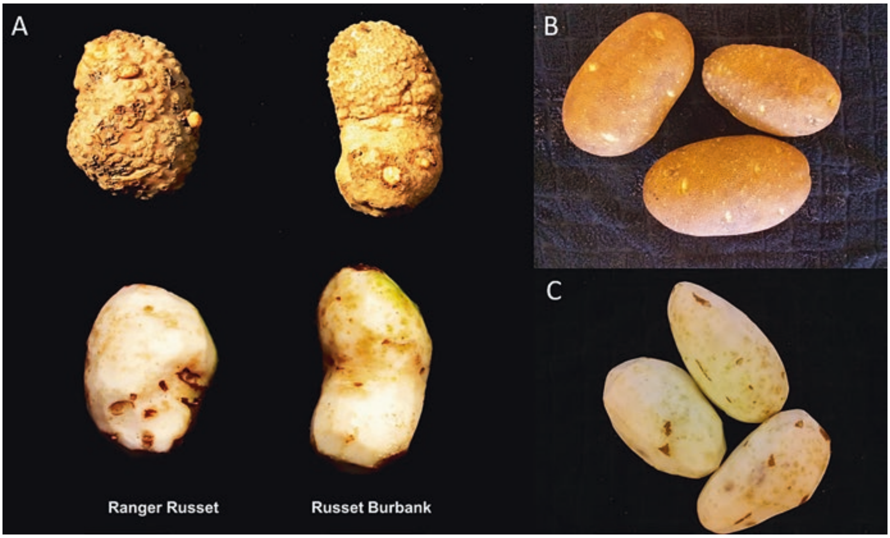

Fig. 8.1 Damage to potato cause plant parasitic nematodes in the Pacific Northwest of the United States. (**a**) External and internal damage to potato (*Solanum tuberosum* 'Ranger Russet' and 'Russet Burbank' by *Meloidogyne chitwoodi*. (**b**) External damage caused by *Paratrichodorus allius*. (**c**) Internal damage caused by *P. allius*. (Photos with permission from B. Charlton and H. Mojtahedi)

Cultivated potatoes lack natural resistance to *M. chitwoodi*. Breeders have identified resistance in several wild *Solanum* species that could be introgressed into the cultivated potato varieties (Brown et al. 1989, 1994, 1995, 2003). The *Solanum bulbocastanum* accession SB22 is resistant to both race 1 and race 2, but it is susceptible to a virulent pathotype of race 2 (previously designated race 3) (Mojtahedi et al. 1995, 1998; Brown et al. 1996). The monogenic resistance trait from SB22 was introduced into cultivated potato and then subjected to backcrossing techniques in order to produce clones with performance characteristics similar to commercial varieties (Brown et al. 2006). The breeding line derived from *S. bulbocastanum*, PA99N82-4, is root resistant to race 1 and contains resistance controlled by a single dominant gene, $R_{Mc1(blb)}$ (Brown et al. 1996, 2009; Zhang et al. 2007). Recently a resistance-breaking nematode pathotype was identified, *M. chitwoodi* 'WAMCRoza'. This nematode pathotype can overcome $R_{Mc1(blb)}$-mediated resistance in PA99N82-4 roots (Brown et al. 2009). Interestingly, PA99N82-4 also possesses a single gene, *RMctuber* that encodes a broad-spectrum resistance of the tubers to penetration by the nematode. In the presence of WAMCRoza, PA99N82-4 will allow reproduction on the roots, but the juveniles cannot penetrate the tuber (Brown et al. 2009). This trait was shown to be under RMc1(blb)-independent, single gene control (Brown et al. 2009).

Meloidogyne chitwoodi has a large host range and potatoes have a low damage threshold. Because of this, the most effective methods to control the nematode are to treat potato fields with pre-plant fumigation, non-fumigant nematicides, or both

(King and Taberna 2013). Common fumigants used for *M. chitwoodi* control are 1,3-dichloropropene (1,3-D) (Telone II), metam sodium (sodium *N*-methyldithiocarbamate) (Vapam HL) and potassium N-methyldithiocarbamate (KS) (K-Pam HL). Fumigation with metam sodium or application of non-fumigant nematicides ethoprop, oxamyl, or aldicarb applied to potato fields via sprinkler irrigation systems alone do not reduce tuber defects caused by *M. chitwoodi* infection (Griffin 1989; Ingham et al. 2007a). The standard for the potato industry has been to use metam sodium simultaneously or sequentially with 1,3-D (Ingham et al. 2007a). A recent report has advocated a more bespoke approach to nematode control where growers identify specific areas in the field for nematicide application, which can reduce the overall use of nematicides and the associated production costs, but still provide effective control (King and Taberna 2013).

8.3.2 Pale Potato Cyst Nematode, **Globodera pallida**

The internationally recognized plant quarantine nematode, *Globodera pallida* (pale potato cyst nematode; PCN) was first detected in 2006 in the PNW during a Cooperative Pest Survey of Idaho samples (Hafez et al. 2007). Surveys to determine the possible origin and distribution of *G. pallida* in Idaho confirmed seven fields infested with this invasive pest totaling 369 ha, all within a 0.4 ha-radius in Bingham and Bonneville Counties, Idaho. Since 2007, an additional twenty PCN-infested fields have been found. All 27 known infested fields are within a 3 ha-radius spanning two counties in Southeast Idaho (Fig. 8.2). Fields associated with infested fields through shared ownership, tenancy, seed, drainage or runoff, farming machinery, or other elements of shared cultural practices have been extensively surveyed and regulated. As of April 2017, 3777 ha of farmland are regulated, of which 1233 ha are infested, which is less than 1% of the total acreage planted to potato in Idaho. Potato production in the U.S. and the viability of international markets for U.S. potatoes, are threatened by the presence and potential geographic spread of this invasive nematode. The discovery of *G. pallida* in Idaho is a significant threat to the Idaho potato industry as it is the state's most economically valuable crop (Table 8.1).

Globodera pallida is one of the most challenging plant pests to control. Damage from *G. pallida* can be extensive; for every 20 eggs/g of soil there can be a 0.4 ton per ha yield loss (Brown 1969). At high levels of infestation, *G. pallida* can reduce tuber yields up to 80% (Brodie 1984; Talavera et al. 1998; Vasyutin and Yakovleva 1998). The narrow host range of cyst nematodes suggests that crop rotation could be effective for their control. However, because of their obligate nature, *G. pallida* hatch only in the presence of a suitable host that produces an appropriate chemical hatching factor necessitating long rotations to prevent injury to potatoes (Whitehead 1995).

In Europe, *G. rostochiensis* (golden potato cyst nematode) and *G. pallida* are managed through a combination of rotation, partial resistance and use of nematicides. However, these measures are not feasible for Idaho growers because there is no resistance in Idaho's signature Russet varieties, the lengthy crop rotation needed

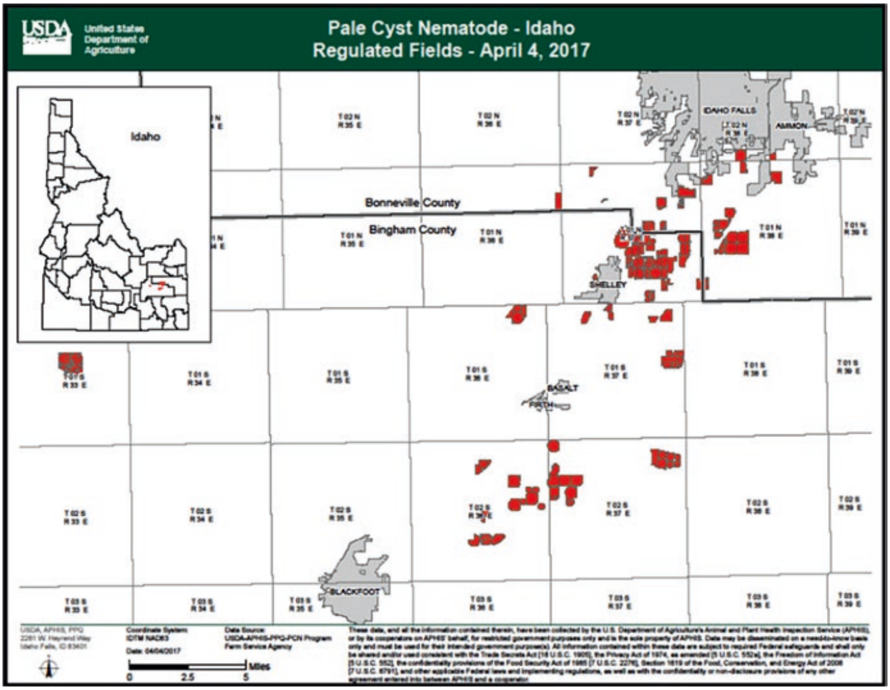

Fig. 8.2 Fields in Bonneville and Bingham Counties, Idaho (red) under regulation by the United States Department of Agriculture-Animal and Plant Inspection Service (USDA-APHIS) for *Globodera pallida* (pale cyst nematode) as of 4 April 2017. Inset map of Idaho showing the limited regulated area for *G. pallida* in the State. For the most recent map of regulated fields https://www.aphis.usda.gov/aphis/ourfocus/planthealth/plant-pest-and-disease-programs/pests-and-diseases/sa_nematode/sa_potato/ct_pcn-maps

for *G. pallida* decline is impractical and because of trade considerations. Consequently, the United States Department of Agriculture-Animal and Plant Health Inspection Service (USDA APHIS) and Idaho State Department of Agriculture (ISDA) have implemented a quarantine program designed to eradicate *G. pallida* and prevent its spread. The program outlines restrictions on the movement of plants and soil, requires sanitation procedures for equipment and enforces zero tolerance for planting potato in infested fields (IDAPA 2010). Stringent adherence to phytosanitary programs has contained the *G. pallida* infestation to only two counties in Idaho. Step-wise measures for the release of infested fields for potato production have been established and include: (1) a negative egg viability assay, (2) inability for *G. pallida* to reproduce from field cysts after three rounds of a greenhouse-conducted potato bioassay, and (3) three additional full field surveys following a susceptible host crop to assure continued negative egg viability (USDA APHIS 2014). Subsequent to planting of three susceptible crops, if no further viable eggs are detected, the field can be released from most regulatory controls except that the field remains restricted for seed potato production. As of 2017, following intensive fumigation with methyl bromide and/or 1,3-D, eight infested fields are eligible to resume host crop production with some regulatory oversight; one field was planted with the first of three rounds of a susceptible potato crop and post-harvest surveys after the susceptible crop did not detect viable *G. pallida* eggs from cyst samples (USDA APHIS 2017).

Millions of dollars have been spent in Idaho on eradication efforts. A critical component of this work has been fumigation of infested fields with methyl bromide. However, use of methyl bromide has been discontinued and USDA-APHIS currently relies on fumigation with 1,3-D, which is in short supply and not as effective. New strategies are needed to protect the investment in eradication efforts as well as to manage potential new infestations. One such strategy is the use of trap crops. These are plants which stimulate *G. pallida* egg hatch, but do not support nematode reproduction. Since hatched juveniles have limited reserves, they will die if they do not successfully parasitize plant roots (Storey 1984). *Solanum sisymbriifolium* (litchi tomato) was investigated as a trap crop because it was shown to be nearly as effective as potato at inducing egg hatching, but was resistant to subsequent nematode development and reproduction (Scholte 2000; Timmermans et al. 2006; Dias et al. 2012). While nematode hatching increases in the presence of a trap crop such as *S. sisymbriifolium*, it is rare to have a high percentage of juveniles hatch from cysts in a single year. Population carry-over could necessitate additional years of rotation with a non-host or trap crop to achieve control (LaMondia and Brodie 1986; Scholte and Vos 2000). However, in a series of greenhouse experiments conducted to mimic a crop rotation, the population density of *G. pallida* was reduced by 95% in potato after a single year of rotation with *S. sisymbriifolium,* regardless of the initial infestation rate (Dandurand and Knudsen 2016). Ongoing field trials indicate similar levels of *G. pallida* reduction in a potato crop subsequent to *S. sisymbriifolium* (Dandurand, unpublished data).

Another non-fumigant strategy for the integrated eradication of *G. pallida* which has proven to be effective against other soil borne pathogens and nematodes, including *G. pallida* and *G. rostochiensis*, is the use of brassicaceous amendments (Brown and Morra 1997; Aires et al. 2009; Mazzola and Brown 2010; Lord et al. 2011; Ngala et al. 2014; Watts et al. 2014). Biocidal activity of biofumigation with brassicaceous materials is attributed to the production of the volatile toxic isothiocyanates (Brown and Morra 1997; Vaughn and Boydston 1997; Buskov et al. 2002; Lazzeri et al. 2004; Zasada and Ferris 2003). Not all brassicaceous sources provide similar nematode suppression. *Brassica juncea* lines containing high concentrations of 2-propenyl glucosinolate (sinigrin) are the most promising of the *Brassica* species evaluated for management of *G. pallida* by biofumigation (Aires et al. 2009; Brolsma et al. 2014; Lord et al. 2011). In vitro and greenhouse assays have demonstrated that *B. juncea* seed meal is 100% effective at killing *G. pallida* when applied at a rate of 1.6 t/ha (Dandurand et al. 2017). However decreasing the application rate to a more feasible rate resulted in variable kill of *G. pallida*. The high application rate needed to achieve control has been an impediment in wide scale adoption of biofumigation with seed meal. Procedures have been developed to extract the active ingredient from *B. juncea* seed meal and formulate it to form a concentrated extract (Popova and Morra 2017). This extract was effective in completely eliminating *G. pallida*, even when applied at low rates (Dandurand et al. 2017).

Unlike potato cyst nematode management in Europe, there are no commercially acceptable russet type varieties suitable for Idaho production with *G. pallida* resistance. To achieve the U.S. goal of eradication and maintain *G. pallida*-free deregulated potato production acreage, growers will need access to potato varieties with resistance to *G. pallida*. Unfortunately, resistance to *G. pallida* is not as well developed as resistance to *G. rostochiensis*, which highlights the risk of the current infestation and future introductions to the industry. Through phenotyping efforts, the breeding clone NY121 from Cornell University has been shown to have some level of resistance to *G. pallida*, and breeding is underway to use this material for development of resistant germplasm (Whitworth et al., unpublished data).

8.3.3 *Cereal Cyst Nematodes*, Heterodera avenae *and* H. fillipjevi

Heterodera avenae and *H. filipjevi* are currently the only two species of cereal cyst nematode (CCN) identified in the PNW. *Heterodera avenae* was first reported in Oregon in 1975 (Jensen et al. 1975). Since this time, *H. avenae* has become widely distributed in the PNW (Hafez and Golden 1984, 1985; Smiley et al. 1994; Smiley 2009a). In 2008, *H. filipjevi* was first reported in Eastern Oregon, representing a new record of occurrence in North America (Smiley et al. 2008); *H. filipjevi* has also been reported in Washington (Smiley and Yan 2015). Current survey efforts suggest the distribution of *H. avenae* is more widespread than *H. filipjevi* in the PNW. However, the exact distribution of *H. filipjevi* is still somewhat unclear, given its recent discovery and lack of systematic surveys. It is likely that the known distribution of *H. filipjevi* will expand in the coming years, as commercial nematode testing laboratories and public research laboratories adopt molecular techniques to distinguish the two species (Yan and Smiley 2010). *Heterodera avenae* and *H. filipjevi* have been recorded in a two-species complex within the same field as well as individually in pure, single-species populations. The dynamics of the *H. avenae* and *H. filipjevi* species complex, including potential virulence, is unknown (Smiley and Yan 2015). The two CCN species have a common host range and cause similar economic damage. The most economically important host for CCN in the PNW is wheat, with yields negatively correlated with initial population densities of CCN in the spring across market classes (Smiley et al. 2005c). Oat, barley, ryegrass and grassy weedy species are also within the CCN host range (Smiley et al. 1994).

Cereal cyst nematodes are obligate sedentary endoparasites and complete one generation in each cropping season. *Heterodera avenae* juvenile populations hatch in response to soil temperatures; in mild winter conditions of Western Oregon, populations peak in March, and in cooler winter conditions of Eastern Oregon, juvenile populations peak from April to May (Smiley 2016). Dynamics of infective *H. filipjevi* juveniles are less understood, but in a preliminary study conducted in Eastern Oregon, *H. filipjevi* populations peaked 14 days earlier than *H. avenae* juvenile populations (Smiley 2016).

Cereal cyst nematode infestations can result in chlorotic patches of unthrifty wheat stands. Below the soil surface, symptoms include shallow rooting and abnormal branching, known as "witch's broom". *Heterodera avenae* infestations can reduce winter wheat yields up to 50% in heavily infested areas or "hot spots" (Smiley et al. 1994). On average, the field wide yield reduction due to *H. avenae* is estimated at 10% or less, leading to an estimated US$3.4 million reduction in overall farm-gate value of wheat across the PNW (Smiley et al. 2009). The effect of CCN on the yield of minor cereals in the PNW, including barley and oat, is less understood. However, research conducted in Sweden indicates tolerance levels of oat and barley are one egg/g of soil for oat and three eggs/g of soil for barley for *H. avenae* (Andersson 1982). Highly susceptible and intolerant spring barley had yield increases of 30.2% and 30.5%, respectively, when treated with aldicarb (Marshall and Smiley 2016). The magnitude of yield loss of cereals due to nematode infestations is often difficult to quantify, due to the strong environmental influence on both nematodes and cultivar, differences in management practices, climates and highly variable/patchy nematode distribution within individual fields (Smiley 2016).

Chemical control of CCN is not economically feasible for cereal producers of the PNW. Instead, CCN population numbers can be reduced by using rotations that do not include a susceptible cereal crop more than once in a 3-year sequence (Smiley et al. 2009). For example, a producer could set a 3-year rotation that includes resistant varieties, broad leaf crops, or fallow with just one crop of susceptible wheat, oat, or barley to keep population densities low (Smiley 2014). If a susceptible crop is grown 2 years in a row, populations can increase.

Genetic resistance to CCN is a measure of a nematode's ability to multiply on roots and is quantified by final density of nematodes remaining in soil to infest the following crop. Genetic tolerance to CCN is a measure of effect on crop yield and is defined by how the yield of the current crop will be affected. Interestingly, tolerance and resistance are genetically independent (Trudgill 1991); growers will have the greatest benefit by planting varieties that are both resistant and tolerant. Major gene resistance and tolerance is available in international wheat, barley and oat germplasm (Smiley et al. 2009; Marshall and Smiley 2016). Breeding efforts are ongoing to introgress specific resistance to CCN into PNW adapted cultivars. However, resistance and tolerance have likely been indirectly selected for both species of CCN simultaneously, as most PNW advanced breeding material has been screened at locations infested with mixed populations of *H. avenae* and *H. filipjevi* (Zemetra, personal communication).

8.3.4 *Root Lesion Nematodes,* Pratylenchus *spp.*

Pratylenchus is the most commonly encountered plant parasitic nematode genus in the PNW (Table 8.3; Hafez et al. 2010). Symptoms of a *Pratylenchus* infection are often difficult to diagnose due to the migratory endoparasitic nature of the species. Nematodes migrates between soil and roots and causes lesions and reduced root growth. Foliar symptoms are non-specific and include very general stunting of plants or patches of weak and wilting plants in the field (Fig. 8.3). Diagnosis must include soil and/or root extractions followed by microscopic and/or molecular confirmation (Davis and MacGuidwin 2000). When the species of *Pratylenchus* were identified in diagnostic samples from the PNW, *P. penetrans* was present in approximately 8% of samples, *P. neglectus* in 6% of samples and *P. thornei* and *P. crenatus* in less than 1% of samples (Zasada, unpublished data). While there have been 13 species of *Pratylenchus* reported in the PNW (Table 8.2), *P. penetrans*, *P. neglectus* and *P. thornei* are the economically important species and will be covered in detail in this section.

8.3.4.1 *Pratylenchus penetrans*

Pratylenchus penetrans is found associated with a wide range of crops in the PNW. With nearly 400 reported plant hosts, many economically-important crops in the PNW are parasitized by *P. penetrans*, including alfalfa, apple, pear, raspberry, peppermint, Easter lily, strawberry, grasses, clover, cherry and onion (Pscheidt and Ocamb 2017). In raspberry, *P. penetrans* was found in 100% of surveyed fields in

Fig. 8.3 (**a**) Reduction in growth of raspberry (*Rubus ideaus* 'Meeker') inoculated (right) and not inoculated (left) with *Pratylenchus penetrans*. (**b**) Stunting of wheat (*Avena sativa* 'Alpowa') caused by *Pratylenchus neglectus* (foreground left) compared to wheat treated with Temik (foreground right) (Photos with permission from I.A. Zasada and R. Smiley)

Northern Washington (Gigot et al. 2013). *Pratylenchus penetrans* is also widely distributed in the major apple growing areas of Washington (Santo and Wilson 1990). While *P. penetrans* is a common pathogen of potato in other growing regions in the U.S., it is rarely recovered from potato in the PNW (Ingham et al. 2005).

Parasitism by *P. penetrans* can lead to reduced yield and vigor of these crops. On peppermint, 0.45 kg of mint oil was lost at 322 *P. penetrans*/g root or 83 *P. penetrans*/100 cm^3 soil (Merrifield and Ingham 1996). In raspberry, 100 *P. penetrans*/100 cm^3 soil at planting and 800 *P. penetrans*/100 cm^3 soil in established plantings can cause reduced yields (McElroy 1992). Many of the most commonly grown varieties of raspberry in the PNW were found to be severely impacted by *P. penetrans* with a greater than 75% reduction in establishment and 1st year yield (Zasada et al. 2015; Fig. 8.3a). *Pratylenchus penetrans* was found associated with orchards exhibiting poor growth and yields in Washington (Santo and Wilson 1990). In the same study, the control of *P. penetrans* in apple with post-plant nematicides resulted in increased yields of 36–80% compared to non-treated plants. The impact of *P. penetrans* on different types of tree fruit including, cherry, pear and peach in other parts the U.S. have been reported (Nyczepir and Halbrendt 1993). In onion, bulb weight reduction ranged from 32% to 64% in microplots inoculated with 430 and 3500 *P. penetrans*/250 cm^3 of soil, respectively (Pang et al. 2009). Direct damage by *P. penetrans* can also occur in onion where bulb quality is compromised by nematode feeding. Additional consequences of *P. penetrans* parasitism can include reduced winter hardiness of mint and an increased severity of *Verticillium* wilt in mint and potato as well as replant issues in apple and cherry (Nyczepir and Halbrendt 1993; Merrifield and Ingham 1996).

Because of the wide host range of *P. penetrans*, nonchemical control measures such as crop rotation and genetic resistance are rarely feasible (Westerdahl et al. 1998). In the PNW, growers producing crops impacted by *P. penetrans* routinely utilize soil fumigation and nematicides to keep population densities of *P. penetrans* below damaging levels and to maintain crop productivity (Westerdahl et al. 2003; Mazzola and Brown 2010; Walters et al. 2017). However, efforts have been made in the PNW to find sustainable alternatives to traditional chemical control. One such effort is plant resistance. To identify sources of resistance with the potential to introgress into raspberry, *Rubus* species and hybrids were evaluated (Zasada and Moore 2010). While most of the tested materials were good hosts for *P. penetrans*, *Rubus niveus* and *Rubus leucodermis* were both identified as poor hosts for *P. penetrans*. However, when these species were then planted in the field and challenged with *P. penetrans*, both were excellent hosts for *P. penetrans* and suffered a 35–73% reduction in biomass compared to non-infested controls (Zasada et al. 2015). Currently, resistance is not an option for managing *P. penetrans* in raspberry. However, plant resistance may be possible in other plant species that are currently impacted by *P. penetrans*. Experimental lines of alfalfa were evaluated for resistance/tolerance to *P. penetrans* (Hafez et al. 2000). In two lines, there were reductions in *P. penetrans* soil and root population densities and corresponding increases in shoot dry weight compared to the susceptible alfalfa ‘Baker’. These sources of *P. penetrans* resistance/tolerance in alfalfa may be available in the future. In apple, the use of Geneva series rootstocks such as G11 and G30 that are poorer hosts for *P. penetrans* compared to Malling or Malling-Merton rootstocks may be effective in reducing the impact of the nematode on tree productivity (Mazzola et al. 2009).

Cultural practices such as crop rotation and cover crops, have also received attention in the PNW as a way to manage *P. penetrans*. A rotational scheme to reduce population densities of *P. penetrans* in Easter lily was evaluated (Westerdahl et al. 1998). Easter lily is often rotated with pasture for cattle and sheep, therefore, different pasture mixes were compared to fallow. Population densities of *P. penetrans* increased on pasture plants (clover and fescue) and decreased under fallow. However, *P. penetrans* were still detectable at the end of a 4 year weed-free fallow period. Because many weeds are hosts for *P. penetrans*, if fallow is implemented as a management strategy every effort should be made to control weeds. As part of a rotational scheme, cover crops may be considered. Thirteen fall and winter cover crops were evaluated for their ability to support population growth of *P. penetrans* (Forge et al. 2000). Results from field experiments suggested that oat (*Avena strigose* 'Saia') or rye (*Secale cereale* 'Wheeler') were better choices for winter cover than weed-contaminated fallow or other cover crops such as meadowfoam or sudangrass in *P. penetrans*-infested fields. Other winter cover crops commonly considered in the PNW are *B. juncea*, *B. napus*, or *S. alba* which are all good hosts for *P. penetrans* (Bélair et al. 2002)

A non-chemical approach that has received attention in the PNW for the suppression of *P. penetrans* is the use of brassicaceous seed meals as a soil amendment. Seed meals of *Brassica napus* 'Dwarf Essex', *B. juncea* 'Pacific Gold and *Sinapis alba* 'Ida Gold' were evaluated for their ability to suppress *P. penetrans* on apple in pots (Mazzola et al. 2009). All of the seed meals reduced population densities of *P. penetrans* compared to the non-treated control. However, *B. juncea* seed meal was the most effective with an 11-fold decrease in *P. penetrans* population densities compared to the non-treated control. The superior ability of *B. juncea* seed meal to suppress *P. penetrans* compared to seed meals derived from other brassicaceous species was further demonstrated in field trials with apple (Mazzola and Brown 2010). In an apple replant situation in Washington, the pre-plant application of a combination of *B. juncea* and *B. napus* seed meals resulted in similar population densities of *P. penetrans* and tree diameter as fumigation with 1,3-D; a similar reduction in population densities of *P. penetrans* compared to the fumigant treatment was not observed for *B. napus* seed meal applied alone. Ultimately, the implementation of brassicaceous seed meals into PNW high value crop production systems may be limited by availability, large application rates and cost. In raspberry, a 3.3 t/ha rate of *B. juncea* seed meal applied pre-plant at an approximate cost of US$1000/ha did not suppress population densities of *P. penetrans* at any sampling date post planting (Rudolph, unpublished data).

8.3.4.2 *Pratylenchus neglectus* and *P. thornei*

Approximately 60% of dryland wheat fields in Eastern Washington host populations of *P. neglectus* and *P. thornei* (Kandel et al. 2013). Overall, it is estimated that these nematodes reduce annual farm gate value of wheat by USD$51 million in the

PNW (Smiley 2009b). *Praytlenchus neglectus* is more abundant than *P. thornei* in the PNW; mixed populations are also common (Smiley et al. 2004). Similar to other *Pratylenchus* spp., the host range of *P. neglectus* and *P. thornei* is quite wide and includes chickpea, pea, lentil, wheat, barley, oat, sudangrass, mustard, canola, camelina, sunflower, flax, safflower, rangeland plants, and many broadleaf and grassy weeds (Smiley et al. 2014). Barley is generally more tolerant and more resistant than wheat, while all commercial wheat cultivars are susceptible (Smiley 2015b). Population densities are highly dependent on many variables, with higher densities observed in spring wheat compared to winter wheat and populations larger in years with mild winter and summer temperatures (Smiley et al. 2004; Kandel et al. 2013).

Symptoms of damage to wheat caused by *Pratylenchus* spp. include reduced plant growth and yield as well as chlorosis (Fig. 8.3b). While *P. neglectus* is more commonly encountered in the PNW than *P. thornei*, *P. thornei* is more damaging. Yield loss of wheat can be up to 50% when *P. thornei* is present (Smiley et al. 2005a). By comparison, *P. neglectus* has been observed to cause yield losses of up to 37% (Smiley et al. 2005b; Smiley and Machado 2009).

Given the wide host range of *P. neglectus* and *P. thornei*, crop rotation to control populations is quite challenging. A multi-year rotational study found that *P. neglectus* populations were larger in mustard, pea and wheat. The study also found that continuously cropped winter wheat or winter wheat rotated with winter pea had the highest population densities of *P. neglectus* (Smiley and Machado 2009). Overall, *Pratylenchus* spp. became more numerous as host-crop frequency increased. In long-term crop rotation experiments in Oregon at both 279 mm and 406 mm of annual rainfall, winter wheat has been shown to select for a dominance of *P. neglectus,* whereas spring barley has selected for a dominance of *P. thornei* (Smiley et al. 2013; Smiley 2015a). In a 9-year study, *Pratylenchus* spp. population density was greater in cultivated dryland crop management compared to chemical fallow management (Smiley et al. 2013); this is likely due to cultivation disturbance breaking the nematode lifecycle.

8.3.5 Stubby Root Nematode, Paratrichodorus allius

Stubby root nematodes are found in several areas in the PNW (Table 8.3). While five species have been reported from the PNW (Table 8.2), they are seldom routinely identified to species. Those which have been identified generally fit the description for *Paratrichodorus allius* (Jensen 1963; Siddiqi 1973). This nematode was described from an onion field in Oregon and was initially believed to be limited in distribution and rarely associated with potato (Jensen et al. 1974). Stubby-root nematodes associated with potato in Central, South Central and Eastern Oregon were identified as *P. teres* (Hooper 1962; Siddiqi 1973), a species originally described from Norfolk, England. In recent years, however, the recognized distribution of *P. allius* has expanded and this nematode is commonly associated with potato in the PNW (Mojtahedi and Santo 1999). *Paratrichodorus teres* has been confirmed from potato fields in Eastern Washington using morphological and molecular diagnostic procedures (Riga and Neilson 2005). Thus, it is likely that both species are present in the PNW, but *P. allius* appears to be the most prevalent. Species designation may not be critical, however, since both species are capable of transmitting Tobacco rattle virus (TRV) and causing corky ringspot (CRS) in potato (Jensen et al. 1974). For the purpose of this chapter, the discussion of stubby-root nematodes in the PNW will be limited to *P. allius* unless stated otherwise.

Paratrichodorus allius has a very wide host range. Mojtahedi and Santo (1999) inoculated 29 plant species belonging to 10 families and evaluated the change in population density after 55 days. The majority of the plants were suitable hosts (Reproduction factor (Rf) = (final population density/initial population density) ≥1) for *P. allius*. Only green pepper (*Capsicum annum* 'California Wonder'), carrot (*Daucus carota* 'Chantenay'), watermelon (*Citrullus vulgaris* 'Charleston Gray'), two common weeds in potato fields, pigweed (*Amaranthus retroflexus*) and Longspine sandburr (*Cenchrus longspinus*) and a species of wild tobacco used as a TRV indicator plant (*Nicotiana clevelandi*) were not hosts. Nevertheless, in spite of its wide host range, *P. allius* is only of concern in onion and potato and, in the case of potato, only if the population is viruliferous with TRV.

Paratrichodorus allius can cause significant direct damage to onions and can reduce yield of dry bulb (storage) onions and those grown for dehydration. The nematode feeds preferentially on root tips, terminating further growth and inducing branching. These branch tips also are attacked, resulting in a root system that is short, branched, swollen and discolored. This alteration of root growth reduces the ability of the plant to take up water and nutrients and causes plants to be unthrifty (Jensen et al. 1983). Yield reduction and disease symptoms on onion are generally most severe when plant growth is reduced during cool, wet springs (Jensen et al. 1964; Ingham et al. 1999). While it is now recognized that *P. allius* is commonly found in potato fields of the PNW, the nematode rarely attains high densities and by itself causes little damage to potato. However, in some fields, *P. allius* (as well as *P. teres*) is a vector for TRV which it transmits to potato roots and/or tubers causing a disease called corky ringspot (CRS). Corky ringspot disease was first reported from the United States in 1946 (Eddins et al. 1946) and in the PNW in Oregon in 1963 (Allen 1963) and in Washington in 1975 (Thomas et al. 1993). Although only a small number of fields appear to be infested with TRV, CRS is routinely found in virtually all potato growing areas of the PNW. Potatoes infected with TRV rarely express symptoms aboveground. Presence of TRV in tubers causes necrotic areas in the form of diffuse brown spots, arcs, or rings which can be quite large (Fig. 8.1c, d). Symptoms can vary by variety. For example, symptoms in 'Russet Burbank' potato tend to be diffuse spots while those in 'Yukon Gold' potato are primarily arcs and rings. These necrotic spots, arcs and rings are considered to be quality defects and tubers with even a small amount of symptoms are considered culls. Crops with as few as 6% culls can be downgraded or rejected. This can occur at densities of 3 *P. allius*/250 g soil, therefore, *P. allius* needs to be managed in any field with a history of CRS (Ingham et al. 2007b).

Because both *P. allius* and TRV have a wide host range, it is virtually impossible to rid a potato or onion field of risk of damage. Therefore, management of this nematode in the PNW is through the use of fumigant and non-fumigant nematicides, either alone or in combination. In onion, fumigation must occur before planting, but the nematicide oxamyl can be applied to growing plants so growers can wait until symptoms are visible before treating. This can allow growers to spot-treat the patches expressing symptoms although they must do so soon after they appear. Onions treated earlier in the season, in early June, had higher yields than those treated later in the season, in late June (Ingham et al. 1999). For the management of CRS, treatment with metam sodium applied through irrigation has not been effective unless used with 1,3-D or nonfumigant (oxamyl, ethoprop) nematicides (Ingham et al. 2000b). Additionally, irrigated applications of oxamyl that began at 55 days after planting or later did not control CRS and were not different from the non-treated control (Ingham et al. 2000b). Therefore, oxamyl applications must be made early in the growing season to be effective in controlling CRS (Charlton et al. 2010b).

Although TRV has a wide host range, there are few crops such as alfalfa (*Medicago sativa*) and scotch spearmint (*Mentha cardiaca*), that rarely serve as hosts for TRV. Growing alfalfa or scotch spearmint in soil containing a viruliferous population of *P. allius* can rid the nematodes of the virus. As individuals carrying the virus die they are replaced by succeeding generations of virus-free individuals that cannot acquire TRV from plants that do not harbor the virus (Boydston et al. 2004; Mojtahedi et al. 2002). Potatoes grown in soil following alfalfa or spearmint are free of CRS symptoms. However, certain weeds found growing in alfalfa and spearmint rotations are hosts for *P. allius* and TRV and can maintain a viruliferous population of *P. allius* if they are not controlled. Tubers harvested from areas where these weeds were adjacent to spearmint or alfalfa were heavily damaged from CRS (Boydston et al. 2004). Charlton et al. (2010a) examined the effect of several cover crops, planted and then incorporated as a green manure, on the population density of *P. allius* and incidence of CRS in the following potato crop. Compared to winter wheat ‘Yamhill’ which was a weak host for *P. allius* (Rf = 2.2) and had a high CRS incidence of 25%, sorghum-sudan ‘Sordan 79’ and arugala ‘Nemat’ were excellent hosts (Rf = 28 and 22, respectively) and resulted in a high incidence of CRS (50% and 23%, respectively). In contrast, radish ‘Colonel’, ‘Doublet’ and ‘Terra Nova’ had low Rf values (2.4, 0.6, 0.4, respectively) and low to moderate levels of CRS (2%, 6% and 14%, respectively). Mustard blends ‘Caliente 61’ and ‘Caliente 199’ also had low Rf values (2.0 and 1.2) but had moderate to high incidence of CRS (12% and 35%). Therefore, while fall incorporated green manure crops may be useful in reducing population increase of *P. allius* and resulting incidence of CRS in a following potato crop, careful selection of the cover crop to be grown is critical.

8.4 Concluding Remarks

Plant parasitic nematodes are a production constraint of many economically-important crops in the PNW. For many of the high-value crops grown in the PNW including potato, onion and small fruits, fumigant and non-fumigant nematicides continue to be the primary management methods utilized. Breeding for genetic resistance is also a critical part of the nematode management strategy in the PNW. In the case of the quarantine nematode *G. pallida* in Idaho whose spread must be controlled, and *M. chitwoodi* and *P. allius* for which infestations can result in crop rejection, controlling these nematode populations is necessary and critically important. For broad acreage crops such as wheat, the use of chemicals to manage CCN and *Pratylenchus* spp. is not economically viable, therefore management strategies such as crop rotation are employed. In spite of the challenges with nematode control discussed in this chapter and the reliance on chemical control, other sustainable management tactics are available and continue to be researched in the PNW including genetic resistance, crop rotation, fallow and cover crops.

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Chapter 9
Plant Parasitic Nematodes in Alaska

Ernest C. Bernard

9.1 Introduction

Compared with every other U.S. state and by any standard, Alaska has a small agricultural base. Cash receipts in 2016 for this largest of states were $33.9 million, less than half that of Rhode Island, the smallest state (USDA ERS 2018) (Table 9.1). Alaska imports more than 95% of its food needs (Alaska Cooperative Extension Service 2011), which is a matter of concern for the state government. Since the 1970s, the state has encouraged and supported large agricultural projects that produce specific products such as feed grains (Lewis and Pearson 1998). In 2008, the Alaska governor issued Administrative Order No. 265 establishing the Alaska Food Resource Working Group (Parnell 2013). The broad goal of this working group was to promote increased use of locally grown and harvested foods within the state and its agencies, institutions and schools. One specific area addressed was to "...provide recommendations to protect, preserve and develop the state's agricultural land for the benefit of all Alaskans." In 2009, the Alaska Department of Natural Resources, Division of Agriculture developed a long-term plan for agriculture with the mission of promoting and encouraging development of a stable and profitable agricultural industry in Alaska (ADNR-DA 2009). Included in this report are recommendations related to plant diseases, including the use of plants as a natural way to solve conservation issues and reestablish ecosystem function; collection, selection and release of high-latitude germplasm; plant solutions to battle invasive species; and production of disease-free seed of potatoes.

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Table 9.1 Important crops grown in Alaska

	2017		2012	
Crop	Hectares	Value ($)	Hectares	Rank in US
Hay	8498	9 million	9775	47
Potatoes	182	2.7 million	274	36
Barley	2225	1.3 million	1799	43
Oats	688	241,000	365	39
All vegetables	NA	NA	429	50

Source: https://www.nass.usda.gov/Quick_Stats/Ag_Overview/stateOverview.php?state=ALASKA

Alaska's agricultural history illustrates the tenacity of growers and researchers in making agricultural production viable (AAFES 1998), with a particularly sustained effort to develop crops adapted to the climate.

9.2 Plant Parasitic Nematodes

Nematodes do not appear to be a factor in crop production. Based on the only significant survey of plant parasitic nematodes in mainland Alaska (Bernard and Carling 1986), the state has a diverse array of species (Table 9.2). Although 520 samples were collected in this survey, these plus Aleutian samples and a few earlier species descriptions are a small effort for a very large area. Thus, our knowledge of Alaskan plant parasitic nematodes remains extraordinarily sparse, resting on no more than a dozen publications (see Andrassy 2000, 2003c for lists of described species). Holovachov (2014) listed the known true Arctic nematodes, including a number of free-living Alaskan nematodes (Dorylaimida, Mononchida, etc.) described by Andrassy (2003a, b, c). Most of these papers are pure taxonomy, but Bernard and Carling (1986) provided the results of a mainland survey aimed at plant parasitic taxa, including earlier Aleutian records and a few other species. In this paper they listed 24 genera and 54 species-level taxa, many of them unidentified and representing undescribed species. In addition to the records reported above, additions to the Alaskan plant parasitic fauna include a series of papers on plant parasitic nematodes of the Aleutian Islands and the mainland (Bernard 1981, 1982, 1984, 1992), three species of *Longidorus* (needle nematodes) (Robbins and Brown 1996), four species of *Nagelus* (Powers et al. 1983) with individual species of *Pararotylenchus* (Baldwin and Bell 1981) and *Pratylenchoides* (Baldwin et al. 1983).

The 1986 survey aimed at getting an overall picture of the Alaskan plant parasitic nematofauna partially to form a baseline of what indigenous nematodes could be present as agriculture expanded. In the survey, only two agricultural sites were sampled: old agricultural sites at the Pt. McKenzie Research area, now covered with mixed vegetation, had a ring nematode, *Criconemoides annulatus*; and a potato field at the Kaslin Agricultural Station on Kodiak Island contained *Helicotylenchus* and

Table 9.2 Plant parasitic nematodes reported from Alaska

Species[a]	Localities	Hosts or associated plants	References
Atalodera crassicrustatus	Adak, Amchitka Islands	*Leymus mollis*	Bernard (1981)
Criconema longulum	Adak, Amchitka Islands, Columbia Glacier region	*Leymus mollis*	Bernard (1982) and Bernard et al. (1995)
Criconema psephinum	Adak Island	*Anemone narcissifolia, Carex macrochaeta, Geranium erianthum, Leymus mollis, Lupinus nootkaensis, Plantago macrocarpa*	Bernard (1982)
Criconemoides annulatus[b]	Widespread	Numerous plant associations	Bernard and Carling (1986)
Helicotylenchus spitsbergensis	Adak, Amchitka Islands	*Toefieldia coccinea*	Bernard (1984)
Hemicycliophora amchitkaensis	Amchitka Island	*Leymus mollis*	Bernard (1982)
Heterodera trifolii	Noorvik	Potato garden	Bernard (1984)
Longidorus alaskaensis	Hess Creek at Dalton Highway	*Alnus* sp., *Rosa acicularis*, *Salix* sp.	Robbins and Brown (1996)
L. bernardi	Hess Creek at Dalton Highway	*Alnus* sp., *Rosa acicularis*, *Salix* sp.	Robbins and Brown (1996)
L. paralaskaensis	Chena and Chatanika Rivers near Fairbanks	*Alnus* sp., *Rosa acicularis*	Robbins and Brown (1996)
Meloidodera eurytyla	Adak Island	*Honckenya peploides, Leymus mollis*	Bernard (1981)
Meloidogyne subarctica	Adak Island	*Leymus mollis*	Bernard (1981)
Merlinius adakensis	Adak Island, southern mainland	*Leymus mollis*	Bernard (1984)
M. joctus	Wrangell	Grasses and herbaceous groundcover	Thorne (1949)
Mesocriconema xenoplax	Adak, Amchitka Islands	*Leymus mollis*	Bernard (1982)
Nagelus borealis	Atigun Pass	Alpine tundra	Powers et al. (1983)
N. leptus	Steese Highway	*Alnus* sp.	Powers et al. 1983
N. obscurus	Fairbanks	*Picea glauca*	Powers et al. (1983)
Ogma seymouri	Adak Island	*Arnica unalaschcensis*	Bernard (1982)
Pararotylenchus megastylus	Summit Lake	*Populus tremuloides*	Baldwin and Bell (1981)
Paratylenchus amundseni	Adak Island	*Leymus mollis*	Bernard (1982)
Pratylenchoides magnicauda	Alaska	*Populus tremuloides*	Baldwin et al. (1983)

(continued)

Table 9.2 (continued)

Species[a]	Localities	Hosts or associated plants	References
P. megalobatus	Adak, Amchitka Islands	*Leymus mollis*	Bernard (1984)
P. variabilis	Adak Island	*Leymus mollis*	Bernard (1984)
Pratylenchus pratensisobrinus	Adak Island	*Arnica unalaschcensis, Platanthera convallariaefolia, Viola langsdorffii*	Bernard (1984)
P. ventroprojectus	Adak Island	*Anemone narcissifolia, Plantago macrocarpa*	Bernard (1984)
Subanguina radicicola	Adak Island	*Elymus arenarius*	Bernard (1979)
Trichodorus aequalis	Elliott Hwy. at Tolavana River	*Picea glauca*	Bernard (1992)
T. californicus	Numerous sites from Prudhoe Bay to Taylor Highway area	*Alnus* sp., *Betula glandulosa*, *Cornus canadensis*, *Epilobium angustifolium*, *Populus balsamifera*, *Salix* spp., *Vaccinium* sp.	Bernard (1992)
T. carlingi	Central Alaska; Unalakleet River	*Betula payrifera, Populus tremuloides, Salix* sp.	Bernard (1992)
T. paucisetosus	Numerous sites in Fairbanks vicinity	*Picea glauca, Rosa acicularis*	Bernard (1992)

This list does not include taxa recognized any further than genus, including species of Criconematidae (*Criconema*, *Mesocriconema*), Telotylenchidae (*Geocenamus*, *Merlinius*, *Nagelus*, *Tylenchorhynchus*), *Dolichodera*, *Hoplolaimus*, *Paratylenchus*, *Pratylenchoides* and *Xiphinema*. A listing of these taxa can be found in Bernard and Carling (1986)

[a]Some generic names have been changed from the original reports to reflect current classification

[b]Called *Criconemella hemisphericaudata* in Bernard and Carling (1986)

Paratylenchus spp. (spiral and pin nematodes, respectively). Among samples made available in 1983, *Trichodorus californicus* was collected from a potato field at Copper Center (Bernard 1992) and a cyst nematode similar to *Heterodera trifolii* was collected from a potato garden at Noorvik. These few records shed little or no light on the vulnerability of Alaskan increased agriculture to plant parasitic nematodes.

Climate change is a phenomenon already affecting Alaska (ADEC 2018). Temperature increase is estimated to be twice that of the global average. Predicted changes in Alaska due to climate change and related to agriculture include hotter and drier summers with increasing evaporation exceeding increased precipitation, increases in wildfires and insect pest outbreaks, and accelerated thawing of permafrost (USGCRP 2009). The effects of this climate shift on indigenous plant parasitic nematodes cannot be predicted, as there has been no research done on their environmental preferences or tolerances. However, a warming climate makes the introduction of known pathogenic species more likely. For instance, potatoes account for most of the consumer food produced in Alaska (Table 9.1). Nematodes such as *Meloidogyne chitwoodi* (Columbia root knot nematode), *Globodera pallida* (pale potato cyst nematode), *M. hapla* (northern root knot nematode) and *Ditylenchus* *destructor* (potato rot nematode) are serious pests of potato. They certainly could become established in a warming Alaska given their environmental preferences elsewhere (Brodie et al. 1993). *Heterodera avenae*, the oat cyst nematode, is an important pest of barley, oats and wheat in many parts of the world and occurs in Canada and several northern U.S. states (Rivoal and Cook 1993). With warming conditions it probably could establish itself in Alaska if given the opportunity.

Nematodes are abundant and diverse in Alaskan soils, with up to 8.9 million/m^2 in taiga forest soils (Freckman et al. 1977; Van Gundy et al. 1978). Nematodes quickly colonize soils newly exposed (<75 years) by glacial retreat (Bernard et al. 1995), with *Paratylenchus* spp. (pin nematodes) and *Criconema* spp. (ring nematodes) the first plant parasites to appear. More expansive studies (Nielsen et al. 2014; Wu et al. 2009) have shown that nematode assemblages in Alaska are diverse and complex. Modifications of these assemblages under the influence of climate change, which may be occurring more rapidly in Alaska than elsewhere, are difficult to predict (Gough et al. 2012). More research should be devoted to the dynamics of the soil biota to better understand Alaska's nematode future.

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