Chapter 7
Nematodes Important to Agriculture in Wisconsin

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7.1 Agriculture in Wisconsin

Agriculture in Wisconsin is very diverse and important to the U.S. economy (Table 7.1). The state is a leader in the dairy industry and the production of corn for silage. Wisconsin produces more snap beans for processing, cranberries and ginseng than any other state and ranks among the top five states for forage, potatoes and processing vegetables (USDA NASS 2017). The state contributes to the forest products industry with significant acreage devoted to silviculture. Organic agriculture is very prominent and Wisconsin is outranked only by California for the number of organic farms.

About 40% of Wisconsin's land mass is devoted to agriculture. The top five commodities in terms of acreage are corn, soybean, hay, wheat and oat (WAS 2017; USDA NASS 2017). In terms of sales value, the ranking changes to corn, soybean, hay, potato and cranberry. The majority of corn and soybean are grown in the south and north central regions of the state on alfisols with a good potential for productivity. Potatoes and processing vegetables are concentrated in the central region of the state on irrigated sandy soils. Cranberry production is focused in Westcentral Wisconsin.

7.2 Nematology in Wisconsin

Root knot nematode on ginseng was the first nematology project in Wisconsin (McClintock 1914), but it was the discovery of *Ditylenchus destructor* in seed potatoes in 1953 that established the need for nematode expertise in Wisconsin. In 1953, Dr. H. Darling, Director of the Wisconsin Seed Certification Program at the University

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Table 7.1 Agricultural crops of Wisconsin

Crop	Harvested hectares[a]	U.S. rank
Corn grain	1,186,000	8
Soybean	866,000	12
Hay	506,000	13
Corn for silage	356,000	1
Wheat	69,000	18
Oat	34,000	4
Potato	27,000	3
Snap bean	25,000	1
Sweet corn	22,000	3
Pea	9,100	3
Cranberry[b]	8,500	1
Cabbage	2,400	2
Cucumber	2,200	6
Carrot	1,800	3
Peppermint[b]	1,250	5

[a]Estimates for 2017 (USDA NASS 2017)

[b]Estimates for 2016 (WAS 2017)

of Wisconsin (UW), went to the Netherlands to study nematology with Drs. M. Oostenbrink and J. W. Seinhorst. Dr. Darling was joined by G. Thorne, who was appointed to the UW faculty in 1956. *Ditylenchus destructor* became the focus of nematology research at UW Wisconsin during this period (Faulkner and Darling 1961; Smart and Darling 1963; Anderson and Darling 1964; Darling 1959). Also at that time, the Wisconsin Department of Agriculture Trade and Consumer Protection (WI DATCP) began a zero-tolerance regulatory program that quarantined fields for seed potato production if *D. destructor* was detected.

With nematology expertise in place, other nematode-plant associations in Wisconsin were studied: *Helicotylenchus* spp. on bluegrass (Perry 1958), *Xiphinema* spp. on spruce (Griffin and Darling 1964; Griffin and Barker 1966), pine (Krebill et al. 1968) and strawberry (Perry 1958), *Pratylenchus penetrans* on potato and corn (Dickerson et al. 1964) and *Meloidogyne* (=*Hypsoperine*) *ottersoni* on reed Canary grass (Webber and Barker 1967; Thorne 1969). Drs. K. Barker and V. Dropkin were in the Department briefly after Thorne's retirement in 1961, but by the time of their departure Dr. Darling had resumed research on seed potatoes and a focused nematology program did not resume until 1983 with the hire of Dr. A. MacGuidwin. Nematode problems that arose in the interim included the soybean cyst nematode *Heterodera glycines* and increased pressure from *P. penetrans*. The Wisconsin DATCP began surveying the state for cyst nematodes of regulatory importance in 1982; an activity that continues to this day.

In 1984, a nematode diagnostic service was established at the UW Department of Plant Pathology. Samples submitted for nematode testing and research projects revealed a wide array of plant parasitic nematodes in the state. Currently, more than

90% of soil samples are positive for *Pratylenchus*, making it the most common genus of plant parasitic nematodes in Wisconsin. Other widely prevalent genera in order of incidence are *Helicotylenchus*, *Paratylenchus* and *Xiphinema*. Common genera associated with particular soil types or hosts include *Heterodera*, *Tylenchorhynchus*, *Hoplolaimus*, *Paratrichodorus* and criconematid genera. Genera that are relatively rare in the agricultural soils of Wisconsin include *Meloidogyne*, *Longidorus* and *Ditylenchus*. The five genera with the greatest economic impact to Wisconsin's most valuable crops are *Pratylenchus*, *Heterodera*, *Meloidogyne*, *Longidorus* and *Ditylenchus*.

7.3 Root Lesion Nematode, *Pratylenchus* spp.

7.3.1 Impact to Wisconsin

The widespread occurrence and extensive host range of *Pratylenchus* spp. make the root lesion nematode the most important nematode pest in Wisconsin. Population densities of *Pratylenchus* spp. are too low in most fields to induce significant yield loss, but nearly every field has the potential for problems to develop. Yield loss has been documented in Wisconsin for *P. penetrans* on potato (MacGuidwin et al. 2012) and corn (MacGuidwin and Bender 2016) and there is anecdotal evidence of damage for many crops. *Pratylenchus* spp. have been recovered from UW diagnostic and research samples for grain (corn, soybean), cereals (wheat, oat), vegetables (potato, pea, sweet corn, carrot, onion, pepper, cabbage, green bean), forage (alfalfa, corn), fruit (cranberry, cherry, apple), ornamental (peony, daisy, marigold, boxwood), cover (rye, sorghum, radish, kale, mustard, rapeseed) and specialty (ginseng, hops, mint) crops. The host range of *P. penetrans* extends well beyond the diagnostic samples received in Wisconsin and includes many weeds (Bélair et al. 2007) present in the state. The majority of infestations have not been identified, but *P. penetrans*, *P. scribneri* and *P. neglectus* are some of the most common species in the state. *Pratylenchus penetrans* has the greatest incidence and impact on specialty crops, while all species are associated with grain and forage crops.

7.3.2 Life History in Wisconsin

There are multiple overlapping generations of *Pratylenchus* spp. in Wisconsin. All life stages overwinter and the roots of annual crops become infected before shoots emerge. Dead roots from previous crops shelter nematodes, so nematode assays that include an incubation step provide the best estimate of initial nematode population densities (MacGuidwin and Bender 2012). Sampling to predict the damage potential of root lesion nematodes in Wisconsin is typically done in the fall. A study on the vertical distribution of *P. scribneri* in the soil profile supports this practice.

There was no evidence of downward migration in fields planted with corn or potato in September or October, indicating an “escape in time” strategy to survive Wisconsin winters (MacGuidwin and Stanger 1991). Estimates of overwinter survival rates for *P. scribneri* over a 3-year period averaged 41% for corn and 25% for potato, with most of the mortality occurring in the soil before soil froze (MacGuidwin and Forge 1991).

7.3.3 Interactions with Other Pathogens

The potato early dying disease caused by the interaction of *P. penetrans* and *Verticillium dahliae*, is a major constraint to potato production in Central Wisconsin (Fig. 7.1). Pioneering research that revealed this disease interaction in Ohio (Martin et al. 1982) was confirmed for potato varieties and conditions common to Wisconsin (Kotcon et al. 1985; MacGuidwin and Rouse 1990b; Morgan et al. 2002b). Very low population densities of these pathogens cause economic loss when the infestations are concomitant, rendering the majority of potato fields vulnerable to reduced yield and quality. The combined effects for yield loss are additive when one or both of the pathogens are present at high population densities. Details of the interaction have been elusive at the molecular level, but it has been demonstrated that the nematode plays an important role that extends beyond root wounding (Rotenberg et al. 2004; Saeed et al. 1999) (Fig. 7.2a, b). There is some evidence that *P. penetrans* may also interact synergistically with *Rhizoctonia solani* to reduce yield of potato under Wisconsin conditions (Kotcon et al. 1985).

Pratylenchus penetrans has also been demonstrated to play a role in the root rot of canning pea in Wisconsin (Oyekan and Mitchell 1972). The recovery of *P. penetrans* from fields damaged by *Aphanomyces euteiches* (Temp and Hagedorn 1967) led to greenhouse studies that showed that symptom expression was synergistic when both pathogens were present at low levels (Oyekan and Mitchell 1972). At higher population densities this nematode can cause severe damage to pea in the absence of *A. euteiches* (Fig. 7.2c).

Interactions for *Pratylenchus* spp., particularly *P. penetrans* and fungi resulting in yield reductions of other crops grown in Wisconsin, have been verified in other states. These associations follow the same pattern in that the combined effects of the pathogens are synergistic at low population densities and additive when one of the organisms is present at levels sufficient to cause disease as the sole pathogen. This was the case for *P. penetrans* and *Rhizoctonia fragariae* on strawberry in Connecticut (LaMondia and Cowles 2005) and *P. penetrans* and *Fusarium oxysporum* on alfalfa in Canada (Mauza and Webster 1982).

Current evidence argues against blanket generalizations suggesting that *Pratylenchus* spp. predisposes roots to fungal infection. Enhanced root infection by fungi in the presence of *P. penetrans* occurred for some fungi such as *R. fragariae* on strawberry (LaMondia and Cowles 2005), but not for others such as *R. solani* and *Colletotrichum coccodes* on potato (Kotcon et al. 1985). Bowers et al. (1996),

Fig. 7.1 Russet Burbank potato in a microplot experiment at the Hancock Research Station, Hancock, WI. The plants in the foreground are showing symptoms of the potato early dying disease

showed that the presence of *P. penetrans* increased infection and colonization of potato roots by *V. dahliae*, but not in the areas where nematodes were feeding. It is intuitive to assume that root wounding by root lesion nematodes attract and facilitate infection by other pathogens. This model may be specific to only certain root-infecting fungi since many are only successful in living tissue or in cases where they control the nature and timing of cell death (Kabbage et al. 2013). Educational tools used in Wisconsin to demonstrate *Pratylenchus* spp. are important pathogens in their own right include root explant cultures infected with only *P. penetrans* (Fig. 7.2d).

7.3.4 Management

There are three challenges to managing *Pratylenchus* spp. in Wisconsin. The first is the widespread distribution of this genus. Management practices for other nematode genera are sometimes conducive to reproduction by *Pratylenchus* spp., which can become problematic as populations of the primary pest decline. A second challenge is the lack of host resistance to *Pratylenchus* spp. Reports of tolerance or resistance are in the literature for alfalfa (Barnes et al. 1990) and wheat (Vanstone et al. 1998), but those cultivars are not grown in Wisconsin. It is well known that there are differences in nematode reproduction among genotypes of corn, soybean and other crops, but the market life of cultivars is too short for screening programs to be feasible for most crops. The final challenge is the lack of data on *Pratylenchus* species.

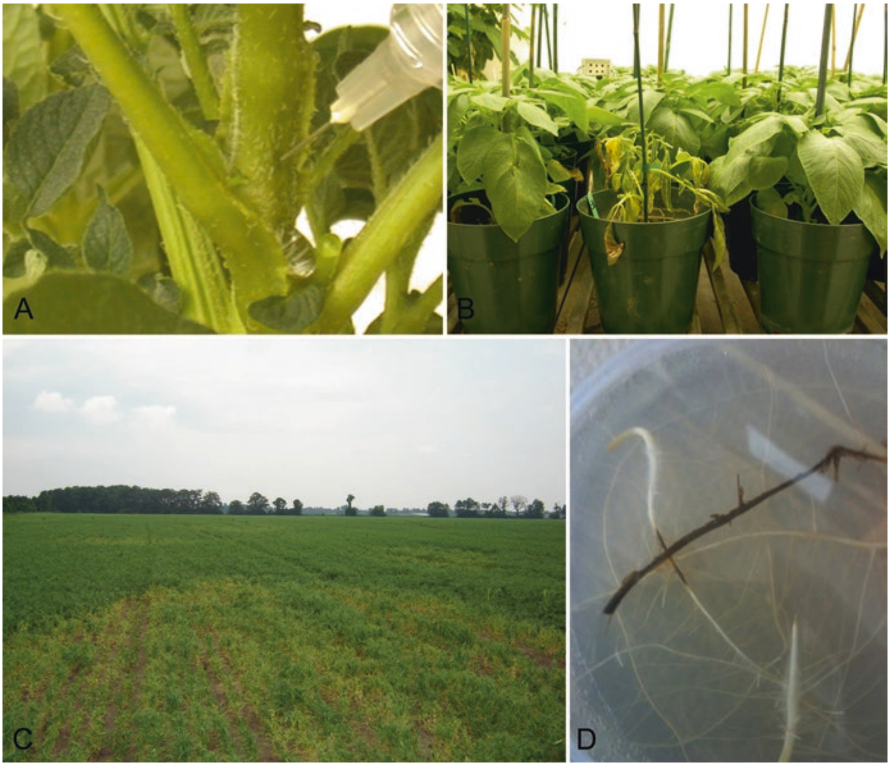

Fig. 7.2 (**a**) Injecting conidia of *Vertcillium dahliae* into the stem of Russet Burbank potato infected with *Pratylenchus penetrans*; (**b**) The fungal and nematode pathogens intecting different plant organs interacted to cause disease as expressed by cholorsis and wilting; (**c**) A pea field in central Wisconsin infested with *Pratylenchus penetrans*. The distribution of the nematode was patchy; (**d**) Root explant of I. O. Chief sweet corn that has been inoculated by placing a root infected with *Pratylenchus penetrans* retrieved from a mature in vitro culture onto healthy roots

Sustainable management recommendations, especially nuanced practices like crop rotation, will be greatly improved when diagnostics and field experiments include that level of detail. Presently, *P. penetrans* is the only species that is routinely singled out. The prevalence of this species in the central sandy vegetable production area of Wisconsin and the distinguishing high incidence of males allow diagnosticians to make a cursory identification of samples. Formal surveys have identified the majority of populations with males as *P. penetrans* (Kutsuwa and MacGuidwin unpublished).

7.3.4.1 Soil Disinfection

Fumigation of soil with biocidal chemicals is a cost effective and common practice in Wisconsin on high value crops such as ginseng, potato and carrot. In Wisconsin, soil is fumigated in the fall when soil temperature is above 10 °C and irrigation systems are still active so as to apply water after the material is injected into soil. Nematodes that come into contact with the fumigant are killed, but many are not, and residual root lesion nematode populations rebound over time (Morgan et al. 2002a). There is often a carry-over effect of fumigation for at least one additional year (Morgan et al. 2002a), but farmers are advised to manage root lesion nematode throughout the rotation to decrease the necessity of fumigating for the next potato crop.

Anaerobic soil disinfection (ASD), the practice of covering green manure with a plastic tarp, was demonstrated to be effective in Wisconsin (MacGuidwin et al. 2012). The study was conducted in potato fields with a high potential from damage due to *P. penetrans* and the Potato Early Dying disease. Inoculum levels of *P. penetrans* and *Verticillium dahliae* were reduced in 1 of 2 years and yields were increased both years in plots receiving ASD. Due to the logistics of applying tarps to large areas, ASD is not practiced in conventional production fields. A study showing that the distribution of *P. penetrans* was stable throughout a 3-year potato rotation in Central Wisconsin (Morgan et al. 2002a) indicates that using ASD as a site-specific approach is feasible.

7.3.4.2 Nematicides and Seed Treatments

Nematicides are used to control *Pratylenchus* spp. in potato and processing vegetables in Wisconsin. Product availability, and therefore use, declined over the past 30 years but has seen a recent upswing as new chemistries and biologicals have entered the market. Seed treatments for corn have generated a lot of interest based on early reports for *P. zeae* (Cabrera et al. 2009). A greenhouse study in Iowa found that nematode population densities of *P. penetrans* were reduced when corn seeds were treated with a nematicide in combination with a fungicide and insecticide (da Silva et al. 2016). The “early mitigation” strategy for seed treatments is supported by a yield loss model developed for corn in Wisconsin that explained yield loss using nematode population densities at planting (MacGuidwin and Bender 2016).

7.3.4.3 Crop Rotation

Crop rotation is difficult for *Pratylenchus* spp. due to the wide host range of multiple species, but there is sufficient variation in the host status of crops common to the state to plan rotations for nematode management in vegetable systems. Corn was a better host for *P. penetrans* (Dickerson et al. 1964; Morgan et al. 2002a) and *P. scribneri* (MacGuidwin and Forge 1991) than potato. Soybean was a better host than corn for *P. penetrans* in Canada (Bélair et al. 2002) and this seems to be the case in Wisconsin (Kutsuwa unpublished). The majority of fields planted with these long-season crops in the year prior to potato are fumigated to mitigate the potato early dying disease. Short season processing crops such as pea or green bean are good hosts to *P. penetrans* but offer opportunity to disrupt the nematode's life cycle with a period of fallow or cover crops which can increase the interval between fumigation events.

7.3.4.4 Cover Crops

In Wisconsin, cover crops are planted after harvest on the majority of potato and vegetable fields. Ninety-two percent of organic vegetable farmers in Wisconsin reported using cover crops (Moore et al. 2016). The most common cover crop grown is cereal rye because it can be planted throughout the state during the month of October. Rye is an excellent host for *P. penetrans* (Bélair et al. 2002), but the late planting and reduced reproduction by *P. penetrans* at low temperature (Thistlethwayte 1970) discourage the increase of nematodes until spring when the cover crop is destroyed. A rye cover crop provides valuable ecological services so farmers concerned about *Pratylenchus* spp. are advised to monitor their situation by soil sampling.

Cover crops reported to reduce root lesion nematodes have had mixed success in Wisconsin. Mustard, rapeseed, and other members of the Brassicaceae, excellent hosts for *P. penetrans*, are planted in the late summer when the nematodes are likely to increase. Sorghum-sudangrass and rapeseed maintained *Pratylenchus* spp. (MacGuidwin et al. 2012; MacGuidwin and Layne 1995). Population densities of *P. penetrans* were reduced at the time of planting potato in plots planted with African marigold (*Tagetes erecta*) and forage pearl millet (*Pennesetum glaucum*) the previous year (MacGuidwin et al. 2012). Subsequent research in Wisconsin supported results from earlier studies (Ball-Coelho et al. 2003; Bélair et al. 2005) showing forage pearl millet to be a good cover crop for managing *P. penetrans*. Millet is planted in August because it is sensitive to frost, so adoption has been highest for vegetable cropping systems.

7.4 Soybean Cyst Nematode, *Heterodera glycines*

7.4.1 Impact to Wisconsin

Heterodera glycines, the soybean cyst nematode, was intercepted from soil associated with cabbage transplants from Tennessee in 1980 and during the following year, a survey by the Wisconsin Department of Agriculture and Consumer Protection (DATCP) revealed an infested soybean field in Southeastern Wisconsin (Phibbs et al. 2016). As of 2016, 52 counties with 96% of the state's soybean acreage were known to be infested. The SCN also affects green bean production in the state. Research in Illinois (Melton et al. 1985) showed that green bean cultivars bred for root rot resistance in Wisconsin suffered less damage from *H. glycines* than other cultivars. Today, green bean cultivars grown for processing range in sensitivity to *H. glycines*, with some supporting even more nematode reproduction than soybean (MacGuidwin unpublished).

Due to its widespread distribution and potential for damage, the soybean cyst nematode is considered the greatest yield-reducing biotic factor affecting soybean production in the state. Studies in commercial fields in Wisconsin have consistently shown an advantage to planting soybean genotypes that limit reproduction by *H. glycines*. The yield advantage of planting a resistant variety was fairly consistent over a range of initial nematode population densities in a sandy soil, with an average gain of at least 30% (MacGuidwin et al. 1995). On silt loam soil the yield gain was at least 17% (Bradley et al. 2003). A regional study that included sites in Wisconsin, showed *H. glycines*-resistant varieties had greater yield than susceptible varieties with the magnitude of the difference depending on cultivar, location and initial population densities (Donald et al. 2006).

7.4.2 Life History in Wisconsin

The distribution of the soybean cyst nematode is aggregated in fields in Wisconsin (Kaszubowski and MacGuidwin 2000). Studies in commercial fields showed the field entrance to be the location most often infested with the nematode, but in some fields *H. glycines* was found only in one or two patches well away from vehicle access points (Kaszubowski unpublished), suggesting that birds or wind are important means of dispersal. One commercial field that was a site for multiple studies showed a remarkable range of pH that was positively associated with population densities of *H. glycines* (Pedersen et al. 2010). Information from these studies has been applied to sampling recommendations for farmers in Wisconsin.

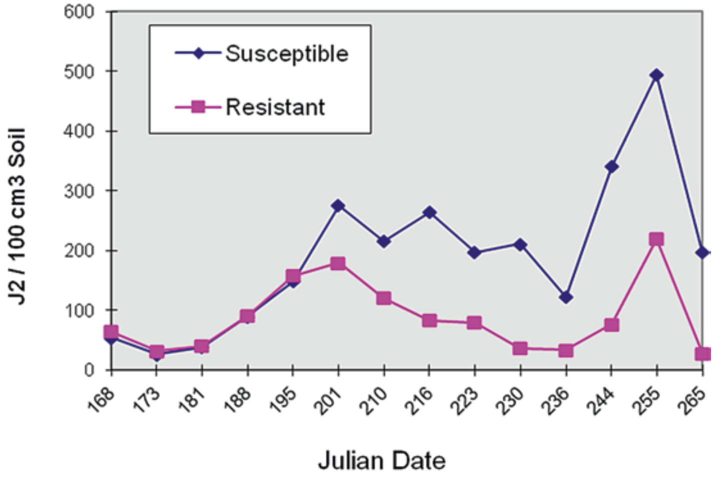

Fig. 7.3 Numbers of second-stage juveniles of *Heterodera glycines* recovered from 100 cm^3 soil samples on multiple dates from two soybean varieties: one susceptible and one resistant to *H. glycines*

The population dynamics of the soybean cyst nematode including temporal changes in the attrition of population densities, guide recommendations for managing this pest in Wisconsin. Soybeans are grown throughout the state, and in all but the northern counties it appears that there are at least two generations per year (Fig. 7.3). Second-stage juveniles can be detected in diagnostic and research samples collected at all times of the year but are particularly abundant in the fall. A collaborative study among northcentral states including Wisconsin, showed the rate of population growth during the season was inversely related to population densities in the spring (Wang et al. 2000). Wisconsin populations appear to be well adapted to winter, at least following the soybean year. In a study comparing *H. glycines* populations collected from five latitudes representing the U.S., populations from Wisconsin showed a high rate of overwinter survival even when they were moved to Florida (Riggs et al. 2001). Soil sampling confirms this finding; population densities are higher in the spring than fall in some years, suggesting that *H. glycine*s can reproduce after soybeans senesce (MacGuidwin unpublished).

7.4.3 Interactions with Other Pathogens

Foliar symptoms of the sudden death syndrome caused by *Fusarium virguliforme* were exacerbated in *H. glycines*-infected plants in microplot studies in Mississippi (McLean and Lawrence 1993). Studies in Nebraska fields infested with both pathogens found the severity of foliar symptoms to be positively associated with initial population densities of the nematode (Brzostowski et al. 2014). The disease potential of the fungus was low in both studies and the presence of the soybean cyst nematode synergistically increased disease severity. Analysis of diagnostic samples in Wisconsin showed a negative association between the incidence of *F. virguliforme* and *H. glycines* (Marburger et al. 2014). Considering the many ways that the soybean cyst nematode can enter fields, farmers with a history of sudden death syndrome disease are advised to test their fields regularly for the nematode so that they can act quickly to amend their disease management plan if the soybean cyst nematode is also a factor.

Brown stem rot disease caused by *Phialophora gregata* was more severe in treatments with *H. glycines* in growth chamber studies in Iowa (Tabor et al. 2003). This fungus is common in Wisconsin soybean fields and often occurs together with the nematode. There is anecdotal evidence that the disease is more severe in joint infestions (Grau unpublished). Understanding the association of *P. gregata* and *H. glycines* in the field is difficult because soil pH has a strong and opposite effect on these pathogens (Pedersen et al. 2010) and many soybean cyst nematode-resistant cultivars derived from PI 88788 are also resistant to *P. gregata*. Crop rotation and host resistance, either alone or together, are the pillars of management plans for both pathogens in Wisconsin.

7.4.4 Management

Soybean fields in Wisconsin can experience yield loss without foliar symptoms, so infestations often escape notice until population densities are very high and difficult to manage. The soybean industry began offering free assays to Wisconsin farmers in the 1990s, yet to date most fields have never been tested. The majority of soybean varieties marketed in Wisconsin has PI 88788 in their pedigree and are labeled as soybean cyst nematode-resistant, so farmers are inadvertently managing the nematode. The challenge is to convince farmers to take a proactive approach by sampling soil to confirm and monitor soybean cyst nematode infestations on their farms.

7.4.4.1 Host Resistance

Most of the soybean varieties sold today in the Northcentral U.S. have resistance to the soybean cyst nematode derived from the source line PI 88788. Since there is significant genetic variation in *H. glycines*, it is not surprising that many populations are now adapted and reproducing on varieties with the PI 88788 source of resistance. One study, with sites ranging from Tennessee to Ontario, Canada, found that most *H. glycines* populations reproduced on PI 88788 (Faghihi et al. 2010). Analysis of 15 years of research data in Iowa verified an increase in the reproduction of *H. glycines* over time (McCarville et al. 2017). Populations of the nematode species from more than 325 farms in Wisconsin have been evaluated and 75% (10-year average) show some level of development (>10%) on PI 88788 (MacGuidwin unpublished). Adapted populations have been detected in Wisconsin on farms with only a brief or no history of planting soybean cyst nematode-resistant varieties, presumably because all populations are exotic to the state and may have been dispersed from a farm elsewhere that had relied on host resistance.

Populations of *H. glycines* adapted to the PI 548402 (Peking) source of resistance have also been detected in Wisconsin. About 25% (10-year average) of the populations tested over the past 10 years developed (>10%) on varieties with Peking-derived resistance (MacGuidwin unpublished). The level of adaptation to the Peking line reported for Tennessee and Ontario were higher and lower, respectively, than the estimate for Wisconsin (Faghihi et al. 2010). Adaptation of the soybean cyst nematode over a 15-year study period was not detected for varieties with the Peking pedigree in Iowa (McCarville et al. 2017).

Understanding the basis for adaptation and educating farmers to manage soybean germplasm resources wisely is a top priority for nematology in Wisconsin. Adaptation is characterized using the HG typing system (Niblack et al. 2002), awarding the "adapted" designation to any population with 10% or more of its members capable of developing on the germplasm being tested. While the majority of *H. glycines* populations in Wisconsin surpass the 10% level on PI 88788, most populations remain below 30%, the threshold commonly used to indicate the point at which growing a resistant variety is no longer economical (Schmitt and Shannon 1992). Data show the average level of adaptation is slowly increasing in the state, underscoring the importance of easing selection pressure on *H. glycines* populations.

7.4.4.2 Crop Rotation

Rotation, for the purpose of breaking the life cycle and minimizing nematode reproduction, is the most important cultural practice for soybean cyst nematode in Wisconsin. Crops of varying host status were planted for 1 or 2 years to create a range of *H. glycines* population densities in order to develop a damage model for soybean (MacGuidwin et al. 1995). The non-hosts, white clover and alfalfa, had the greatest impact on population attrition. Pea and hairy vetch treatments showed there is value to planting a host crop of another species as compared to a soybean monoculture. Rotating soybean varieties, even soybean cyst nematode-resistant varieties, is recommended in Wisconsin because many traits including root mass and architecture, affect the population dynamics of SCN.

7.4.4.3 Noxious Chemicals

Some of the practices to supplement host resistance involve noxious chemicals that must be taken up by *H. glycines* juveniles in soil. Examples include synthetic chemicals coated on to seeds, plant-derived compounds released during the breakdown of cover crop green manures such as glucosinolates, and toxins released by fungal antagonists. Schroeder and MacGuidwin (2007, 2010a) showed that juveniles, within eggs or hatched, accumulated fluorescein isothiocyanate in the intestine and the mode of entry was the stoma and other body openings. They demonstrated that the uptake of four plant-derived compounds varied according to the mobility of the nematode. Quiescent nematodes had decreased sensitivity compared to those that were actively moving (2010b). Based on these results, it is recommended that management practices based on noxious chemicals are deployed when conditions are warm and soil moisture is not limiting, thereby enhancing active movement of the nematodes.

7.5 Root Knot Nematode, *Meloidogyne hapla*

7.5.1 Impact to Wisconsin

The impact of *Meloidogyne hapla* in Wisconsin was first documented in a M.S. thesis in 1914 (McClintock 1914). Field and laboratory studies were conducted in Michigan and Wisconsin respectively, to control *M. hapla*, then called *Heterodera radicicola*, on ginseng. Soil treatments of carbon bisulfide, formalin, sulfuric acid, naphthaline, ammonia, nicotine, kerosene, gasoline and tobacco dust were unsuccessful in alleviating galling, and the author provided advice which is still followed today, "...the best solution of the problem is to take great pains to keep their soil free from this pest by planting only such seeds and roots as are known to be free from the parasite...".

Meloidogyne hapla, the northern root knot nematode, is distributed throughout Wisconsin today on a wide range of crops. Crops represented in diagnostic and research samples positive for the *M. hapla* include carrot, ginseng, potato, alfalfa, mint, onion, green bean, soybean, daisy and basil. Research in other locales has shown the host range to be extensive including crops and weeds that grow in Wisconsin (Bélair and Benoit 1996; Faulkner and McElroy 1964).

Reduced yields of potato have been demonstrated in the state (MacGuidwin and Rouse 1990a). The northern root knot nematode is often not diagnosed in potato fields because there is little to no galling and the primary impact is on tuber production rather than quality (MacGuidwin 2008). Crop quality is the major impact of *M. hapla* on carrot and nematode damage thresholds established for carrot in New York (Gugino et al. 2006) also apply to Wisconsin. Wisconsin produces about one third of the processing carrots in the U.S. (USDA NASS 2017), and farmers in Wisconsin consider the potential impact of the northern root knot nematode when managing the crop. Wang and Goldman (1996) identified resistance to Wisconsin populations of the nematode species in inbred carrot lines, however, commercial resistant cultivars are currently not available.

7.5.2 Life History in Wisconsin

Carrot, ginseng and other root crops are very sensitive to early season damage by the northern root knot nematode, so studies in Wisconsin were conducted to learn how the nematode survived winter conditions. Sampling during the winter months revealed second-stage juveniles as an abundant overwintering stage. Laboratory studies showed that exposure to low temperatures prior to freezing, as would occur in the field, increased survival of frozen conditions (Forge and MacGuidwin 1992a). Conditions of low water potential had the same effect (Forge and MacGuidwin 1992b). Manipulating temperature and water potential indicated that there were two mechanisms that allowed juveniles to escape freezing at subzero temperature: removal of water through desiccation (Fig. 7.4a) and the accumulation of cryoprotectant compounds. These studies suggest that the greatest mortality of *M. hapla* occurs during autumn with warm temperatures and high rainfall; conditions that might be manipulated, at least in part, in irrigated fields.

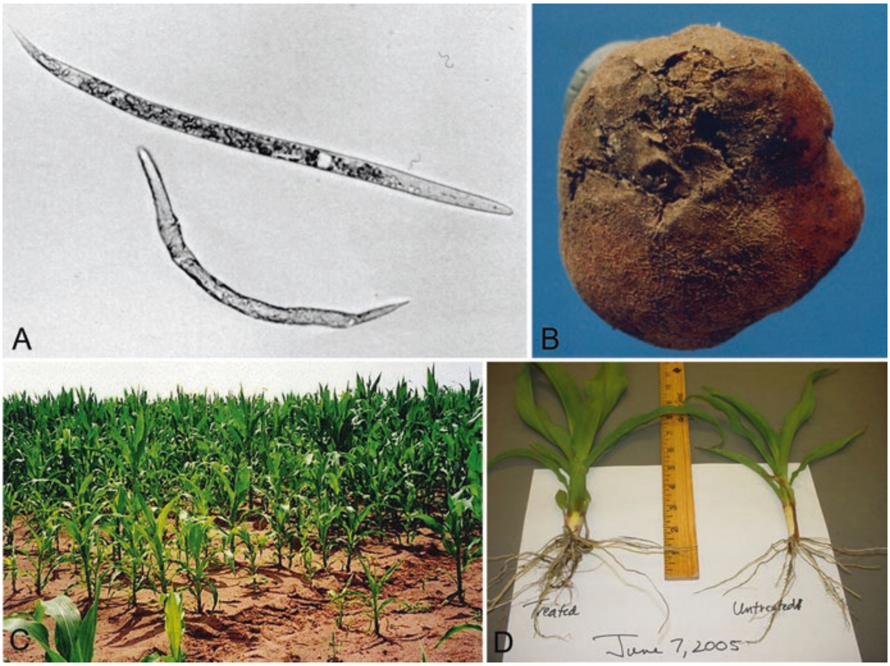

Fig. 7.4 (**a**) Second-stage juveniles of *Meloidogyne hapla*. The nematode below was preconditioned by exposure to 4 °C for 4 h and then the temperature was lowered to −10 °C. The nematode above was maintained at 24 °C for the entire period; (**b**) Potato tuber with dry rot symptoms following exposure to the potato rot nematode, *Ditylenchus destructor*; (**c**) A field near Spring Green Wisconsin showing stuting symptoms caused by the corn needle nematode, *Longidorus breviannulatus*; (**d**) Corn plants from field trials showing the benefit of a nonfumigant nematicide for mitigating damage caused by the corn needle nematode, *Longidorus breviannulatus*

7.5.3 Interactions with Other Pathogens

The northern root knot nematode is not known to have synergistic interaction with fungi in Wisconsin. Microplot experiments showed the effects of *M. hapla* and *V. dahliae* to be additive for potato (MacGuidwin and Rouse 1990a). Association between *M. hapla* and *F. oxysporum f. sp. medicaginis* on alfalfa have not been studied to determine if synergism between these two pathogens, reported for Utah (Griffin and Thyr 1988), also applies to populations in Wisconsin.

7.5.4 Management

Sampling before planting to determine nematode population densities is particularly important for *M. hapla* because many crops can't "outgrow" the damage inflicted by the nematode at the seedling stage. The challenge in making that assessment is that most *M. hapla* are deep in the soil profile in the spring. Sampling at the end of the preceding summer or in the fall to estimate population densities for the following spring is recommended for developing nematode management plans in Wisconsin.

7.5.4.1 Soil Disinfection

Many of the northern root knot nematode infestations in Wisconsin are in high organic soils that are difficult to fumigate because of their binding properties. Soil fumigants must penetrate deep within the soil profile in order to reach the nematode, and residual nematode populations are a concern. Biofumigation, the incorporation of *Brassica* spp. at flowering, is problematic because population densities of the *M. hapla* increase during the cover crop phase. Due to these issues, soil disinfection is either usually not practiced in Wisconsin for the northern root knot nematode or is done in combination with nematicides or seed treatments.

7.5.4.2 Nematicides and Seed Treatments

Nonfumigant nematicides are commonly used on carrot in Wisconsin. The product is targeted to the plant for protection against infection by nematodes. There is anecdotal evidence that systemic nematicides increase yield as documented for New York (Gugino et al. 2006). New seed treatments for nematodes have begun to enter the market and will likely become an important tool for managing the northern root knot nematode.

7.5.4.3 Crop Rotation and Cover Crops

Crop rotation is the cornerstone of northern root knot nematode management. The host range of *M. hapla* does not include corn or small grains, so planting these crops the year before carrot or other sensitive crops reduces nematodes below the detection level (MacGuidwin unpublished). Studies in New York (Viaene and Abawi 1998) concluded that rye, oat, and sudangrass grown for 7 weeks were not hosts for *M. hapla* and would, therefore, be good candidates to include as full season rotation crops or partial season cover crops. The authors also examined the benefit of incorporating sudangrass as a green manure, which they concluded, was superior to growing it as a cover crop. This practice has not been widely adopted in Wisconsin, because it has the unintended consequence of increasing root lesion nematode which does reproduce on sudangrass (MacGuidwin and Layne 1995).

7.6 Potato Rot Nematode, *Ditylenchus destructor*

7.6.1 Impact to Wisconsin

Wisconsin is one of seven U.S. states infested with *Ditylenchus destructor*, the potato rot nematode. The majority of the detections have been in one northern county and new infestations are relatively rare. The typical symptom on tubers is cracking and a dry rot that can spread among tubers in storage as the nematode multiplies (Fig. 7.4b). Since *D. destructor* is a nematode of regulatory concern worldwide, the WI DATCP (2017) places infested fields under quarantine for the production of seed potatoes and inspects new production fields, as well as fields with a prior history for the potato rot nematode. The seed potato farmers, DATCP, and the University of Wisconsin have worked together since 1953 to limit the impact of *D. destructor*, and no shipment of seed or commercial potatoes from the state has ever tested positive for the nematode.

7.6.2 Life History in Wisconsin

Much of what is known about the life cycle of *D. destructor* was based on populations from Wisconsin. Anderson and Darling (1964) determined that the gender of juveniles could be discerned by the third stage and that soon after the final moult, females mate with multiple males. These studies were facilitated by the studies of Faulkner and Darling (1961) that showed *D. destructor* can be cultured in vitro on more than 64 species of fungi. MacGuidwin and Slack (1991) expanded the host range of this highly polyphagus nematode to include corn and green bean, two crops commonly grown in Wisconsin, and detailed its proclivity to infect seed and to mature and survive in above-ground plant tissues (MacGuidwin et al. 1992).

One of the most important aspects of the life cycle is the low incidence of *D. destructor* in soil. This observation was made by Darling from field studies (Darling 1959; Darling et al. 1983), and MacGuidwin and Slack (1991) and MacGuidwin et al. (1992) found very few nematodes in soil in greenhouse studies. The probability of detecting *D. destructor* in soil is further thwarted by the large number of *Ditylenchus* species, all with very similar morphology in the juvenile stage. All discoveries of *D. destructor* in Wisconsin have only been from potato tubers.

7.6.3 Interactions with Other Pathogens

During the 1950s, fungi were detected from tubers infected with the potato rot nematode, therefore, it was important to verify that *D. destructor* was the primary cause of disease rather than a secondary invader. Faulkner and Darling (1961) were able to do so by rearing the nematodes in monoxenic callus culture. Today, fungi such as *Fusarium* spp. and *Rhizoctonia solani*, contribute to disease; their effects are considered to be additive to those of *D. destructor*.

7.6.4 Management

The challenge of managing *Ditylenchus destructor* is the inability to detect infestations by soil sampling prior to planting potato. Best management practices are aimed at seed potatoes in order to prevent the dispersal of potato rot nematode and regulatory procedures for Wisconsin are enforced (WI Administrative Code 2017). Seed potato fields new to certification and fields released from quarantine are inspected for potato rot nematode in Wisconsin. Commercial farmers are advised to plant only seed potatoes that are certified to be free from *D. destructor* and to be vigilant for symptoms on tubers during harvesting and washing activities.

7.6.4.1 Soil Disinfection

Experiments to eliminate potato rot nematode in the 1950s showed the soil fumigant ethylene di-bromide to be effective (Darling 1959). Soil fumigation was written into the state's regulatory standards and on the basis of case studies over 29 years, Darling et al. (1983) declared that potato rot nematode had been eradicated by fumigation in Wisconsin. However, soon afterward, some fumigated fields were found to be positive for potato rot nematode. Therefore, fumigation is now considered to be a mitigation measure that requires validation through crop inspection. Current regulations do not name a particular soil fumigant and fields are released from quarantine after fumigation and two successive potato crops with no detections of *D. destructor*. Fumigation is also recommended for fields in the 1st year of seed production until inspectors verify the field to be free of potato rot nematode at harvest. Additional recommended measures for 1st-year fields are to plant them last and disinfect equipment before exiting fields.

7.6.4.2 Crop Rotation

Fields adjacent to sites of potato rot nematode detection may also be placed under quarantine, but even if they are not, it is recommended to lengthen the interval between potato crops. Many crops can maintain *D. destructor* in the greenhouse, but oat was a poor host for a Wisconsin population even under greenhouse conditions (MacGuidwin and Slack 1991), thereby, making it a good candidate for fields at risk. Until more is known about the persistence of *D. destructor* in fields, crop rotation should be considered an important, but not the primary, practice for management.

7.7 Other Nematode Pests in Wisconsin

The corn needle nematode, *Longidorus breviannulatus*, causes severe stunting in sandy soils of Wisconsin (Fig. 7.4c). Infestations are highly aggregated as patches in fields, and in most cases, the patch size is small. Seasonal migration in the soil profile occurs as corn plants mature (MacGuidwin 1989), so detecting infestations beyond the seedling stage can be problematic. Nonfumigant nematicides are used to mitigate damage (Fig. 7.4d).

The stubby root nematode, *Paratrichodorus* spp., is commonly recovered from potato fields in Wisconsin. Crop loss due to nematodes alone has not been reported, but the corky ringspot disease, vectored by the nematode, was discovered in Wisconsin in 2007 (Phibbs and Leisso 2009). Detection of corky ringspot means total loss for infested fields since the potatoes are destroyed to prevent the spread of disease. Farmers are advised to plant only certified seed potatoes, as infected tubers are a known means of introducing the virus into potato fields.

The pine wood nematode (PWN), *Bursaphelenchus xylophilus*, was detected in Wisconsin in 1981 and 1982, associated primarily with insects in the family Cerambycidae (Wingfield and Blanchette 1983). Diagnostic samples positive for the pine wood nematode are detected periodically, accompanied by reports of tree death.

A number of other plant parasitic nematode species have been reported from Wisconsin (Table 7.2). The extent of damage and yield loss attributable to most of these species today has not been assessed. Some such as *Helicotylenchus digonicus* and *Pratylenchus penetrans*, are fairly common in agricultural fields across the state. Others such as *Meloidogyne ovalis* and *Nothocriconema sphagni*, have not been detected since the original report.

Table 7.2 Nematode species reported from Wisconsin

Species	Host	References
Bakernema inaequale	Maple	Hoffman (1974)
Bursaphelenchus xylophilus	Pine	Wingfield and Blanchette (1983)
Cactodera milleri	Lambsquarters	Schroeder et al. (2008)
C. rosae	Corn	Phibbs et al. (2017)
C. weissi	Unknown	Phibbs et al. (2017)
Criconema octangulare	Unknown	Hoffman (1974)
Crossonema menzeli	Unknown	Hoffman (1974)
Ditylenchus destructor	Potato	Darling (1959)
D. dipsaci	Phlox, garlic	WI DATCP (2017)
Helicotylenchus digiatus	Cranberry	Barker and Boone (1966)
H. digonicus	Blue grass, corn	Perry (1959) and Griffin (1964)
H. microlobus	Blue grass, corn	Perry (1959) and Griffin (1964)
H. platyurus	Blue grass, corn	Perry (1959) and Griffin (1964)
H. pseudorobustus	Cranberry	Barker and Boone (1966)
Hemicycliophora obtusa	Cranberry	Barker and Boone (1966)
H. typica	Maple	Riffle (1962)
Heterodera glycines	Soybean	MacGuidwin et al. (1995)
H. trifolii	Corn	WI PIB (2016)
Hirschmanniella gracilis	Unknown	Sher (1968)
Hoplolaimus galeatus	Pea	Temp and Hagedorn (1967)
Lobocriconema thornei	Unknown	Powers et al. (2017)
Longidorus breviannulatus	Corn	MacGuidwin (1989)
Meloidogyne hapla	Ginseng	McClintock (1914)
M. ottersoni	Canary grass	Thorne (1969)
M. ovalis	Maple, elm	Riffle (1963)
Nanidorus minor	Cranberry	Barker and Boone (1966)
Nothocriconema sphagni	Maple	Riffle (1962)
Ogma octangularis	Unknown	Powers et al. (2017)
Pratylenchus crenatus	Corn	Dickerson et al. (1964)
P. neglectus	Corn	Dickerson et al. (1964)
P. penetrans	Corn	Dickerson et al. (1964)
P. scribneri	Potato, corn	MacGuidwin and Stanger (1991)
P. vulnus	Corn	Griffin (1964)
P. thornei	Corn	Griffin (1964)
Rotylencus buxophilus	Corn	Griffin (1964)
R. pumilus	Blue grass	Perry (1959)
Tylenchorhynchus maximus	Corn	Griffin (1964)
Trichodorus californicus	Corn, cranberry	Griffin (1964) and Barker and Boone (1966)
Xiphinema americanum	Strawberry, corn	Perry (1958) and Griffin (1964)
X. chambersi	Strawberry	Perry (1958)

7.8 Sustainable Nematode Management in Wisconsin

Wisconsin farmers have been leaders in agricultural sustainability. Collaborations between the University of Wisconsin and commodity groups advance science-based programs to promote environmental stewardship and inform management decisions. The Healthy Grown Program, an industry-led initiative to use best-management practices, reduce pesticides, and to support native plants and animals (Zedler et al. 2009), developed standards and third-party certification for the sustainable production of potatoes and onions. The National Soybean Initiative, piloted in Wisconsin, developed an assessment process to help soybean farmers document practices and quantify progress in adopting sustainable approaches to soybean production (Dong et al. 2016). Farmers in both of these programs include nematodes in pest management plans, but much work remains in educating the agricultural industry at large about the importance of plant parasitic nematodes and the yield gains that can be realized when pest nematodes are maintained at low population densities. Collaborations between nematologists in the Northcentral region of the U.S. and nationally bolster Wisconsin efforts to evaluate and develop management practices for nematodes and to advance awareness of important nematode pests.

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