Sustainability in Plant and Crop Protection

Sergei A. Subbotin
John J. Chitambar *Editors*

Plant Parasitic Nematodes in Sustainable Agriculture of North America

Vol.2 - Northeastern, Midwestern and Southern USA

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Preface

Many changes globally affect the evolution of cropping systems today. There is hence a substantial need to periodically update our knowledge on the present and expected factors determining the performance of crops on continental scales. These two volumes on plant parasitic nematodes of North America are in line with this perspective. Both provide an impressive amount of updated information arising from one of the most technologically advanced agricultural system in the world. Topics include species composition, pathogenicity and losses, spatial distribution, and management approaches identified for most important nematode species. The volumes represent a rich source of information, also providing several historical reports and records, together with the description of main quarantine issues, related legislation, and adopted measures.

The chapters cover the whole continental range of geographic areas and crops, spanning from Mexico to Alaska. Although the same species are sometimes treated in different chapters, a *repetita juvant* approach has been considered necessary to provide a complete, detailed data source for the reader, including detailed geographic distribution patterns and incurred losses. The authors describe in fact the problems by regions, highlighting the different solutions that have been locally adopted and the main traits of the management approaches which have been identified and made available to farmers. These include, among others, use of rotation and resistant germplasm; nonhost or cover crops; agronomic management technologies; organic, integrated, or nematicide-based methods; as well as informations on the institutional initiatives aiming at the containment and exclusion of most threatening pests. All chapters have a stand-alone structure and represent a useful citation source.

In most intensive agricultural systems in the world, there is an increased need for new methods of nematode and other pest management, possibly with low environmental impacts, being sustainable in the long term. This view is today more necessary than ever due to the limitations in natural resources such as soil and water, the lack of traditional tools such as fumigants and nematicides, in part already banned or abandoned, or due to environmental issues. These factors have been considered by the authors, reporting prevalence data, updated quantitative estimations of losses, and data on the economic value of crops and products, in a broad regional context.

The two volumes result from the long-term work and experience of the authors, who represent a leading edge in the field of applied nematology, either for their experience or comprehensive research contributions. The volumes' compilation and production largely arose thanks to the careful and exhaustive coordination efforts that the editors, Sergei Subbotin and John J. Chitambar, deployed. Thanks to their excellent work, the readers will find a manual with complete source of information, literature data, and references, useful for any technical, teaching, and scientific need.

Bari, Italy

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Chapter 1
Plant Parasitic Nematodes of New England: Connecticut, Massachusetts and Rhode Island

James A. LaMondia, Robert L. Wick, and Nathaniel A. Mitkowski

1.1 Introduction

New England is a compact, northern region of the United States comprised of Connecticut, Rhode Island, Massachusetts, New Hampshire, Vermont and Maine. It has a small agricultural base compared to other regions of the country that benefit from longer growing seasons and more amenable soil types. New England states are not often associated with agriculture, but the economic value of agriculture is very important for these small states. A recent study (Lopez et al. 2017) estimated the 2015 economic impact of agriculture on the Connecticut economy to be $3.3–4 billion in direct sales, generating 21,000 jobs and approximately $800 million in wages. Sales of agricultural products in Massachusetts were over $490 million (Anon 2015) and were approximately $100 million in Rhode Island (Anon 2011). In addition, the green industry including landscaping and golf courses, adds significantly to both economic values and the quality of life in these states.

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1.2 Connecticut Agriculture

Agriculture has been important in Connecticut since colonial times and continues to be, with the total impact of agricultural industry in the state worth between $3.3 and 4 billion (Lopez et al. 2017). The green industry including ornamentals such as greenhouse, nursery, floriculture and sod production, accounts for 42% of the total agricultural products sold, nearly $500 million per year. Animal based production including dairy, poultry and cattle, accounts for about $340 million in sales and vegetable, fruit and cigar wrapper tobacco constitute 8, 7 and 6% of sales for an additional $200 million per year, respectively. Approximately 176,400 ha (12% of the land area) is classified as farmland. Much of the plant-based agriculture including ornamental production, vegetables and cigar tobacco, is located within the Connecticut River Valley running north-south through the center of the state (and north through Western Massachusetts). While only 23% of soils in Connecticut are classified as prime agricultural soils, 45% of the Connecticut River Valley and lowland soils are prime soils. These soils are the result of sedimentation from an ancient glacial lake and floodplain valley (Hartshorn and Colton 1967) and represent some of the most agriculturally productive soils in the state, New England, and the nation.

1.3 Massachusetts Agriculture

Massachusetts, the sixth smallest state has 20,305 km^3 of land. There are approximately 7800 farms with 210,400 ha under cultivation making agriculture worth about $492 million dollars annually. Ornamentals including sod, have the highest value, $144 million, followed by fruits and berries at $ 125 million; $69 million of which are from cranberries. Vegetables comprise the third highest market value at $81 million (USDA NASS 2012). In 1875 there were 14,549 farms in Massachusetts with 369,284 ha under cultivation (Census of Massachusetts 1876).

1.4 Rhode Island Agriculture

As the smallest state in the country, Rhode Island has a limited amount of agricultural production. Of 3140 km^3, approximately 20% of the state is comprised of the Providence area urban complex, in which 57% of the population resides. The total value of crop production in Rhode Island as of 2012 was approximately $49 million, ranking 49th in the nation (USDA NASS 2012). Greenhouse, nursery, floriculture and sod constitute the largest value at approximately $32.8 million. Within this group, turfgrass sod covers the largest area and averages 1214 ha annually, distributed among 15 farms. The mostly widely grown commodity group is forage grasses, with approximately 3318 ha in hay and other grains located on 285 farms (USDA

NASS 2012). Vegetable production constitutes the next largest commodity group at 890 ha distributed among 243 farms. The majority of crop producing farms in Rhode Island are less than 10 ha in size and are located throughout the rural and forested southern and western portions of the state. Surprisingly, Rhode Island was one of the few states to show an increase in agricultural production from 2007 to 2012, amounting to a 10% increase, and income from agritourism doubling to $1.4 million (USDA NASS 2012). Unfortunately, between 1981 and 2004, 25% of Rhode Island's prime farmland soils were converted to suburban or urban development and are no longer usable for agriculture (Turenne and Payne 2011).

1.5 Golf Course Industry

Turfgrasses are a significant agricultural commodity in all three states. The golf course industry in New England is worth approximately 10.6 billion dollars annually and there are more than 900 golf courses in the region. Massachusetts leads the New England states, where 377 golf courses generate about $5 billion and employ more than 57,000 people (Raub et al. 2015) (Table 1.1). While the sting nematode (*Belonolamius longicaudatus*) is typically considered the most damaging of turfgrass nematodes in the United States, it does not occur in northern climates. Consequently, nematode-related damage in northern golf course putting greens is frequently overlooked, even though multiple nematode genera are capable of causing severe turfgrass decline. The first significant survey of plant parasitic nematodes on golf course putting greens, from temperate regions in the United States, was undertaken in 1954. Researchers identified at least a dozen plant parasitic genera at variable levels from 41 putting greens throughout Rhode Island (Troll and Tarjan 1954). Although the study did not attempt to assign damage threshold numbers to populations of different genera, the researchers did notice observable turf declines in areas of extremely high *Tylenchorynchus claytoni*. As a final note, the authors stated, *"It had been assumed that plant nematodes were of only slight significance*

Table 1.1 Golf course statistics for New England States

State	Number of courses	Direct sales (dollars in millions)	Total value added (dollars in millions)	Total output (dollars in millions)
Connecticut	178	2473	1813	2853
Maine	140	1067	547	918
Massachusetts	377	4270	3157	4976
New Hampshire	113	1164	689	1098
Rhode Island	57	772	541	855
Vermont	69	928	356	609
All States	934	10,672	7102	11,308

After Raub et al. (2015)

in areas of the country subject to colder climates. It is hoped that surveys such as the one reported in this paper eventually will result in the abandonment of this fallacious view."

1.6 Historical Overview

In this chapter we will present some of the nematological problems that occur in Connecticut, Massachusetts and Rhode Island, with a historical perspective and overview of past and current management tactics. As agriculture including horticulture in New England is high-value and diverse, it is no surprise that nematode parasites of economically important plants are also diverse and can cause significant losses.

An early and informative study of the root knot nematode in Massachusetts can be found in Massachusetts Agricultural College Bulletin No. 55, *Nematode Worms* (Stone and Smith 1898). In this historical publication, the authors refer to the nematode as *Heterodera radicicola* since at the time, all root knot nematodes were considered to be the same species. The 68-page bulletin describes what nematodes are, symptoms produced in plants due to nematode infestations, histology of galls, life cycle of the nematode, and physical and chemical attempts to control the disease. Also included are some excellent drawings of different life stages of the nematode. They recognized the root knot nematode as the cause of decline in vegetable production. During the last decade of the 1800s, the value of vegetable crops propagated in glasshouses during the winter doubled and were worth $1,749,070 in 1895, according to a Massachusetts census of that year. However, root knot nematode often killed cucumber plants, and tomatoes were stunted and wilted, resulting in significant reduction and loss of crop growth. *"Realizing the impossibility of making definite recommendations to those seeking advice in the matter and feeling that the subject was one of great importance to the gardeners of Massachusetts, we finally undertook investigations, the results of which are contained in this bulletin"* (Stone and Smith 1898).

One of the first nematologists to work in New England, B. F. Lownsbery, conducted an extensive survey of plant parasitic nematodes on a wide variety of crops throughout the State of Connecticut from 1951 to 1953. The results were not published, but are summarized here. Plant parasitic nematodes were recovered from vegetables in 28 of 36 fields and included *Pratylenchus*, *Meloidogyne hapla* and *Tylenchorhynchus*. It was noted that *Pratylenchus* was associated with *Verticillium* wilt-affected plants. Tree and small fruit crops (16 farms) were affected by *Pratylenchus*, *Aphelenchoides*, *Meloidogyne hapla*, *Hoplolaimus*, *Mesocriconema* and *Xiphinema*. Ornamentals were positive for *Pratylenchus*, *Aphelenchoides*, *Meloidogyne hapla* and *Xiphinema* in 21 of 24 fields sampled. From over 300 tobacco fields sampled, the tobacco cyst nematode, *Globodera tabacum*, was found on one tobacco farm, while *Pratylenchus* and *Tylenchorhynchus* were present in several tobacco fields. Finally, in one of the first surveys of plant parasitic nematodes in turf in New England, *Tylenchorhynchus* and *Mesocriconema* were recovered from seven of nine golf course and turf farms. *Tylenchorhynchus* was noted as being associated with dead spots on golf greens. No comprehensive state-wide survey of nematode populations has been conducted in Connecticut since.

1.7 Root Lesion Nematode, *Pratylenchus penetrans*

Root lesion nematodes, primarily *Pratylenchus penetrans*, have been and continue to be the most commonly recognized nematode parasites of plants in the Northeast United States (Mai et al. 1960). Much of what we know about lesion nematodes in the Northeast was determined by coordinated research conducted in Connecticut, Illinois, Maryland, Massachusetts, New Jersey, New York, Ohio, Pennsylvania, Rhode Island and West Virginia as a part of the Regional Research Project (NE-64) and published in a collaborative Bulletin that outlined nematode biology and pathogenicity (Mai et al. 1977). The differences in lesion nematode impacts on crops that may exist between New England and other areas of the country may be due to the effects of lesion nematodes in interaction with certain fungal pathogens resulting in complex diseases. Lesion nematodes have been widely demonstrated to interact with vascular wilt pathogens (Rowe et al. 1985, 1987). Research in Connecticut has documented that *P. penetrans* can also interact with the fungal pathogen *Rhizoctonia fragariae* to increase the incidence and severity of cortical root rot in the strawberry black root rot disease complex (Fig. 1.1a) (LaMondia and Martin 1989; LaMondia 2003, 2004), which is a serious problem in strawberry replant situations or after several years in perennial plantings.

Lesion nematode populations fluctuate over time in response to strawberry growth and root biology (Szczygiel and Hasior 1972). LaMondia (2004) investigated the relation between strawberry root type, biomass, and nematode populations in roots and soil over time and determined that *Pratylenchus penetrans* primarily infected feeder and structural roots rather than perennial roots. In addition, *Rhizoctonia fragariae* was consistently isolated from both healthy and diseased perennial roots. Nematode feeding and movement directly resulted in cell damage and death. The indirect effects of lesion nematode infection were early periderm formation, initially seen as discoloration of the endodermis, followed by localized areas of secondary growth and cortical cell senescence and death. Weakened or dying cells resulting from the direct or indirect effects of *P. penetrans* were more susceptible to *R. fragariae*, and thereby, increased the extent of infection and cortical root rot.

Rhizoctonia fragariae and *P. penetrans* pathogens are widespread and common in strawberry plantings, making management of strawberry black root rot disease difficult, but necessary, in order to avoid serious losses. Martin (1988) was able to isolate *R. fragariae* from more than 70% of strawberry plants cultivated in commercial fields for more than 1 year. A survey of 41 commercial strawberry fields in Connecticut demonstrated that lesion nematodes occurred in greater than 75% of

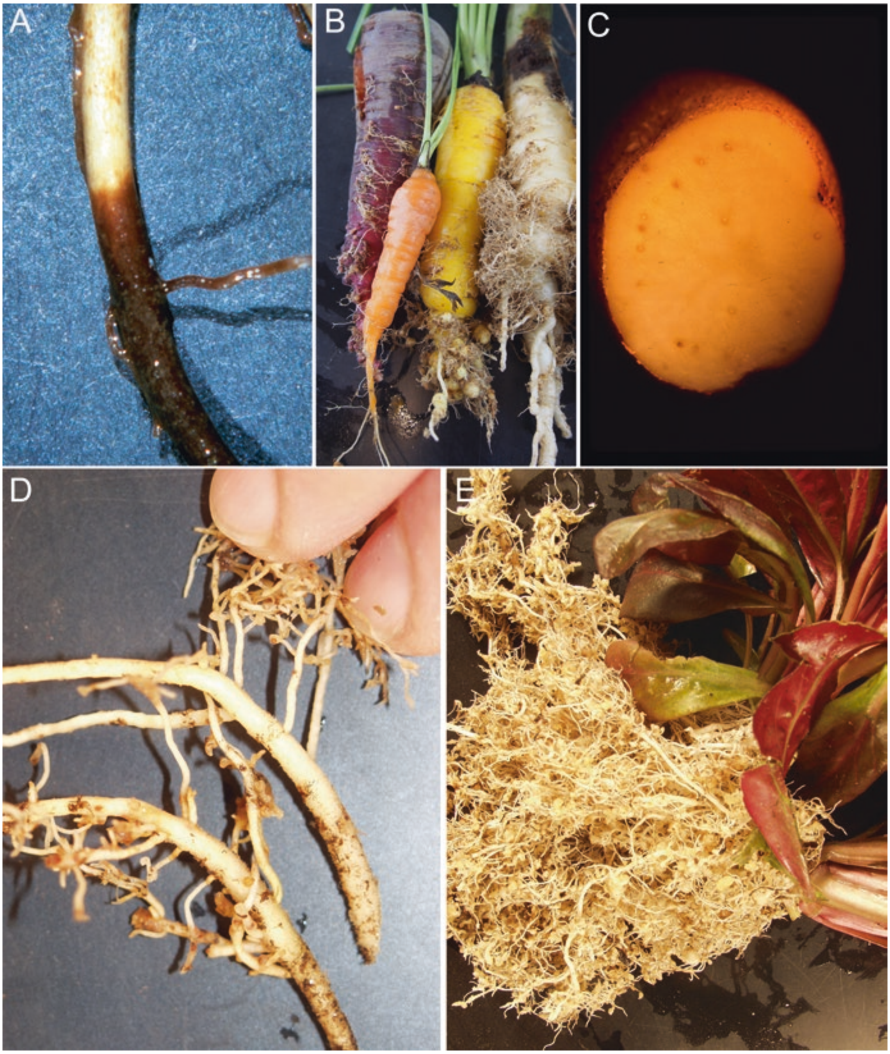

Fig. 1.1 (**a**) Strawberry black root rot; (**b**) *Meloidogyne hapla* infected carrots; (**c**) *Meloidogyne hapla* infecting potato tuber; (**d**) *Meloidogyne hapla* infected *Hosta undulata*; (**e**) *Meloidogyne hapla* infected *Lobelia cardinalis*

sampled plants, especially in replanted fields, and that nearly half of growers were unaware of significant lesion nematode infestations in their fields. Stunted plants had nearly twice the *Pratylenchus* populations of adjacent healthier plants and populations ranged from undetectable to 2350/g root (LaMondia et al. 2005). Black root rot caused by co-infection of *R. fragariae* and *P. penetrans* can have severe economic consequences. An economic analysis of lesion nematode populations in *R. fragariae*-infested field soils was conducted based on a regression model

(DeMarree and Riekenberg 1998) using yield data with *P. penetrans* populations in small plots at the Connecticut Agricultural Experiment Station Valley Laboratory in Windsor, Connecticut. Based on 4 years of projected fruiting from a planting, strawberry profit, expressed as a percentage of gross sales, was predicted to be 33%, 30%, 18% or operation at a cumulative loss over four harvest years at initial densities of 0, 12, 50, or 125 *P. penetrans* per g root, respectively. Half of the samples recovered from surveyed growers' fields had populations in excess of 125 nematodes per g of root (LaMondia et al. 2005).

1.7.1 Management: Crop Rotation

Management of black root rot and lesion nematodes has historically relied on preplant soil fumigation. While fumigation had short-term effects that reduced nematode densities the next year and temporarily increased yields, sampling from fumigated fields still resulted in damaging lesion nematode populations (LaMondia et al. 2005). Rotation away from strawberry to unspecified crops reduced *R. fragariae* to about one third of that seen from continuous strawberry production (Martin 1988). A dense planting of small grains reduces broadleaf weeds, but the lesion nematode has a wide host range including most small grains (Mai et al. 1960) and rotation with grains has been associated with increased lesion nematode damage to potato (Florini and Loria 1990). Growers in Connecticut that rotated away from strawberry to small grains continued to observe poor strawberry growth and black root rot symptoms in the following crop. Rotation with cover crops that suppress nematodes such as 'Saia' oat, sorgho-sudangrass, *Rudbeckia hirta*, pearl millet '101' and 'Polynema' marigold can be effective (LaMondia 1999; LaMondia and Halbrendt 2003). Not all of these plants are suitable as they can be difficult to establish, may not compete well with weeds, or may be difficult to obtain. Strawberry growers in Connecticut who have had losses due to lesion nematodes and black root rot have reported that growing sorgho-sudangrass or millet before replanting strawberry greatly reduced lesion nematodes disease severity, especially after several cycles of rotation and strawberry. Additional rotational plant species need to be evaluated for non-host or antagonism efficacy against *P. penetrans*, the black root rot complex, seed availability, low cost and ease of establishment.

1.8 Northern Root Knot Nematode, *Meloidogyne hapla*

Root knot nematodes are some of the most important and damaging plant pathogens world-wide (Sasser and Carter 1985). The northern root knot nematode, *Meloidogyne hapla,* is common in Connecticut, Massachusetts and Rhode Island. It was relatively wide-spread in Connecticut in the 1951–1953 survey and continues to be a problem on a large number of crops due to its cold tolerance and wide host range.

Galls resulting from *M. hapla* infection are usually much smaller than the southern root knot species, but nonetheless may have a great economic impact. Most vegetable and fruit crops are hosts, and aboveground symptoms are often subtle. Plants can be stunted and grow and ripen unevenly with reduced yields and quality; for example, forking and galling on carrot (Fig. 1.1b) and lesions within the vascular ring of potato (Fig. 1.1c). Unlike some root knot nematode species, there are no resistant vegetable varieties available for *M. hapla* and nematode management has relied either on chemical controls (Gugino et al. 2006) or on rotation to a non-host plant such as a small grain crop.

High value nursery and greenhouse crops represent some of the most valuable components of agriculture in Connecticut, Massachusetts and Rhode Island. We have observed many ornamental plants, especially herbaceous perennials, to be infected with *M. hapla* (Fig. 1.1d, e) (LaMondia 1995c, 1996b). Not only may these plants be stunted, they may also have reduced winter survival and ornamental quality. Many of these infected plants are vegetatively propagated and their movement may result in distribution of the nematode to new previously uninfested areas. Once infected propagation stock is planted, the nematode will continue to spread in that field, garden or planting.

1.8.1 Management: Host Resistance

Management of the northern root knot nematode in ornamentals with the use of plant resistance has become very important, particularly in the absence of chemical control options. Resistance to *M. hapla* has been observed in many ornamental species (LaMondia 1995c, 1996b) and can aid in management in different ways. Inspection of incoming planting stock can be time consuming and expensive. Knowledge of *M. hapla* host status allows application of limited resources to the most likely host plant species to be infected. Some resistant plants such as *Rudbeckia fulgida* and *Aster novi-belgii,* can greatly reduce or eliminate *M. hapla* nematodes from potted nursery soil, garden beds or field soils in as little as 2–6 months, presumably due to both non-host and antagonistic effects against *M. hapla* (LaMondia 1997). This would be useful in controlling infestations in field-grown nurseries, landscapes and gardens after northern root nematodes have been introduced.

There may be instances when infected planting stock may be the only material available for a certain cultivar. *Meloidogyne hapla* juveniles typically infect roots at or near root tips (Christie 1936). This may explain why selective pruning of only the fibrous roots was successful in reducing *M. hapla* infection as well as the spread and establishment of *M. hapla* in propagation material from a known infested source (LaMondia 1997). This root-pruning sanitation is an alternative to heat treatment of propagation material. Heat treatment to kill *M. hapla* in roots is often difficult and may result in plant death.

1.8.2 Sustainable Management

Meloidogyne hapla infestation in soil may also be controlled by biofumigation, the incorporation of green manures such as Brassicas with high glucosinolate contents, which break down to nematicidal isothiocyanates (Halbrendt 1996). However, even the most effective biofumigant crops may be hosts of the northern root knot nematode, so there may be a danger of population increase if conditions are not suitable for biofumigation after green manure incorporation (LaMondia and Halbrendt 2003).

1.9 Tobacco Cyst Nematode, *Globodera tabacum*

While not generally recognized, tobacco has been grown as a high value agricultural crop in New England for a very long time and Connecticut and Massachusetts continue to have economically important tobacco producing areas in the Connecticut River Valley. Many high quality cigars are wrapped with tobacco leaves from Connecticut and Massachusetts. Native Americans in the Northeast grew *Nicotiana rustica* and tobacco was adopted along with corn as one of the first crops grown by European settlers, who first planted *N. rustica* but quickly switched to cultivation of the more palatable *Nicotiana tabacum*. Tobacco was important enough that Connecticut, settled in 1633, enacted legislation concerning tobacco by 1640. Tobacco was grown, not only for local consumption, but also for export, although exports were less than 10 tons per year until the end of the 1700s. Tobacco was primarily used in pipes until Colonel Israel Putnam, of revolutionary war fame, was credited with introducing cigars to Connecticut after a military expedition to Havana, Cuba in 1762. Cigars became popular and by 1810 numerous cigar factories had been established in and around the tobacco producing area of the Connecticut River Valley. Since that time, Connecticut tobacco has been grown and used almost exclusively for cigar production. Broadleaf cigar tobacco was introduced about 1833 as a new improved all-purpose strain that could be used for cigar filler, binder and wrapper and shade tobacco was developed in 1900 as a high quality cigar wrapper leaf (Jenkins 1925). Tobacco acreage was first officially recorded in Connecticut as approximately 2430–2840 ha during the US Civil War, and increased to over 12,140 ha in 1920 (Anderson 1953). Both broadleaf and shade tobacco continue to be grown in Connecticut as natural leaf cigar wrapper, with 1214–1618 ha of production.

In 1951, B. F. Lownsberry found a round cyst nematode to be the cause of a disease on shade tobacco in the Hazardville section of Enfield in Hartford County, Connecticut and subsequently described it as *Heterodera tabacum* (Lownsbery and Lownsbery 1954) (Fig. 1.2a), which was later transferred to the genus *Globodera* as *G. tabacum* (Behrens 1975; Stone et al. 1983). A major concern at the time of its description was its morphological similarity to the potato cyst nematode *Globodera rostochiensis,* which had just recently been quarantined as a potato pest in New York

Fig. 1.2 (**a**) Tobacco cyst nematode *Globodera tabacum* females and males on roots; (**b**) Damage to shade tobacco due to *G. tabacum*; note treated areas surrounding the plot; (**c**) Fusarium wilt of broadleaf tobacco due to *Fusarium oxysporum* and *G. tabacum*

State in an effort to reduce or eliminate spread (Spears 1968). However, after further official evaluation, quarantine restrictions were not placed on Connecticut crops or acreage as the host ranges of *G. tabacum* and *G. rostochiensis* were demonstrated to be different (Lownsbery 1953; Harrison and Miller 1969) and morphological differences between the two nematodes demonstrated that the tobacco cyst nematode was a closely related, but new and distinct species (Lownsbery and Lownsbery 1954). The most important fact was that *G. tabacum* did not reproduce on potato and *G. rostochiensis* did not reproduce on *N. tabacum*. The host range of *G. tabacum* included all *N. tabacum* types tested as well as *N. rustica*. The ornamental tobacco species *N. alata*, *N. sanderae* and *N. longiflora* were not hosts. *Solanum nigrum*, eastern black nightshade, a common weed in the northeast and in tobacco fields, was shown to be the preferred host, with four to five times the number of cysts produced from the same amount of inoculum, in comparison to tobacco (Lownsberry 1953).

Once potential quarantine issues were resolved, further research demonstrated that *G. tabacum* significantly impacted tobacco growth and yields (Lownsbery and Peters 1955) (Fig. 1.2b). More recent research quantified yield losses by *G. tabacum* densities as low as 10–20% in soil at nematode densities over 50 J^2 per cm^3 soil and as high as 40–60% in shade and broadleaf tobacco at nematode densities of 500–1000 J^2 per cm^3 (LaMondia 1995a, 2002b). Tobacco cyst nematode increase in infested fields was greater in shade than broadleaf tobacco due to increased plant density and a longer growing season of over 100 days *versus* 75–80 days respectively. In addition, when *G. tabacum* occurred in combination with *Fusarium oxysporum* f.sp. *nicotianae*, broadleaf plants often died from Fusarium wilt before the nematodes could complete their life cycle (Fig. 1.2c). This not only seriously impacted the tobacco crop but also decreased cyst nematode populations (LaMondia 1992, 2015). Unlike broadleaf, shade tobacco cultivars are resistant to Fusarium wilt and the tobacco cyst nematode did not break that resistance. The introduction of wilt resistance genes to a new broadleaf tobacco release (C9) that has dominated subsequent commercial production (LaMondia and Taylor 1992) allowed broadleaf tobacco to be grown in wilt-infested fields, and also allowed increases in nematode populations to the point where damage thresholds were routinely exceeded.

The tobacco cyst nematode was initially found only on a single farm in Connecticut. The source of that infestation was unknown. Surveys, from 1951 to 1953, in 168 tobacco fields spread across all three tobacco producing counties (Hartford, Tolland and Middlesex) did not recover any additional tobacco cyst nematode infestations. Over a relatively short period of time, the tobacco cyst nematode infestation spread so that nearly 100% of the shade and broadleaf tobacco fields were infested by the 1980s. It is likely that the movement of soil from farm to farm on equipment and vehicles played a very important role in that spread.

The genus *Nicotiana* likely has its origin in South America and *Nicotiana tabacum* is a natural allopolyploid that has not been found in nature, being derived from the interspecific hybridization of the ancestors of *Nicotiana sylvestris* (maternal) and *Nicotiana tomentosiformis* (paternal) about 200,000 years ago (Leitch et al. 2008). The tobacco cyst nematode is also a likely native to the Andes of South America, similar to other round cyst nematodes, and now is world-wide in distribution (CAB International 2004; Bélair and Miller 2006). Genetic differences in nematode populations have been associated with tobacco farms operated by different companies in France, and it can therefore be assumed that both within-region and long-distance cyst spread has been unintentionally accomplished through human activities (Alenda et al. 2014).

1.9.1 Management: Chemical

For decades, tobacco cyst nematode management in Connecticut and Massachusetts relied almost exclusively on chemical controls: soil fumigation with 1, 3-Dichloropropene, ethylene dibromide, or methyl-isothiocyanate, oxamyl application as a non-fumigant nematicide in shade tobacco and either oxamyl or two or more years of rotation in broadleaf tobacco. Methyl bromide was not used as it had negative effects on tobacco quality characteristics, particularly, burn. Other tactics for managing nematode numbers involved crop root destruction immediately after harvest to kill nematodes which had not yet completed development in the roots

(LaMondia 2008) and trap cropping with plants that stimulated nematode hatch, again before reproduction could occur (LaMondia 1995b, 1996a).

1.9.2 Resistance

Breeding for resistance to tobacco cyst nematodes has been ongoing in Connecticut since the late 1980s. The incorporation of a single dominant-effect resistance gene, originally transferred to *N. tabacum* from *N. longiflora* (LaMondia 2002a) into an adapted and widely grown broadleaf variety, B2, has resulted in yield and leaf quality increases while reducing nematode populations (LaMondia 2012). Resistant plants stimulate cyst nematode hatch but the juveniles which infect roots do not establish viable feeding cells and do not reproduce. Cyst-nematode resistant shade tobacco lines are under development. An additional source of resistance to *G. tabacum* associated with black shank resistance has been documented to have a different inheritance and mode of action and can also be used in breeding programs (Johnson et al. 2009). Should a population of *G. tabacum* be able to reproduce on currently available single-gene resistance plants, the additional source of resistance will be available for continued management.

1.10 Nematodes on Turfgrasses in New England

Nematodes occur in all turfgrasses such as residential lawns, athletic fields, cemeteries, sod farms, school grounds and golf courses; however, in New England, damaging populations tend to occur primarily on golf course putting greens. Golf course greens in New England are particularly susceptible to nematode damage because of the intense utilization and management practices. This management results in shallow root systems due to low cutting heights, drought conditions and extreme soil compaction. While the authors have observed damage to golf course fairways and commercial sod farms from plant parasitic nematodes, these occurrences are the exception, not the rule.

New England has some of the oldest golf courses in the United States, several of them 100 or more years old. Most of the golf courses in the region have what are known as “pushup greens”, that is, greens formed by mounding-up field soil so that the greens surface is elevated from the approach and fairway. Top dressing with core aerification over the last 50 or more years has resulted in a cap of sandy soil (75–95% sand) 7–10 cm deep. Most turf-parasitic nematode populations are restricted to the sandy cap, although *Longidorus* can be found well below. New England greens are comprised mostly of *Poa annua* and *Agrostis stolonifera* with a few having mixtures that include *Agrostis canina.* Unlike field crops, golf greens are uniquely suited to propagate plant parasitic nematodes and very high populations often occur. Golf greens have a long season with a perennial host that forms a dense root system

Table 1.2 Occurrence and frequency of plant parasitic nematodes above damage threshold values from University of Rhode Island (URI) and University of Massachusetts (UMASS) sampling data (UMASS data derived from records of UMASS Extension Nematology Lab)

	URI 2003–2004		UMASS 2011–2017	
Nematode genus	Greens w/ nematode (%) (n = 114)[a]	Samples above threshold (%)[b, c]	Courses w/ nematode (%) (n = 692)	Samples above threshold (%)
Criconemoid species	97.4	7.0	57.6	1.8
Helicotylenchus	100.0	2.6	53.3	3.8
Tylenchorhynchus	100.0	35.1	95.4	24.4
Hoplolaimus	89.5	9.6	74.1	45.7
Heterodera juveniles	94.7	7.9	23.7	1.8
Meloidogyne J2's	50.0	1.8	29.8	6.8
Pratylenchus	–	–	27.1	5.9
Trichodorus	–	–	0.7	20
Other parasitic genera[d]	76.3	n/a	29.1	n/a

[a]URI sample was taken from 114 putting greens on 38 golf courses (Jordon and Mitkowski 2006
[b]Based on damage threshold data from Table 1.3
[c]Refers to the percent of total samples with nematode levels above damage threshold at any of the six sampling dates in 2003 and 2004
[d]Other genera include *Longidorus, Tylenchus*, *Paratylenchus* and *Xiphinema*

throughout the entire surface. This, coupled with the sandy texture and daily irrigation, make an ideal environment for nematode feeding and reproduction.

At least 12 genera of plant parasitic nematodes are found in golf course greens with *Tylenchorhynchus, Helicotylenchus, Hoplolaimus* and criconemoid nematodes most commonly encountered (Table 1.2). In 2003 and 2004, Jordon and Mitkowski (2006) undertook a sampling study of 114 putting greens from 38 different golf courses in Rhode Island, southern Connecticut and eastern Massachusetts. Golf courses were chosen based on previous history of nematode injury to turf. More currently, 2011–2017 data from the University of Massachusetts (UMASS) Extension Nematology Lab are also included in Table 1.2. While the percentages between the two data sets are different, the four most common turf-parasitic nematodes are the same. It should be noted that the University of Rhode Island (URI) sampling was focused on golf courses which were known to have high nematode populations, while the UMASS data is based on submissions from golf courses with suspected (but not necessarily confirmed) nematode issues at the time of submission. Additionally, sampling at both sites was conducted a decade apart from each other and the URI data is representative of a much narrower geographic area.

For the purposes of rapid diagnosis, turfgrass parasitic nematodes are typically only identified to genus, so the number and diversity of species encountered in the region are unclear. Within New England, *Tylenchorhynchus claytoni* and *T. dubius* have most commonly been reported (Troll and Tarjan 1954; Miller 1976; Blackburn

Table 1.3 Damage threshold levels for nematodes that parasitize turfgrasses (number of each genus/100 cm[3] soil)

Nematode genera	New England[a]	Other[b]
Criconemoids	1500	1500
Tylenchorhynchus	800	300
Hoplolaimus	400	150
Helicotylenchus	1500	600
Longidorus	100	–
Meloidogyne	500	100
Heterodera	500	–
Pratylenchus	100	150
Hemicycliophora	200	200
Trichodoroids	100	100
Xiphinema	–	200

[a]Developed by Robert Wick, PhD, University of Massachusetts
[b]From: Eric Nelson, PhD, Cornell University, Turfgrass Trends, Oct. 1995 (Nelson 1995)

et al. 1997). Recent ITS sequencing of *Tylenchorhynchus* nematodes from Massachusetts golf course greens confirms the presence of *T. claytoni* (N. Mitkowski, personal communication). However, *T. maximus* has been identified in New Jersey and is likely to be present in New England (Myers et al. 1992). As the name implies, *T. maximus* is noticeably longer than most species of the genus and unusually large *Tylenchorhynchus* individuals have been observed from different locations in the region over the past decade. *Tylenchorhynchus nudus* has been reported from turfgrasses in the Midwestern United States, but it is unclear if it is present along the east coast (Smolik and Malek 1972; Malek 1980). Malek (1980) reported *T. clarus* parasitizing creeping bentgrass in Ohio, but once again, it is unclear if it is present in New England.

To date, only a single species of *Hoplolaimus* has been reported in New England on golf course turfgrasses, *Hoplolaimus galeatus* (Troll and Tarjan 1954; Miller 1976) (Fig. 1.3a–c). Although the genus *Hoplolaimus* is not nearly as diverse as *Tylenchorhynchus*, with only 29 currently known species (Handoo and Golden 1992), ITS sequencing and morphological data have never identified any other species of *Hoplolaimus,* besides *H. galeatus,* parasitizing golf course turf in New England or elsewhere in the US (Lucas et al. 1978; Wick and Vittum 1988; Blackburn et al. 1997; Settle et al. 2006). While *Helicotylenchus* spp. are extremely common in New England turfgrass soils, the only attempt to identify populations of these nematodes to species was undertaken by Troll and Tarjan (1954) when they sampled 41 golf course putting greens in Rhode Island and identified *H. erythrinae* from half of the sampled greens. While prevalent, these nematodes rarely appear to reach high population levels, although Fushtey and McElroy (1977) did report significant numbers of *Helicotylenchus* spp. from different locations in Southern British Columbia. The most commonly reported species of *Helicotylenchus* found on turf in North America is *H. dihystera* (Sumner 1967; Lucas et al. 1978; Zeng et al. 2012). Davis et al. (1994b) reported *H. cornurus* from golf course putting greens in Chicago, IL

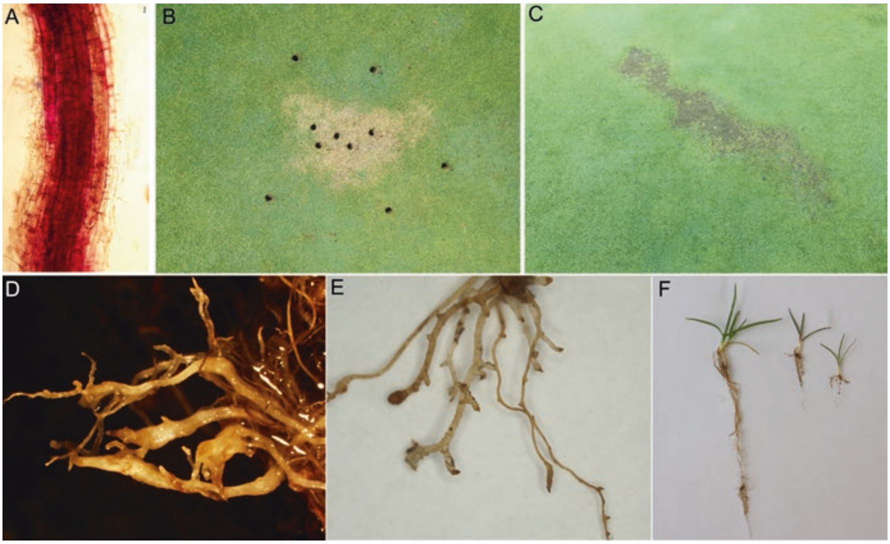

Fig. 1.3 (**a**) Four lance nematodes, *Hoplolaimus galeatus* in the bentgrass root; (**b**) This patch of dead turf on a golf green has more than 5000 lance nematodes per 100 cm^3 of soil. In surrounding patch the population is about 1500 lance nematodes per 100 cm^3 of soil; (**c**) This patch had 11,340 lance and 380 stunt nematodes/100 cm^3 soil; (**d**) Root-knot galls of grass roots caused by *Meloidogyne naasi*; (**e**) Galled and necrotic root tips of Kentucky bluegrass as the result of feeding injury by *Longidorus*, the needle nematode; (**f**) Healthy Kentucky bluegrass on the left, stunted galled roots as the result of about 50 *Longidorus* nematodes/100 cm^3 of soil

but the species has never been reported from additional locations. *Helicotylenchus pseudorobustus* has also been reported from New York State, a short distance from Connecticut (Feldmesser and Golden 1974). The most extensive list of *Helicotylenchus* found on turfgrasses comes from Kentucky bluegrass lawns, athletic fields and pastures in Wisconsin and includes *H. digonicus, H. dihystera* (=*H. nannus*), *H. erythrinae* (= *H. melancholicus*), *H. platyurus* and *H. microlobus* (Perry et al. 1959). Of the identified species, *H. digonicus* appeared to be the most pathogenic. As is the case with *Tylenchorhynchus,* distinctions between *Helicotylenchus* species can be subtle and there are currently 193 recognized species within the genus (Marais 2001).

Species of ring or criconemoid nematodes are very commonly found parasitizing turfgrasses. In the 1954 study by Troll and Tarjan, *Mesocriconema* (= *Criconemoides*) was reported from a single putting green in Rhode Island. While it is unclear which species of criconemoids are common in New England, in 1976, Miller reported *Criconemoides lobatum* from Connecticut, now recognized by some as *Mesocriconema rustica* (Ebsary 1991). No other reports of specific criconemoid taxa on turf from New England have been reported. Feldmesser and Golden reported *M. rustica* from West Point, NY in 1974, approximately 20 miles from the Connecticut border. *Criconema mutabile* has been reported from Rhode Island on unspecified hosts (Mai et al. 1960) and its ability to parasitize turf would make it a likely turfgrass pathogen in New England (Bernard 1980). *Mesoscriconema* spp. have been reported from turf in various locations in the USA (Bernard 1980; Zeng et al. 2012), and having been positively reported from New Jersey, it is likely present at some level in New England turfgrasses (Mai et al. 1960).

Meloidogyne naasi, the barley root knot nematode, commonly occurs in golf greens in New England and New York causing root galls (Fig. 1.3d). It was previously thought to be *M. graminis* (Rungrassamee et al. 2003). *Meloidogyne naasi* was first described in Great Britain (Franklin 1965) and later reported in Los Angeles and Orange Counties in California (Radewald et al. 1970). It has also been reported in Nevada, Oregon, Utah, Washington (McClure et al. 2012); Illinois, Kentucky, and Kansas (Michell et al. 1973). *Meloidogyne naasi* is not restricted to feeding on grasses; dicotyledonous hosts include alfalfa, clover, pea, soybean, chickweed and sugar beet. *Meloidogyne naasi,* either alone or in combination with *Tylenchorhynchus agri* or *Pratylenchus penetrans,* was very pathogenic to potted creeping bentgrass 'Toronto C-15' (Sikora et al. 1972). In another trial, inoculation of potted bentgrasses 'Toronto C-15 and 'Northmoor 9'' with *M. naasi* resulted in a significant reduction of clipping weight 8 months after inoculation (Michell et al. 1973). Pathogenicity in golf greens has not been well established but circumstantial evidence suggests that several thousand juveniles/100 cm^3 of soil will result in compromised turf. In New England, this assessment must be made in the month of April when the juveniles are still in the soil. Regardless of the numbers in April, few juveniles will be seen throughout the growing season as there is only one hatch period per year. *Meloidogye naasi* is unique in that it requires a chilling period before the eggs will hatch. Diapause affects about 95% of the population so that in *M. naasi*-infested golf greens, a few juveniles can be recovered throughout the summer and fall. Depending on the year and location, high populations of *M. naasi* can be found between December and the end of April.

Pratylenchus penetrans has been reported from turfgrasses in New England (Troll and Tarjan 1954), but the species does not appear to be particularly aggressive on putting green turf. When *P. penetrans* was inoculated on the roots of greenhouse-grown *Poa annua*, very little damage was observed, even at the highest concentrations of 5000 nematodes/100 cm^3 soil (Bélair and Simard 2008). In fact, after 9 weeks, nematode concentrations had declined significantly from inoculation levels. Sikora et al. (1972) demonstrated significant pathogenicity of *P. penetrans* on *Agrostis palustris* but only in the presence of other pathogenic nematodes, particularly *Meloidogyne naasi.* While *P. penetrans* could reproduce on *A. palustris* in the absence of other plant parasitic nematodes, population levels had dropped significantly below inoculation concentrations after 6 months in the greenhouse and *A. paulstris* was described as a poor host for the nematode. Between 1992 and 1996, *Pratylenchus* spp. were only identified in an average of 7.2% of the approximately 2600 soil samples processed by the University of Rhode Island Turf Diagnostic Lab, with the vast majority of samples containing 40 or fewer nematodes/100 cm^3 soil. Roots were not extracted for *P. penetrans* in any of these cases. From 2011 to 2017, the University of Massachusetts (UMASS) Extension Nematology Lab reported 27.1% of submitted samples contained *P. penetrans* but only 5.9% of samples were above damage threshold levels (Table 1.2). The discrepancy between these two data sets is likely a result of the counting methodology used. The University of Rhode Island (URI) samples were all counted at a 1:20 dilution, meaning that if less than 20 nematodes of any type were present, they were statistically unlikely to be observed. The UMASS data set was derived by counting each nematode in an extracted sample. Interestingly, Qing et al. (1998) identified four species of *Pratylenchus* from Southern Ontario, an area relatively close to New England, but did not identify *P. penetrans.*

Longidorus spp. are relatively uncommon in turfgrass soils, but can cause significant damage even at low population levels. In 2006, the authors identified populations of *Longidorous* spp. attacking newly seeded Kentucky Bluegrass sod in Southern Maine, with damage resulting from only 50 nematodes/100 cm^3 soil. Hundreds of square feet of turf were killed and surviving seedlings had severely damaged root systems (Fig. 1.3e, f). Troll and Tarjan (1954) identified *L. sylphus* from 5 of 41 sampled Rhode Island golf courses. Although very little work has been undertaken on *Longidorus* on turf, *L. breviannulatus* was identified in Pennsylvania on creeping bentgrass greens (Forer 1977) and as few as 20 nematodes/100 cm^3 soil have been documented to cause severe damage to corn (Niblack 2003). *Longidorous elongatus* has also been observed to parasitize perennial ryegrass (*Lolium perenne*) under experimental conditions, but this grass is not used as putting surface, and while the grass was a host, no damage to affected plants was observed (Taylor 1967).

Plant parasitic nematodes vary widely in their virulence (Table 1.3), and their genus and number per given volume of soil needs to be considered when assessing their potential for damage. Damage threshold levels in Table 1.3 were not determined experimentally but were based on field observations and laboratory assays from golf courses in the New England region. As with all nematodes, the conditions in which turf-parasitic nematodes exist have a significant impact on their damage potential. Soil type (highly organic *vs*. sand *vs*. silt) and moisture content have the most significant impact on the success of turf-parasitic nematodes and can also affect the health of the turf grown in site-specific conditions. It has been shown that turf-parasitic nematodes are less prevalent in organically managed golf courses (Allan et al. 2015). Golf course age can also have a significant impact. In one study, older courses were shown to have higher nematode populations, with *Poa annua* and *Agrostis canina* being more susceptible to nematode increases, in general, than *A. palustris* (Jordan 2005). In addition, nematodes species can also play a role in virulence. While damage thresholds have been developed for the genus *Tylenchorhynchus,* no assumptions have been made as to the virulence of individual *Tylenchorhynchus* species. As a result, damage thresholds may be higher or lower than is appropriate as thresholds are applied to different *Tylenchorhynchus* species. Other extenuating circumstances such as geographic location, method of sample collection, time of the year, assay methods and prevailing environmental conditions, can affect the numbers and interpretation of threshold levels.

In addition to the difficulty of applying a single damage threshold to a variety of different potential environments, determining a threshold experimentally can be difficult and experimental conditions rarely correspond to real-world conditions on a golf course. As a consequence, turfgrasses in a greenhouse that can withstand very high populations of nematodes without showing symptoms may collapse when subjected to golf course traffic, drought and cutting heights. In addition, the determination of "damage" on golf turf is difficult to quantify because a clear and measurable yield is never achievable. Some researchers have chosen to examine clipping yield and rooting depth as a measure of nematode virulence but these parameters fluctuate throughout a growing season in cool-season turfgrasses and are often dependent on fertilization level and soil temperatures. The single most damaging nematode in the region is *Hoplolaimus*, which feeds both ecto- and endoparasitically on grass roots (Fig. 1.3a). Populations of 4000 nematodes/100 cm^3 of soil can result in dead patches of turf (Fig. 1.3b, c). Settle et al. (2006) utilized visual and multispectral radiometry to examine the effects of *H. galeatus* on *Agrostis palustris* "A-4". Researchers observed that damaging populations of *H. galeatus* ranged from 177 to 845 nematodes/100 cm^3 soil and that quality rating decreased 10% for each additional 400 nematodes counted (maximum counts of *H. galeatus* reached 1600 nematodes/100 cm^3 soil). Unfortunately, *H. galeatus* frequently burrows into roots and this study did not account for those nematodes, which cannot be removed via sugar flotation. When researchers examined the effect of turfgrass cultivar on nematode populations numbers and turfgrass injury, the error induced by varietal differences appeared to mask any possible correlation with nematode population levels.

Laughlin and Vargas (1972) observed significant reductions in foliar and root dry weight on both *Agrostis palustris* 'Toronto' and *Poa pratensis* 'Merion' in sand-based greenhouse trials using 500 and 1000 *Tylenchorhynchus dubius* nematodes/100 cm^3 soil. In similar greenhouse experiments, Davis et al. (1994a) were able to demonstrate pathogenicity on both *A. palustris* 'Penncross' and *P. annua* by *Tylenchorhynchus nudus*, indicated by reduced root mass of both species in the presence of approximately 1500 nematodes/100 cm^3 soil. This study also demonstrated that reduction in rooting was more severe on *A. palustris* than on *P. annua* and regression analysis suggested that as few as 120 *T. dubius* nematodes/100 cm^3 soil could potentially reduce root length by a centimeter, but the regression coefficient was very low ($R^2 = 0.31$). A study on the effect of *T. claytoni* on multiple cultivars of *A. palustris* indicated that cultivar had no effect on nematode reproduction. All six tested cultivars supported the nematode reproduction and visual decline in turfgrass quality was observed above 600 nematodes/100 cm^3 soil (Walker and Martin 2001).

As mentioned previously, *Longidorus* spp. were found to be very damaging in a turf farm with very sandy soil in Maine, in 2006. Populations as low as 30–50 nematodes/100 cm^3 of soil were capable of killing seedlings, where galled root tips and necrotic meristems were evident. In the 3rd edition of Couch's treatise on turfgrass diseases (Couch 1995), *Longidorous* spp. are listed at 20 nematodes/100 cm^3 soil, which approximates the experiences of the authors in 2006. Forer's (1977) work on *L. breviannulatus* also suggested a minimum number of 20 nematodes/100 cm^3 soil to cause observable damage, derived from an actual *A. palustris* putting green.