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Spatial and temporal dynamics of *Meloidogyne minor* on creeping bentgrass in golf greens

K. Morris[ab]*, F. G. Horgan[b]† and C. T. Griffin[a]

[a]*Department of Biology, National University of Ireland, Maynooth, Ireland; and* [b]*Teagasc, Oakpark Research Centre, Co. Carlow, Ireland*

Meloidogyne minor, first reported on potatoes in the Netherlands in 2004, is an emerging nematode pest in Europe. It damages turfgrass, particularly creeping bentgrass (*Agrostis stolonifera*) grown on sandy soils such as those of golf greens. However, little is known of the nematode's life history and pathology. In this study, the spatial and temporal distribution of *M. minor* on a creeping bentgrass green in Ireland was determined over a 15 month period. Cores were taken on transects across yellowing patches of grass caused by nematode damage. Second-stage juveniles (J2) were absent from the soil from November to February, when soil temperatures were below 10°C. Both galls and egg masses were present throughout the year but were more abundant in late summer and early autumn. More J2, galls and egg masses were present in the top 10 cm of soil than at a depth of 11–20 cm. The nematode population tended to decrease as distance from the centre of the yellow patches increased. The diameter of visual symptoms (yellow patches) was also recorded over the 15 months. The mean diameter of five sampled patches increased from 23·7 cm in June 2003 to 45·2 cm in August 2004. There were 158–193 galls per 100 cm^3 soil at the margin of the visible infested area, indicating that this could be the threshold level for visible symptoms.

Keywords: horizontal distribution, population dynamics, root-knot nematode, turfgrass, vertical distribution, yellow patch disease

Introduction

Root-knot nematodes, *Meloidogyne* spp., are amongst the most damaging of plant parasitic nematodes. They can cause extensive root damage, affecting water and nutrient uptake in plants (Karssen & Moens, 2006). With reductions in the use of chemical nematicides, the importance of the genus in Europe is increasing (Wesemael *et al.*, 2011). *Meloidogyne minor,* first described in 2004 (Karssen *et al.*, 2004), is considered an emerging pest species in Europe (Moens *et al.*, 2009). To date, *M. minor* has been primarily a pest of creeping bentgrass (*Agrostis stolonifera stolonifera*) on golf greens and other turf grass amenities in England, Wales and Ireland, where it causes yellow patches (Karssen *et al.*, 2004; Lammers *et al.*, 2006). Reduction of root density due to nematodes can produce depressions in the turf (Fleming *et al.*, 2006; Turner & Fleming, 2006). The resulting unevenness of the turf, together with unsightly yellow patches, reduces the amenity value of the affected courses. Therefore, the disease is a major concern to the golf industry (Fleming *et al.*, 2008). Symptoms are most pronounced on golf greens with a high sand content, including those constructed according to United States Golf Association (USGA) guidelines where the root zone has up to 85% sand (minimum 60%; USGA, 2004). *Meloidogyne minor* is also a potential threat to certain crop plants. In 2000, the species was found heavily infesting potato roots in a field in the Netherlands (Karssen *et al.*, 2004) and controlled experiments indicate that it can reproduce on tomato, carrot, wheat, barley and oats (Karssen *et al.*, 2004; Lammers *et al.*, 2006). However, in field trials, only potato supported a significant reproduction of *M. minor* (Thoden *et al.*, 2012). *Meloidogyne minor* is now known to occur in Britain, Ireland, the Netherlands and Belgium (Viaene *et al.*, 2007; Vandenbossche *et al.*, 2011); however, the full extent of its geographic distribution is unknown (Lammers *et al.*, 2006).

Little is known of the biology of *M. minor*, and there are no studies on its population dynamics or spatial distribution. Factors such as temperature, soil type, crop management strategies and root spatial distribution can affect nematode population densities and distribution in soil (Franklin *et al.*, 1971; Carpenter & Lewis, 1991; Windham & Barker, 1993; Zhang & Schmitt, 1995). *Meloidogyne* spp. are sedentary endoparasitic nematodes and deposit all their eggs in egg masses. This results in the nematodes typically exhibiting a highly aggregated and uneven distribution (Goodell & Ferris, 1980). Knowledge of the spatial distribution of nematodes is important in understanding their epidemiology. Population densities are usually enumerated in a composite

*E-mail: Karen.morris@nuim.ie
†Present address: International Rice Research Institute, DAPO Box 7777, Metro Manila, The Philippines

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sample composed of many subsamples (Duncan & Phillips, 2009), providing limited information on the nature of the spatial distribution. Spatial distributions of nematodes have been described in relation to certain discrete host plants (e.g. Zhang & Schmitt, 1995), but studies of nematode spatial distribution in turf grass or pastures are rare. This study determines the spatial and temporal dynamics of *M. minor* on a USGA golf green over a 15 month period and describes the relationship between the nematodes and visible disease symptoms (yellow patches).

Materials and methods

Sampling was conducted on a golf course nursery in County Kildare in the east of Ireland. The nursery was planted in 2002 with creeping bentgrass (cv. Providence). Five patches of root-knot nematodes were located based on visible symptoms (yellowing) and the presence of galls on roots. The nematodes were identified as *M. minor* based on morphological criteria and esterase patterns (Karssen *et al.*, 2004). The centre of each patch was permanently marked by a wooden dowel, the top of which was flush with the soil surface. Each patch was sampled monthly from June 2003 to August 2004 (except July 2004). Cores (1·9 cm diameter) were taken to a depth of 20 cm, divided into 0–10 and 11–20 cm portions (total volume of 20 cm core = 45·4 cm^3). Cores were taken at 5 cm intervals along a radial transect starting either 5 or 10 cm from the centre of the patch and extending beyond the area with visible symptoms. Each radius was sampled only once. Fewer samples were taken at 5 cm from the centre due to the limited area available at that circumference. The sampled radius was extended over time from 25 to 40 cm, as the patch increased in size. Second-stage juveniles (J2) were extracted using the tray method (Whitehead & Hemming, 1965) for 24 h at 20°C. Following extraction of J2, roots were gently cleaned of adhering soil and blotted dry with tissue paper, the upper 2 cm of root thatch was removed and the remaining roots were weighed. The roots were examined with the aid of a dissecting microscope (×25) and the numbers of galls and egg masses were recorded. When they could be distinguished, the diameters of visible symptoms (yellow patches) were measured at each sampling time; symptoms were most apparent during the summer months. Meteorological data (soil temperature at 10 and 20 cm) were obtained from the Met Éireann Casement climate station, 15 miles (24·1 km) from the field site. Rainfall levels are not presented as golf greens are liberally irrigated.

Statistical analysis

The effects of soil depth, distance from patch centre and sampling time on number of J2, number of galls, number of egg masses and the percentage of galls with egg masses were analysed using ANOVA on transformed data. The numbers of J2, galls or egg masses were transformed using a square root ($x + 0{\cdot}5$) transformation. The percentage of galls with egg masses was transformed using an arcsine [square root (n)] transformation. The full data sets were unbalanced, as not all sampling distances were included at each time point; therefore a restricted data set was used in the ANOVA. This balanced data set included data for 10, 15, 20 and 25 cm from the centre of the patch. The full data sets were analysed using general linear models and confirmed the main effects. Residuals were plotted after analyses and found to be normal and homogeneous.

Results

Meloidogyne minor showed distinct temporal and spatial patterns of abundance (Fig. 1). Time of sampling, distance from centre of patch and soil depth all had a highly significant effect on the numbers of J2, galls and egg masses; there were also significant two-way interactions (Tables 1 and 2).

Seasonal trends in numbers of J2

J2 were absent during the winter months of November 2003 to February 2004, but were detected at all other times, with up to 374 J2 per 100 cm^3 soil (Figs 1 and 2c). The seasonal pattern of J2 numbers differed between the upper and lower cores (depth × time, $P < 0{\cdot}001$; Table 1). For example, 10 cm from the centre of the patch, the number of J2 in the upper core increased steeply in March 2004 and remained high to the end of the sampling period in August of that year, while in the lower core (11–20 cm), the number rose more gradually, and reached a more distinct peak in May 2004 (Fig. 2c). Soil temperature remained below 10°C (the critical temperature for hatching of *M. minor*; Morris *et al.*, 2011) from October to February; mean daytime temperature first approached 10°C in March at 10 cm depth (Fig. 2a) and in April at 20 cm depth (Fig. 2b). The general trend, shown for all locations across the transect, was for J2 numbers to decline in autumn (September–October 2003) from a peak in August 2003. Then, following the winter absence, numbers increased from March 2004 onwards, reaching higher levels in summer 2004 than in the previous summer at the same location (Figs 1 and 2c).

Seasonal trends in numbers of galls and egg masses

Galls and egg masses were present throughout the year (Fig. 1). Numbers of galls tended to be low in winter and to increase towards late summer, but the exact nature of the change over time depended both on depth in soil and on distance from the centre of the patch (significant interactions, $P < 0{\cdot}001$; Table 2). At 10 cm from the patch centre, the number of galls in the upper core doubled from June to September 2003, then declined steeply to January, remained comparatively constant until April and rose steeply again to May 2004 (Fig. 2d). Seasonal changes were less pronounced in the lower core (Fig. 2d). The pattern illustrated in Figure 2d is typical for locations towards the centre of the patch (5–20 cm), with two fairly equal peaks around September–October 2003 and June–August 2004, but towards the edge of the patch (25–40 cm) the earlier peak was smaller or absent as the infestation expanded outwards over time (Fig. 1).

There were similar seasonal trends in the abundance of egg masses, but the number of egg masses was notably low in December 2003 (Figs 1b and 2e). The proportion

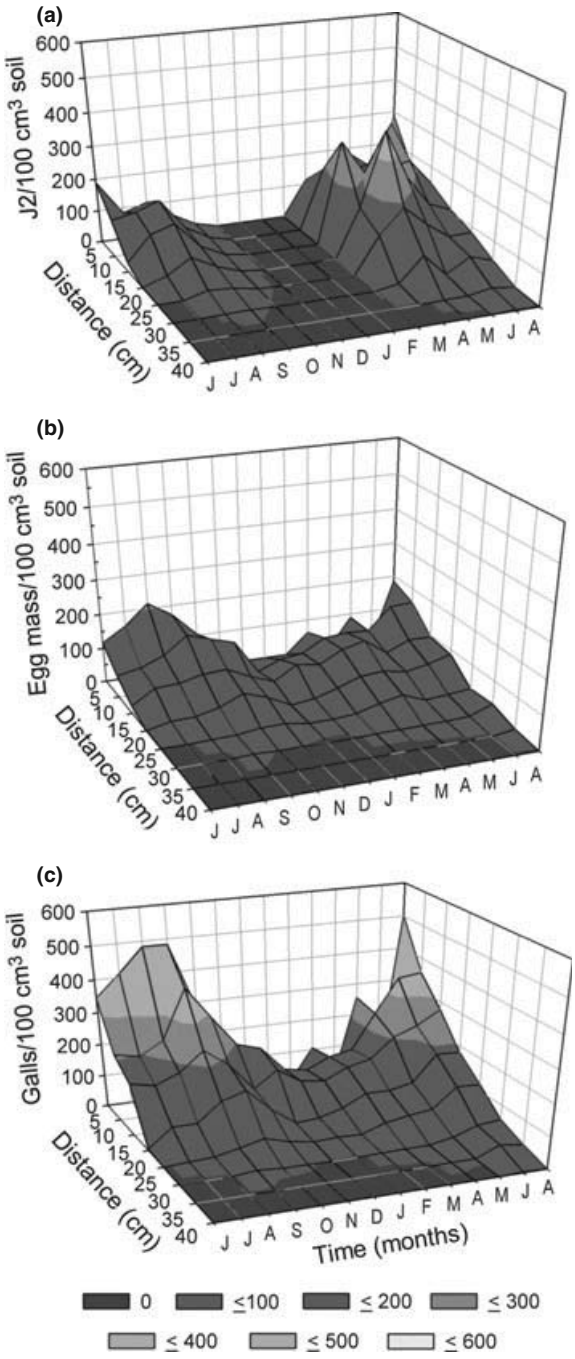

Figure 1 Mean number of root-knot nematode J2 (a), egg masses (b), and galls (c) per 100 cm^3 soil in transects across five patches of *Meloidogyne minor* sampled from June 2003 to August 2004. No samples were taken at 5 cm from November 2003 to February 2004, or during April and June 2004. Variance estimates are not included.

of galls with attached egg masses also varied seasonally (Table 2). There were two peaks, one in October–November 2003 and one in March–April 2004 (Fig. 2f). The November peak of 60% galls with egg masses was followed by a decline to 10% in December 2003. At other times the proportion of galls with egg masses was relatively constant (30–40%).

Table 1 Analysis of variance of the effect of distance from the centre of the *Meloidogyne minor* patch, sampling time and depth on numbers of J2 (10–25 cm from centre of the patch)

Factor	df	*F*	*P*
Depth	1	137·93	<0·001
Distance (from patch centre)	3	19·70	<0·001
Time	13	35·39	<0·001
Depth × Distance	3	1·94	0·124
Depth × Time	13	6·18	<0·001
Distance × Time	39	1·58	0·030
Depth × Distance × Time	39	0·45	0·995
Error	352		

Spatial distribution of J2

J2 density was strongly influenced both by soil depth and by distance from the centre of the patch ($P < 0{\cdot}001$, Table 1). There were more J2 in the upper core than the lower core at each sampling date and location. There was a significant depth × time interaction ($P < 0{\cdot}001$). Usually, there were 2–4 times as many J2 in the upper core as in the lower core, but in March 2004 the difference was tenfold (Fig. 2c).

The number of J2 per core tended to decline towards the edge of the patch (Fig. 1). The exact pattern varied over time (distance × time, $P < 0{\cdot}03$; Table 1). A steady decline from centre to edge was evident in some months (e.g. August 2004; Fig. 3a), while in others the highest number of J2 occurred at 10, 15 cm or 20 cm from the patch centre, and then declined towards the patch margin. For example, in August 2003, J2 were most abundant at 10 cm from the patch centre (Fig. 3a). The area within which J2 were recovered increased in radius over the sampling period from 15 cm in June 2003 to a maximum of 40 cm in June 2004 (Fig. 1).

Spatial distribution of galls and egg masses

As for J2, numbers of galls and egg masses were high in the centre of the patch and declined towards the edge (Fig. 1). Numbers were also higher in the upper than in the lower core throughout the patch (data not shown). There was a significant depth × distance interaction for both galls and egg masses ($P < 0{\cdot}001$; Table 2): the decline in numbers from the centre of the patch was steeper in the upper than in the lower core (Fig. 4a,b). The proportion of galls with attached egg masses was influenced by distance but not by depth (Table 2); from 5 to 20 cm from the patch centre, at least 40% of galls had attached egg masses, but this declined to <5% at 35 cm (Fig. 4c), where new galls were forming. Figure 3 shows the spread of the infestation over a 1-year period. In August 2003, galls and egg masses were

Table 2 Analysis of variance of the effect of distance from the centre of the *Meloidogyne minor* patch, time and depth, on numbers of galls per core, numbers of egg masses per core, and percentage of galls with egg masses (data from 10 to 25 cm along radius of the patch)

		Galls		Egg masses		Percentage of galls with egg masses	
Factor	df	*F*	*P*	*F*	*P*	*F*	*P*
Depth	1	393·16	<0·001	220·26	< 0·001	1·16	0·282
Distance (from patch centre)	3	152·08	<0·001	96·1	< 0·001	13·54	< 0·001
Time	13	20·12	<0·001	12·45	< 0·001	12·04	< 0·001
Depth × Distance	3	21·62	<0·001	11·63	< 0·001	0·77	0·846
Depth × Time	13	5·09	<0·001	2·91	< 0·001	2·05	0·106
Distance × Time	39	2·08	<0·001	1·38	0·069	1·72	0·054
Depth × Distance × Time	39	0·87	0·694	0·61	0·969	0·99	0·492
Error	448						

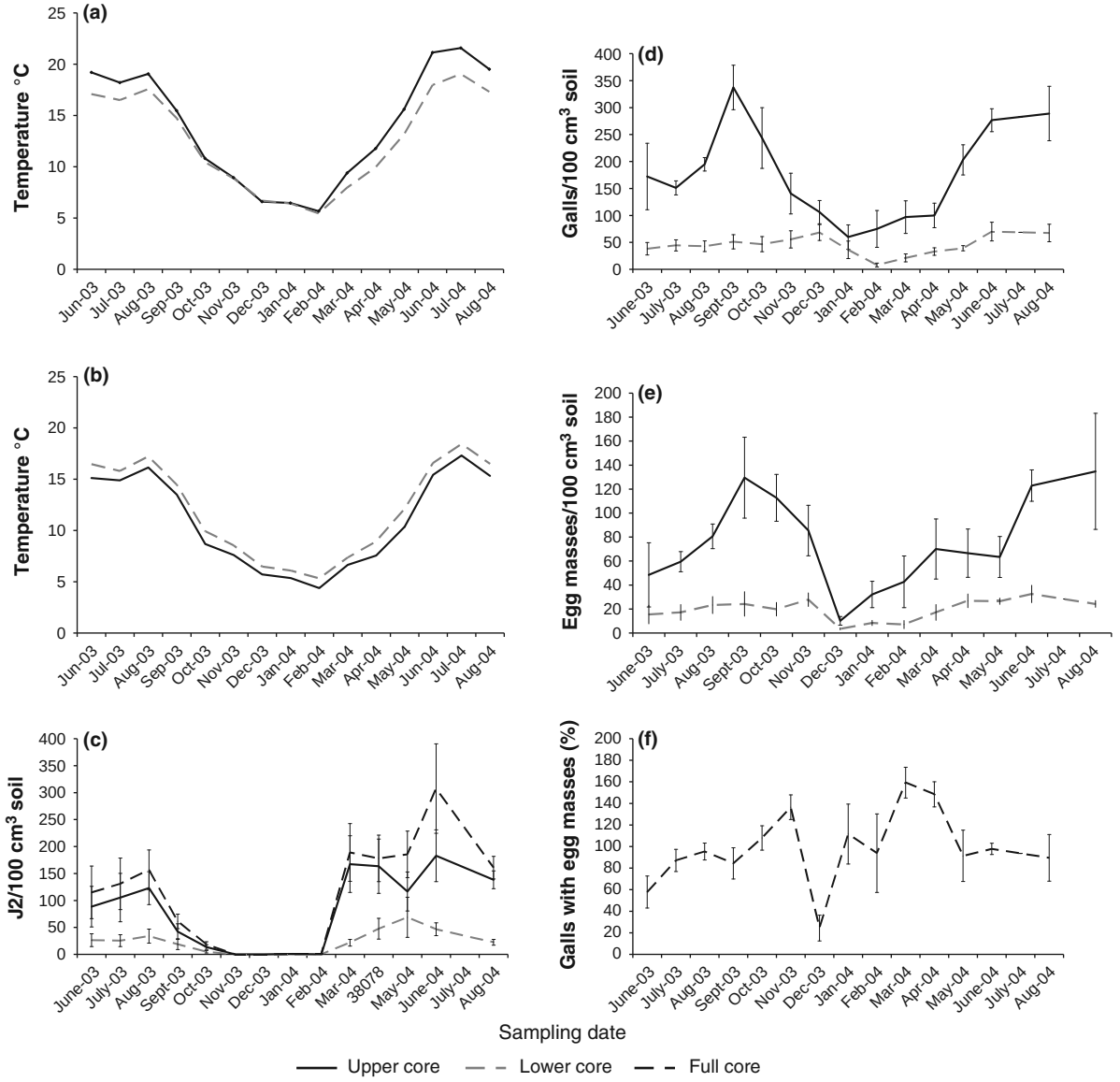

Figure 2 Seasonal changes in number (mean ± SE) of root-knot nematodes in cores taken 10 cm from the centre of *Meloidogyne minor* patches from June 2003 to August 2004. (a) Mean daytime temperature at two soil depths; (b) mean night time temperature at two soil depths; (c) J2 per 100 cm^3 soil; (d) galls per 100 cm^3 soil; (e) egg masses per 100 cm^3 soil; (f) percentage of galls with egg masses. Number of patches per month = 5. (c–f: mean (±SE), upper core = 0–10 cm deep, lower core = 11–20 cm deep, full core = 0–20 cm deep).

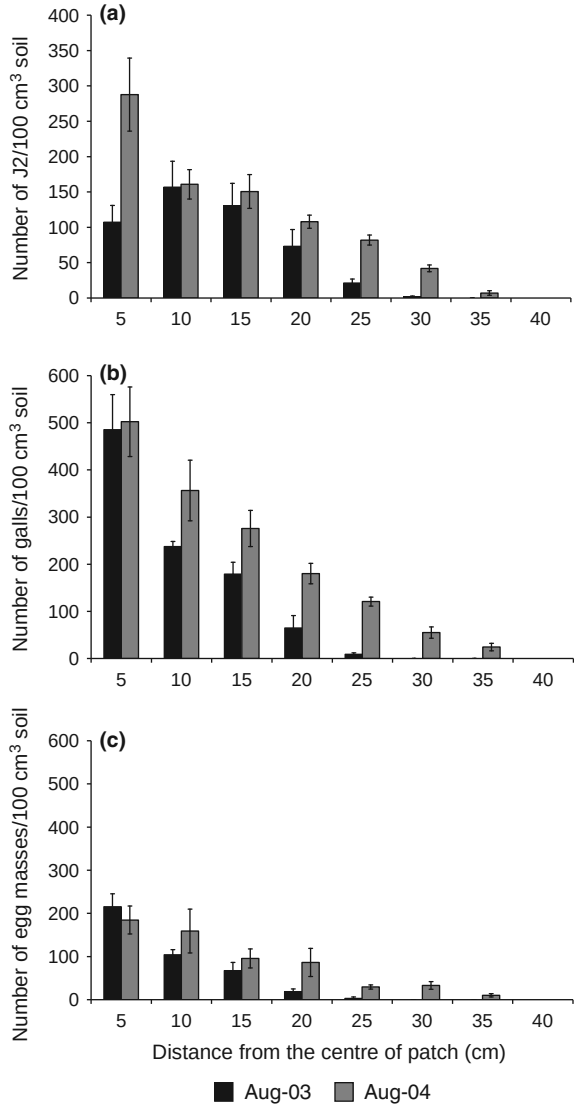

Figure 3 Horizontal distribution of *Meloidogyne minor* across patches sampled in August 2003 and August 2004. Mean (±SE), (a) J2, (b) galls and (c) egg masses per 100 cm^3 soil (n = 5).

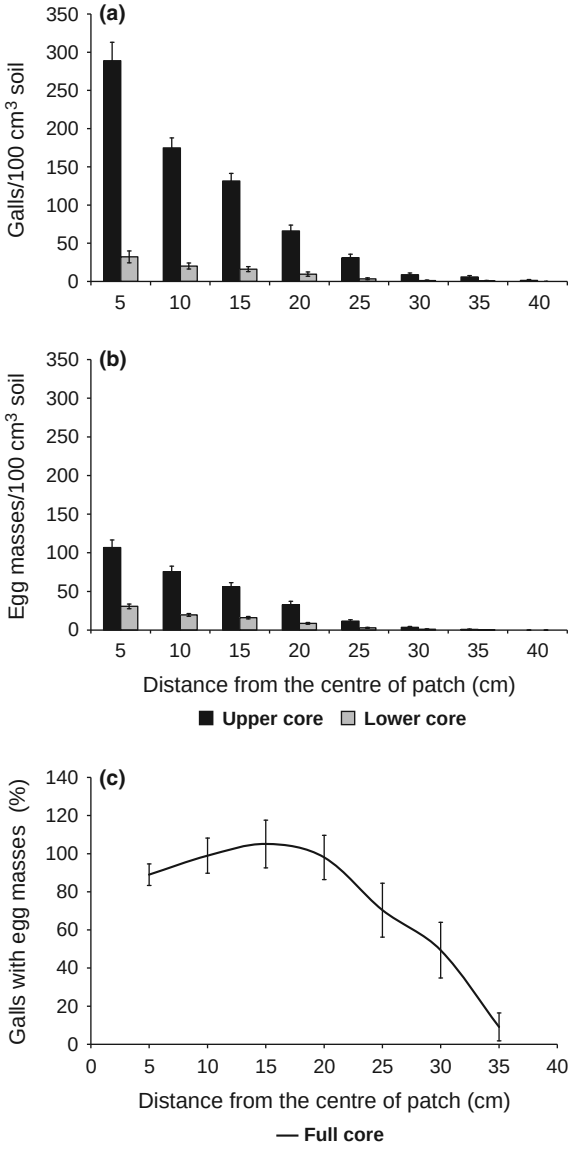

Figure 4 Horizontal distribution of *Meloidogyne minor* at two soil depths across five replicated patches of infested turfgrass. Points show mean (±SE) values of galls (a) and egg masses (b) per 100 cm^3 soil, and the percent of galls with eggs (c), for the period June 2003–August 2004 (upper core = 0–10 cm, lower core = 11–20, full core = 0–20 cm).

recorded at a maximum of 25 cm from the centre of the patch. By August 2004 this had increased to 35 cm (Fig. 3b,c).

Relationship between *Meloidogyne* and visible symptoms

Visible symptoms (primarily yellowing of the grass) could only be seen in the warmer months of the year, when the grass was actively growing. At these times, the diameter of the yellow patch was measured. The patch nearly doubled in size over the 15-month study period, from an average diameter of 23·7 cm in June 2003 to 45·2 cm August 2004 (Table 3). The gall density at the visible patch margin (estimated by linear interpolation from values shown in Table 3) was 159 to 194 galls per 100 cm^3 soil in most months, but was lower in August of both years (108 and 150 galls per 100 cm^3 soil in 2003 and 2004, respectively). Throughout this study there was no evidence for a recovery in turf quality.

Discussion

Plants infested with *Meloidogyne* show stunted growth, wilting, and discoloured foliage (chlorosis; Karssen &

Table 3 Extent of visual symptoms caused by *Meloidogyne minor* over 15 months, and number of galls per 45 cm^3 core at the perimeter of the symptom patch (estimated by linear interpolation between adjacent sampling points)

Sampling time	Diameter of visible symptoms (cm, mean ± SE)	Estimated number of galls at perimeter of visible symptoms
June 2003	23·7 ± 0·51	88·0
July 2003	27·9 ± 1·43	72·1
August 2003	34·2 ± 1·21	49·1
September 2003	35·9 ± 1·49	78·1
October 2003	32·0 ± 2·23	80·0
June 2004	41·3 ± 1·62	79·4
August 2004	45·2 ± 1·63	67·8

Moens, 2006). The above-ground symptoms are similar to those caused by a variety of pathogens and nutritional deficiencies; in the case of *Meloidogyne*, these are explained by the nematodes affecting water and nutrient uptake and translocation by the root system, and interfering with the rate of photosynthesis in leaves (Karssen & Moens, 2006). Root systems may show deformities, most notably the characteristic galls caused by the endoparasitic females.

Meloidogyne minor may result in extensive turf loss when combined with other severe stresses (Fleming *et al.*, 2006), but even the visual symptoms and reduced quality of infested patches have a significant effect on high value turfgrass. When referring to the visible symptoms caused by *M. minor,* Karssen *et al.* (2004) stated that 'on affected greens the patches appeared in new positions each season'. While it is true that new patches may appear, this study shows that symptom patches that are visible in one season reappear in the same location next season, and that the patch of nematodes remains throughout the season. Over a year, visible patches can nearly double in size. Between 159 and 194 galls per 100 cm^3 soil were located at the margin of the visible symptoms in most months, indicating that this could be the usual threshold level for these symptoms. There were fewer galls at the patch margin in August of each year, suggesting a lower damage threshold at this time of year. This may be attributed to a combination of increased numbers of egg masses and active egg laying putting an increased demand on the plant (Karssen & Moens, 2006). The visible symptoms were less distinct during the winter months when the *M. minor* population is lower.

While *M. minor* is the main root-knot nematode causing problems on golf greens, *M. naasi* has been found together with *M. minor* on golf greens (Karssen *et al.*, 2004; Lammers *et al.*, 2006; Viaene *et al.*, 2007). Detailed morphological examination of J2 from 10 affected patches (including the five patches used in the present study) on the golf course where this study took place confirmed that *M. minor* was present in all of them, and that *M. naasi* was present as an additional minor component in one. In routine checks on samples of recovered J2 throughout this study, all examined specimens conformed to the description by Karssen *et al.* (2004). Esterase patterns on a sample of females detected *M. minor* but not *M. naasi* (Morris, 2008). While the possibility that some of the *Meloidogyne* in the study was *M. naasi* cannot be excluded, the above evidence indicates that the vast majority was *M. minor*.

This is the first study to document the spatial and temporal distribution of *M. minor*. Both galls and egg masses were present on bentgrass roots throughout the year. These tended to be more abundant in late summer and early autumn (up to 502 galls per 100 cm^3 soil). Following a peak in September 2003, numbers declined steadily until January 2004, presumably due to the death of the previous year's generation. The gradual increase in the number of galls from February to April and the more dramatic increase in the proportion of galls bearing egg masses in March could be due to the nematodes that had entered roots in the autumn maturing and producing egg masses. The larger galls seen in May could have resulted from the invasion of newly hatched J2 from March onwards. There may thus be two generations of *M. minor* females co-existing: one that resulted in the appearance of J2 from March, and another that developed from those J2. *Meloidogyne* species typically have many generations, though some species such as *M. naasi* may have only one (Karssen & Moens, 2006). Factors including food availability and temperature affect the number of generations per year. For example, in England *M. naasi* completed only one generation per year on wheat, but it was able to complete a second on perennial ryegrass (Franklin *et al.*, 1971). Turfgrass, managed as a perennial crop, provides a constant source of food for nematodes (Crow, 2005). The development of *M. minor* from egg mass to egg mass can take place in 12 weeks at 15–20°C (Fleming *et al.*, 2006), which would allow for a complete generation to develop during the summer months.

Meloidogyne minor J2 were absent from soil between November and February, despite the constant availability of egg masses from which J2 hatched when incubated at 20°C (Morris *et al.*, 2011). A large number of hatched J2 was present in March, when average daytime temperatures at a depth of 10 cm approached 10°C. As this is the average, temperature at this depth would have exceeded 10°C some of the time. Moreover, temperatures in the upper few centimetres of soil are normally higher, and many of the egg masses were located there. These field data correspond to the results of constant temperature experiments that indicate that the minimum temperature for *M. minor* hatch lies between 10 and 15°C (Morris *et al.*, 2011). The majority of *M. minor* was found at a depth of 0–10 cm in the soil, rather than 11–20 cm. The vertical distribution of plant parasitic nematodes is influenced by root distribution (Barker & Imbriani, 1984). The tendency for more nematodes to occur in the upper core may be explained by the greater mass of roots present at this depth compared to 11–20 cm. Usually, there were 2–4 times as many J2 in the

upper core, but in March 2004 the difference was tenfold. In March, mean daytime temperatures had reached 10°C at a soil depth of 10 cm but not at 20 cm.

While not specifically designed to aid in prediction or control of the pest, the findings here lead to some preliminary recommendations. The timing of application is important for control measures that target J2, such as mustard-based soil amendments (Fleming *et al.*, 2008). The onset of J2 hatch in spring can be predicted by monitoring soil temperature; when soil temperatures reach 10°C, control agents could be applied. It was found that J2 numbers in the soil remained high for most of the year, without the summer decrease seen in some studies and associated with massive root invasions (Franklin *et al.*, 1971; Belair, 1998). This suggests that reproduction and root invasion rates are in balance for much of the year. As an alternative to the expense of repeated widespread application, the discrete and visible nature of root-knot induced damage lends itself to targeted application. Although symptoms are not obvious throughout the year, it should be possible to adapt methods from precision agriculture (Wrather *et al.*, 2002; Starr *et al.*, 2007) to locate patches in the summer and target application to these areas during the following spring.

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