Eur J Plant Pathol (2008) 120:249–257
DOI 10.1007/s10658-007-9213-x

FULL RESEARCH PAPER

Vertical distribution of the plant-parasitic nematode, *Meloidogyne chitwoodi*, under field crops

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Received: 13 April 2007 / Accepted: 9 August 2007 / Published online: 1 September 2007

Abstract The root-knot nematode *Meloidogyne chitwoodi* is a severe pest on sandy soils in Belgium and causes quality damage to economically important crops such as carrot, potato and black salsify. Pre-planting soil sampling to detect infestations has proven useful to farmers when taking decisions on the crop rotation. To develop an adequate sampling strategy, the vertical distribution of *M. chitwoodi* was examined under summer barley, carrot, fodder beet, bean, marigold and black fallow on two fields with a sandy soil. Soil samples were collected at monthly intervals from April 2004 to April 2006. Cores were taken to a depth of 70 cm and split into 10 cm segments. Nematodes were extracted by zonal centrifugation. Fodder beet increased the population of *M. chitwoodi* immensely; carrot was also a good host. Barley was a moderate host and under bean and marigolds the population decreased. The relative distribution of *M. chitwoodi* over the different soil layers during two successive years was consistent in each field. The different successions with good, moderate and poor hosts did not influence this distribution significantly. A logistic model was fitted to the mean cumulative percentages of nematodes at increasing soil depth. Farmers are advised to take soil samples for detection of *M. chitwoodi* immediately after harvest, especially after crops with a long field period. Adapting the depth of the cores taken to the vertical distribution of the population can increase the chances of detection. Our results suggest that this distribution is persistent in crop rotations and depends on field characteristics.

Keywords Crop rotations · Host plants · Population dynamics · Root-knot nematodes · Soil sampling

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Introduction

The root-knot nematode, *Meloidogyne chitwoodi*, was first described by Santo et al. (1980). It has a wide host range (Santo et al. 1980; O'Bannon et al. 1982; Ferris et al. 1993; Brinkman et al. 1996) and causes severe damage to economically important crops such as potato, black salsify and carrot. In 1998 *M. chitwoodi* was listed as quarantine pest in the EU. *Meloidogyne chitwoodi* has multiple generations during a crop-growing season and can build up to high population levels; however, the population

decreases markedly during winter and under fallow (Noling and Becker 1994; Pinkerton et al. 1991). The nematode became a major problem in the culture of field vegetables for the food canning industry in the Belgian provinces of Antwerp and Limburg (Waeyenberge and Moens 2001). Farmers need to prove, through soil sampling, that their fields are free of *M. chitwoodi* before a contract for growing carrots or black salsify is given to them. In general, fields are sampled between December and March to a standard depth of 25 cm. Crops grown on fields declared free of *M. chitwoodi*, based on these sampling practices, were sometimes severely damaged. The presence of nematode populations below detection levels, and extensive sampling and nematode extraction errors, can be a reason for non-detection. However, it is also possible that damage was caused by nematodes originating from soil layers deeper than 25 cm. Nematodes can migrate towards the roots of a host plant and deep-rooting crops can reach soil layers with a higher density of nematodes. Johnson and McKeen (1973) found that a population of *M. incognita* situated at a depth of 120–125 cm was able to induce galls on tomato roots that were present in the top 15 cm of a sandy loam glasshouse soil. Pinkerton et al. (1987) found that *M. chitwoodi* migrated 30 cm upwards and the recovered J2 were able to penetrate tomato plants. The authors did not observe a difference in migration in the presence or absence of a suitable host. In a vineyard in California, juveniles of *Meloidogyne* spp. were detected in relatively high numbers 120 cm below surface and still occurred at 330 cm depth (Ferris and McKenry 1974). Although Mojtahedi et al. (1991) showed that only a small fraction of the *M. chitwoodi* population in a potato field migrated upwards and remained infective, this migration was sufficient to cause significant damage to potato tubers in the field.

The objective of this work was to examine the importance of the vertical distribution of *M. chitwoodi* for their detection by soil sampling in rotations with field-grown vegetables. The population density of *M. chitwoodi* in different soil layers was monitored on two fields naturally infected with *M. chitwoodi* during two successive years. The host status of summer barley, carrot, fodder beet, bean and marigold, and the distribution of *M. chitwoodi* at different depths in these field-grown crops are discussed in order to improve sampling schemes.

Materials and methods

Pre-sampling

Based on sampling results provided by the Flemish Diagnostic Centre for Plants, Merelbeke, Belgium, two fields (sandy soil, organic matter: 2.3–4%, pH: 5.2) naturally infected with *M. chitwoodi* were selected. *Meloidogyne chitwoodi* was the only species of root-knot nematodes present in the fields. Other plant-parasitic nematodes present included *Pratylenchus crenatus*, *Pratylenchus penetrans*, *Tylenchorhynchus* spp. and *Rotylenchus* spp. In each of the fields the experiments were established in the area with the highest *M. chitwoodi* infection as established by preliminary soil sampling.

Crops and field characteristics

On both fields, maize (*Zea mays*) and summer wheat (*Triticum aestivum*) were cultivated in 2002 and 2003, respectively. The succession of crops used for experimentation on both fields is shown in Table 1. Preliminary tests under glasshouse conditions showed that carrot (*Daucus carota* cv. ABK) was a good host, bean (*Phaseolus vulgaris* cv. Polder) a poor host and marigold (*Tagetes patula* cv. Single gold) a non-host for *M. chitwoodi*. Fodder beet (*Beta vulgaris*) and barley (*Hordeum vulgare*) are considered as moderate

Table 1 Succession on the fields selected for data collection

	Host	Sowing date	Harvest date
Field 1			
2004	Summer barley, *Hordeum vulgare* cv. Prestige	8th April	12th August
2005	Carrot, *Daucus carota* cv. ABK	28th April	13th September
Field 2			
2004	Fodder beet, *Beta vulgaris* (cv. unknown)	12th April	24th November
2005	Bean, *Phaseolus vulgaris* cv. Polder	26th May	3rd August
	Marigold, *Tagetes patula* cv. Single gold	3rd August	9th November (mulched + incorporated)

to good hosts (O'Bannon et al. 1982; Ferris et al. 1993).

The fields were ploughed in the first week of April 2004 and the second week of April 2005 and April 2006. In between crops the fields were manually kept weed free (black fallow). Fertilization, pesticide applications and irrigation were according to farmers' usual practice.

Data on the mean monthly air temperature were obtained from the Royal Dutch Meteorological Institute (KNMI). The temperature was recorded in a thermometer shelter located at the weather station of Eindhoven, 35 and 36 km from the experimental fields. No data on soil temperatures or rainfall were collected.

Experimental design and sampling

In each field an experimental plot of 20×2 m was set out. From 14 April 2004 to 27 April 2005 stratified soil samples were taken every 3 weeks, then every 4 weeks. At each sampling date, 15 soil cores (2.5 cm diameter, 70 cm depth) were taken along the plant rows. From 14 April 2004 to 27 April 2005 five replicates were taken, thereafter 4. Each core was divided into seven segments of 10 cm. For each replicate, the 15 segments from corresponding depths were pooled.

Sample processing

Each soil sample was thoroughly mixed and a 200 g sub-sample was taken. Roots were separated from the mineral soil fraction by washing the sub-sample through an 850 μm sieve; the mineral soil fraction that passed through the sieve was collected in a 1 l beaker. Roots and soil particles that were retained on the sieve were washed from the sieve into a beaker and stirred. After 3 s without stirring, during which the soil particles settled to the bottom, the suspension was poured onto a 250 μm sieve so that the roots, but not the soil particles, were collected. If present, stems and leaves were removed. The root fraction was blotted, weighed and then macerated for 1 min at high speed with a commercial Waring blender.

Nematodes were extracted from both the organic and mineral soil fractions with an automated zonal centrifugal machine (Hendrickx 1995). This machine follows the principles of conventional centrifugation but the process is fully automated. After extraction the nematodes were collected in a glass beaker. Nematodes from mineral and organic fractions were pooled after extraction.

Nematode counts

Juveniles and adults of *M. chitwoodi* were counted. Eggs were not counted because of the presence of other plant-parasitic nematodes. Eggs could not be distinguished from each other based on their morphology. Nematode eggs look the same irrespective of the size of the adult (Perry 2002) and therefore we could not measure their abundance and focused on the motile hatched stages and adults. The results were expressed as nematodes per 100 g soil.

Host plant status

To determine the host plant status, the nematode counts of the sampling dates closest to the sowing and harvest of the different crops represented the initial (Pi) and the final (Pf) populations respectively.

Statistical analysis

The total number of *M. chitwoodi* juveniles and adults per soil layer were expressed as % of the total number found in the soil profile between 0 and 70 cm. A multifactor analysis of variance (ANOVA) was carried out to determine the effect of sampling date, soil layer and the interaction between both on the total % nematode values.

The mean cumulative % of *M. chitwoodi* were fitted to the logistic model $Y = 100/(1 + \exp(-b \times (d - m)))$, where Y is the cumulative % *M. chitwoodi* at soil depth d, 100 is the total cumulative % over all soil layers (100%), b is the slope of the curve, and m is the soil depth where 50% cumulative % of nematodes is obtained. For the statistical analyses Statistica 7 was used.

Results

Plant growth and development

There were no visible above-ground symptoms in either of the crops. Root galls were detected on the

roots of barley, fodder beet and carrot. At harvest time, 15% of the carrots showed severe quality damage on the tap-root, but the size or weight of the roots were not different from uninfected carrot roots (data not shown). Fresh roots were found up to 70 cm depth under summer barley, fodder beet and carrot and up to 60 cm depth under bean and marigold. From the middle of the fallow periods until the following crop, roots were limited to the first 50 cm.

Host plant status

Figure 1 shows the mean total numbers of *M. chitwoodi* (juveniles + adults) found in the examined soil profile from 0 to 70 cm depth and the mean air temperature at Eindhoven (source: KNMI, The Netherlands) from spring 2004 until spring 2006. In field 1 the population of *M. chitwoodi* decreased during spring 2004. Under summer barley the population increased but did not reach the same numbers as in early spring. Under black fallow during the following autumn and winter the population decreased, but in spring 2005 a small peak appeared. Soon after this peak the numbers of *M. chitwoodi* continued to decrease, even after the sowing date of carrot. Under carrot the population increased near the end of the growing season and reached the highest numbers at the time of harvest. During the autumn of 2005 the level of nematodes stayed high but decreased in the following winter. In spring 2006 a peak appeared.

In field 2 the initial population greatly increased under fodder beet at the end of the summer 2004 but started to decrease before the harvest of the crop. In spring 2005 a peak appeared after ploughing. Afterwards the population decreased and this continued under bean and marigold.

To determine the host plant status of the crops, the population densities before sowing (Pi) and immediately after harvest (Pf) were compared for the different soil layers separately (Figs. 2 and 3). For summer barley Pf was lower than Pi in all soil layers. No nematodes were found after the harvest in the soil layers 50–60 and 60–70 cm. For carrot, Pf was considerably higher than Pi for the soil layers between 0 and 50 cm. In the layers from 50 to 70 cm no nematodes were found. In field 2 fodder beet gave a substantial increment in the population of *M. chitwoodi* in all soil layers except the layer 0–10 cm. The Pf for bean and marigold was lower than Pi in all soil layers except for the layers 50–60 and 60–70 cm in marigold.

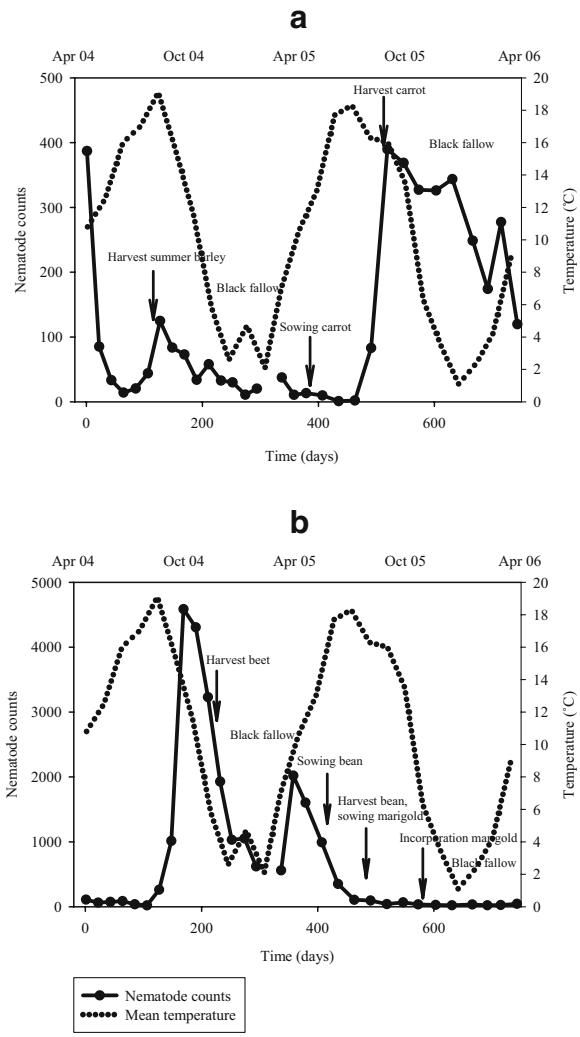

Fig. 1 Mean total numbers of *M. chitwoodi* (adults + juveniles) in the soil profile from 0 to 70 cm depth on field 1 (**a**) and field 2 (**b**) and the mean monthly air temperature. Day 1, the first sampling date, is 14 April 2004

Distribution of *M. chitwoodi* over different soil layers

The densities of *M. chitwoodi* for each soil layer separately for field 1 and 2 are shown in Fig. 4. In field 1 nematode densities were highest in the soil layer 10–20 cm under summer barley. After carrot the highest densities were present in the layer 20–30 cm. Ploughing in spring 2006 resulted in more nematodes in the layer 0–10 cm. In field 2 the highest numbers

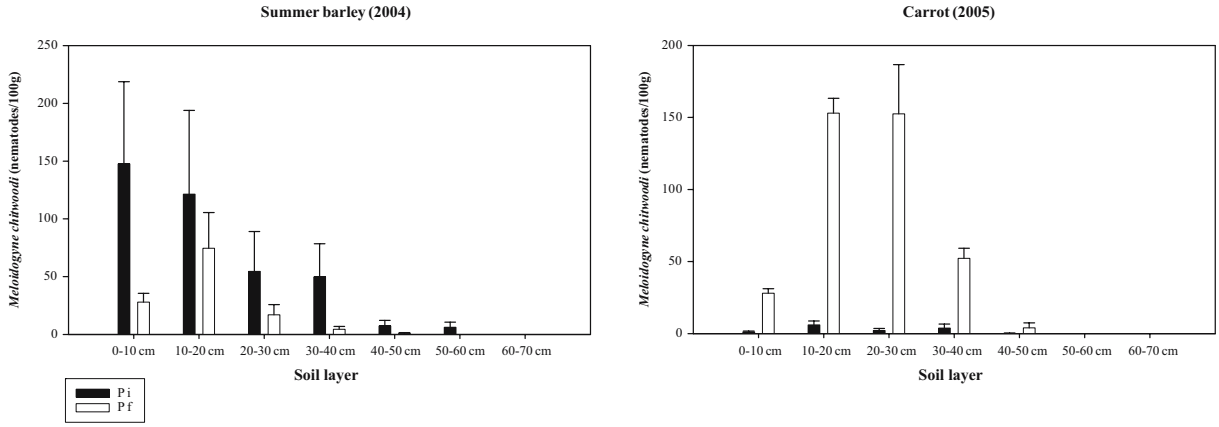

Fig. 2 The initial (Pi) and final (Pf) population per soil layer (means ± standard error) of *M. chitwoodi* for summer barley and carrot (different scales) on field 1

of *M. chitwoodi* were found in the layer 30–40 cm under fodder beet. After ploughing in spring 2005, layer 20–30 cm contained the highest number of nematodes. In both fields, in general, the nematode densities followed a similar pattern for all soil layers although there seemed to be a delay in the deeper soil layers. The multifactor ANOVA performed on the nematode counts per soil layer, expressed as %, did not show any significant effect of the sampling date (Table 2) for both fields. Based on the calculated *P* values of the F test, both soil layer and the interaction between soil layer and sampling date were

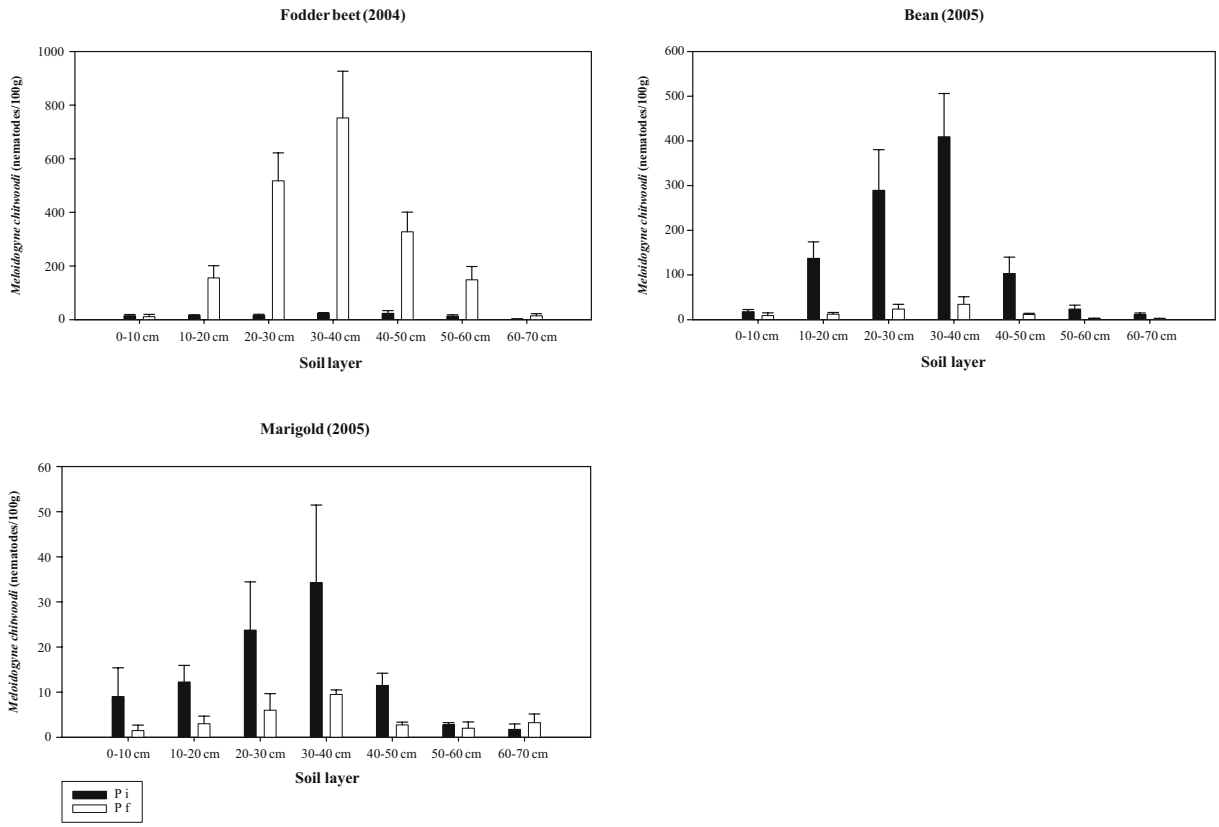

Fig. 3 The initial (Pi) and final (Pf) population per soil layer (means ± standard error) of *M. chitwoodi* for fodder beet, bean and marigold (different scales) on field 2

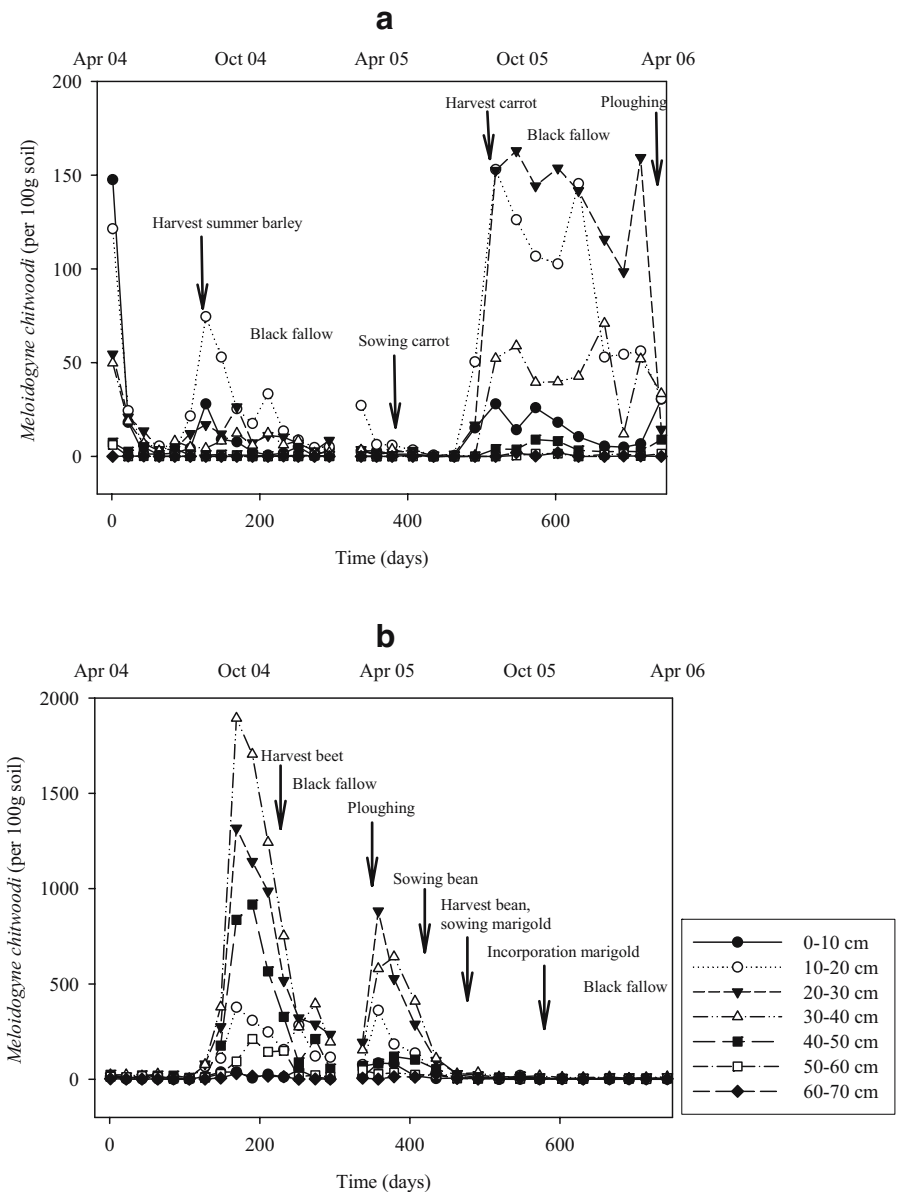

Fig. 4 The mean numbers of *M. chitwoodi* (adults + juveniles) per 100 g soil in different soil layers on field 1 (**a**) and field 2 (**b**). Day 1, the first sampling date, is 14 April 2004

significant sources of variation in nematode densities in both fields. However, the variance explained by the interaction was very small compared with the variance explained by the soil layer. Therefore, we concluded that increases and decreases in population densities of *M. chitwoodi* took place simultaneously in the different soil layers and that the % could be averaged over time for further analysis. The mean cumulative % of nematodes at increasing soil depth were described by a logistic model. Parameter *b* indicates the steepness of the slope and parameter *m* represents the required soil depth to detect 50% of the nematodes. Higher values of *m* indicate a deeper distribution of nematodes. Figure 5 shows the models for the different crops and intercrop (fallow) periods and the overall model for fields 1 and 2. The models for the crops and intercrop periods were calculated based on the sampling data collected between the sowing dates and the dates of harvest of the crops. The values of parameters *b* and *m* are shown in

Table 2 Significance of main and interaction effects of variables for the vertical distribution of *M. chitwoodi* in two infected fields under two different successions

Source of variation	*F* test	*P* value
Field 1		
Sampling date	0.138	1.000
Soil layer	164.064	0.000
Sampling date × soil layer	2.282	0.000
Field 2		
Sampling date	0.000	1.000
Soil layer	147.915	0.000
Sampling date × soil layer	2.099	0.000

Table 3. In field 1 soil sampling to a depth of 19.6 cm was required to detect 50% of the *M. chitwoodi* population. Parameter *m* was highest for the fallow period after carrot and lowest for the fallow period after summer barley. The slope of the curve (*b*) was highest for carrot and lowest for summer barley. In field 2 soil sampling to a depth of 33.5 cm was required to detect 50% of the *M. chitwoodi* population. Parameter *m* was highest in the fallow period after marigold and lowest in the fallow period after fodder beet. Parameter *b* was highest in the fallow period following beet.

Discussion

Preventive soil sampling to detect infestations with *M. chitwoodi* is very important to avoid quality damage to field-grown vegetables. The results from this study show that the relative distribution of *M. chitwoodi* over the different soil layers examined in two fields was consistent during two successive years. The different successions with good, moderate and poor hosts did not significantly influence this distribution. For each field a logistic model could be fitted to the cumulative %. Based on these models the required depth to detect a given % of the *M. chitwoodi* population could be calculated. In field 1 the distribution was shallower than in field 2. In the 2 years before the starting date of the in-depth soil sampling the same crops (maize and summer wheat) were grown in both fields. Therefore, the difference in vertical distribution in the two fields is most likely due to reasons other than crop rotation. Mojtahedi et al. (1991) found that the ability of *M. chitwoodi* to migrate and cause damage appeared to depend on soil texture. Soil with a higher silt and/or clay content may hinder the motility of root-knot nematodes (Prot and Van Gundy 1981). Although both fields were categorized as sandy soils, field 2 contained a greater sand fraction, the moisture level in each soil layer was higher compared to field 1, and the water table increased faster (data not shown). These features might enable *M. chitwoodi* to survive winter through migration and acclimation to greater depths. Our data showed no evidence of *M. chitwoodi* moving to deeper layers during colder spells.

Although increases and decreases in population densities of *M. chitwoodi* took place simultaneously in the different soil layers, we cannot conclude that no migration took place. Therefore, more knowledge is required about the number of eggs in the soil profile,

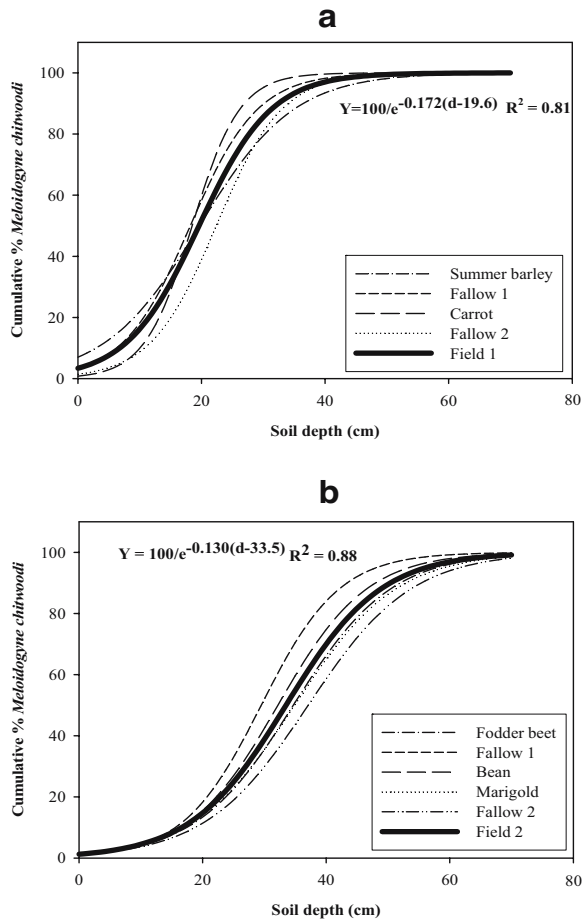

Fig. 5 The logistic models fitted to the cumulative % of *M. chitwoodi* present in the soil layers on field 1 (**a**) and field 2 (**b**). Explanation of model parameters in described in text (R^2 with $P<0.001$)

Table 3 Parameters of the logistic model $Y = 100/(1 + \exp(-b \times (d - m)))$fitted to the cumulative % of nematodes present in the soil layers, where Y is the cumulative % *M. chitwoodi* at soil depth d

	m	b
Field 1		
Summer barley	19.7±0.70	0.131±0.0116
Fallow 1	18.2±0.35	0.184±0.0111
Carrot	18.5±0.61	0.260±0.0417
Fallow 2	22.4±0.26	0.189±0.0084
Total model	19.6±0.23	0.171±0.0065
Field 2		
Fodder beet	34.7±0.43	0.127±0.0061
Fallow 1	29.5±0.35	0.158±0.0079
Bean	32.2±0.51	0.139±0.0089
Marigold	34.9±0.66	0.122±0.0087
Fallow 2	37.1±0.52	0.120±0.0066
Total model	33.5±0.24	0.130±0.0036

Means ± the standard error of the soil depth where 50% cumulative % of nematodes is obtained (m) and the slope of the curve (b).

their survival and the rate of hatch of juveniles. It is possible that migration of J2 was masked by continuous hatching. Starr and Jeger (1985) found that eggs are as important as J2 in winter survival of *M. incognita* and *M. arenaria*. They reported an increase in numbers of J2 during the early winter months while eggs and the total nematode population declined. Viable eggs were detected up to March. Pinkerton et al. (1991) reported that second-stage juvenile densities of *M. chitwoodi* after potato, declined through winter and increased slightly as soil temperatures increased in the spring. The decline continued soon after this peak. A similar pattern was recorded in our fields. The peaks in the population densities recorded in spring in both fields can be explained by hatching of juveniles from eggs. After these peaks the densities continued to decline. *Meloidogyne* species are obligate parasites and in the absence of a host their numbers decline. For summer barley and carrot the highest nematode numbers (adults + juveniles) were found immediately after harvest. However, in fodder beet, the number of *M. chitwoodi* decreased before the harvest date. The field period of summer barley and carrot is much shorter than that of fodder beet. The low temperature requirements of *M. chitwoodi* for reproduction (Griffin 1985; O'Bannon and Santo 1984) enable more generations to be formed on crops with long field periods. The later generations can be formed on crops that are starting to senesce. Wesemael et al. (2006) found that egg masses of *M. chitwoodi* collected from senescing tomato plants contained a % of unhatched J2 that required root diffusate to cause hatch and 6–10% remained unhatched. This pattern could be a reason for the decline of the population in fodder beet before the harvest date and the slow decline after carrot. Nematode eggs present in the soil and changes in the hatching of juveniles from eggs during the growing season and the successive fallow could have influenced our results. However, high aggregations of eggs in the soil (Been and Schomaker 2006) can result in great variation.

The activity and presence of plant-parasitic nematodes are correlated to the distribution of the root system (Ingham et al. 1985; Verschoor et al. 2001). The final population densities (Pf) we found were greatest in the soil layers corresponding to the highest root densities for summer barley, fodder beet and carrot but this did not change the relative vertical distribution. The cultivars of bean and marigold used in this work were poor or non-hosts. In crop rotations with poor or non-hosts and fallow in winter, the field period of host plants might be too short to influence the vertical distribution of a population of *M. chitwoodi* which is already established in the field. In monocultures it is more likely that the vertical distribution is closely related to the root system of the host plant. Rodríguez-Kábana and Robertson (1987) suggested a direct relationship between juvenile numbers of *M. arenaria* and the root density of peanut on light texture soil in a field that had been continuously cropped with peanut as a winter crop for 10 years.

Based on the results from the present work, we would advise farmers to take soil samples immediately after harvest, especially after crops with a long field period. Samples taken soon after harvest gave the highest detection for *M. chitwoodi*. This was also found by Been et al. (2002) in a potato field. As the time after harvest increases, the numbers of juveniles in the soil decrease and detection becomes more difficult. Incubation could increase the chances for detection of small population densities but is time-consuming and raises the costs. Detection based on the presence of juveniles and adults enhances the speed of diagnosis. Therefore, we suggest adapting the depth of the cores taken to the vertical distribution

of the population. Our results suggest that this distribution is persistent in crop rotations and dependent on field characteristics. However, a longer observation period of *M. chitwoodi* populations under different crop rotations and in fields with different soil characteristics is required to enable us to develop a better sampling strategy for the detection of this quarantine pest.

Acknowledgements The authors wish to thank E. De Smet, H. Van De Sype and M. Vermassen for their technical assistance during the collection of soil samples. P. Roost and W. Smeets are acknowledged for providing the fields and seeds used in this investigation and for their advice on the farmers' usual practice. We kindly thank Drs T. Been, C. Schomaker and R. Perry for their never ending support and advice. We thank the international growers associations BND and Rijke Oogst for funding this research.

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