A literature review of the root-knot nematodes (*Meloidogyne* species) that pose a threat to potato production in GB

Ref:11120024

Report Authors: Katy James (Harper Adams University), Matthew Back (Harper Adams University), Thomas Prior (Fera Science Limited)

Report No. 2019/11

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Summary points

- It is important to recognise the difference between *Meloidogyne* species in terms of their host range, impact on potatoes and geographical distribution. Not all *Meloidogyne* species present in GB attack potatoes. For example, *Meloidogyne naasi* (Barley Root-Knot Nematode) and *Meloidogyne artiellia* have not been recorded parasitising potato.
- There are four species of potential concern to GB potato growers: *Meloidogyne fallax* (False Columbia Root Knot Nematode – an A2 quarantine species), *Meloidogyne hapla* (Northern Root Knot Nematode) and *Meloidogyne minor* are pathogenic to potatoes and have been detected in UK soils. *Meloidogyne chitwoodi* (Columbia Root Knot Nematode - an A2 quarantine species) is also pathogenic to potatoes but has not been detected in the UK, although it is found in Belgium, Germany and the Netherlands.
- Awareness of *M. minor* and *M. hapla* nematode species by growers and agronomists and early identification and reporting of suspected infestations will provide a better understanding of the distribution and occurrence of these species. Without this it is difficult to prioritise the current threat posed by *Meloidogyne* species.
- Evidence from the European continent suggests that *M. chitwoodi* and *M. fallax* would constitute a significant threat should they become established, and as such, these species are listed as A2 quarantine pests.
- The most likely methods of introducing *Meloidogyne* species into a new geographical area are through infected soil or the movement of infected or contaminated plant material.
- Crop rotation is one of the most widely used control measures to suppress damage by, and population build-up of, *Meloidogyne* species.
- Correct identification of *Meloidogyne* species is important for the effective use of crop rotation as non-host crops may suppress one species but increase another.
- Preventative soil sampling in the Netherlands has reduced losses due to *Meloidogyne* species.
- Green cover crop fodder radish with partial resistance to *M. chitwoodi*, *M. fallax* and *M. hapla* have been developed and are used by farmers in the Netherlands and Belgium.
- There are some potato genotypes with resistance to *M. chitwoodi.* Not all potato genotypes show external symptoms of infection.

Glossary of terms

A2 quarantine species	Pathogens or pests with a limited distribution in the EPPO (European Plant Protection Organisation) region, presenting a risk of further spread.
Cortical cells	The outer layer of cells directly beneath epidermal cells
Dimorphic	Occurring in two distinct forms
Edaphic	Relating to the soil
Genotype	The genetic makeup of an individual organism. Within a species, there may be a variety of genotypes (*syn.* sub-groups or strains).
Isozymes	Enzymes with the same function by different structure. Isozyme patterns can be useful for distinguishing separate species.
Moult	Progress to the next life-stage
Parenchyma	Soft plant tissue, comprised of thin walled cells
Parthenogenetic	Reproducing asexually/ no requirement for males
Pathogenicity	Measure of the organisms' ability to cause disease
Rhizosphere	Zone around the roots
Vermiform	Worm like appearance

Background

The genus *Meloidogyne* (root-knot nematodes - RKN) contains some of the most damaging species of nematodes found in crops worldwide. To date, over 100 putative species of *Meloidogyne* have been described and their host range spans most vascular plant species (Jones *et al*., 2013). Although numerous *Meloidogyne* species are known to infect potato crops across the globe, less is known about their occurrence and potential impact in the UK. *Meloidogyne fallax* (False Columbia RKN – An A2 quarantine species), *M. hapla* (Northern RKN) and *M. minor* are pathogenic to potatoes and have been detected in UK soils. *Meloidogyne chitwoodi* (Columbia RKN - an A2 quarantine species), has not been detected in the UK, but is found in Belgium, Germany and the Netherlands (EPPO, 2018).

Root-knot nematodes are considered economically significant due to the stunted growth and yield loss to host plants resulting from infection, and reduction in quality of potato tubers. For example, species belonging to the *Meloidogyne chitwoodi*-lineage can cause defects to tubers such as external galling and internal necrotic spotting. Effective management of each species of *Meloidogyne* requires a clear understanding of the host range, lifecycle and preferred edaphic conditions.

In order to evaluate the threat posed by *Meloidogyne* species to GB potatoes, a review of published and grey literature was conducted for *M. chitwoodi*, *M. fallax*, *M. minor* and *M. hapla* to include the following: 1) Geographical distribution 2) Host plant range 3) Description of

organism 4) Life cycle variation between species 5) Symptoms on potatoes 6) Sampling and identification 7) Economic impact 8) Control methods.

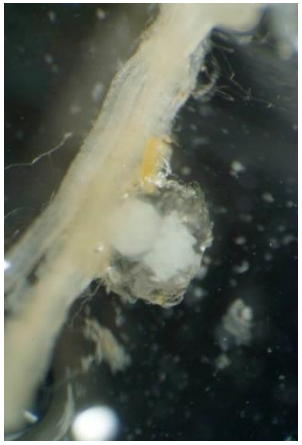
The review prioritises *Meloidogyne* species in terms of the risks that they pose to potatoes. *Meloidogyne chitwoodi* and *M. fallax* are considered first as they are quarantine organisms and highly pathogenic to potatoes. In contrast, *M. minor* and *M. hapla* are considered to be widespread in the UK. Actions to mitigate the risks that these species pose to potatoes are identified and discussed. Finally, the review considers knowledge gaps and how these should be best addressed.

Life cycle of *Meloidogyne* species

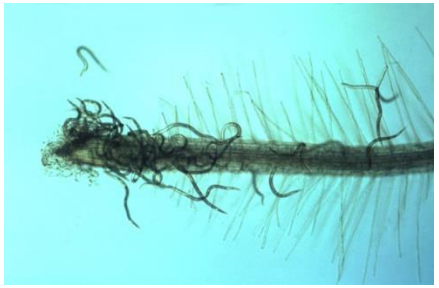
All root-knot nematodes are sexually dimorphic and follow a similar life cycle. Females are pear or sac shaped and males are vermiform in shape (Wale, Platt and Cattlin, 2008). First stage juveniles develop within the egg, and moult once to become second stage juveniles (J2) which hatch out of the egg and are vermiform and motile (Wale, Platt and Cattlin, 2008). Hatching is driven by temperature and moisture and in general occurs without requiring stimulus from plant roots, although root exudates can, in some cases, stimulate hatching (Karssen *et al.* 2013). When the J2 hatch, most species migrate through the soil and penetrate root tips through epidermal cells, wounds or entry sites of other juveniles and move into the cortical region (EPPO not dated). The J2 set up permanent feeding sites and injection of pharyngeal gland secretions stimulate parenchyma or cortical cells to become multinucleate and form giant cells, causing the surrounding root tissue to produce a gall (Moens *et al*., 2009; Mermans, 2015; Prior *et al*., 2015). These 'giant cells' serve as a source of nutrients for the developing nematode (Mermans, 2015). The J2 develop within the gall and if the root tip enlarges, root growth may stop for a period of time (Prior *et al*. 2015). Root galling is variable within the genus and plant hosts. The J2 swell, stop feeding, loose mobility and undergo three rapid successive moults to become adult males or females (EPPO not dated). The total time for the J3 and J4 stages is generally no more than 4–6 days, much shorter than that for the J2 or the adult (Moens *et al*., 2009). Males may be found in parthenogenetic species and generally only develop under unfavourable conditions for female development (e.g. high population densities), and when they do develop, they do not feed as adults (Moens *et al*. 2009). Any adult males produced leave the root and are found free in the rhizosphere or near the protruding body of the female. It is thought, that males are largely functionless and reproduction is nearly always parthenogenetic (EPPO not dated). Adult females are usually embedded within plant roots or tubers. Eggs are laid by the female in a gelatinous sac which is attached to the females' posterior. The egg masses may be seen on the surface of galled roots, or embedded within the gall tissue (Moens *et al*., 2009). In potato tubers, modified host cells form a protective layer around the egg mass and the juveniles as they hatch (Bay 2004; EPPO not dated, a).

Figure 1 (below). shows the generalised life cycle of *Meloidogyne* spp. in potato. Specific detail about the lifecycle of individual species and symptoms of infestation on potato roots and tubers are presented in each species section of this review.

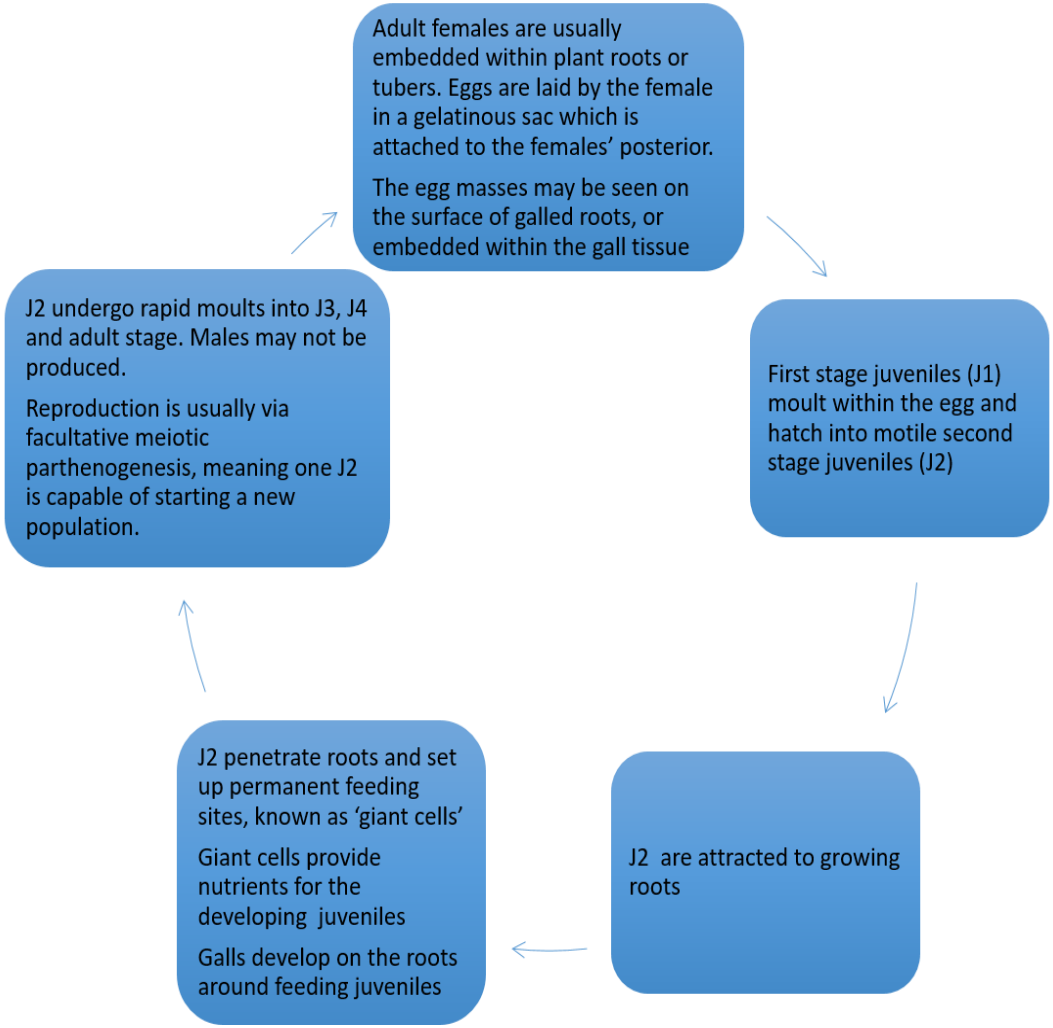
Figure 1. Generalised life cycle of *Meloidogyne* spp. in potato



Mature female and egg mass
(UK Crown Copyright - courtesy of Fera)



Infective J2 invading roots
(Courtesy of Nemapix)



Meloidogyne chitwoodi (Columbia root-knot nematode)

Geographical distribution

M. chitwoodi was first described in the USA in 1980, and is now present in many states in the USA (California, Colarado, Idaho, Nevada, New Mexico, Oregon, Texas Utah, Washington), Mexico, Argentina, South Africa and Mozambique (CABI/EPPO, 2012; EPPO Global Database, *M. chitwoodi*, 2018). The nematode was first detected in the European and Mediterranean region in the 1980s in the Netherlands. However, a review of old illustrations and specimens of *Meloidogyne* suggests that it may have been present as far back as the 1930s (Bay, 2004). In Europe, *M. chitwoodi* has been recorded in Belgium (NPPO of Belgium 2007, 2004; Waeyenberge and Moens 2001; Wesemael and Moens 2008 a,b; NPPO, 2007, 2014), France (NPPO of France, 2010, 2011, 2012, 2012; Gamon and Lenne 2012), Germany (Heinicke, 1993; Muller et al., 1996; NPPO of Germany 2005, 2011, 2011); Italy (CABI/EPPO, 2012), Netherlands (NPPO of the Netherlands, 2007, 2009, 2011, 2012, 2013, 2014, 2015, 2017), Portugal (Powers *et al*., 2005; da Conceiçao *et al*., 2007), Maderia (CABI/EPPO, 2012), and Sweden (NPPO of Sweden 2017). It is also present in Turkey (Ozarslandan *et al*., 2009).

M. chitwoodi may have a wider undetected distribution in Europe. Comprehensive surveys are required to obtain more data on distribution. To date, *M. chitwoodi* is not thought to be present in the UK.

Host range

M. chitwoodi has a wide host range, which includes weed species and economically important crops. Potato plants are a particularly suitable host species for the nematode (O'Bannon and Santo, 1984; Korthals *et al.,* 2001). Glasshouse experiments have shown that barley, corn, and wheat are also good hosts for *M. chitwoodi*, whereas lucerne is a poorer host, however, this depends on the putative race of *M. chitwoodi*, which is discussed below (O'Bannon *et al*., 1982; Mojtahedi *et al*., 1988). Other experimental studies have shown the following plants to be potential hosts for *M. chitwoodi*: oats, rye, quinoa, barley, *Poaceae* (grasses and weeds), sudangrass hybrids, sorghum-sudangrass hybrids, celery, *Arrhenatherum elatius*, sugar beet, borage, chicory, carrot, maize, buckwheat, *Festuca rubra*, tomato, lucerne, evening primrose, parsley, common bean, pea, salsify, tomato, radish, *Tagetes patula*, wheat and *Valeriana officinalis* (Griffin *et* al., 1982; O'Bannon *et al*., 1982; Mojtahedi *et al*., 1993; Goossens, 1994; Umesh and Ferris, 1994; Brinkman *et al*., 1996; Korthals *et al*., 2001; den Nijs *et al*., 2004; Wesemael and Moens, 2008b; Wesemael *et al*., 2011). In the Netherlands, host crops recorded to be attacked by *M. chitwoodi* are carrots, cereals, maize, peas, potatoes, salsify, sugarbeet and tomatoes (OEPP/EPPO, 1991). It should be noted that the host status of these plants/crops are often dependent on cultivar meaning that it is not always possible to make general statements about their susceptibility.

In the United States, different "host races" (Hartman and Sasser, 1985) have been described based on their host preference. Two putative races of *M. chitwoodi* are recognised: race 1 and race 2 which are distinguished with regard to their pathogenicity on Thor lucerne and Red Cored Chantenay carrot, with *M. chitwoodi* race 2 able to reproduce on lucerne but not on carrot and for race 1 lucerne was a poor host and carrots were suitable (Mojtahedi *et al*., 1988). Both races cause serious damage on potato and some isolates are able to reproduce on clonal selection PI275187.10 of wild potato species *Solanum bulbocastanum*, a source of resistance in breeding programmes (Mojtahedi and Santo 1994).

Currently, no valid evidence exists on the presence of different races in Europe (van der Beek *et al*., 1999) although there are indications of differences in the level of aggressiveness between different *M. chitwoodi* populations in Europe (Mermans, 2015). In general the concept of 'host races' is not fully accepted outside of the US, partly because it measured only a small portion of the potential variation in parasitic ability (Moens *et al*., 2009).

Little is known about the presence of M. *chitwoodi* in natural habitats (Wesemael *et al*., 2011) and it probably has a wider host range than presently known.

Description of organism

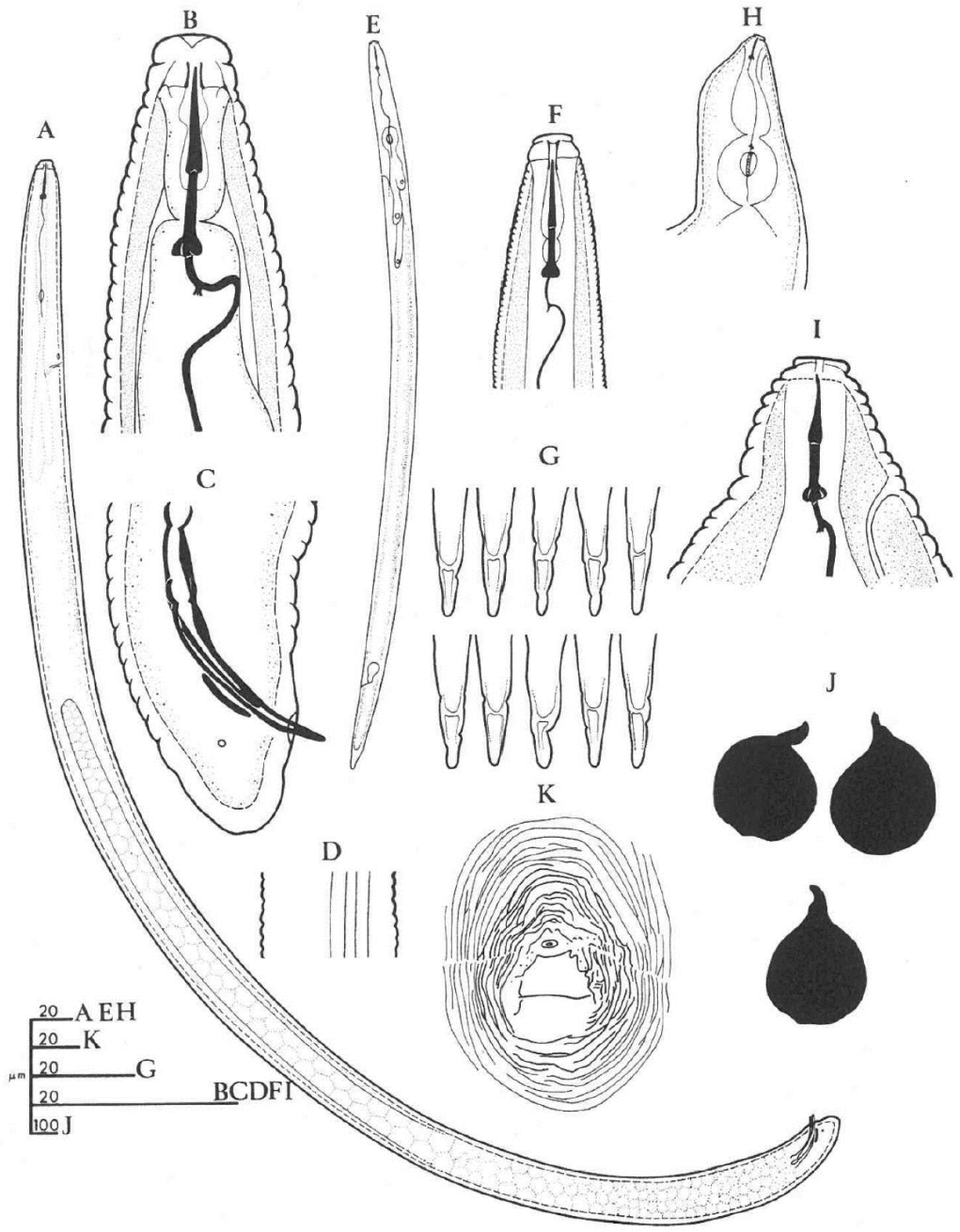


Figure 2. *Meloidogyne chitwoodi*. Male A: entire, lateral view; B: anterior, lateral view; C: posterior, lateral view; D: lateral field. Second stage juvenile E: entire, lateral view, F: anterior, lateral view; G: posteriors. Female H, I: anterior; J: entire; K: perineal pattern. After Jepson (1985), courtesy CAB International.

Adult males and the second-stage juveniles (J2) are vermiform, motile animals, similar in general appearance to free-living soil nematodes. The male is larger than the J2, has a slight taper at each end, and the tail is short and rounded, the stylet is larger than the females but similar in shape (Karssen *et al*., 2013).

The J2 have a conical tail that ends in a hyaline part with an acutely rounded tail tip. They are the only infective stage and similar to all plant-parasitic nematodes possess a stylet. The head is male-like but with a weakly sclerotized cephalic framework. The third- and fourth-juvenile stages possess no stylet and are swollen and sedentary inside the root where the nematode develops within the J2 cuticle (Karssen *et al*., 2013).

Females are sedentary and characteristically pear-shaped, pearly-white and have a short and slightly posterior protruding neck. The third and fourth juvenile stages are swollen and sedentary inside the root where the nematode develops within the J2 cuticle. These stages possess no stylet (Karssen *et al*., 2013).

M. chitwoodi and *M. fallax* are often found in mixed populations. Two of the main differences between *M. fallax* and *M. chitwoodi* include a longer stylet length in *M. fallax*, and the stylet knob is rounded and prominent in *M. fallax* as opposed to irregular and small in *M. chitwoodi*. These differences and a more in-depth description of the morphological characteristics of both nematodes are provided in EPPO (2016).

Life cycle

The life cycle of *M. chitwoodi* takes approximately 3-4 weeks under optimal conditions (Wesemael *et al*., 2006). Females are capable of producing up to 1000 eggs and *M. chitwoodi* usually reproduces by facultative meiotic parthenogenesis, which means that one second-stage juvenile is capable of starting a new population (Santo, 1989; van der Beek and Karssen, 1997; EPPO not dated, a).

M. chitwoodi can begin development when the soil temperature rises above 5 °C requiring 600–800 degree-days to complete the first generation, whilst subsequent generations require 500–600 degree-days (Pinkerton *et al*., 1991). This species, therefore, has a potentially high reproduction rate and ability to rapidly increase population levels in a single season. Baker and Dickens (1993) concluded from their pest risk analysis that *M. chitwoodi* would be likely to produce three generations per year in the UK. Brommer and Molendijk (2001) reported that there were at least two generations per year in fields naturally infected with *M. chitwoodi* in the Netherlands.

M. chitwoodi passes the winter as eggs or juveniles and whilst it can survive extended periods of sub-zero temperatures, low soil temperatures during the winter can reduce population densities (Tiilikkala *et al*., 1995; Thoden *et al*., 2012). As temperatures rise in spring the majority of eggs hatch. *M. chitwoodi* requires a temperature of at least 4°C for hatching and penetrating roots (shown for wheat, Inserra *et al*., 1985), and 6°C for development within potato plants (Charchar, 1997). Infectivity of J2 is correlated to food reserves stored in the intestine, which are consumed during periods outside of plant roots (Karssen *et al*. 2013). Khan *et al*. (2014) also investigated hatching, migration, invasion and post-penetration (on potato and maize) development of *M. chitwoodi* at 15, 20 and 25°C. Optimum temperature for hatching of J2 of *M. chitwoodi* was 20°C and no higher than 25°C. The authors also found that optimum temperature for migration was 20°C.

Wesemael *et al*. (2006) carried out comparative studies on the effects of tomato root diffusates and host age on *in vitro* hatching of *M. chitwoodi*. Hatching of J2 did not require host root diffusate stimulus which confirmed previous work by Inserra *et al*. (1983) and Perry (1997). At

the end of the plant growing season, however, egg masses contained a percentage of unhatched J2 that require host root diffusate to cause hatch. Wesemael *et al*. (2006) also found the number of eggs per egg mass of *M. chitwoodi* decreased with plant age.

Symptoms

Above-ground symptoms are often not obvious but may consist of varying degrees of stunting, yellowing, lack of vigour and a tendency to wilt under moisture stress, all leading to reduced yield (Prior *et al*., 2015). *Meloidogyne* infection is thought to affect water and nutrient uptake and upward translocation by the root system (Prior *et al*., 2015). Therefore, above ground symptoms are similar to those produced by any plant having a damaged root system that is not functioning correctly (Prior *et al*., 2015). The severity of these above ground symptoms is thought to be related to the number of juveniles penetrating and becoming established within the root tissue of young plants (Prior *et al*., 2015).

Potato roots may be infected, and the spherical bodies of females may protrude from the surface of small rootlets surrounded posteriorly by a large egg-filled sac which becomes dark-brown with age (EPPO not dated, a). On potato tubers, *M. chitwoodi* causes numerous small, pimple-like raised areas on the surface of most cultivars (Moens *et al*. 2009) (Figure 3). Internal potato tissue just below the skin can be necrotic and brownish (Figure 4) with adult females usually visible just below the surface, in the cortical layer, as white, pear-shaped bodies surrounded by a brownish layer, which is usually indicative of the presence of eggs (EPPO, 2006). However, potatoes often remain free from visible external symptoms, even though they are heavily infested, particularly in some cultivars (although none of the cultivars listed are grown in GB: Been *et al*., 2007; EPPO, 2006).

Figure 3. *M. chitwoodi* external potato tuber symptoms (UK Crown Copyright - courtesy of Fera)

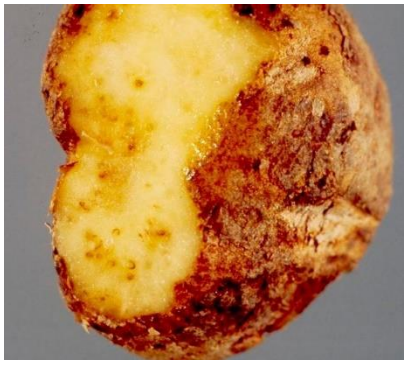


Figure 4. *Meloidogyne* infesting potato tuber (UK Crown Copyright - courtesy of Fera)

Sampling and identification

The following section discusses EPPO sampling and identification guidance for both *M. chitwoodi* and *M. fallax* which frequently occur in mixed infestations and are similar in terms of symptoms, distribution, life cycle and biology.

Sampling

Specific guidance on sampling of potato tubers, by which potato lots are tested to determine area freedom, place of production freedom and/or lot freedom for the detection of *M. chitwoodi* and *M. fallax*, is given in EPPO, 2006 Phytosanitary Procedure PM 3/69. In summary, after harvest 200 tubers are randomly sampled from the lot (typically 25t), the tubers are then processed using the visual method, inspected for symptoms after incubation, and nematodes extracted for diagnosis; or the isolation method, where mature females and/or other developmental stages are extracted for identification from tubers using standardised methods (EPPO 2013b PM 7/119 Nematode extraction).

Guidance for soil sampling is given in the EPPO 2013a National Regulatory Control System PM 9/17. This guidance specifies that it is important to get a representative sample and that detection of the nematodes through field inspection and soil sampling is more sensitive if done as close as possible to the time of harvest of a host crop. The guidelines suggest sampling hectare blocks in a grid pattern (10 x 10 m). Composite soil samples should be taken to a depth of 25cm and the volume of each core should be 40 ml. Plant health clinics (testing laboratories) are advised use a 200ml sub sample.

Identification

Identification is based on a combination of morphological/morphometric characteristics and biochemical or molecular methods (isozymes or PCR). Guidance on the extraction of nematodes for identification is given in EPPO 2013b PM 7/119 Nematode extraction. A flow diagram describing the diagnostic procedure for *M. chitwoodi* and *M. fallax* when found in soil, roots or tubers can be found in EPPO (2016).

Morphological/morphometric characteristics

Morphological characteristics can be used to differentiate between *Meloidogyne* species, but it is labour intensive and requires specialist experience and knowledge. It is recommended that for identification, biochemical techniques and/or molecular methods should be used in addition to morphology and morphometrics (EPPO, 2016). Detailed morphological characteristics for *M. chitwoodi* and *M*. *fallax* are given in EPPO (2016).

Biochemical methods

Reliable isozyme electrophoresis methods are available for the identification of single young egglaying *Meloidogyne* females, including *M. chitwoodi* and *M. fallax*. The method was originally developed by Esbenshade and Triantaphyllou (1985) and modified and adapted for PhastSystem, (an automated electrophorectic apparatus) by Karssen *et al*. (1995). Isozymes of glucose 6phosphate dehydrogenase (EC 1.1.1.49) are also useful to differentiate between (*M. hapla*), *M. fallax* and *M. chitwoodi* (van der Beek and Karssen, 1997; EPPO, 2016). Further detailed information about the isozyme electrophoresis method recommended by EPPO is available in EPPO (2016).

Molecular methods

PCR tests can be performed on all developmental stages of nematodes and multiplex PCR methods allow the detection of one or more species in a nematode mixture by a single PCR

test. EPPO recommend seven PCR molecular tests, which are detailed in full in EPPO (2016). Additionally, a portable field diagnostic kit, based on loop mediated isothermal amplification (LAMP), is being developed by Fera Science Ltd.

Economic impact

M. chitwoodi infection can reduce the yield of potatoes but this is rarely observed (EPPO, 2013a). The major impact is reduction in quality as a result of internal necrosis and external galling, which reduce market value. Necrotic spots in the flesh of tubers of as little as 5% of a crop can make it commercially unacceptable (EPPO, not dated, a).

There is little information on the economic impact on potatoes in Europe, however, the preventative soil sampling conducted in Belgium and the Netherlands to detect *M. chitwoodi* in potatoes and the costs associated with sampling and diagnostic analysis are likely to be compensated by the reduction of heavily infected and valueless crops (Wesemael *et al*., 2011). For example, prior to preventative soil sampling in the Netherlands 7% of vegetables harvested for the canning industry were rejected due to damage by root-knot nematodes, this was reduced to 1.5% in 2003 when soil sampling was implemented (Wesemael *et al*., 2011).

If *M. chitwoodi* is detected in the Netherlands, a radius of 1Km around the infected site is placed under quarantine. The crop will not be sold as seed potatoes but in general the grower will receive the average pool price of their trading company (Phaff Export Marketing, unpublished). Rejected seed potatoes may be treated using a steam machine and sold as ware potatoes after treatment, processed as starch potatoes or even processed as consumer products by approved processors (although this final option is uncommon) (Phaff Export Marketing, unpublished).

In The Netherlands, ca. 425 findings of *M. chitwoodi* or *M. fallax* were reported from plant lots and propagation material in the period between 1995 and 2016, the majority of which consisted of *M. chitwoodi* (Plant Protection Service, 2010 – 2017), indicating that despite the quarantine regulations imposed, the number of infestations is still increasing (Teklu, 2018).

In 1993, Baker and Dickens conducted a plant risk assessment for *M. chitwoodi*, and whilst they thought the nematode would be likely to produce three generations per year under UK conditions, they were not able to predict the potential economic impact of the pest, as this could depend on a number of other unknown factors such as soil wetness, varietal susceptibility and quality control thresholds.

Control

The most likely method of introducing *M. chitwoodi* into a new geographical area is through the movement of infected or contaminated planting material, as the nematode has very limited potential for natural movement (only second-stage juveniles can move in the soil and, at most, only a few tens of centimetres). Infected tubers can easily transport the nematode as both eggs and females survive and propagate in tubers, therefore seed potatoes are a primary challenge that needs to be met (Been *et al*., 2007).

The movement of non-host seedling transplants, nursery stock, machinery or other products, which are contaminated with soil, sand or gravel (including clothing, containers, packaging etc) infested with *M. chitwoodi* could also result in spread (EPPO, not dated, a). Infective larvae of this genus have been known to persist for more than one year in the absence of host plants. Nematode movement can also be facilitated by contaminated irrigation water or animals moving between fields (Wale, Platt and Cattlin, 2008).

Chemical Control

Nematicides are currently used in two major forms; fumigants and non-fumigants. Fumigants are phytotoxic and limited to pre-plant application. Non-fumigants can be used as pre-plant or post-harvest treatments to control nematodes in potato fields.

Whilst nematicides are able to reduce populations of *M. chitwoodi*, Teklu (2018) suggested that it is unlikely that densities below the threshold level for quality damage will be attained based on evidence in the literature (e.g. Griffin, 1985; Ingham *et al*., 2000; Hafez and Sundararaj, 2002; Runia and Molendijk, 2007). The damage threshold on potato for *M. chitwoodi* is: 1 J2/250 cm^3 soil (Santo *et al*. 1981); 10 J2/100 cm^3 soil (Norshie *et al*., 2011). Degree-day accumulation, however, is thought to be more important than density (Griffin, 1985). Tuber damage in potatoes may occur when soil temperatures exceed 1000 degree days above 5°C but the threshold for significant tuber damage is assessed to be about 1500 degree days above 5°C (Macleod *et al*., 2012). The drastic decline of soil fumigation in the last decades, used to control potato cyst nematodes (PCN), is thought to be one of the main reasons for the emergence of *M. chitwoodi* and *M. fallax* (Teklu, 2018).

Furthermore, EU legislation has led to a decline in nematicides and nematistats available. Those nematistats remaining (*e.g.* oxamyl, ethoprophos, and fosthiazate) reduce yield loss rather than reduce the final nematode population. Teklu (2018) hypothesised, therefore, that with the current trend to try and phase out many actives, it is not likely that chemical crop protection will be a major part of a future management system for *M. chitwoodi*.

Novel chemical approaches, as potentially safer alternatives to nematicides, include laboratory experiments using essential plant oils (e.g. essential oils isolated from *Dysphania ambrosioides*, *Filipendula ulmaria*, *Ruta graveolens*, *Satureja montana* and *Thymbra capitate*) to inhibit *M. chitwoodi* hatching which have had some positive results (Faria *et al*., 2016). However, further work is needed to test the practicality of these options, such as assessing their phytotoxicity to the crop (Faria *et al*., 2016).

Crop rotation

Options for controlling *M. chitwoodi* through crop rotations are limited due to its wide host range. Winter fallow can reduce populations by 90% (Been *et al*., 2007). European policy, however, discourages fallow periods and green manure crops are encouraged as winter cover to prevent soil erosion, nitrogen leaching and to add organic matter to the soil. Many green manure crops (e.g. grasses or grains) are highly susceptible to *M. chitwoodi*, and this practice is regarded as the second major cause of the increased presence of *M. chitwoodi* and *M. fallax*, with green manure crops maintaining or even increasing populations (Teklu, 2018). Exemption to allow fallow periods in Europe have been made for fields infested with *M. chitwoodi* because other control options are so limited (Wesemael *et al*., 2011).

Only a few crops are reported as non-hosts or poor hosts, these include chicory cultivars (*Cichorium intybus*), borage, French beans, spinach and some green manure crops like *Tagetus patula*, fodder radish, sudangrass hybrids or sorghum-sudangrass hybrids (Mojtahedi *et al*., 1993; Brinkman *et al*., 1996; Korthals *et al*., 2001; den Nijs *et al*., 2004; Hafez and Sundararaj, 2009). More recently researchers have been using population dynamic models to investigate host status and these models have revealed that many crops previously thought to be good hosts are in fact poor hosts, for example Carrot cv. Nerac (Heve *et al*., 2015). A degree of uncertainty about host status of many crops therefore exists.

Effective management for *M. chitwoodi* is still in development but some useful information is available for Dutch farmers on a website hosted by Wageningen University and Research

(http://www.aaltjesschema.nl/) which provides information on identifying and controlling nematodes on farms. This website helps Dutch farmers avoid unfavourable crop rotations and suggests the cultivation of early potato varieties to limit damage. Wesemael and Moens (2008b) also showed that quality damage on carrots caused by low population densities of *M. chitwoodi* can be avoided by a reduction of the period the crop is in the field.

Natural enemies

Whilst a number of potential natural enemies have been identified for *M. chitwoodi* (e.g. Inserra and Davis 1983; Jaffee and Muldoon, 1995; Wishart *et al*., 2004), Lammers *et al*. (2007), suggested that nematodes are not likely to be controlled by natural enemies.

Host resistance

The best strategy for the management of *M. chitwoodi* in potato rotations would be the use of resistant potato cultivars. Research to identify resistant genes in wild and primitive cultivars of potato started in the 1990s, in the Netherlands. Sources of resistance were obtained from *S. bulbocastanum, S. cardiophyllum, S. brachistotrichum, S. fendleri* and *S. hougasii* (Janssen *et al*., 1995). In 2000, the EU-funded project QLRT-1999-1462 Durable Resistance against *M. chitwoodi* and *M. fallax* (Zoon et al., 2002) was initiated focussing on, identifying and incorporating resistance genes in arable crops including potato and green manure crops. Following the completion of the project, several breeding companies managed to successfully produce potato genotypes with a single resistance gene against *M. chitwoodi* and possibly *M. fallax* (Draaistra, 2006).

A number of breeding companies were also successful in selecting cultivars of the green cover crop fodder radish with (partial) resistance for *M. chitwoodi*, *M. fallax* and *M. hapla*. Farmers in Belgium and The Netherlands are using these cultivars on a regular basis during the intercrop season (Wesemael *et al*., 2011). In the UK, a number of these cultivars (E.g. Doublet and Terranova) are available through RAGT Seeds Ltd.

Tolerance.

Potato cultivars differ in their tolerance to *M. chitwoodi*, with early cultivars showing a lower percentage of symptoms compared with later maturing cultivars (van Riel, 1993; see www. aaltjesschema.nl).

Legislation

Since 1998, *M. chitwoodi* and *M. fallax* have been listed as quarantine pests in the EU.

In the Netherlands, a range of phytosanitary measures have been implemented to contain *M. chitwoodi* and *M. fallax*, including general surveys (in all hosts) and specific surveys (potatoes), checking seed potato tubers after harvest and incubation for presence of the nematode in each lot and restriction of growing seed potatoes in a radius of 1 km around an infected site (Plant Protection Service, 2017). Contaminated areas are subject to containment with the aim of preventing the further spread of the nematode (EPPO, 2013a). If contamination is detected, the phytosanitary certificate is refused and the product has to be cleaned, if possible, or destroyed. Infested fields lose their registration for potato seed production and all propagation material from these fields is checked for the following 3 years (den Nijs, 2004).

Teklu, 2018 recently stated that In The Netherlands, *ca*. 425 findings of *M. chitwoodi* or *M. fallax* were reported from plant lots and propagation material between 1995 and 2016, the majority of which consisted of *M.chitwoodi* (Plant Protection Service, 2010 – 2017), indicating that despite the quarantine regulations imposed, the number of infestations are still increasing.

In Belgium, a similar policy to the Netherlands is employed but in addition, growing root crops such as carrot, beet and black salsify is prohibited in fields infested with *M. chitwoodi* for as long as the nematode can be detected in those fields, a strategy that prevents transportation of the nematodes with the soil adhering to the crop after harvest (Wesemael *et al*., 2011).

In France, the response to outbreaks has been to destroy all plants and plant products or treated adequately in an authorised factory under the supervision of the NPPO; it is forbidden to remove soil from the contaminated field, and machines and equipment must be cleaned immediately at the exit of the field; contaminated fields placed into bare fallow for 5 years and cropping restrictions are placed on other fields; extensive national surveys and soil testing have also been carried out (Gammon and Lenne, 2012). Placing contaminated fields in fallow for 5 years had a large economic impact, and financial aid had to be provided each year to support the farmers affected (Gammon and Lenne, 2012). Soil analyses carried out in fields after 2 years of bare fallow showed that neither *M. chitwoodi* nor *M. fallax* was detected in 99% of cases, and measures have now been reduced so that if the nematodes are not detected after 2 years of fallow, crops such as cereals are allowed in these fields, but no tubers or root crops can be grown. All eradication measures are lifted from previously contaminated fields after 3 additional years on the condition that two analyses per hectare test negative (Gammon and Lenne, 2012).

The quarantine status of *M. chitwoodi* in Europe means that potato seed tubers must be free from these nematodes before they are allowed to enter EU. Detection is based on visual inspection for symptoms on host plants grown in the same field as the seed potatoes or on the seed itself (Anon., 2006). Symptoms, however, are not always visible and therefore Wesemael *et al*. (2011) suggested that for detection of *M. chitwoodi* in potatoes the tubers are peeled and nematodes are subsequently extracted from these peels to increase the chances of detection (Anon., 2006; Viaene *et al*., 2007a).

Meloidogyne fallax (false Columbia root-knot nematode)

Geographical distribution

Meloidogyne fallax was first detected in 1992 in the Netherlands in maize (Karssen, 1996). Within Europe the species has been recorded from Belgium (Waeyenberge and Moens, 2001), France (Dahler *et al*., 1996; NPPO of France, 2010, 2011, 2012, 2013), Germany (Schmitz *et al*., 1998; Sturhan, 2014), Switzerland (Eder *et al*., 2010) and the UK (NPPO of the United Kingdom, 2013, 2015). It has also been detected outside Europe in New Zealand (Marshall *et al*., 2001), Australia (Nobbs *et al*., 2001) and South Africa (Fourie *et al*., 2001). In France in 2008, *M. chitwoodi* and *M. fallax* were detected in Picardie region on black salsify and ware potatoes (NPPO of France, 2010). *Meloidogyne fallax* has not been recorded from natural habitats and so its geographic origin is unknown (Everatt *et al*., 2016).

This species was first recorded in the UK in 2011 in sports turf (NPPO of the United Kingdom, 2013). In 2013, NPPO recorded the species in an organic leek crop in Staffordshire where it caused substantial stunting of part of the crop. The pest may have been introduced into the infested field with plant waste and soil resulting from the on-site processing of leeks produced in other EU member states. The infested field was close to the pack house and had received processing waste for many years (NPPO of the United Kingdom, 2013).

In October 2015, outbreaks were reported in North Western England in sports turf, at three locations (2 brownfield sites in urban locations and one rural location surrounded by arable land) very close to each other. All locations had used the same contractor to build and maintain

the grounds and the nematode may have been spread by machinery and soil (NPPO of the United Kingdom, 2015). According to DAERA (not dated), *M. fallax* may be an emerging native pest in the British Isles. However, there is no published information to support this, and where it has been found, there has been an import association (Defra, unpublished). In order to minimise further introductions and potential spread, growers and agronomists are strongly advised to send samples with suspicious symptoms to Fera Science Ltd. or SASA for diagnosis.

Host range

M. fallax has a wide host range including potato (Nobbs *et al*., 2001; Marshall *et al*., 2001; den Nijs *et al*., 2004; NPPO of France, 2010), leek (NPPO of the United Kingdom, 2013), sugar beet (Rohan *et al*., 2015), carrots (Goossens, 1995; den Nijs *et al*., 2004), strawberries (Sommen *et al*., 2005) , lettuce (NPPO of France, 2010), tomato (Goossens, 1995; NPPO of France, 2010), black salsify (Goossens, 1995; den Nijs *et al*., 2004; NPPO of France, 2010), white clover (Rohan *et al*., 2016), turf grasses (NPPO of the United Kingdom, 2015) and artichoke (Greco *et al*., 2005). den Nijs *et al*. (2004), also reported the following as host plants: asparagus, wheat, barley rye, buckwheat, lucerne, chicory, raddish, perennial and Italian ryegrass, white mustard, tagetes, common bean, fennel, celery, phacelia (also reported by Brinkman *et al*., 1996) and evening primrose (also reported by Brinkman *et al*., 1996).

Shah *et al*. (2010) also recorded *M. fallax* on field grown (from a potato field) hairy nightshade (*Solanum physalifolium*) and black nightshade (*S. nigrum*) in New Zealand. Pathogenicity of *M. fallax* from field-grown nightshade plants was confirmed by inoculating glasshouse-grown tomato and potato plants.

Maize is a poor host for *M. fallax* (Brinkman *et al*., 1996; Davis and Venette, 2004).

Description of organism

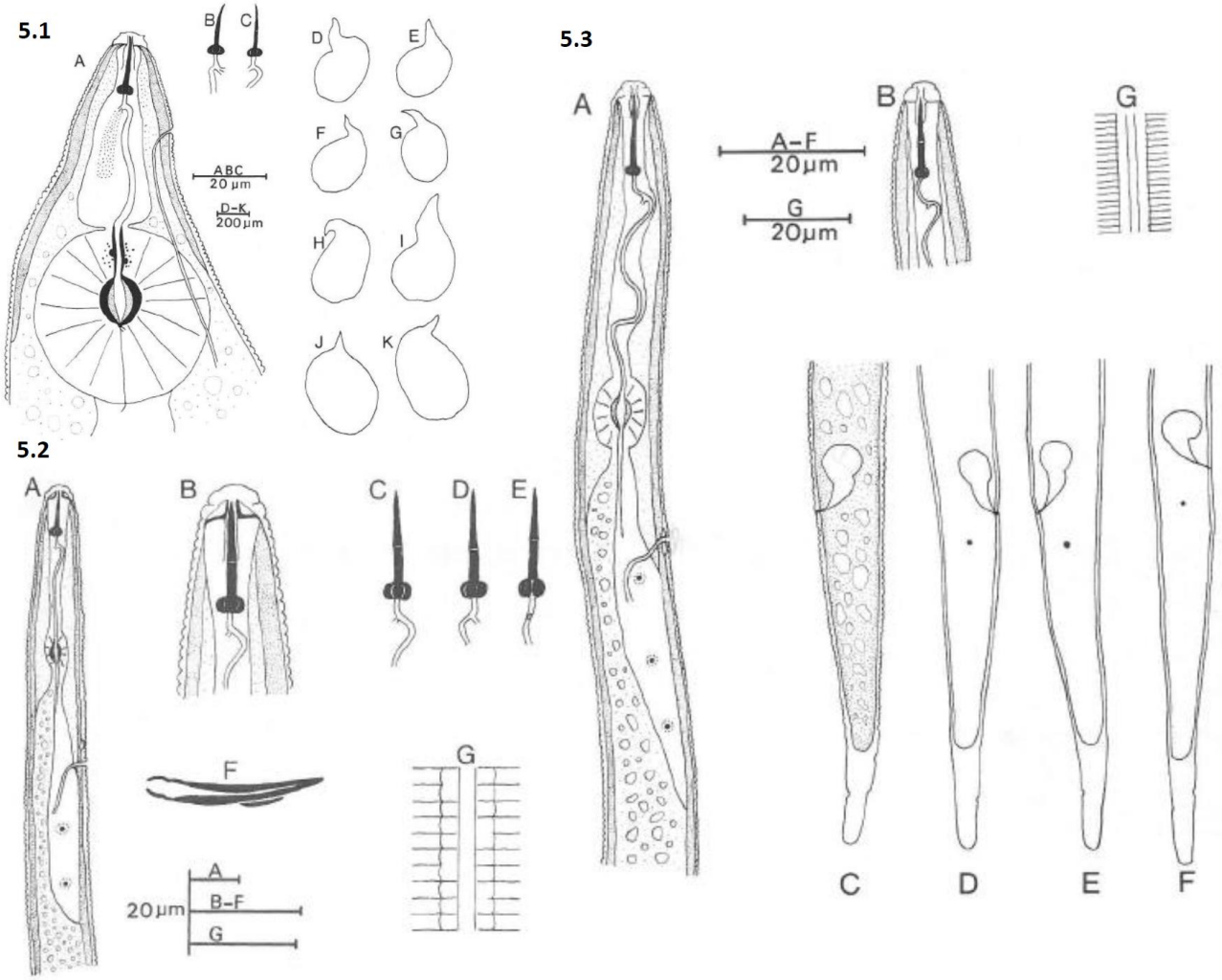


Figure 5. *Meloidogyne fallax*. 5.1 Females A: anterior, lateral view; B, C: stylets; D: entire. 5.2 Males A: pharyngeal region, lateral view; B: anterior; C – E: stylets; F: spicule & gubernaculum; G: lateral field. 5.3 second-stage juvenile A: pharyngeal region, lateral view; B: anterior; C – F: tails. After Karssen (1996), courtesy Fundamental & Applied Nematology.

M. fallax is similar in appearance to other *Meloidogyne* species, females are sedentary, thin, annulated, pearly white and globular to pear-shaped. Adult males and the second-stage juveniles are vermiform, motile and slightly tapered at each end. *M. chitwoodi* and *M. fallax* are often found together. Two of the main differences between the *M. fallax* and *M. chitwoodi* include a longer stylet length in *M. fallax*, and the stylet knob is rounded and prominent in *M. fallax* as opposed to irregular and small in *M. chitwoodi*. These differences and a more in depth description of the morphological characteristics of both nematodes is given in EPPO (2016).

Life cycle

The life cycle of *M. fallax* is in general the same as that for *M. chitwoodi* (please see above section for life cycle of *M. chitwoodi*) with respect to root penetration, gall induction, symptomatology, number of moults, and parthenogenetic reproduction (EPPO/CABI, 1997).

The species can begin development when soil temperature rises above 5 °C (Pinkerton *et al*., 1991). Khan *et al*. (2014) also investigated hatching, migration, invasion and post-penetration (on potato and maize) development of *M. fallax* at 15, 20 and 25°C. *M. fallax* hatched in greater number at temperatures below 20°C and no lower than 15°C and optimum temperature for migration being 25°C for *M. fallax*.

A virulence study on potato by van der Beek (1997) indicated that *M. fallax* has a shorter life cycle than *M. chitwoodi*, whilst Kahn *et al*. (2014) found similar degree-days (DD5, base temperature 5°C) required for life cycle completion on potato 555-740 DD5 and maize 705-740 DD5 for both species of nematode. As for *M. chitwoodi*, the life cycle of *M. fallax* from J2 until egg production takes approximately 3-6 weeks under optimal conditions (Wesemael *et al*., 2006). This species therefore has a potentially high reproduction rate and ability to rapidly increase population levels in a single season. Furthermore, as for *M. chitwoodi*, *M. fallax* usually reproduces by facultative meiotic parthenogenesis (van der Beek and Karssen, 1997), which means that one second-stage juvenile can start a new population.

Wesemael *et al*. (2006) investigated the effect of tomato root diffusate on hatching of *M. fallax* and found that this species does not require hatch stimulation from root diffusate, irrespective of plant age. The authors hypothesised that if *M. fallax* J2 are able to survive the absence of a host plant and other adverse conditions for a longer time period (e.g. over the winter period) then they can immediately penetrate host roots when they appear. However, survival as hatched J2 requires energy and it is not known whether the energy reserves of J2 after a winter period are sufficient for invasion.

Khan *et al*. (2014) suggested the lower temperature optimum for hatching of *M. fallax* observed in their study supports the survival strategy hypothesised by Wesemael *et al*. (2006) where due to the limited migration at lower temperatures, J2 of *M. fallax* can restrict their energy utilisation enabling them to survive longer in the soil. Khan *et al.* (2014) recommended further research on energy reserves, survival and infectivity of these this nematode species to develop effective management programmes.

Symptoms

In trials, *M. fallax* caused the same symptoms on potato tubers as *M. chitwoodi*, namely external galling and internal necrosis just below the skin (Brinkman *et al*., 1996; van Riel and Goossens, 1996). Natural outbreaks of *M. fallax* on potato also showed these external symptoms (Karssen, 1996).

The root galls produced by *M. chitwoodi* and *M. fallax* are comparable to those produced by several other root-knot species, relatively small galls in general, without secondary roots emerging from them (as found in *M. hapla*). This may be difficult to detect as often little or no galling occurs even in heavy infestations (EPPO, 2006). On potato tubers, *M. chitwoodi* and *M. fallax* cause numerous small, pimple-like raised areas on the surface (Moens *et al*., 2009). Some potato cultivars, however, may remain free from visible external symptoms, even though they are heavily infested (EPPO, 2006). Internal potato tissue just below the skin is necrotic and brownish and adult females are usually visible just below the surface, in the cortical layer,

as white, pear-shaped bodies surrounded by a brownish layer, which is usually indicative of the presence of eggs (EPPO, 2006).

Above-ground symptoms are often not obvious but may consist of varying degrees of stunting, yellowing, lack of vigour and a tendency to wilt under moisture stress, all leading to reduced yield (Prior *et al*., 2015).

Sampling and identification

Please refer to the section on *M. chitwoodi*.

Economic impact

At present no direct information is available to show the extent of economic damage caused by *M. fallax*. This species frequently occurs in mixed infestations with *M. chitwoodi* and is thought to have a pest status similar to that of *M. chitwoodi* (EPPO undated, b).

Like *M. chitwoodi*, *M. fallax* infection may reduce the yield of potatoes but this is rarely observed (EPPO, 2013a). The major impact is reduction in quality as a result of internal necrosis and external galling, which reduce market value. Necrotic spots caused by *M. chitwoodi* in the flesh of tubers of as little as 5% of a crop can make it commercially unacceptable (EPPO, not dated, a) and it is likely *M. fallax* will have a similar impact.

Preventive soil sampling is conducted in Belgium and The Netherlands to detect *M. chitwoodi* and *M. fallax* and the extra costs associated with sampling and diagnostic analysis are most likely compensated by the reduction of heavily infected and valueless crops (Wesemael *et al*., 2011).

Prior to preventative soil sampling, in the Netherlands 7% of the vegetables harvested for the canning industry were rejected due to damage caused by root-knot nematodes, this was reduced to only 1.5% in 2003 when soil sampling was implemented (Wesemael *et al*., 2011). The efficacy of detection increases if soil sampling is conducted shortly after harvest of previous crops (Wesemael and Moens, 2008a).

Phytosanitary measures, where *M. fallax*, is a problem can include the inspection of seed potatoes, which also increases production costs (Wesemael *et al*., 2011).

Control

As for *M. chitwoodi*, the most likely method of introducing *M. fallax* into a new area is through the movement of infected or contaminated planting material as the nematode has very limited potential for natural movement (only second-stage juveniles can move in the soil and, at most, only a few tens of centimetres). Infected tubers can easily transport the nematode as both eggs and females survive and propagate in tubers, therefore seed potatoes are a primary challenge that needs to be met (Been *et al*., 2007).

The movement of non-host seedling transplants, nursery stock, machinery or other products which are contaminated with soil, sand or gravel (including clothing, containers, packaging etc) infested with *M. fallax* could also result in spread. Nematode movement can also be facilitated by contaminated irrigation water or animals moving between fields (Wale, Platt and Cattlin, 2008).

Chemical control

Whilst nematicides are able to reduce populations of *M. fallax*, if host plants are not controlled the effect of treatment will be short lived. The drastic decline of soil fumigation in the last

decades in the Netherlands, used to control PCN, is thought to be one of the main reasons for the emergence of *M. chitwoodi* and *M. fallax* (Teklu, 2018).

Crop rotation

Options for crop rotations in Europe for the control *M. fallax* are limited due to its wide host range on crops (den Nijs *et al*., 2004; Wesemael *et al*., 2011). Maize and *Phaseolus vulgaris* (except cv. Masai), however, are not considered good hosts for *M. fallax* (Brinkman *et al*., 1996; Davis and Venette 2004) and may therefore be useful where management of this nematode is important. Furthermore, farmers in Belgium and The Netherlands are using cultivars of the green cover crop fodder radish with (partial) resistance for *M. chitwoodi*, *M. fallax* and *M. hapla* on a regular basis during the intercrop season (Wesemael *et al*., 2011).

Less is known about *M. fallax* host range on weed species and requirement for control in crop rotations. As mentioned previously, hairy nightshade and black nightshade have been recorded as hosts for *M. fallax* in New Zealand (Shah *et al*., 2010).

In crop rotations of potato with pasture (which is sometimes carried out to control PCN) *M. fallax* may build up in potatoes, and in both the white clover and ryegrass components of pasture. In areas where *M. fallax* is known to be a problem, it is recommended to check for the presence of *M. fallax* prior to planting a potato crop from pasture (Rohan *et al*., 2016). Maize may be a useful part of any pasture rotation where management of this nematode is required (Rohan *et al*., 2016).

Population densities of root-knot nematodes have been shown to decrease markedly during winter and under black fallow (Been *et al*., 2007; Wesemael and Moens, 2008a). Whilst European policy discourages fallow periods to prevent erosion, exemptions have been made for fields infested with *M. chitwoodi* or *M. fallax* because other control options for these nematodes are so limited (Wesemael *et al.,* 2011).

Manipulating planting or harvest date

Manipulating planting or harvest dates may reduce damage caused by nematodes (Hooper and Evans, 1993). For example, Molendijk and Brommer (1998) reported the production of good quality carrots in fields that were heavily infested with *M. fallax* after postponing sowing date. This practice, however, is not always practical as planting and harvest depend strongly on both climate conditions and market demands (Wesemael *et al*., 2011).

Host resistance

Research to identify resistant genes to *M. fallax* in wild and primitive cultivars of potato started in the nineties, in the Netherlands. Sources of resistance were obtained from *S. bulbocastanum, S. cardiophyllum, S. brachistotrichum, S. fendleri* and *S. hougasii* (Janssen *et al*., 1995). In 2000, the EU-funded project QLRT-1999-1462, Durable Resistance against *M. chitwoodi* and *M. fallax* (Zoon et al., 2002) was initiated focussing on, identifying and incorporating resistance genes in arable crops including potato and green manure crops. Following the completion of the project, several breeding companies managed to successfully produced potato genotypes with a single resistance gene against *M. chitwoodi* and possibly *M. fallax* (Draaistra, 2006). A number of breeding companies were also successful in selecting cultivars of the green cover crop fodder radish with (partial) resistance for *M. chitwoodi*, *M. fallax* and *M. hapla*. Farmers in Belgium and The Netherlands are using these cultivars on a regular basis during the intercrop season (Wesemael *et al*., 2011)

Legislation

Since 1998, *M. chitwoodi* and *M. fallax* have been listed as quarantine pest in the EU.

In the UK, an outbreak on organic leeks was attributed to plant waste and soil resulting from the on-site processing of leeks produced in other EU member states (NPPO of the United Kingdom, 2013). Where similar operations occur strict pest and hygiene measures should be put in place to minimise the possibility of spread of infection.

In the Netherlands, a range of phytosanitary measures have been implemented to contain *M. fallax*, including general surveys (in all hosts) and specific surveys (potatoes), checking seed potato tubers after harvest and incubation for presence of the nematode in each lot, and restriction of growing seed potatoes in a radius of 1 km around an infected site (Plant Protection Service, 2017). Contaminated areas are subject to containment with the aim of preventing further spread of the nematode (EPPO, 2013). If contamination is detected, the phytosanitary certificate is refused and the product has to be cleaned, if possible, or destroyed. Infested fields lose their registration for potato seed production and all propagation material from these fields is checked for the following 3 years (den Nijs, 2004).

In France, the response to outbreaks has been to destroy all plants and plant products or treated adequately in an authorised factory under the supervision of the NPPO; it is forbidden to remove soil from the contaminated field, and machines and equipment must be cleaned immediately at the exit of the field; contaminated fields placed into bare fallow for 5 years and cropping restrictions are place on other fields; extensive national surveys and soil testing have also been carried out (Gammon and Lenne, 2012). Placing contaminated fields in fallow for 5 years had a large economic impact, and financial aid had to be provided every year to support the farmers affected (Gammon and Lenne, 2012). Soil analyses carried out in in fields after 2 years of bare fallow showed that neither *M. chitwoodi* nor *M. fallax* was detected in 99% of cases, and measures have now been reduced so that if the nematodes are not detected after 2 years of fallow crops such as cereals are allowed in these fields, but no tubers or root crops can be grown. All eradication measures are lifted from previously contaminated fields after 3 additional years on the condition that two analyses per hectare test negative (Gammon and Lenne, 2012).

In Belgium, a similar policy to the Netherlands is employed but in addition, growing root crops such as carrot, beet and black salsify is prohibited in fields infested with *M. chitwoodi* or *M. fallax* for as long as the nematode can be detected in those fields. This strategy prevents transportation of the nematodes with the soil adhering to the crop after harvest (Wesemael *et al*., 2011).

The quarantine status of *M. fallax* in Europe means that potato seed tubers must be free from these nematodes before they are allowed to enter EU. Detection is based on visual inspection for symptoms on host plants grown in the same field as the seed potatoes or on the seed itself (Anon., 2006). Symptoms, however, are not always visible and therefore Wesemael *et al*. (2011) suggested that for detection of *M. fallax* in potatoes the tubers are peeled and nematodes are subsequently extracted from these peels to increase the chances of detection (Anon., 2006; Viaene *et al*., 2007). There is also a risk from strawberry plants regards introduction of the nematode to the UK, and again these plants are often symptomless (Sommen *et al*., 2005).

Meloidogyne minor

Geographical distribution

Meloidogyne minor is thought to be native to the UK (Lammers *et al*., 2007). In the UK, *M. minor* can be found in coastal sand dunes (Lammers *et al*., 2007) and has been reported on sports pitches, particularly golf courses, where it causes yellow patches on *Agrostis stolonifera var. stolonifera* (L.) (creeping bent grass) (Lammers *et al*., 2007; Entwistle *et al*., 2014). In 2007, *M. minor* was also detected infecting a potato crop in Northern Ireland (Fleming *et al*., 2016) and a survey of grassland pasture or cereal-growing fields in Northern Ireland between October 2011 and July 2013 indicated that *M. minor's* distribution is widespread (Fleming *et al*., 2016).

The nematode has also been reported in the Netherlands, Belgium, Republic of Ireland, Portugal, Chile and the United States (Viaene *et al*., 2007b; Wesemael *et al*., 2011; McClure *et al.*, 2012; Prior *et al*., 2015). *M. minor* has been recorded twice in potatoes in the Netherlands, once in 2000 from a potato field in Zeijerveld where the nematode caused strong growth reduction on potato plants, but no damage to potato tubers (Karssen, 2004) and once in 2005, in a post-harvest potato sample (Lammers *et al*., 2007).

The geographical distribution of this species, however, has not yet been fully recorded as it has only relatively recently been described (Prior *et al*., 2015) and surveys have not been carried out in many countries (Lammers *et al*., 2007). Comprehensive surveys are required to obtain more data on distribution.

Host range

Grasslands and dune areas are thought to be the natural habitat of *M. minor* (Prior *et al*., 2015). Golf courses in the UK that have been affected by the nematode use coastal sand for construction and maintenance (Lammers *et al*., 2007).

In the Netherlands, Northern Ireland and England, the nematode has been reported in pasture, and in Wales and Ireland in coastal dunes (Lammers *et al*., 2007; Fleming *et al*., 2016; T. Prior unpublished data). The potato crops affected in the Netherlands in 2000 and 2005 were grown in fields that were pasture land for several years prior to potatoes being grown (Lammers *et al*., 2007).

M. minor has, however, been reported on a wide host range on grasses, broadleaved weeds and crops in the UK. Of relevance to UK potato production these include: *Trifolium pratense* (red clover), *Trifolium repens* (white clover), *Phleum pratense* (timothy) and *Festuca arundinacea* (tall fescue) (Fleming 2004, Department of Applied Plant Science (APS), The Queen's University of Belfast, unpublished results: In Lammers *et al*., 2007), *Lolium perenne* (perennial ryegrass), *Solanum tuberosum* (potato), Festuca sp. (fescue) (Karssen *et al*., 2004), *Anagallis arvensis* (scarlet pimpernel), *Medicago lupulina* (black medick), *Poa* sp. (bluegrass) (Prior *et al*, 2015). Reproduction on potato has been observed on roots as well as potato tubers (Karssen *et al*., 2004).

M. minor has also been shown to reproduce on the following hosts under experimental conditions: *Avena sativa* (oat), *Dacus carota* (carrot), *Lactuca sativa* (lettuce), *Lolium multiflorum* (Italian ryegrass), *Lolium perenne* (perennial ryegrass), *Lolium* sp. (ryegrass), *Medicago sativa* (alfalfa), *Phacelia tanacetifolia* (phacelia), *Solanum esculetum* (tomato), *Vicia sativa* (vetch) (Wageningen University and Research centre, unpublished data: In Lammers *et al*., 2007), *Hordeum vulgare* (barley) and *Triticum sativum* (Fleming 2004, Department of Applied Plant Science (APS), The Queen's University of Belfast, unpublished results: In Lammers *et al*., 2007)

Under experimental glasshouse conditions the nematode failed to reproduce on marigold and maize (Karssen, 2004). In a field experiment conducted in 2008 by Thoden *et al*. (2012), no substantial reproduction of *M. minor* was present on rye (*Secale cereale* cv. Sorum), sugar beet (*Beta vulgaris* cv. Shakira), maize (*Zea mays* cv. Expert) or annual ryegrass (*L. multiflorum* cv. Bartali). Furthermore, no nematodes were found in the roots of sugar beet or maize. Annual ryegrass had a statistically significant higher population density of *M. minor* than the control fallow but densities were very low.

Description of organism

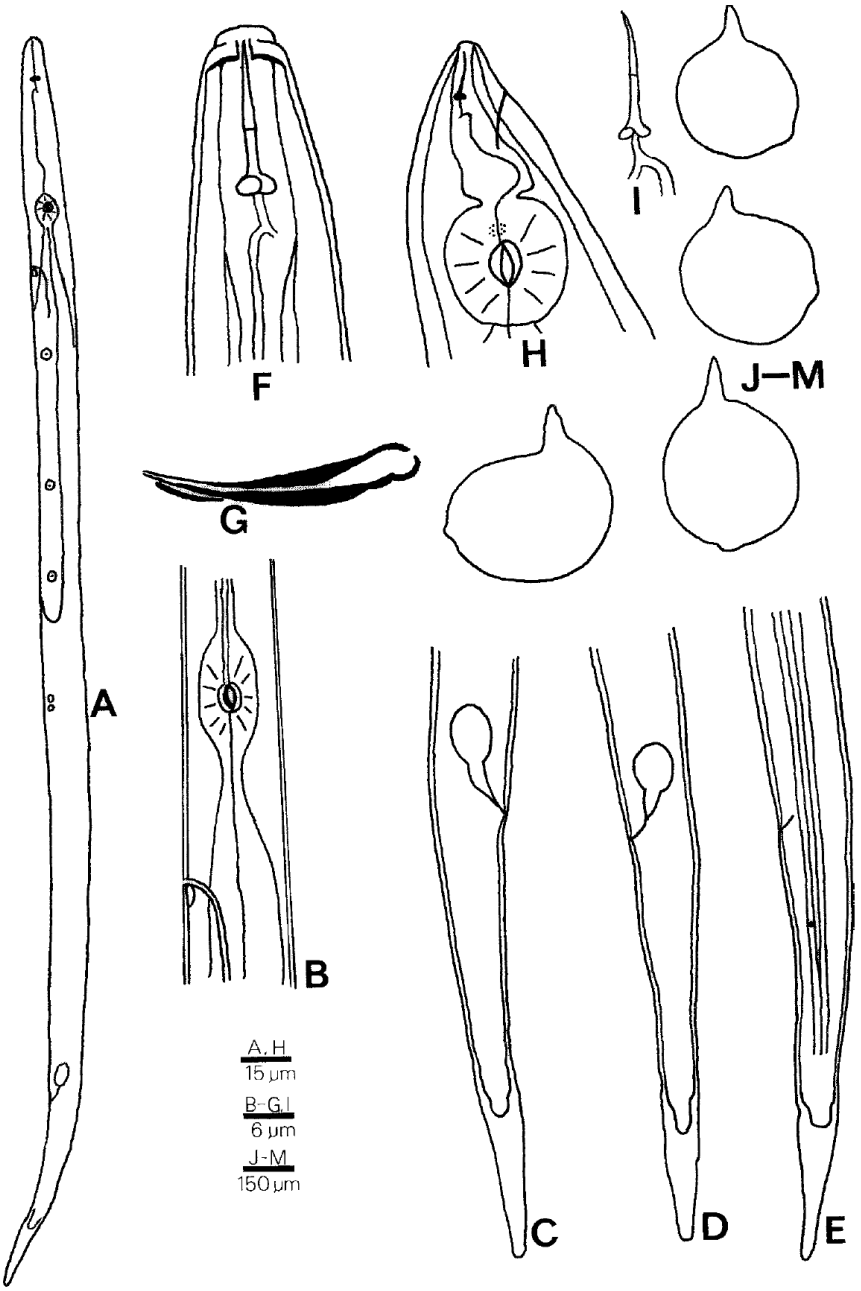


Figure 6. *Meloidogyne minor* Second-stage juvenile A: entire, lateral view; B: region of metacorpus; C – E: tails; Male F: anterior; G: gubernaculum & spicule; Female H: Anterior; I: stylet; J – M: entire. After Karssen et al. 2004, courtesy *Nematology*.

An in depth description of *M. minor* is provided by Karssen *et al*. (2004). *M. minor* adult female nematodes are pearly white, globose in shape with a distinctly offset neck region (Karssen *et al*., 2004; Prior *et al*., 2015). The adult females are usually embedded within plant roots or tubers. The eggs are very small and are contained within a gelatinous matrix, roughly five to six times the size of the adult female and usually attached to the posterior of the female (Karssen *et al*., 2004; Prior *et al*., 2015). Infective juveniles and males are soil borne, vermiform in shape (Karssen *et al*., 2004; Prior *et al*., 2015). The body of the male is annulated, usually not twisted, and the tail region curved ventrally, is short, conical and with bluntly rounded tip (Karssen *et al*., 2004). The second-stage juvenile body is relatively short, annulated with the anterior part tapering behind stylet-knob level, and posterior part slightly ventrally curved when heat relaxed. The tail is straight, sometimes slightly curved ventrally, and gradually tapering until finely pointed at the tail tip (Karssen *et al*, 2004).

Life cycle

M. minor passes through an embryonic stage, four juvenile stages and an adult stage, similar to that of the lifecycle of other root-knot nematode species.

Under set temperature conditions, Wesemael *et al*. (2014) calculated that *M. minor* requires 606-727 DD 5 to complete its life cycle on potato, which is similar to that found for *M. chitwoodi*, which required 600-800 DD 5 (Pinkerton *et al*., 1991). This suggests that as for *M. chitwoodi* and *M. fallax*, *M. minor* is capable of producing several generations during one growing season corroborating findings by Turner and Fleming (2005). In a survey of cereal growing crops and pasture in Northern Ireland by Fleming *et al*. (2016), the authors found a higher abundance of *M. minor* J2s in autumn suggesting a second major hatch in a year, evidence which also supports Wesemael *et al*. (2014).

In contrast, under field experimental conditions in the Netherlands of *M. minor* infesting potatoes, Thoden *et al*. (2012), suggested that only one generation per season is likely to develop. Wesemael *et al*., (2014), however, disputed these findings and speculated that the nematodes found by Thoden *et al*. (2012) were second generation females.

In the UK, therefore, it is likely that *M. minor* is able to complete 1-2 generations (Lammers *et al*., 2007).

Research has shown that *M. minor* usually reproduces by facultative meiotic parthenogenesis (Karssen *et al*, 2004), which means that one second-stage juvenile can start a new population. The life span of an adult female may extend to three months (Prior *et al*., 2015) and *Meloidogyne* spp females are able to lay 100 – 500 eggs (CAB International, 2004; Enneli and Toros, 1996). Egg hatching is temperature driven with the optimum temperature for hatching at 20-25°C and the optimum temperature for activity 15-25°C (Morris *et al*., 2011). Females can continue egg laying after the harvest of aerial parts of the plant and the survival stage between crops is generally within the egg (Prior *et al*., 2015).

This mode of reproduction and ability to produce hundreds of eggs, combined with the most likely absence of specific natural enemies, and the fact that *M. minor* is able to reproduce on monocotyledonous and dicotyledonous species, makes it likely that small populations of *M. minor* are likely to establish in a new area (Lammers *et al*., 2007).

Thoden *et al*. (2012), found nearly the same numbers of *M. minor* in samples taken in autumn or the following spring when samples were stored at 4°C and have speculated that *M. minor* overwinters unharmed by the cold temperatures, probably within its egg masses. The authors pointed out that this differs markedly from *M. chitwoodi*, which shows a drastic population decrease during Dutch winters.

Symptoms

As for other root-knot nematodes symptoms of infestation includes gall formation on the roots and tubers of potatoes. Symptoms caused by *M. minor* may be difficult to differentiate with the symptoms caused by other *Meloidogyne* species or other nematodes species (Lammers *et al*., 2007). Where infestations are light symptoms may not be easily seen and in new infestations, the females are still immature, opaque and difficult to see in tubers, while galls on roots are less prominent (Lammers *et al*., 2007).

In a pest risk analysis (PRA) for *M. minor*, Lammers *et al*. (2007), reported that *M. minor* may cause quality damage to particular potato varieties, as shown by an infested potato field in the Netherlands and a small greenhouse experiment in the Netherlands (trial tubers were heavily infested with *M. minor* and showed gall symptoms). The authors also reported that potatoes grown after pasture land, on sandy soils (crop damage associated with *Meloidogyne* spp. is often observed in sandy soils Braasch *et al*., 1996) in warm summers (when temperatures are optimal for activity and egg hatching Morris *et al*., 2011) are most likely to suffer damage. They also suggested that the extent to which *M. minor* is sensitive to competition from other nematode species in the soil may be a significant factor in damage levels.

In 2000, when *M. minor*, was found in a potato field in Zeijerveld symptoms included strong growth reduction but there was no damage/sign of infection to tubers, and juveniles of *M. minor* were only isolated from the potato roots (Karssen *et al*., 2004).

In a more recently reported study, Wesemael *et al*. (2014), investigated damage development of *M. minor* on potato in a pot experiments. Symptoms (galling on the tubers) were similar to those caused by *M. chitwoodi* and *M. fallax* and a damage threshold of 41 J2 (100 cm3 soil) suggesting *M. minor* is capable of developing on potato and causing severe damage at low initial population densities.

Meloidogyne infection is thought to affect water and nutrient uptake and upward translocation by the root system (Prior *et al*., 2015). Therefore above ground symptoms are similar to those produced by any plant having a damaged root system that is not functioning correctly, for example, suppressed shoot growth, chlorosis of the foliage, and wilting even when soil moisture is adequate (Prior *et al* ., 2015). The severity of these above ground symptoms is thought to be related to the number of juveniles penetrating and becoming established within the root tissue of young plants (Prior *et al*., 2015).

Sampling and identification

EPPO standards and guidelines for the sampling and detection of *M. minor* in potatoes are not available as for *M. chitwoodi* and *M. fallax*. It is likely, however, that sampling procedures would be similar to those for *M. chitwoodi* and *M. fallax*.

As for *M. chitwoodi* and *M. fallax* morphological characteristics can be used to identify *M. minor* and an in depth description of *M. minor* is provided by Karssen *et al*. (2004). The isozyme electrophoresis methods available described for *M. chitwoodi* and *M*. *fallax* can also be used for identifying *M. minor*. This method, however, requires females for diagnosis. A real-time PCR method for detection of *M. minor* that can be used for any developmental stage has also been developed and is described by de Weerdt *et al*., (2010).

Economic impact

The economic importance of most root-knot nematodes is, in general, related to yield reduction, growth reduction and deformation or similar kinds of damage to host crops, which reduces the marketability of produce (Davis and Venette, 2004; Potter and Olthof, 1993).

Evidence indicates that *M. minor* is capable of causing damage in potatoes (Karssen *et al*., 2004). Outbreaks of *M. minor* in potato have shown both ware and seed crops to be vulnerable, with tuber weight reductions of 70% recorded in affected plants (C Fleming, unpublished data; In Fleming *et al*., 2008). However, at present it is not known what the true economic impact could be if the species establishes widely in potato growing areas.

Control

As for *M. chitwoodi* the most likely method of introducing *M. minor* into a new area is through the movement of infected or contaminated planting material as the nematode has very limited potential for natural movement (only second-stage juveniles can move in the soil and, at most, only a few tens of centimetres). This could be through the movement of non-host seedling transplants (Wale, Platt and Cattlin, 2008) or via infected tubers which can easily transport the nematode as both eggs and females survive and propagate in tubers. Therefore seed potatoes are a primary challenge that needs to be met (Been et al., 2007).

It is possible that *M. minor*, like other nematodes, can also be spread on a limited scale throughout a field and between fields by natural drainage, water run-off, flood water, soil attached to machinery, (Lammers *et al*., 2007), clothing, packaging or animals (Wale, Platt and Cattlin, 2008).

Chemical control

Whilst nematicides reduce the impact of *M. minor*, the effect of treatment will be short lived if the crop is not rotated with non-host plants (Prior *et al*., 2015). The damage threshold for *M. minor* on potato is 41 J2/100 cm^3 soil (Wesemael *et al*. 2014)

Crop rotation

As reported by Lammers *et al*. (2007), potatoes grown after pasture land on sandy soils in warm summers (when temperatures are optimal for activity and egg hatching) would likely be of most risk to *M. minor*. The pest is very likely to be associated with seed potatoes (Lammers *et al*., 2007).

Availability of host plants is an important factor in the population development of nematodes. Bare fallow may help to prevent *M. minor* establishing over a longer period of time (Lammers *et al*., 2007) and growing of non-host crops (e.g. maize Karssen, 2004) in a rotation may be effective but at present farmers have few control options.

Natural enemies

At present it is unknown whether *M. minor* has any natural enemies. Second-stage juveniles originating from a coastal sand dune had spores of *Pasteria* attached to the cuticle, which is a known parasite of nematodes (Poinar and Jansson, 1988; Lammers *et al*., 2007). Lammers *et al*. (2007), suggested however that nematodes are not likely to be controlled by natural enemies.

Meloidogyne hapla (Northern root knot nematode)

Geographical distribution

Meloidogyne hapla has a very widespread distribution worldwide, occurring in countries in Asia, Africa, the Americas, the Caribbean, Oceania and Europe, including the UK (for a comprehensive list of countries please refer to CABI, 2018). In depth, distribution records for the occurrence of *M. hapla* in the UK are not available. However, *M. hapla* is considered to be widespread in the UK, and is usually associated with certain vegetables and soft fruits (T. Prior pers. comm.)

Host range

M. hapla is extremely polyphagous, attacking a wide (over 500) range of crops and weeds (Goodey *et al*., 1965; Carter, 1985).

In temperate climates, nearly all vegetables of economic importance, including potatoes, onion, radish, beets, brassicas, carrots, parsnips, peas and beans are liable to attack as well as crops such as clover and lucerne (Clark, 1963; Dale, 1971 & 1972; Santo *et al*., 1980). Weed hosts include for example *Cirsium arvense* (perennial thistle) (Dale, 1972), *Cirsium vulgare* (spear thistle) (Dale, 1972), *Convolvulus arvensis* (field bindweed) (Dale, 1971) and *Chenopodium album* (fat hen) (Clark, 1963).

In pot experiments, *M. hapla* has been shown not to reproduce successfully on maize and cereals, including wheat, oats and barley (Santo *et al*., 1980). *M. hapla* reproduces poorly or not at all on most grasses (Moens *et al*., 2009; Magnusson and Hammeraas 2000).

Description of organism

M. hapla is similar in appearance to other *Meloidogyne* species, females are sedentary, thin, annulated, pearly white and globular to pear-shaped. Adult males and the second-stage juveniles are vermiform, motile and slightly tapered at each end. The stylet in both sexes is small and rounded. An in depth description of the morphological characteristics of *M. hapla* can be found in Williams (1974).

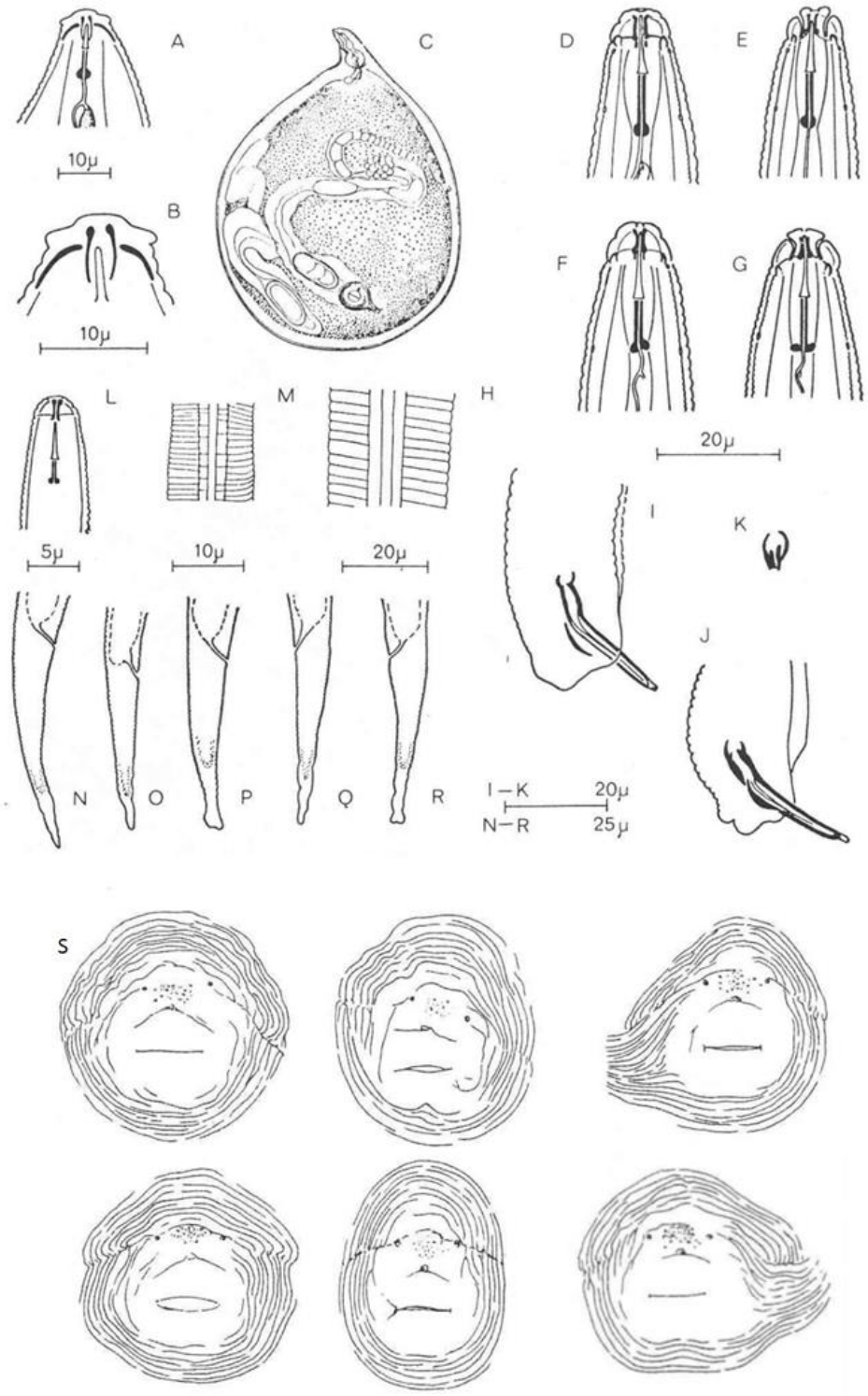


Figure 7. *Meloidogyne hapla*. Female A, B: anterior, lateral view; C: entire; Male D – G: anterior; H: lateral field; I, J: spicular region and tails; K: spicular head; Second-stage juvenile L: anterior, lateral view; M: lateral field; N – R: tails. After Whitehead, 1968 (except C, which is after Chitwood, 1949). Plate by Orton Williams,1974 and reproduced courtesy of CAB International.

Life cycle

The life cycle of *M. hapla* is similar to that of *M. chitwoodi* which takes approximately 3-4 weeks under optimal conditions (Wesemael *et al*., 2006), requiring 600–800 degree-days to complete the first generation, whilst subsequent generations require 500–600 degree days (Pinkerton *et al*., 1991). Research has shown that *M. hapla* usually reproduces by facultative meiotic parthenogenesis (Triantaphyllou, 1966), which means that one second-stage juvenile can start a new population. It is likely that *M. hapla* as for *M. chitwoodi* can produce two to three generations per year (Baker and Dickens, 1993; Brommer and Molendijk, 2001) and a single female can lay thousands of eggs. *M. hapla*, therefore, has the ability to rapidly build up a population in a single season.

M. hapla is able to withstand the cold. Eggs and juveniles able to survive field temperatures below 0°C, with some studies recording survival down to -15 °C in the soil for a prolonged period of time (Bergeson, 1959; Daulton and Nusbaum, 1961; Dao, 1970; Vrain and Barker, 1978; Belair, 1985; Wu *et al*., 2018). The minimal temperature for development of J2 is 8.8°C and eggs 6.74°C (Vrain and Barker, 1978). The climate in the UK is therefore suited to *M. hapla*.

Symptoms

M. hapla produces relatively small, subspherical galls on roots, often combined with extensive secondary root proliferation from the galls (Sasser, 1954; EPPO, 2016). This secondary root proliferation in not seen in infestations by *M. minor*, *M. chitwoodi* and *M. fallax*.

Where populations of *M. hapla* are high the outer layers of tubers may be invaded producing wart like protuberances and thin slices of tuber may reveal adult females (pearly white, round pear-shaped bodies surrounded by brown layer) below the protuberances (Wale, Platt and Cattlin, 2008). These symptoms, however, are not always apparent.

Above-ground symptoms are often not obvious but may consist of varying degrees of stunting, yellowing, lack of vigour and a tendency to wilt under moisture stress, all leading to reduced yield (Prior *et al*., 2015). Hafez and Sundararaj, (2007) stated that root knot nematode field damage in potatoes in Idaho is often localized in circles of various sizes, or spread throughout an entire field with random plants becoming chlorotic and stunted.

M. hapla is also known to increase the severity of disease caused by some plant pathogenic fungi, particularly *Verticillium* and *Fusarium*. For example, in field and greenhouse experiments *M. hapla* increased the severity of *Verticillium* wilt of potato (Jacobsen *et al*., 1979).

Soil sampling and identification

EPPO standards and guidelines for the sampling and detection of *M. hapla* in potatoes are not available as for *M. chitwoodi* and *M. fallax*. It is likely, however, that sampling procedures would be similar to those for *M. chitwoodi* and *M. fallax*.

Morphological characteristics can be used to identify *M. hapla* and an in depth description of *M. hapla* is provided by (Williams, 1974), but this method of identification requires specialist knowledge and experience and is labour intensive.

The isozyme electrophoresis methods available described for *M. chitwoodi* and *M*. *fallax* can also be used for identifying *M. hapla*. This method, however, requires females for diagnosis. Isozymes of glucose 6- phosphate dehydrogenase (EC 1.1.1.49) is also useful to differentiate between *M. hapla*, *M. fallax* and *M. chitwoodi* (van der Beek and Karssen, 1997; EPPO, 2016).

PCR tests can be performed on all developmental stages of nematodes and multiplex PCR methods allow the detection of one or more species in a nematode mixture by a single PCR test. PCR tests recommended by EPPO (2016) for identification of *M. chitwoodi* and *M. fallax* can also be used to identify *M. hapla*.

Economic impact

M. hapla attacks nearly all temperate vegetables of economic importance and is well known as being capable of causing considerable reductions in yield, particularly in crops such as carrot, onions and lettuce (Viaene and Abawi, 1996; Widmer *et al*., 1999; Gugino *et al*., 2006; Pang *et al*., 2009). *M. hapla* infection can reduce the yield of potatoes and the quality as a result of internal necrosis and external galling, which reduces market value or renders them useless for either fresh packing or processing. Economic data on the impact of *M. hapla* on potatoes in Europe is not readily available. Experimental studies by Olthof and Potter (1972), showed that marketable yield of potatoes and total weight of tuber was reduced at low densities of *M. hapla* (666 nematodes/kg soil) and many of the tubers suffered large amounts of blemishing. The highest nematode density (18,000 nematodes/kg soil) caused 46% yield reductions in potato. In Idaho, Hafez and Sundararaj (2007) found that damage in potatoes is usually most severe following alfalfa hay crops and during years with high spring temperatures.

Tiilikkala *et al*., (1988) suggested that in Finland, *M. hapla* may overwinter but survival and damage is considered very limited, and in Canada where *M. hapla* has been found in potatoes, populations are small and damage has not been significant (New Brunswick Canada, not dated). Furthermore, *M. hapla* is not generally considered to be a serious pest of potato in the Midwest of the US. However, where potatoes are grown in rotations with highly susceptible vegetables, *M. hapla* infestations may be exacerbated (Melakeberhan, Douches, and Wang, 2012).

Control

As for *M. chitwoodi* the most likely method of introducing *M. hapla* into a new area is through the movement of infected or contaminated planting material as the nematode has very limited potential for natural movement (only second-stage juveniles can move in the soil and, at most, only a few tens of centimetres). Infected tubers can easily transport the nematode as both eggs and females survive and propagate in tubers, therefore seed potatoes are a primary challenge that needs to be met (Been *et al*., 2007).

The movement of non-host seedling transplants, nursery stock, machinery or other products which are contaminated with soil, sand or gravel (including clothing, containers, packaging etc) infested with *M. hapla* could also result in spread. Nematode movement can also be facilitated by contaminated irrigation water or animals moving between fields (Wale, Platt and Cattlin, 2008).

Chemical control

Whilst nematicides are able to reduce populations of *M. hapla* if host plants are not controlled the effect of treatment will be short lived.

Crop rotation and green manures

Wageningen University and Research host a website for Dutch farmers to identify and control nematodes, including *M. hapla* on their farms (http://www.aaltjesschema.nl/). Whilst crop

rotations for the control of *M. hapla* are limited due to its wide host range, it is recommended that grasses (e.g. annual ryegrass, timothy, sudangrass), cereals (e,g. barley) and maize which are non-hosts can be incorporated into rotations to help reduce populations (e.g. Bélair, 1996; Viaene and Abawi, 1998; Widmer and Abawi, 2002). Good weed control is essential, however, as many weeds are hosts. The website also recommends that if grasses or grains are used as green manures, where *M. hapla* is a problem, that this is destroyed before winter to prevent propagation of other problematic nematodes (e.g. *M. chitwoodi* and *fallax*). Furthermore, it is recommended that cultivation of legumes on plots infected by *M. hapla* is avoided as the nematode can multiply well in these crops.

Solanum sisymbriifolium which has been tested and assessed as a potential trap crop for controlling PCN, and is used by some potato growers in the UK, has also been shown not to be a host for *M. hapla* (Scholte and Vos, 2000; Clayton *et al*., 2008).

Alternative chemical control

Pot experiments have indicated that plant extracts, for example from *Artemisia annua*, may have potential for the formulation of new nematicides suitable for sustainable *M. hapla* management (D'Addabbo *et al*., 2017). Field trials, however, are needed to effectively demonstrate the potential of any plant extracts for commercial exploitation.

Host resistance

Research to identify resistant genes to *M. hapla* in wild and primitive cultivars of potato has been conducted (Janssen *et al*., 1995a & b) but at present no potato cultivars have been developed for growers with full resistance against this nematode species.

Breeding companies have been successful in selecting cultivars of the green cover crop fodder radish with (partial) resistance for *M. hapla* and farmers in Belgium and The Netherlands are using these cultivars on a regular basis during the intercrop season (Wesemael *et al*., 2011).

Meloidogyne knowledge gaps

Strategic research

- The geographical distribution of *M. fallax* and *M. minor* in the UK is unknown, as is the incidence of *M. hapla* in UK potato land. Comprehensive surveys, both general (in all hosts) and specific (i.e. potatoes), are required to obtain more information on distribution.
- *M. chitwoodi* may have a wider distribution in Europe than currently documented. Comprehensive surveys would provide a better understanding of the nematodes' distribution.
- Standards for the sampling and detection of *M. minor* and *M. hapla* in potatoes have not been fully developed as for *M. fallax* and *M. chitwoodi*.
- More knowledge about the host range on weed species and requirement for control in GB crop rotations, particularly for *M. fallax* and *M. chitwoodi* is required.

Applied research

- There are currently no potato cultivars with complete resistance to *M. chitwoodi*, *M. fallax*, *M. minor* and *M. hapla* available to growers.

- Novel chemical or biological control methods need to be field tested to effectively demonstrate whether there is any potential for commercial exploitation.
- At present there are few options for non-host crops of *M. minor* in rotations.
- Greater certainty about the host status of crops is required, particularly for *M. chitwoodi*.

Knowledge transfer/exchange

- It is not known what the true economic impact of *M. chitwoodi*, *M. fallax*, *M. minor* and *M. hapla* would be if the species established widely in potato growing areas in the UK.
- Easily accessible information, about suitable crop rotations would be invaluable for UK growers. Information from this review should be condensed into simpler guides.

Conclusions

This review has highlighted that significant knowledge gaps exist for *Meloidogyne* species that pose a potential threat to potato production in the UK.

Nematicides have historically been used to control nematode problems. The currently available nematicides can be used to control *Meloidogyne* species (although this is often not specified on the label of nematicides available in the UK), but if alternative host plants are not controlled the effect of treatment will be short lived. Novel chemical or biological control methods identified by researchers still need to be field tested to effectively demonstrate whether there is any potential for commercial exploitation. Some scientists, however, suggest that nematodes are unlikely to be controlled by natural enemies.

Crop rotation is the most widely used control measure to suppress damage by and population build-up of *Meloidogyne* species. This method of control is complicated by the wide host range of *Meloidogyne* species and lack of availability and low profits of various poor- and non-host crops. It is important for growers to know which *Meloidogyne* species occur in their soils as complications may arise from trying to control more than one species of *Meloidogyne* using non-host crops (i.e. non-host crops may control one species but increase another). Easily accessible information, about suitable crop rotations would be invaluable for UK growers.

A better understanding about the host range on weed species and requirement for control in crop rotations particularly for *M. fallax* and *M. chitwoodi* is also needed.

Plant resistance is an effective, economical and environmentally safe alternative to control root-knot nematodes but at present no potato cultivars are available that have complete resistance to these nematodes and this is an area for future research.

Lack of knowledge about geographical distribution in the UK of *M. minor* and *M. fallax* (the latter may be an emerging native pest in the British Isles according to DAERA (not dated) but there is no published information to support this, and where it has been found, there has been an import association (Defra, unpublished)) and the incidence of *M. hapla* in UK potato fields, makes it difficult to prioritise the current threat of these species. Comprehensive surveys would provide a better understanding of the nematodes distribution and host range. Awareness of *M. minor* and *M. hapla* nematode species by growers and agronomists and early identification

and reporting of suspected infestations will also provide a better understanding of the distribution and occurrence of these species.

Whilst it is not known what the true economic impact of *M. chitwoodi*, *M. fallax*, *M. minor* and *M. hapla* would be if the species established widely in potato growing areas in the UK, evidence from the European continent suggests that should *M. chitwoodi* and *M. fallax* become established they would constitute a significant threat, and as such these species are listed as A2 quarantine pests. The importance of ongoing surveillance, via preventative soil sampling, for *Meloidogne* spp. is highlighted by data from Belgium and the Netherlands. Prior to preventative soil sampling in the Netherlands 7% of vegetables harvested for the canning industry were rejected due to damage by root-knot nematodes, this was reduced to 1.5% in 2003 when soil sampling was implemented (Wesemael *et al*., 2011).

Detection of *M. chitwoodi* and *M. fallax* on potatoes and other host plants (e.g. strawberry plants for *M. fallax)* is based on visual inspection, but symptoms are not always visible. *M. fallax* is also thought to have been previously introduced into the UK via plant waste and soil resulting from the on-site processing of leeks produced in other EU member states. Quarantine inspections and continued vigilance and awareness of theses nematodes by growers and agronomists will help to limit the risk of these two species becoming established in the UK.

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