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## Review article

# The carrot cyst nematode *Heterodera carotae*: a major plant-parasitic nematode requiring more investigation

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**Summary** – The present study reviews the knowledge to date on the carrot cyst nematode *Heterodera carotae*, which has become the primary threat to the carrot sector following the withdrawal of the last chemical soil fumigants in Europe. A keyword co-occurrence network was used to structure this review into five research areas: *i*) biology and epidemiology of *H. carotae*; *ii*) molecular identification and phylogeny; *iii*) population genetics and genomics; *iv*) control methods and strategies; and *v*) root exudates and hatching stimulation. Our findings indicate that *H. carotae* is an under-studied plant-parasitic nematode species, with several identified alternative control methods that require further investigation.

**Keywords** – bibliographical analysis, CorTexT manager, *Daucus carota*, hatching, molecular identification, molecular phylogeny, non-chemical control.

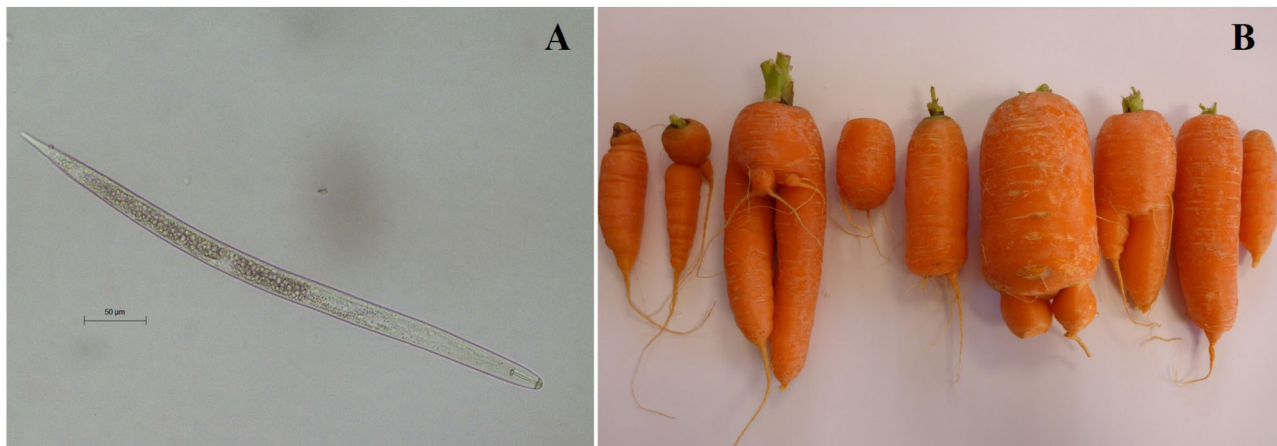
The carrot cyst nematode, *Heterodera carotae* (Fig. 1A), was first described and named in England in 1950 by F.G.W. Jones (Jones, 1950a). It was then found in Scotland in 1970 (Osborne, 1971) before being reported across all European carrot-growing areas, including Denmark, France, Germany, Hungary, Italy, Ireland, The Netherlands, Portugal, Poland, Russia, Serbia, Slovenia, Slovakia, Sweden and Switzerland (Subbotin *et al.*, 2010). After its first report in Michigan, USA (Graney, 1985), its precise distribution in this state was described by Berney & Bird (1988, 1992) who found the nematode in 67.4% of the investigated fields. More recently, *H. carotae* was identified in the province of Ontario in Canada (Yu *et al.*, 2017), in an important Mexican carrot-producing area (Escobar-Avila *et al.*, 2018), in Algeria (Mehalaine *et al.*, 2020) and in South Africa (Subbotin *et al.*, 2010; Shubane *et al.*, 2021). The carrot cyst nematode is still not reported in Australia. Thus, this nematode is a serious threat to

Australia's vegetable industry and is classified as a notifiable plant pest in New South Wales.

In the fields, infestation by *H. carotae* results in irregular areas of stunted plants, characterised by small, abnormally developed and unmarketable carrots (Fig. 1B). Estimated carrot crop losses related to *H. carotae* damage ranged from 20 to 90% in Italy, the USA and Canada (Greco *et al.*, 1993; Koenning *et al.*, 1999; Yu *et al.*, 2017). In a glasshouse experiment, Escobar-Avila & Tovar-Soto (2020) demonstrated that carrot cyst nematodes could cause an average yield loss of 70% over a 10-month period in carrot cultivation.

To carry out this review, we performed a bibliographical analysis using the simple query “*Heterodera carotae*” in the Web of Science core collection (on July 11, 2024). This query led to 42 papers, which have all been checked for relevance. As the bibliographical analysis was only available from 1955 to 2024, we manually added

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**Fig. 1.** Second-stage juvenile of *Heterodera carotae* (A) and the damage it causes on carrots (B).

two papers published by F.G.W. Jones before 1955. With only 44 papers since the first publication (Jones, 1950a), *i.e.*, fewer than one paper per year, this plant-parasitic nematode can be considered as a poorly studied species. For comparison, similar analyses on other cyst nematodes resulted in 561, 943, 1086, 1086 and 2257 papers, using the queries “*Heterodera avenae*”, “*Globodera pallida*”, “*Globodera rostochiensis*”, “*Heterodera schachtii*” and “*Heterodera glycines*”, respectively. This analysis even reached 6388 papers using the query “*Meloidogyne incognita*”. While the relevance of the papers was only checked for *H. carotae*, results obtained for the other nematodes clearly showed that the carrot cyst nematode has been understudied since its identification. However, a temporal analysis (Fig. 2) suggested that the publication dynamic on *H. carotae* is increasing as 15 of the 44 papers were published since 2018.

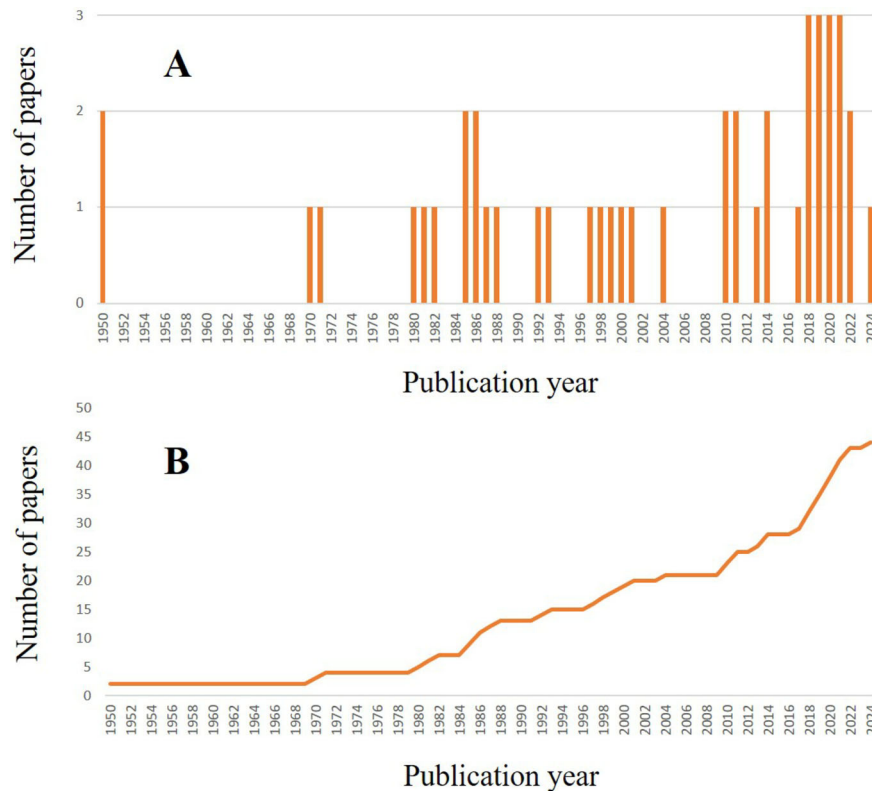
Using titles and abstracts of the 44 papers, a term co-occurrence analysis, performed using CorTexT Manager (Breucker *et al.*, 2016), identified five distinct fields of research on *H. carotae*: *i*) biology and epidemiology; *ii*) molecular identification and phylogeny; *iii*) population genetics and genomics; *iv*) control methods and strategies; and *v*) root exudates and hatching stimulation (Fig. 3). The present study aims to review the existing knowledge published on these five different fields and to identify priorities for further research.

## Biology and epidemiology

*Heterodera carotae* cysts are light brown and lemon-shaped with small vulval cones and contain from 50 to

300 eggs (Escobar-Avila *et al.*, 2018). From the first observations, Jones (1950a) highlighted the presence of a gelatinous egg sac (or egg mass) attached to the cyst of *H. carotae* and showed that this egg sac is as large as the cyst. Second-stage juveniles (J2) in the egg sac hatch once soil moisture and temperature conditions are suitable regardless of host presence, while J2 in the cyst require host presence to hatch. Full descriptions and morphometrics of *H. carotae* females, cysts, males and juveniles are available in the literature (*e.g.*, Subbotin *et al.*, 2010).

As with other cyst nematodes, *H. carotae* enters plant roots as a second-stage juvenile (J2) and establishes a specialised feeding structure, the syncytium, which is a severe nutrient sink for the plant. It uses anti-oxidant enzymes to deal with the active oxygen species produced by the plant during the interaction (Molinari & Miacola, 1997). The penetration of J2 into carrot roots induces the growth of secondary roots, thus increasing the number of potential infection sites for the nematode (Bossis & Mugniéry, 1987). Once juveniles reach the adult stage, males exit the roots in order to mate with females. After mating, the females continue to feed from the syncytium. When egg development is completed, females die and form the cysts, which protect the eggs. To complete its life cycle, *H. carotae* requires 510 day-degrees (Greco & Brandonisio, 1986). Thus, this polyvoltine species can achieve between two and four generations during a carrot-growing season, depending on the local climatic conditions (Greco & Brandonisio, 1986; Subbotin *et al.*, 2010; Shubane *et al.*, 2021).



**Fig. 2.** Distribution of the number (A) and the cumulative number (B) of papers in the corpus by year of publication.

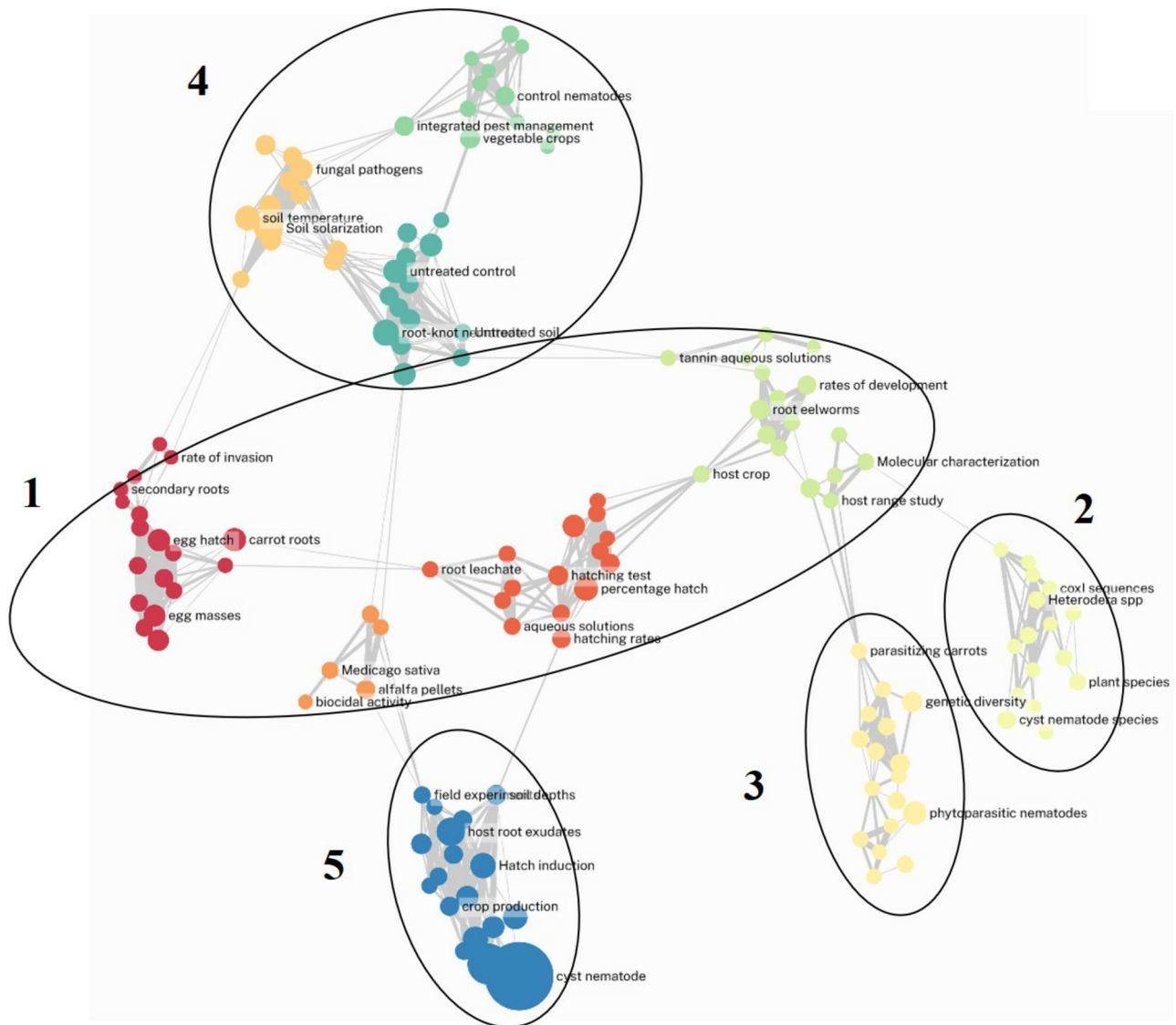
Greco & Brandonisio (1980) produced the relationship between the initial population density and the yield of carrots and estimated a tolerance limit at  $T = 0.8$  eggs  $(\text{ml soil})^{-1}$ . The yield losses in relation to initial densities of eggs were 10% at 4 eggs  $\text{ml}^{-1}$ , 20% at 8 eggs  $\text{ml}^{-1}$ , 40% at 16 eggs  $\text{ml}^{-1}$ , 70% at 32 eggs  $\text{ml}^{-1}$ , 90% at 64 eggs  $\text{ml}^{-1}$  and 100% from 128 eggs  $\text{ml}^{-1}$  and above.

Jones (1950b) showed that *H. carotae* has a very narrow host range as it only attacked cultivated and wild carrots (*Daucus carota*) among the 105 distinct plants tested. The 16 other Umbelliferae tested in the study, including *Pastinaca sativa* (parsnip), were found to be non-host plants for this nematode. The only other wild Umbelliferae reported to support the complete development of *H. carotae* were *Torilis leptophylla* (bristlefruit hedge parsley) (Mugniéry & Bossis, 1988) and *Daucus pulcherrimus* (Oriental Astrodaucus) (Winslow, 1954). From an evolutionary point of view, an interesting prospect would be to explore the wild component and to study the occurrence of *H. carotae* on wild *Daucus* species and the potential genetic relationship between *H. carotae* populations from wild and cultivated carrots.

## Molecular identification and phylogeny

*Heterodera carotae* belongs to the *Goettingiana* group, one of the nine groups in which the *Heterodera* species are distributed (Handoo & Subbotin, 2018). While the *Avenae*, *Humuli* and *Schachtii* groups have recently been revisited (Subbotin *et al.*, 2018, 2022, 2024), the *Goettingiana* group has not yet benefited from this update. However, two studies have proposed the addition of new species within this group: *H. persica* (Maafi *et al.*, 2006) and the new species recently described in China, *H. microulae* (Li *et al.*, 2020). Until now, the closest relatives of *H. carotae* are *H. urticae*, *H. cruciferae* and *H. goettingiana* (Sabo *et al.*, 2001; Subbotin & Skantar, 2018). For instance, a recent phylogenetic analysis grouped the *H. carotae* population identified in 2008 from the Tarlton area in South Africa together in a clade with *H. cruciferae* and *H. urticae* (Shubane *et al.*, 2021). In test carried out *in vitro*, *H. carotae*, *H. cruciferae* and *H. goettingiana* do not interbreed (Yeates, 1970).

Madani *et al.* (2004) produced a phylogenetic tree, based on the ITS-rDNA sequences, which showed a



**Fig. 3.** Network of the co-occurrence of terms. Considering only terms composed of two or three words (*i.e.*, monograms forbidden) with a minimum frequency of two, a list of 200 terms was extracted from titles and abstracts of the 44 papers and then reduced to 153 terms through the exclusion of terms corresponding either to a nematode species name (*e.g.*, *Heterodera carotae*), a locality (*e.g.*, South Africa) or non-informative terms (*e.g.*, aim of the work). This network was prepared using the network mapping tool on CorTeX Manager platform (<https://www.cortext.net>). Nodes represent terms; lines between nodes represent links that measure the mutual occurrence of the terms among papers. The five identified research fields are circled and numbered. An interactive version of this network is available online at <https://retina.cortext.net/#/graph/?url=https%3A%2F%2Fassets.cortext.net%2Fdocs%2F95ab075c4f0ef84393b6a966bb5c571>.

strong homology between *H. carotae* and *H. cruciferae*. A diagnostic tool using conventional and real-time PCR has been developed specifically to recognise *H. carotae* based on a primer pair targeting the *COXI* gene sequence (*i.e.*, the cytochrome oxidase subunit I of mito-

chondrial DNA), with a single J2 detection limit (Madani *et al.*, 2018). However, using the available molecular tools, Escobar-Avila *et al.* (2018) showed that it was not possible to differentiate *H. carotae* from *H. cruciferae*. Accordingly, Huston *et al.* (2022) showed that *COXI*

sequences enabled identification of the different *Heterodera* species except the *H. carotae*/*H. cruciferae* pair. As these two nematodes are morphologically identical, only a time-consuming host range test can distinguish them. To fill this significant diagnostic gap, Fouville *et al.* (2024) have developed two primer sets targeting specifically the two species and validated them through real-time PCR protocols (SYBR Green singleplex and TaqMan multiplex real-time PCR). These new diagnostic tools appear promising as they were successfully validated using a set of European populations, even if their reliability could be improved by using populations from other parts of the world.

### Population genetics and genomics

So far, the available molecular markers enabled exploration of the inter-species genetic relationship, but not the intra-specific genetic diversity. Recently, Gautier *et al.* (2019) have developed a set of 13 polymorphic microsatellite markers and used them to genotype several European populations of *H. carotae*. Their results revealed that these populations belong to two distinct genetic clusters, one located in the north of Europe and the second one located in the south of Europe. Esquibet *et al.* (2020) used these microsatellite markers to explore the genetic structure of *H. carotae* populations in a French carrot-growing area located in west Normandy and highlighted a strong gene flow among populations (with a maximum distance between fields of 120 km). The authors hypothesised that soil transport with agricultural machinery and leek seedlings was responsible for migration of *H. carotae* cysts among fields. These two studies (Gautier *et al.*, 2019; Esquibet *et al.*, 2020) also showed that, as for other cyst nematode species (*e.g.*, Montarry *et al.*, 2015), *H. carotae* populations were characterised by a strong heterozygote deficit (*i.e.*,  $F_{IS} > 0$ ), which suggests consanguineous mating due to the low dispersal capability of J2 hatched from the same cyst.

In terms of genomics, Wram *et al.* (2022) recently provided the first draft genome of *H. carotae*, which was generated from short reads (Illumina HiSeq technology). This genome of 95 Mb was composed of 17 839 scaffolds and contained 17 212 predicted protein coding genes. However, an effort is still needed to produce a high-quality reference genome (*i.e.*, with a reduced number of scaffolds and a high N50 value), using third generation sequencing technologies producing longer sequence reads, and also

RNAseq reads to help future annotation of this new cyst nematode genome.

### Control methods and strategies

Before the withdrawal of most pesticides, several studies have explored the efficiency of nematicides to control *H. carotae*. The efficacy of isazofos and benfuracarb was analysed in field trials in Italy (Greco *et al.*, 1986) and results showed that applications of isazofos gave yield increases, while benfuracarb was not effective against *H. carotae*. Under laboratory conditions, it was demonstrated that aldicarb and fenamiphos suppressed emergence and movement of *H. carotae* J2 (Greco & Elia, 2000). A survey published by Greco *et al.* (2019) highlighted the need for very effective chemical fumigation as part of an integrated pest management programme (IPM). Fritsch *et al.* (2014) and Curto *et al.* (2014) showed that dimethyl disulfide (DMDS) appeared to be a promising alternative to existing fumigants (*e.g.*, 1,3-dichloropropene) to control *H. carotae*. However, the fumigants 1,3-dichloropropene and DMDS are now both banned in Europe for their use as fumigants on carrot crops.

Gasparic *et al.* (2022) reviewed the non-chemical methods available to control *H. carotae* populations. Among these methods, solarisation allows soil disinfection by increasing the soil temperature (up to 60°C). The best effect is achieved by placing transparent plastic sheets on moist and loose soil for 4-6 weeks during the warmest period of the year (D'Addabbo *et al.*, 2010a). This technique is particularly suitable in regions with high summer temperatures. Indeed, a former study conducted by Greco *et al.* (1998), analysing the effect of both the temperature and exposure time on the mortality of *H. carotae*, showed that solarisation could be an effective control method in warm and sunny countries but not in colder regions. Moreover, the authors showed that *H. carotae* was less affected than *H. schachtii* by heat stress. Indeed, a 24 h exposure time at 45°C was sufficient to obtain a 98.5% loss of viability for *H. schachtii*, whereas cysts of *H. carotae* required 60 h at the same temperature to reach the same result (Greco *et al.*, 1998).

Nematicidal plants may also play an important role as biofumigants in the sustainable control of phytoparasitic nematodes through the phytochemical compounds they secrete in the soil (D'Addabbo *et al.*, 2014). For example, Brassicaceae extracts – glucosinolates and related hydrolysis products, mainly isothiocyanates – have been shown to be toxic to the carrot cyst nematode in *in vitro*

experiments (Avato *et al.*, 2013). These toxic compounds have a broad spectrum of biocidal activity against bacteria, soil-borne pathogens, insects, nematodes and weed seeds (Lazzeri *et al.*, 2009; Caboni *et al.*, 2012). Therefore, soil biofumigation using Brassicaceae plant species could be a promising solution but needs to be investigated more because the efficacy of the isothiocyanates depends on the pH, the temperature and soil moisture (Buskov *et al.*, 2002). It has also been shown that soil amendments composed of *Medicago sativa* (alfalfa) pelleted meal, containing saponins, allowed both a decrease in *H. carotae* population density and an increase in carrot yield (D'Addabbo *et al.*, 2010b, 2011). Other plants could also be biofumigated; *Sorghum bicolor* (sorghum), which produce dhurrin, has been shown to be effective against root-knot nematodes (Djian-Caporalino *et al.*, 2019) and needs to be tested against *H. carotae*. The use of *Castanea sativa* (chestnut) tannin aqueous solutions, which have a nematocidal activity, could also be favourably considered for protection of carrot against *H. carotae* (Maistrello *et al.*, 2018).

Biocontrol solutions have also been explored. An example of an alternative product against parasitic nematodes is abamectin, an anthelmintic produced by the soil bacterium *Streptomyces avermitilis* (Khalil, 2013). This anthelmintic is already registered as an insecticide and nematicide. This product can be used as a seed treatment to protect early growth stage plants from nematodes and insects that attack the root system (Khalil, 2013). Abamectin has recently been shown to have nematocidal activity against *H. carotae* (Sasanelli *et al.*, 2020). This *in vitro* study reported more than 80% mortality rate when exposing the nematode to the highest abamectin tested dose ( $36 \mu\text{g a.s. ml}^{-1}$ ) (Sasanelli *et al.*, 2020).

In their recent reviews, McDonald & Telfer (2019) and Gasparic *et al.* (2022) considered that crop rotation using non-host plants (*i.e.*, any cultivated plant other than a carrot) combined with resistant host plants is the most promising long-term control measure for *H. carotae*. However, several carrot cultivars have been screened for resistance (*e.g.*, Mugniéry & Bossis, 1985) but there is currently no commercial resistant cultivar. This reinforces the needs to search for resistant carrot cultivars and to combine the above-mentioned available alternative solutions – with partial and/or variable effects – in an integrated pest management strategy.

## Root exudates and hatching stimulation

The first studies describing the hatching process of *H. carotae* showed that J2 hatched after 2 months from eggs in newly-formed cysts, whereas J2 in egg sacs hatched promptly (Greco, 1981). Hatching is reportedly greater at 15–20°C, substantial at 5–10°C and negligible at 25°C (Greco & Brandonisio, 1986). The age of carrot plants affected the hatch and most juveniles emerged with root exudates from 5- to 7-week-old carrots (Greco *et al.*, 1982).

The strong dependence for hatch of *H. carotae* on root exudates from its host plant offers an opportunity to use this feature as a new control method. This had recently motivated Ngala *et al.* (2021) to test root exudates from 33 distinct plant species for their *in vitro* ability to induce hatching of *H. carotae*. Their results showed that only exudates from carrots were efficient. Under control conditions, carrot exudates, crude or diluted 2× in water, stimulated hatching of J2 from cysts placed at 10 and 20 cm soil depth (Ngala *et al.*, 2021). In addition, Gautier *et al.* (2021) showed that populations from both genetic clusters (four from *H. carotae* cluster 1 and four from cluster 2; Gautier *et al.*, 2019) exhibited a high level of hatching with carrot root exudates. Finally, Ngala *et al.* (2024) tested a 'lure and starve' or 'suicide hatching' strategy in field trials, based on stimulating hatching of J2 in the absence of their host plant. The results showed that after two applications, one in autumn followed by another one in spring, the decline of *H. carotae* density reached up to 54% in field plots drenched with carrot root exudates.

The application of host root exudates can reduce the population densities of *H. carotae*, but the required quantities of root exudates to treat large cropping areas is clearly the main technical and industrial challenge to solve. So, the next step would be the identification of the molecule(s) which is(are) exuded in the soil by carrots and stimulate *H. carotae* J2 hatching.

## Conclusion and prospects

Despite decades of research, *H. carotae* still remains a poorly known species, even though it is a major threat to carrot production all over the world. Found worldwide in cultivated areas, nothing is known about its presence in wild ecosystems and its evolutionary history. Its genetic and morphological proximity to *H. cruciferae* also raises questions even though their host ranges are radically different. Recently, the withdrawal of nematicides

(e.g., 1,3-dichloropropene) creates a favourable context for the development of more specific new control strategies, which require the acquisition of new specific knowledge and thus new research efforts. In this sense recent studies have provided valuable information on its biology, molecular identification, population genetics and alternative control methods. Among the various topics of interest regarding *H. carotae*, we first observed that the impact of climate change on the epidemiology and management of the carrot cyst nematode is poorly studied (only one among the 44 publications on *H. carotae*). Using a modelling approach, Colagiero & Ciancio (2011) showed that a mean daily temperature increase of 1.5°C or 2.0°C would cause an additional *H. carotae* generation during the cropping season. In addition to this important topic, we propose a list of actions that we consider to be priorities.

A first interesting prospect would be to explore the wild component and to study the genetic relationship, potential gene flow and life history traits between *H. carotae* populations from wild and cultivated carrots. Indeed, populations of crop pathogens have necessarily wild relative populations on wild host plants that may be considered as potential reservoirs of diversity. As an example, Gracianne *et al.* (2014) showed that *H. betae*, which was previously described as a crop species in the field in The Netherlands, was largely distributed from the south to the north of Europe on the wild sea beet *Beta maritima*. Thus, there is no reason for assuming that *H. carotae* is present only in the field. We have initiated investigation into this aspect by sampling soil in Brittany (France) under the wild species *Daucus carota* subsp. *gummifer*, and some samples contained cysts that morphologically resemble *H. carotae* cysts but which need now to be biologically and genetically characterised. These investigations would be extended to other wild *Daucus* and larger geographic areas in order to explore the co-evolution between *H. carotae* and the genus *Daucus* and to measure potential gene flow between both (wild and cultivated).

In terms of control methods, the control of pest populations is now quickly changing with the demand and the need for more agro-ecological environmentally-friendly methods. Plant-parasitic nematodes and *H. carotae* are no exception to this new direction, especially with the ban of the last nematicides with a wide target broad spectrum. Thus, pest management will no longer be based on a single solution but on several complementary solutions, each being less effective than the replaced solution but

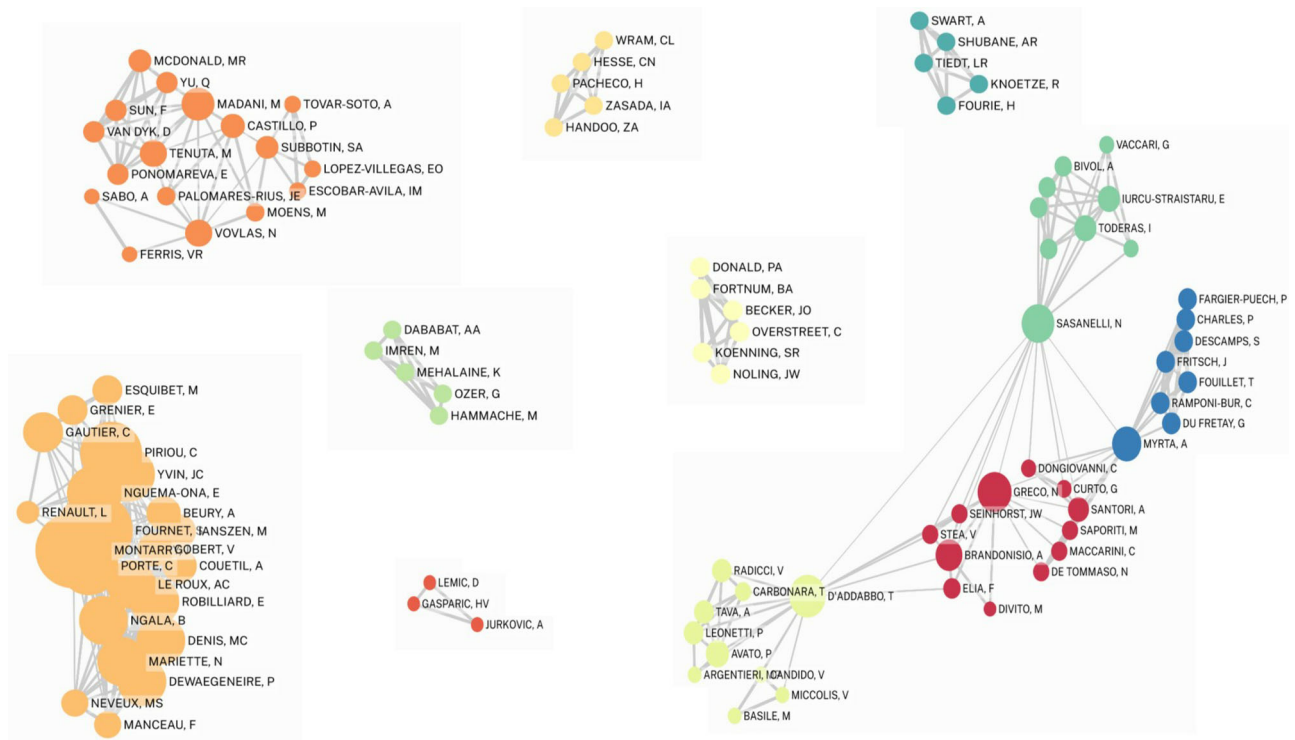
together enabling a satisfactory control level. In the case of *H. carotae*, exploring alternative and more specific control methods as well as combining them in an integrated pest management (IPM) approach has become a matter of urgency. This means first to be sure of the identity of the target. It is therefore crucial to deploy the recently developed molecular tools (Fouville *et al.*, 2024) to allow carrot farmers to distinguish *H. carotae* from *H. cruciferae*. Second, IPM involves pursuing the development of a control strategy based on plant resistance, on the biofumigation (e.g., sorghums), on the stimulation of *H. carotae* hatching in the absence of the host plant, and on the use of soil antagonists.

Identifying organisms within the soil microbiota with direct regulatory capacities is also a promising avenue that can provide effective answers where high population densities of *H. carotae* occur. Current technology makes it possible to scan a large number of candidate bacteria and fungi in a relative short time. Two methods would then be available: using the identified and validated organism as a biocontrol agent by inoculating it into the soil, or managing the soil and the crop rotation in a way that allows natural enemies to play a role in managing nematode populations.

Discovering the molecules involved in the chemical dialogue established between the host plant and the nematode is obviously a challenge for developing new biocontrol strategies. To do so, one may rely on recent advances in LC- or GC-(HR)MS based metabolomics approaches to be compatible with the low concentrations expected in the analysed matrices (root exudates). Once identified, the molecule could be bio-sourced to ease its use in fields. The identification of the molecule(s) which is(are) exuded in the soil by carrots and stimulate(s) *H. carotae* hatching may also make it possible to understand the J2 hatching process better and to define more precisely the factors that play a role in this critical step in the *H. carotae* life cycle.

Within cyst nematodes, a notable feature of *H. carotae* is its parasitic hyper-specialisation, which makes it a biological model for research questions about the specialisation (as opposed to polyphagia) both from an evolutionary and functional point of view. Using an improved reference genome, comparative genomics approaches would be performed to compare *H. carotae* with *H. cruciferae*, which are genetically close with distinct size of host ranges, *i.e.*, distinct level of specialisation.

To improve both our fundamental and applied knowledge of this plant-parasitic nematode, further research on



**Fig. 4.** Co-authorship network using the 44 papers. This network was prepared using the network mapping tool on CorTexT Manager platform (<https://www.cortext.net>).

*H. carotae* is essential. However, it is equally important to enhance international collaborations among research teams. Indeed, a network based on the co-authorship of the 44 publications on *H. carotae* (Fig. 4) highlighted eight distinct groups of authors. While two of these groups involve authors from different institutions/countries, the other six are limited to national collaborations. More dynamic international partnerships are therefore crucial to define the best strategies to manage *H. carotae* populations in a sustainable and eco-friendly way.

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### References used in the bibliographical analyses (n=44)

Avato, P., D'Addabbo, T., Leonetti, P. & Argentieri, M.P. (2013). Nematicidal potential of Brassicaceae. *Phytochemistry Reviews* 12, 791-802. DOI: 10.1007/s11101-013-9303-7

Berney, M.F. & Bird, G.W. (1988). Distribution of *Heterodera carotae* in Michigan. *Journal of Nematology* 20, 628.

Berney, M.F. & Bird, G.W. (1992). Distribution of *Heterodera carotae* and *Meloidogyne hapla* in Michigan carrot production. *Journal of Nematology* 24, 776-778.

Bossis, M. & Mugniéry, D. (1987). Variability within *Heterodera carotae* in the ability to stimulate production of secondary roots in carrots. *Nematologica* 33, 322-327. DOI: 10.1163/187529287X00452

Colagiero, M. & Ciancio, A. (2011). Climate changes and nematodes: expected effects and perspectives for plant protection. *Redia-Giornale di Zoologia* 94, 113-118.

Curto, G., Dongiovanni, C., Sasanelli, N., Santori, A. & Myrta, A. (2014). Efficacy of dimethyl disulfide (DMDS) in the control of the root-knot nematode *Meloidogyne incognita* and the cyst nematode *Heterodera carotae* on carrot in field condition in Italy. *Acta Horticulturae* 1044, 405-410. DOI: 10.17660/ActaHortic.2014.1044.55

- D'Addabbo, T., Miccolis, V., Basile, M. & Candido, V. (2010a). Soil solarization and sustainable agriculture. *Sociology, Organic Farming, Climate Change and Soil Science* 3, 217-274. DOI: 10.1007/978-90-481-3333-8\_9
- D'Addabbo, T., Radicci, V., Avato, P. & Tava, A. (2010b). Use of pelleted *Medicago sativa* meal for the control of root-knot and cyst nematodes. *Acta Horticulturae* 883, 303-308. DOI: 10.17660/ActaHortic.2010.883.37
- D'Addabbo, T., Carbonara, T., Leonetti, P., Radicci, V., Tava, A. & Avato, P. (2011). Control of plant parasitic nematodes with active saponins and biomass from *Medicago sativa*. *Phytochemistry Reviews* 10, 503-519. DOI: 10.1007/s11101-010-9180-2
- Escobar-Avila, I.M., Lopez-Villegas, E.O., Subbotin, S.A. & Tovar-Soto, A. (2018). First report of carrot cyst nematode *Heterodera carotae* in Mexico: morphological, molecular characterization and host range study. *Journal of Nematology* 50, 229-242. DOI: 10.21307/jofnem-2018-021
- Esquibet, M., Gautier, C., Piriou, C., Grenier, E., Fournet, S. & Montarry, J. (2020). Evidence of strong gene flow among French populations of the carrot cyst nematode *Heterodera carotae*. *Plant Pathology* 69, 168-176. DOI: 10.1111/ppa.13102
- Fritsch, J., Fouillet, T., Charles, P., Fargier-Puech, P., Ramponi-Bur, C., Descamps, S., Du Fretay, G. & Myrta, A. (2014). French experiences with dimethyl disulfide (DMDS) as a nematicide in vegetable crops. *Acta Horticulturae* 1044, 427-433. DOI: 10.17660/ActaHortic.2014.1044.59
- Gasparic, H.V., Jurkovic, A. & Lemic, D. (2022). Integrated pest management approaches for two major carrot pests – the carrot root fly and carrot cyst nematode. *Journal of Central European Agriculture* 23, 69-81. DOI: 10.5513/JCEA01/23.1.3380
- Gautier, C., Esquibet, M., Fournet, S., Piriou, C., Yvin, J.C., Nguema-Ona, E., Grenier, E. & Montarry, J. (2019). Microsatellite markers reveal two genetic groups in European populations of the carrot cyst nematode *Heterodera carotae*. *Infection, Genetics and Evolution* 73, 81-92. DOI: 10.1016/j.meegid.2019.04.011
- Gautier, C., Montarry, J., Piriou, C., Renault, L., Porte, C., Yvin, J.C., Nguema-Ona, E. & Fournet, S. (2021). Impact of the genetic diversity of three cyst nematodes on the effectiveness of root exudates to induce hatching. *European Journal of Plant Pathology* 161, 553-563. DOI: 10.1007/s10658-021-02341-5
- Graney, L.S.O. (1985). Observations on the morphology of *Heterodera carotae* and *Heterodera avenae* in Michigan. *Journal of Nematology* 17, 519.
- Greco, N. (1981). Hatching of *Heterodera carotae* and *Heterodera avenae*. *Nematologica* 27, 366-371. DOI: 10.1163/187529281X00377
- Greco, N. & Brandonisio, A. (1980). Relationship between *Heterodera carotae* and carrot yield. *Nematologica* 26, 497-500. DOI: 10.1163/187529280X00440
- Greco, N. & Brandonisio, A. (1986). The biology of *Heterodera carotae*. *Nematologica* 32, 447-460. DOI: 10.1163/187529286X00327
- Greco, N. & Elia, F. (2000). Effects of the nematicides albicarb and fenamiphos on the egg hatch, movement, and root penetration of the carrot cyst nematode, *Heterodera carotae*. *Acta Horticulturae* 532, 189-194. DOI: 10.17660/ActaHortic.2000.532.24
- Greco, N., Divito, M. & Brandonisio, A. (1982). Effect of temperature and plant-age on the hatching of *Heterodera carotae* and *Heterodera fici*. *Journal of Nematology* 14, 443.
- Greco, N., Elia, F. & Brandonisio, A. (1986). Control of *Heterodera carotae*, *Ditylenchus dipsaci*, and *Meloidogyne javanica* with fumigant and nonfumigant nematicides. *Journal of Nematology* 18, 359-364.
- Greco, N., D'Addabbo, T., Brandonisio, A. & Elia, F. (1993). Damage to Italian crops caused by cyst-forming nematodes. *Journal of Nematology* 25, 836-842.
- Greco, N., D'Addabbo, T., Sasanelli, N., Seinhorst, J.W., Stea, V. & Brandonisio, A. (1998). Effects of temperature and length of exposure on the mortality of the carrot cyst nematode, *Heterodera carotae*. *International Journal of Pest Management* 44, 99-107. DOI: 10.1080/096708798228392
- Greco, N., Saporiti, M., Maccarini, C., Santori, A., De Tommaso, N. & Myrta, A. (2019). Sustainability of southern European carrot production in relation to fumigation practices. *Acta Horticulturae* 1264, 183-190. DOI: 10.17660/ActaHortic.2019.1264.22
- Jones, F.G.W. (1950a). A new species of root eelworm attacking carrots. *Nature* 165, 81. DOI: 10.1038/165081a0
- Jones, F.G.W. (1950b). Observations on the beet eelworm and other cyst-forming species of *Heterodera*. *Annals of Applied Biology* 37, 407-440. DOI: 10.1111/j.1744-7348.1950.tb00966.x
- Koenning, S.R., Overstreet, C., Noling, J.W., Donald, P.A., Becker, J.O. & Fortnum, B.A. (1999). Survey of crop losses in response to phytoparasitic nematodes in the United States for 1994. *Journal of Nematology* 31, 587-618.
- Madani, M., Vovlas, N., Castillo, P., Subbotin, S.A. & Moens, M. (2004). Molecular characterization of cyst nematode species (*Heterodera* spp.) from the Mediterranean basin using RFLPs and sequences of ITS-rDNA. *Journal of Phytopathology* 152, 229-234. DOI: 10.1111/j.1439-0434.2004.00835.x
- Madani, M., Palomares-Rius, J.E., Vovlas, N., Castillo, P. & Tenuta, M. (2018). Integrative diagnosis of carrot cyst nematode (*Heterodera carotae*) using morphology and several molecular markers for an accurate identification. *European Journal of Plant Pathology* 150, 1023-1039. DOI: 10.1007/s10658-017-1342-2
- Maistrello, L., Sasanelli, N., Vaccari, G., Toderas, I. & Iurcu-Straistaru, E. (2018). Control of the carrot cyst nematode *Heterodera carotae* by tannin aqueous solutions. *Scientific Papers. Series A. Agronomy* 61, 316-321.

- McDonald, M.R. & Telfer, Z. (2019). Sustainable carrot production. In: Hochmuth, G. (Ed.). *Achieving sustainable cultivation of vegetables*. London, UK, Burleigh Dodds Science Publishing, pp. 437-458.
- Mehalaine, K., Imren, M., Özer, G., Hammache, M. & Dabat, A.A. (2020). Molecular identification and phylogenetic diversity of cereal cyst nematodes (*Heterodera* spp.) populations from Algeria. *Nematropica* 50, 134.
- Molinari, S. & Miacola, C. (1997). Antioxidant enzymes in phytoparasitic nematodes. *Journal of Nematology* 29, 153-159.
- Mugniéry, D. & Bossis, M. (1985). Influence of host competition and physiological-state of infective juveniles on penetration, development and sex of *Heterodera carotae* Jones. *Nematologica* 31, 335-343. DOI: 10.1163/187529285X00391
- Ngala, B., Mariette, N., Ianszen, M., Dewaegeneire, P., Denis, M.C., Porte, C., Piriou, C., Robilliard, E., Couetil, A., Nguema-Ona, E. et al. (2021). Hatching induction of cyst nematodes in bare soils drenched with root exudates under controlled conditions. *Frontiers in Plant Science* 11, 602825. DOI: 10.3389/fpls.2020.602825
- Ngala, B., Dewaegeneire, P., Robilliard, E., Mariette, N., Manceau, F., Denis, M.C., Porte, C., Neveux, M.S., Le Roux, A.C., Fournet, S. et al. (2024). Lure and starve: Host root exudates to suppress field populations of cyst nematodes. *Applied Soil Ecology* 201, 105490. DOI: 10.1016/j.apsoil.2024.105490
- Osborne, P. (1971). First report of *Heterodera carotae* in Scotland. *Plant Pathology* 20, 148. DOI: 10.1111/j.1365-3059.1971.tb00534.x
- Sabo, A., Vovlas, N. & Ferris, V.R. (2001). Phylogenetic relationships based on ribosomal DNA data for four species of cyst nematodes from Italy and one from Syria. *Journal of Nematology* 33, 183-190.
- Sasanelli, N., Toderas, I., Iurcu-Straistaru, E., Bivol, A., Rusu, S., Konrat, A. & Andoni, C. (2020). *In vitro* effect of abamectin from *Streptomyces avermitilis* on the survival of the cyst nematodes *Globodera pallida*, *Heterodera carotae* and *Heterodera schachtii*. *Scientific Papers. Series B. Horticulture* 64, 456-461.
- Shubane, A.R., Swart, A., Knoetze, R., Tiedt, L.R. & Fourie, H. (2021). Characterization of *Heterodera carotae* from the Tarlton area, South Africa, and determination of its life cycle under field conditions: a baseline study. *Journal of Plant Diseases and Protection* 128, 1637-1655. DOI: 10.1007/s41348-021-00503-5
- Wram, C.L., Hesse, C.N., Handoo, Z.A., Pacheco, H. & Zasada, I.A. (2022). Genome announcement: the draft genome of the carrot cyst nematode *Heterodera carotae*. *Journal of Nematology* 54, e2022-1. DOI: 10.2478/jofnem-2022-0014
- Yeates, G.W. (1970). Failure of *Heterodera carotae*, *H. cruciferae* and *H. goettingiana* to interbreed *in vitro*. *Nematologica* 16, 153-154. DOI: 10.1163/187529270X00586
- Yu, Q., Ponomareva, E., Van Dyk, D., McDonald, M.R., Sun, F., Madani, M. & Tenuta, M. (2017). First report of the carrot cyst nematode (*Heterodera carotae*) from carrot fields in Ontario, Canada. *Plant Disease* 101, 1056. DOI: 10.1094/PDIS-01-17-0070-PDN

## Other cited references

- Breucker, P., Cointet, J., Hannud Abdo, A., Orsal, G., de Quatrebarbes, C., Duong, T., Martinez, C., Ospina Delgado, J.P., Medina Zuluaga, L.D., Gómez Peña, D.F. et al. (2016). *CorText Manager (version v2)*. Available online at <https://docs.cortext.net>.
- Buskov, S., Serra, B., Rosa, E., Sorensen, H. & Sorensen, J.C. (2002). Effect of intact glucosinolates and products from glucosinolates in myrosinase-catalyzed hydrolysis on the potato cyst nematode (*Globodera rostochiensis* Woll.). *Journal of Agricultural and Food Chemistry* 50, 690-695.
- Caboni, P., Sarais, G., Aissani, N., Tocco, G., Sasanelli, N., Liori, B., Carta, A. & Angioni, A. (2012). Nematicidal activity of 2-thiophenecarboxaldehyde and methylisothiocyanate from caper (*Capparis spinosa*) against *Meloidogyne incognita*. *Journal of Agricultural and Food Chemistry* 60, 7345-7351. DOI: 10.1021/jf302075w
- D'Addabbo, T., Laquale, S., Lovelli, S., Candido, V. & Avato, P. (2014). Biocide plants as a sustainable tool for the control of pests and pathogens in vegetable cropping systems. *Italian Journal of Agronomy* 9, 616. DOI: 10.4081/ija.2014.616
- Djian-Caporalino, C., Mateille, T., Bailly-Bechet, M., Marteu, N., Fazari, A., Bautheac, P., Raptopoulo, A., Duong, L.V., Tavoillot, J., Martiny, B. et al. (2019). Evaluating sorghums as green manure against root-knot nematodes. *Crop Protection* 122, 142-150. DOI: 10.1016/j.cropro.2019.05.002
- Escobar-Avila, I. & Tovar-Soto, A. (2020). Population dynamics of the carrot cyst nematode *Heterodera carotae* under greenhouse conditions. *Revista Mexicana de Fitopatología* 39, 1. DOI: 10.18781/r.mex.fit.2007-1
- Fouville, D., Biget, M., Montarry, J., Fournet, S. & Grenier, E. (2024). A diagnostic gap to fill: Development of molecular tools to distinguish the plant-parasitic nematodes species *Heterodera carotae* and *Heterodera cruciferae*. *Physiological and Molecular Plant Pathology* 134, 102434. DOI: 10.1016/j.pmpp.2024.102434
- Gracianne, C., Petit, E.J., Porte, C., Renault, L., Fouville, D., Rouaux, C., Arnaud, J.-F. & Fournet, S. (2014). Spatial distribution and basic ecology of *Heterodera schachtii* and *H. betae* wild populations developing on sea beet, *Beta vulgaris* ssp. *maritima*. *Nematology* 16, 797-805. DOI: 10.1163/15685411-00002809
- Handoo, Z.A. & Subbotin, S.A. (2018). Taxonomy, identification and principal species. In: Perry, R.N., Moens, M. & Jones, J.T. (Eds). *Cyst nematodes*. Wallingford, UK, CAB International, pp. 365-394.

- Huston, D.C., Khudhir, M. & Hodda, M. (2022). Reliability and utility of standard gene sequence barcodes for the identification and differentiation of cyst nematodes of the genus *Heterodera*. *Journal of Nematology* 54, 20220024. DOI: 10.2478/jofnem-2022-0024
- Khalil, M.S. (2013). Abamectin and azadirachtin as eco-friendly promising biorational tools in integrated nematodes management programs. *Journal of Plant Pathology & Microbiology* 4, 174. DOI: 10.4172/2157-7471.1000174
- Lazzeri, L., Curto, G., Dallavalle, E., D'Avino, L., Malaguti, L., Santi, R. & Patalano, G. (2009). Nematicidal efficacy of biofumigation by defatted Brassicaceae meal for control of *Meloidogyne incognita* (Kofoid & White) Chitw. on a full field zucchini crop. *Journal of Sustainable Agriculture* 33, 349-358. DOI: 10.1080/10440040902773202
- Li, W., Li, H., Ni, C., Peng, D., Liu, Y., Luo, N. & Xu, X. (2020). Description of *Heterodera microulae* sp. n. (Nematoda: Heteroderinae) from China – a new cyst nematode in the *Goettingiana* group. *Journal of Nematology* 52, e2020-97. DOI: 10.21307/jofnem-2020-097
- Maafi, Z.T., Sturhan, D., Subbotin, S.A. & Moens, M. (2006). *Heterodera persica* sp. n. (Tylenchida: Heteroderidae) parasitizing Persian Hogweed *Heracleum persicum* (Desf. ex Fisch.) in Iran. *Russian Journal of Nematology* 14, 171-178.
- Montarry, J., Jan, P.-L., Gracianne, C., Overall, A.D.J., Bardou-Valette, S., Olivier, E., Fournet, S., Grenier, E. & Petit, E.J. (2015). Heterozygote deficits in cyst plant-parasitic nematodes: possible causes and consequences. *Molecular Ecology* 24, 1654-1667. DOI: 10.1111/mec.13142
- Mugniéry, D. & Bossis, M. (1988). *Heterodera carotae* Jones, 1950. 1. Gamme d'hôtes, vitesse de développement, cycle. *Revue de Nématologie* 11, 307-313.
- Subbotin, S.A. & Skantar, A.M. (2018). Molecular taxonomy and phylogeny. In: Perry, R.N., Moens, M. & Jones, J.T. (Eds). *Cyst nematodes*. Wallingford, UK, CAB International, pp. 399-418.
- Subbotin, S.A., Mundo-Ocampo, M. & Baldwin, J.G. (2010). *Systematics of cyst nematodes (Nematoda: Heteroderinae). Nematology Monographs and Perspectives 8B* (Series Editors: Hunt, D.J. & Perry, R.N.). Leiden, The Netherlands, Brill.
- Subbotin, S.A., Toumi, F., Elekcioğlu, I.H., Waeyenberge, L. & Tanha Maafi, Z. (2018). DNA barcoding, phylogeny and phylogeography of the cyst nematode species of the *Avenae* group from the genus *Heterodera* (Tylenchida: Heteroderidae). *Nematology* 20, 671-702.
- Subbotin, S.A., Roubtsova, T.V., Bostock, R.M., Tanha Maafi, Z. & Chizhov, V.N. (2022). DNA barcoding, phylogeny and phylogeography of the cyst nematode species of the *Humuli* group from the genus *Heterodera* (Tylenchida: Heteroderidae). *Nematology* 24, 873-886. DOI: 10.1163/15685411-bja10176
- Subbotin, S.A., Roubtsova, T.V., Bostock, R.M., Tanha Mafi, Z., Chizhov, V.N., Palomares-Rius, J.E. & Castillo, P. (2024). DNA barcoding, phylogeny and phylogeography of the cyst nematode species of the *Schachtii* group from the genus *Heterodera* (Tylenchida: Heteroderidae). *Nematology* 26, 71-97. DOI: 10.1163/15685411-bja10292
- Winslow, R.D. (1954). Provisional lists of host plants of some root eelworms (*Heterodera* spp.). *Annals of Applied Biology* 41, 591-605. DOI: 10.1111/j.1744-7348.1954.tb01156.x