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ORIGINAL RESEARCH PAPER

Populations of parasitic nematodes colonizing Jerusalem artichoke (*Helianthus tuberosus* L.)

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Abstract

The populations of parasitic nematodes colonizing the rhizosphere of *Helianthus tuberosus* L. grown in Polish plantations were studied in the summer of 2016 and the spring of 2017. A total of 35 nematode species were identified: *Paratrichodorus pachydermus*, *Trichodorus cylindricus*, *T. viruliferus*, *Longidorus attenuatus*, *L. elongatus*, *L. leptocephalus*, *Criconema annuliferum*, *Criconemoides informis*, *Mesocriconema rusticum*, *M. solivagum*, *M. xenoplax*, *Paratylenchus nanus*, *P. neoamblycephalus*, *P. projectus*, *Bitylenchus dubius*, *B. maximus*, *Merlinius brevidens*, *M. nothus*, *Scutylenchus quadrifer*, *S. tartuensis*, *Helicotylenchus digonicus*, *H. pseudorobustus*, *H. vulgaris*, *Rotylenchus pumilus*, *R. robustus*, *Pratylenchus crenatus*, *P. fallax*, *P. neglectus*, *Hirschmanniella gracilis*, *Aphelenchoides fragariae*, *Aphelenchus avenae*, *A. eremitus*, *Ditylenchus dipsaci*, and *D. medicaginis*. *Aphelenchoides fragariae* and *Ditylenchus dipsaci* could be foliar pathogens of *H. tuberosus* L. This is the first study to demonstrate the presence of *A. fragariae* on the leaves of the Jerusalem artichoke in Poland. The frequencies of occurrence and population densities of the 35 nematode species were determined.

Keywords

nematodes; plant viruses; long-term monoculture; Jerusalem artichoke

Introduction

Jerusalem artichoke (*Helianthus tuberosus* L.) is a versatile plant native to North America, and has a variety of applications, including in energy generation, feed and food production, and phytoreclamation. This species is mostly prized for its tubers and aerial parts. The stems and leaves of Jerusalem artichoke are used as animal feed. The Jerusalem artichoke is an alternative crop for human consumption and has numerous benefits, although it is not very popular in Poland. Its tubers, shoots, and flowers contain valuable phytochemicals that can be used for producing medicines, cosmetics, and food. Jerusalem artichoke is a rich source of inulin and other fructooligosaccharides suitable for the production of functional foods. Inulin induces a smaller increase in blood sugar levels than other carbohydrates do, and it is particularly recommended for diabetic patients [1,2]. Inulin has also been found to have probiotic effects in humans [3,4]. Jerusalem artichoke tubers are characterized by high content of fructans, dietary fiber, and phenolic compounds. They also contain polyhydric alcohols, peptides, proteins, vitamins, choline, lecithin, polyunsaturated fatty acids, and phytochemicals [5–7]. The plant is rich in proteins with high biological value, and it contains all exogenous amino acids, including methionine [8]. The tubers typically contain 80% water, 15% carbohydrates, and 1–2% proteins, and are also a source of minerals, mostly iron (0.4–3.7 mg 100 g^{-1}), calcium (14–37 mg 100 g^{-1}), and potassium (420–657 mg 100 g^{-1}) [7,8].

Similar to *Miscanthus ×giganteus*, *H. tuberosus* L. is particularly suitable for biofuel production. The Jerusalem artichoke is an excellent source of biomass owing to its high yields and high lignin and cellulose content. However, long-term monocultures can compromise the plant's genetic diversity. The plant is an attractive substrate for energy generation, including direct combustion, combined combustion with coal, and biogas production [9,10].

Pathogenic nematodes are small (approximately 1 mm in length, with only *Longidorus* and *Xiphinema* reaching up to 6 mm in length) worm-like animals that live in soil and feed on plant roots and stems. Nematodes pierce plant cells with a needle-like structure known as a stylet and suck plant sap. Parasitic nematodes feed on the roots and stems of many plant species in Poland, including the Jerusalem artichoke. Communities of plant and soil nematodes are influenced by various factors, including the soil environment. The plant's health largely determines tolerance to pathogens and parasites. Soil quality is influenced by the structure of the soil food web. Nematodes feed on different types of organic matter and they belong to various trophic types: microbivores that feed on microorganisms; parasites that feed on fungi, algae, and lichens; higher-plant feeders; omnivores; and predators. They are involved in soil processes such as decomposition and circulation of soil organic matter, energy flow, and circulation of plant nutrients [11–13].

Herbivorous nematodes and pathogenic bacteria and fungi cause diseases with complex etiologies. Nematodes of the genera *Longidorus*, *Xiphinema*, and *Trichodorus* are vectors of soil-borne viruses that are transmitted to plant roots [14]. There is a general scarcity of research into parasitic plant nematodes [15], and nematodes of the genera *Longidorus* and *Xiphinema* that colonize *H. tuberosus* L. in Poland have not been studied so far. Jerusalem artichoke tubers seem to be fairly resistant to nematodes [16]. However, long-term monocultures of energy crops can compromise plant resistance to pathogens and diseases. In view of the above, the objective of this study was to analyze the populations of parasitic nematodes colonizing the root zone of *H. tuberosus* L. in Poland.

Material and methods

The study was carried out in the summer of 2016 and spring of 2017. Soil and plant tissue samples were collected in five locations in Poland where Jerusalem artichoke is cultivated:

- Ujkowice (49.85° N, 22.72° E), Podkarpackie (Subcarpathian) Province,
- Poznań (52.40° N, 16.92° E), Wielkopolska (Greater Poland) Province,
- Wołczkowo (53.47° N, 14.42° E), Zachodniopomorskie (West Pomerania) Province,
- Lisewo (53.30° N, 18.66° E) and Rumia (54.37° N, 18.23° E), Pomorskie (Pomerania) Province.

The soil of the areas where the trials were conducted was heavy loam. The agronomic soil category was heavy soil, with the overall sum of fractions less than 0.02 mm amounting to 37.7%. Based on particle size, the soil can be categorized as heavy soil, with its agricultural suitability classified as class IV according to the Polish soil classification system.

According to the data from the Institute of Meteorology and Water Management in Warsaw, mean total precipitation in 2016 was lower (455 mm) than the multiannual mean (610 mm) precipitation, while in 2017, it was higher (755 mm). The rainfall observed in July in 2016 and 2017 beneficially affected the level of moisture on the soil surface, as well as the growth and development of root crops. During the remaining months, precipitation was significantly lower. Mean air temperature during the first vegetation season (2016), 11.3°C, was similar to mean air temperature during the second vegetation season (11.4°C); both values were slightly higher than the multiannual mean (10.6°C). During the periods of April–May and June–August, the mean monthly air temperatures were similar to the multiannual mean values. The temperatures observed from October to December were higher than the multiannual mean, by 2°C on average. In 2017, the mean air temperature of 11.3°C exceeded the multiannual mean by 0.7°C. The high temperature in November supported continued vegetation. The weather conditions in December did not pose any significant hazards for the wintering plants. The temperature was favorable for the continued growth of the plants. The short-term decrease in air temperature, occurring locally at the ground level, did not result in excessive cooling of the soil. Hydration of the surface soil layers at the start of the vegetation period effectively satisfied the water requirements of the plants. The weather conditions in April were also favorable for agriculture and promoted rapid growth of the plants. As a result of a cold spell in May, the pace of plant growth and maturation was slower. In June, the agrometeorological conditions were varied as they were in the remainder of the season.

Soil samples were collected from the rhizosphere at a depth of 40 cm. Nematodes were collected in two steps, according to the different types of plant-parasitic nematodes associated with three sources of samples: soil, roots, and stems.

Fresh roots and stems of Jerusalem artichoke were cut into segments having a diameter of 1 cm and weight of 20 g. The samples were placed in 100-μm sieves, immersed in water, and incubated for 5 days according to the method described by Baermann [17]. After incubation, nematodes were collected separately from each sample (roots and stems). Nematodes from the soil samples were collected by centrifugation. A subsample of 100 cm^3 of soil from each sample was centrifuged.

Nematodes obtained were killed with heated 6% formaldehyde and processed in glycerin, according to the method described by Seinhorst [18]. They were permanently fixed on slides. Nematode species were identified at the species level based on the morphological traits of male and female individuals following the identification keys developed by Brzeski [19] and Andrássy [20]. Species dominance index C was calculated as follows: $C = (Na\ N^{-1}) \times 100\%$, where: Na = number of samples containing a given species, N = total number of samples.

The analyzed nematode species were classified on the basis of the calculated values of index C: (***i***) 0–25%: occasional species, (***ii***) 26–50%: accessory species, (***iii***) 51–75%: dominant species.

The nematodes were also divided into the following trophic groups, according to the classification proposed by other authors [12,13,21–23] and the system approved by Fauna Europaea (cited in [24,25]), as follows:

- A1: migratory endoparasites (Pratylenchidae; occurs mainly in the roots; Anguinidae and Aphelenchoididae, occur mainly in the stem, leaves, and seeds [23]),
- A2: semiendoparasites (Hoplolaimidae; feeds on the roots, with only part of its body inside the plant),
- A3: ectoparasites and A3, V: vectors of plant viruses (nematode species belonging to the families Longidoridae, Xiphinematidae, and Triochodoridae [14,26]),
- A4: sedentary parasites,
- V: vectors of viral infections,
- F: hyphal and root hair feeders.

For every species found in each sample (consisting of specimens isolated from 100 cm^3 of soil by centrifugation, and individuals isolated on Baermann sieves), the following parameters were calculated:

- population density (number of individuals in 100 cm^3 of soil or 20 g of the roots and stem),
- frequency of occurrence (number of occurrences of a species out of the total number of 24 samples), expressed in %.

Results

The nematode species identified in the 24 soil, root, and stem samples from *H. tuberosus* L. plantations are presented in Tab. 1. Population density in 100 cm^3 of soil and the frequency of occurrence were determined for each species. Based on the values of index C, 22 species were classified as occasional, 10 species were classified as accessory (frequency of occurrence <20%), and three species were classified as dominant (frequency of occurrence >50%).

Tab. 1 Species of herbivorous nematodes collected in five plantations of *Helianthus tuberosus* L. in Poland.

Species	Trophic type	Nematodes/100 cm³		Frequency of occurence (%)	Species dominance status
		Range	Mean ±*SD*		
TRICHODORIDAE					
***Paratrichodorus* Siddigi, 1974**					
pachydermus Seinhorst, 1954	A3, V	2–24	13.0 ±8.50	16	O
***Trichodorus* Cobb, 1910**					
cylindricus Hooper, 1962	A3, V	4–12	8.0 ±4.00	8	O
viruliferus Hooper, 1963	A3, V	2–32	12.0 ±9.44	28	A
LONGIDORIDAE					
***Longidorus* Micoletzky, 1922**					
attenuatus Hooper, 1961	A3, V	2–26	13.0 ±8.16	20	O
elongatus de Man, 1876	A3, V	2–48	22.6 ±16.4	20	O
leptocephalus Hooper, 1961	A3, V	6	6.0 ±0.00	4	O
CRICONEMATTIDAE					
Criconemoides					
informis Micoletzky, 1922	A3	4–64	25.3 ±20.3	28	A
Criconema					
annuliferum de Man, 1921	A3	2–20	9.75 ±6.50	16	O
Mesocriconema					
rusticum Micoletzky, 1915	A3	6–64	23.7 ±23.5	16	O
solivagum Andrassy, 1962	A3	4–24	14.0 ±10.0	8	O
xenoplax Raski, 1952	A3	6–82	33.7 ±27.2	28	A
PARATYLENCHIDAE					
***Paratylenchus* Micoletzky, 1922**					
nanus Cobb, 1923	A3	4–120	50.4 ±43.5	28	A
neoamblycephalus Geraert, 1965	A3	28–80	54.0 ±26.0	8	O
projectus Jenkis, 1960	A3	8–128	60.3 ±38.7	28	A
TELOTYLENCHIDAE					
***Bitylenchus* Filipjev, 1934**					
dubius Butschli, 1873	A3	4–180	41.5 ±49.2	54	D
maximus Allen, 1955	A3	8–94	57.1 ±29.3	28	A
***Merlinius* Siddiqi, 1970**					
brevidens Allen, 1955	A3	2–120	33.5 ±39.3	54	D
nothus Allen, 1955	A3	6–96	39.0 ±28.2	32	A
***Scutylenchus* Jairajpuri, 1971**					
quadrifer Andrassy, 1974	A3	6–94	54.8 ±34.0	20	O
tartuensis Krall, 1959	A3	8–120	55.0 ±42.7	20	O
HOPLOLAIMIDAE					
***Helicotylenchus* Steiner, 1945**					
digonicus Perry, 1969	A2	24–140	66.0 ±38.0	24	O
pseudorobustus Steiner, 1914	A2	6–98	50.4 ±39.5	36	A

Tab. 1 Continued

Species	Trophic type	Nematodes/100 cm³ Range	Mean ±*SD*	Frequency of occurence (%)	Species dominance status
vulgaris Yuen, 1964	A2	18–42	30.0 ±12.0	8	O
		Rotylenchus **Filipjev, 1936**			
pumilus Perry in Perry, Darlings & Thorne, 1959	A2	6–68	28.4 ±23.6	20	O
robustus de Man, 1876	A2	14–120	57.3 ±37.4	24	O
		Pratylenchus **Filipjev, 1936**			
crenatus Loof, 1960	A1	16–62	40.0 ±18.8	12	O
fallax Seinhorst, 1968	A1	8–126	53.9 ±39.6	32	A
neglectus Rench, 1924	A1	16–94	52.8 ±30.8	20	O
		Hirschmanniella			
gracilis de Man, 1880	A1	4	4.0 ±0.00	4	O
		APHELENCHOIDAE			
		Aphelenchoides **Fisher, 1894**			
fragariae Ritzema Bos, 1891	A1, F	120–280	212.0 ±65.5	20	O
Aphelenchoides sp. 1	A1, F	42–95	67.5 ±22.9	16	O
		Aphelenchus **Bastian, 1865**			
avenae Bastian, 1865	F	2–98	42.8 ±35.9	54	D
eremitus Thorne, 1961	F	24–46	35.0 ±11.0	8	O
		ANGUINIDAE			
		Ditylenchus **Filipjev, 1936**			
dipsaci Kuhn, 1857 complex	A1, F	8–180	69.1 ±54.2	32	A
medicaginis Wasilewska, 1965	F	12	12.0 ±0.00	4	O

A1 – migratory endoparasites; A2 – semi-endoparasites; A3 – ectoparasites; A4 – sedentary parasites; V – vectors of viral infections; F – hyphal and root hair feeders. O – occasional species; A – accessory species; D – dominant species.

A total of 35 herbivorous nematode species belonging to 17 genera were identified in the analyzed samples. The population densities of *A. fragariae* (Ritzema Bos, 1891) and *Ditylenchus* sp. were high, with up to 280 and 180 individuals, respectively, in 20-g samples of fresh stems. The pathogenicity of the above species will be analyzed in a greenhouse experiment in future. *Aphelenchoides fragariae* had previously been found to colonize the leaves of *H. tuberosus* L. in the Korean provinces of Gyeonggi and Gwangweo [15]. The above species were extracted from infected tissues. The leaves of Jerusalem artichokes collected in Ujkowice, Wołczkowo, and Rumia exhibited characteristic symptoms of nematode infection, including brown discoloration of plant tissue, necrotic lesions, and large necrotic patches on leaves (Fig. 1). The observed symptoms were not associated with any fungi or bacteria.

Nematode vectors of viral diseases (a total of six species with frequency of occurrence of 4–28%) are deemed potentially harmful for plants. Half of the analyzed samples were colonized by *Trichodorus viruliferus* and *Paratrichodorus pachydermus*, which are able to transfer TOBRA viruses to the roots of several plant species. Three species of the genus *Longidorus*, capable of transmitting several NEPO viruses to other plants, were also identified: *L. attenuatus* (Fig. 2), *L. elongatus*, and *L. leptocephalus* (Tab. 1). Ectoparasitic nematodes of the genera *Mesocriconema*, *Paratylenchus*, *Bitylenchus*, and *Scutylenchus* were characterized by small population densities that were unlikely to exert significant effects on plant yield. The population densities of endoparasitic nematodes of the genus *Pratylenchus* (Fig. 3) and semiendoparasitic nematodes of the genera

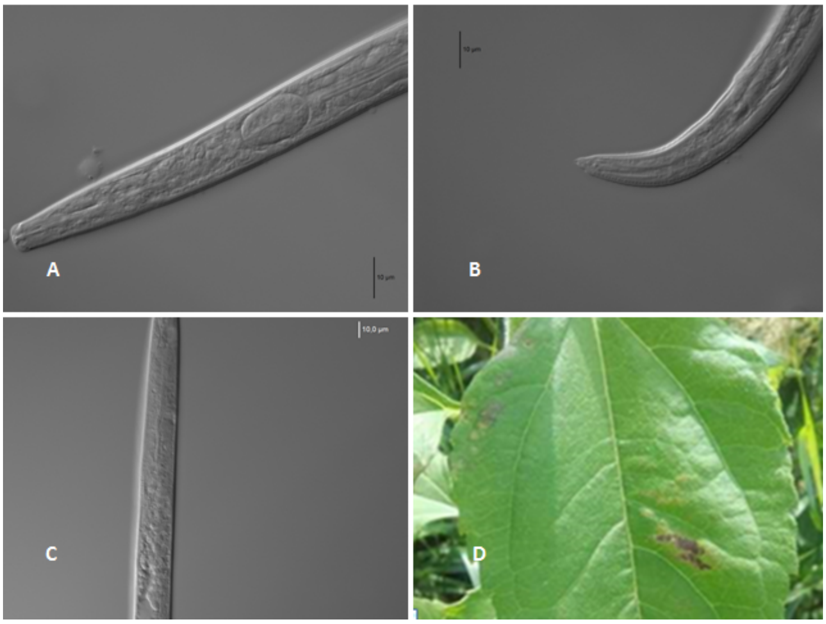

Fig. 1 *Aphelenchoides* sp. and symptoms of infection in Jerusalem artichoke. (**A**) head; (**B**) tail; (**C**) postvulval sac with vulva; (**D**) symptoms in leaves.

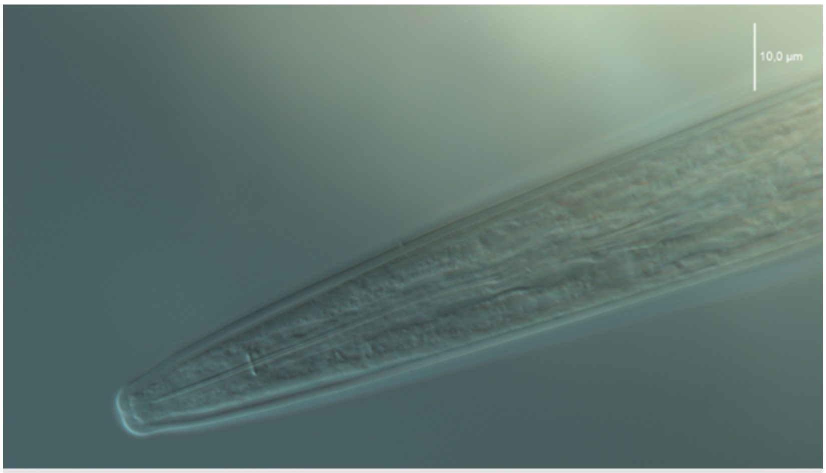

Fig. 2 *Longidorus attenuatus*, head.

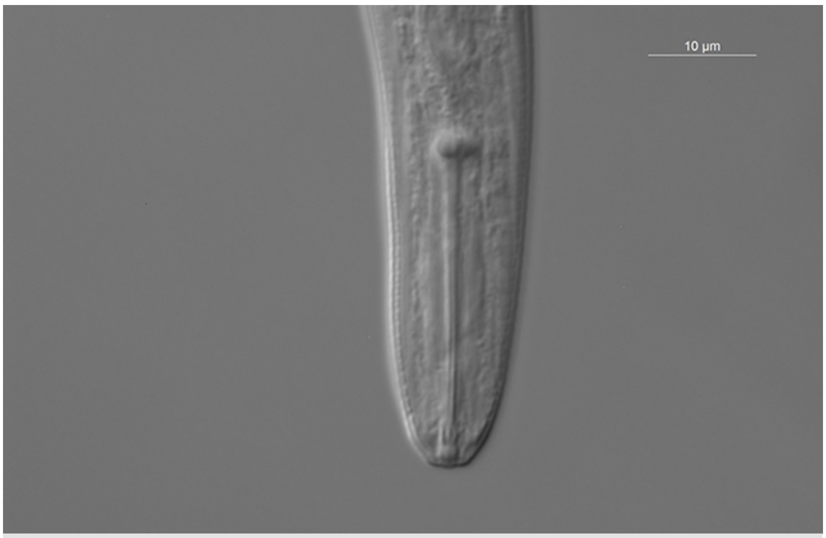

Fig. 3 *Paratylenchus neoamblycephalus*, head.

Helicotylenchus and *Rotylenchus* were low. Owing to their occurrence (28%) and high population densities, the ectoparasites *Paratylenchus nanus* and *P. projectus* should be monitored in future. Species of the families Aphelenchoididae and Anguinidae were identified on the basis of the fact that selected aphelenchids species are herbivores. Half of the analyzed samples contained two species of enthomoparasitic nematodes of the genera *Mermis* and *Steinernema* (a total of six specimens). However, bacteria-feeding nematodes play key roles in the decomposition of organic matter in ecosystems. In the analyzed samples, the following species of bacteria-feeding nematodes were identified: *Cylindrolaimus* de Man, 1880; *Rhabditis* sp. Dujardin, 1845; *Plectus* sp. *Bastian*, 1865; *Anaplectus* de Coninck and Schurmann Stekhoven, 1933; and *Aporcelaimus* sp. Their population densities reached up to 50 specimens in 100 cm^3 of soil, and their frequency occurrences were estimated at 50–75%.

The observed changes in nematode communities in the rhizosphere of *H. tuberosus* L. plants indicate that further research is needed to explain the role of two species of *Aphelenchoides* and *Ditylenchus* sp., which colonized the stems of Jerusalem artichokes. They were classified as herbivores based on the presence of well-defined stylets.

Discussion

Helianthus tuberosus L. is generally susceptible to infections caused by fungi, bacteria, and tobacco mosaic viruses [26]. It is also colonized by nematodes *Caconema radicicola*, *Ditylenchus dipsaci*, *Aphelenchoides ritzemabosi*, *Heterodera marioni*, *Meloidogyne* sp., and *Puccinia helianthi* [24]. In this study, the analyzed samples of *H. tuberosus* L. were colonized by a total of 22 occasional species, seven accessory species, and three dominant species of nematodes (Tab. 1). The members of the *D. dipsaci* complex cause serious infections in many plants grown in Europe. *Ditylenchus gigas*, for example, is pathogenic to broad beans [27]. The specimens of *Ditylenchus* isolated from the stems of *H. tuberosus* L. require molecular analysis to confirm their species identities in a further study. Migratory endoparasites of the genus *Pratylechus* feed on cortical plant tissues, causing necrotic changes in roots and leading to plant death. The results of this study and published data indicate that *A. fragariae* is a ubiquitous pathogen in *H. tuberosus* L. *Aphelenchoides fragariae* infects stems and leaves by migrating to the stem and entering the stomata. The analyzed stems and leaves were significantly (20%) contaminated with *A. fragariae* (Fig. 1). The initial symptoms of infection in Jerusalem artichoke leaves were irregular, water-containing lesions between leaf veins, which spread gradually and caused necrotic changes in plant tissues – symptoms that are very similar in both infested Jerusalem artichoke [15] and in other hosts, for example silver birch [28], among diverse ornamental plants [29–31]. The genus *Aphelenchoides* Fischer, 1894 is composed of ubiquitous fungi-feeding species, as well as species that infect insects and plants. These nematodes feed on both fungi and plants [32]. Numerous plant species are colonized by the foliar nematodes [28] that are the most widespread parasitic nematodes in Poland. Nematodes of the genus *Aphelenchoides* are usually transmitted via clothing, footwear, containers, packaging (wood), land vehicles, paper, soil, sand, and gravel [33]. According to the Center for Agriculture and Biosciences International (CABI), *Hirsutella rhossiliens* is a natural enemy to *Aphelenchoides*; however, it can also be used to fight *Ditylenchus dipsaci*, *Globodera pallida*, *Heterodera avenae*, and *H. schachtii* [26].

This study has revealed that six nematode species could be vectors of viral diseases in the Jerusalem artichoke in Poland. The greatest threat is posed by *Trichodorus viruliferus* (vector of several TOBRA viruses), characterized by a high frequency of occurrence (28%) and high population density, as well as by *Longidorus attenuatus*, which commonly occurs in Polish soils (Fig. 2) [14,25,34,35]. The ectoparasite feeds on roots, and it can transmit NEPO viruses to healthy plants. The prevalence of nematode vectors of viral plant diseases suggests that viral symptoms in leaves should be closely monitored, and that virology tests should be performed to detect latent viruses in *H. tuberosus* L. plantations [36].

Conclusions

- Further research is required to monitor the spread of parasitic nematodes colonizing the rhizosphere of *H. tuberosus* L. in long-term monocultures.
- The roles of two unidentified species of *Aphelenchoides* sp. and *Ditylenchus* sp. in colonizing *H. tuberosus* L. stems should be determined using seedlings grown in a pot experiment under in vitro conditions.
- Six nematode vectors of viral diseases were identified in 40% of the 24 analyzed samples, and further research is needed to identify the causes of viral diseases in plants, in particular in *H. tuberosus* L.

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