J. Trop. Plant Pests Dis.
Vol. 26, No. 2, September 2026
Pages: 473–484

ISSN: 1411-7525
E-ISSN: 2461-0399
DOI : 10.23960/j.hptt.226473-484

RESEARCH PAPER

Identification of *Meloidogyne* spp. (Tylenchida: Meloidogynidae) as potato tuber-borne nematodes (PTBN) in the potato production center of Java Island, Indonesia

Wawan Kurniawan[1,2], Supramana[1], Abdul Munif[1], & Giyanto[1]

Manuscript received: 17 October 2025. Revision accepted: 23 December 2025. Available online: 28 July 2026

ABSTRACT

Root-knot nematodes (*Meloidogyne* spp.) are among the most destructive plant-parasitic nematodes affecting potato production worldwide. However, information on *Meloidogyne* spp. associated with potato tubers and their potential as potato tuber-borne nematodes (PTBN) in Indonesia remains limited. This study aimed to identify *Meloidogyne* species associated with potato tubers and determine their distribution in major potato-producing regions of Java, Indonesia. Surveys were conducted from January 2023 to December 2024 in West, Central, and East Java. Symptomatic potato tubers were collected and examined using morphological, morphometric, and molecular approaches. Tubers were stored under refrigerated conditions for 3–24 months to evaluate nematode persistence. Molecular identification was performed using species-specific SCAR markers, followed by phylogenetic and sequence homology analyses. Root-knot nematodes were detected in all surveyed production areas and were associated with characteristic symptoms, including knobby, branched, elongated, and russeted tubers. Two species were identified: *Meloidogyne incognita*, which was widely distributed throughout Java, and *Meloidogyne javanica*, which was detected only in Cikandang Village, Garut, West Java. The nucleotide sequences were deposited in GenBank under accession numbers LC894939–LC894951 (*M. incognita*) and LC894966 (*M. javanica*). Both species remained viable in potato tubers for up to 24 months, confirming their potential as PTBN. These findings provide a scientific basis for strengthening nematode-free seed certification and phytosanitary measures to reduce the spread of *Meloidogyne* spp. through seed tubers.

Keywords: *Meloidogyne incognita*, *Meloidogyne javanica*, phylogenetic analysis, potato tuber-borne nematodes, seed certification

INTRODUCTION

Root-knot nematodes (*Meloidogyne* spp.; Tylenchida: Meloidogynidae) are among the most economically destructive plant-parasitic nematodes worldwide, causing substantial yield losses in a wide range of agricultural crops. These nematodes infect more than 3000 plant species, including economically important members of the Solanaceae such as potato (*Solanum tuberosum* L.). Infection by *Meloidogyne* spp. induces root gall formation, disrupts water and nutrient transport, reduces plant vigor, and ultimately decreases both tuber yield and quality (Jones et al., 2013; Moens et al., 2009; Przybylska & Obrępalska-Stęplowska, 2020; Yadav et al., 2025). In tropical and subtropical regions, *M. incognita, M. javanica*, and *M. arenaria* are among the most prevalent species. However, their occurrence and distribution vary considerably among regions depending on environmental conditions, cropping systems, and host availability (Hunt & Handoo, 2009; Sikora et al., 2018).

Indonesia is one of the major potato-producing countries in Southeast Asia, with most commercial production concentrated in the highlands of Java Island, which account for more than 60% of the national potato production. Despite its economic importance, potato productivity is frequently constrained by soil-borne pathogens, including root-knot nematodes. In addition to reducing yield, infestations of *Meloidogyne* spp. may compromise the phytosanitary quality of seed tubers, increasing the risk of nematode dissemination through infected planting materials. Several studies have reported the occurrence of *Meloidogyne* spp. in potato-growing regions of Indonesia (Aprilyani et al., 2015; Mutala'liah, 2019; Utami et al., 2017). More recently, Hamidi et al. (2022) identified Meloidogyne species associated with symptomatic potato tubers in

Corresponding author:
Wawan Kurniawan (wawan.kurniawan@apps.ipb.ac.id)

[1]Department of Plant Protection, Study Program of Phytopathology, Faculty of Agriculture, IPB University, Jalan Kamper IPB Dramaga Bogor Campus, West Java 16680

[2]Department of Pests and Plant Diseases, Faculty of Agriculture, Universitas Padjadjaran, Jalan Raya Bandung Sumedang Km. 21 Jatinangor, Sumedang 45363

three potato production centers in Sumatra using both morphological and molecular approaches. However, most previous studies have focused on nematode populations associated with roots or rhizosphere soil, whereas comprehensive information on the occurrence and geographical distribution of potato tuber-borne *Meloidogyne* spp. in the major potato production areas of Java remains unavailable. Previous studies from several countries have demonstrated that potato tubers bearing galls and egg masses can serve as an important pathway for long-distance dissemination of root-knot nematodes through seed movement (Patel et al., 2019; Patel et al., 2020). Unlike root infestations that remain confined to production fields, tuber-borne infestations may facilitate the introduction of nematodes into previously uninfested production areas, posing serious phytosanitary challenges for sustainable potato production.

Accurate identification of *Meloidogyne* species is essential because pathogenicity, host range, and management strategies differ among species. Morphological identification, particularly based on female perineal patterns, male stylet morphology, and morphometric characters of second-stage juveniles (J2), remains the foundation of nematode taxonomy. However, these morphological characteristics often overlap among closely related species, making species identification difficult when used alone (Eisenback et al., 1980; Eisenback & Triantaphyllou, 1991; Hunt & Handoo, 2009). To overcome these limitations, molecular diagnostic approaches targeting ribosomal DNA regions (ITS and 28S D2–D3) and mitochondrial genes (COI and COII) have become widely adopted because they provide greater taxonomic resolution and support phylogenetic inference within the genus *Meloidogyne* (Marquez & Hajihassani, 2023; Patel et al., 2020; Semblat et al., 2000). Consequently, integrating morphological, morphometric, and molecular analyses provides a robust framework for accurate species identification, particularly for closely related or geographically variable populations.

Although potato tuber-borne nematodes (PTBN) have received increasing attention worldwide, information regarding the occurrence, species composition, and geographical distribution of *Meloidogyne* spp. associated with potato tubers in Indonesia remains scarce. Considering that potato farmers in Indonesia commonly use seed tubers derived from previous harvests, infected tubers may represent an important pathway for the dissemination of root-knot nematodes among production centers. Therefore, this study aimed to identify *Meloidogyne* spp. associated with potato tubers collected from the major potato-producing regions of Java Island using an integrated approach combining morphological, morphometric, and molecular analyses, and to determine their geographical distribution. To our knowledge, this is the first comprehensive study documenting the occurrence and distribution of *Meloidogyne* spp. as PTBN in Indonesia. The findings provide baseline information for phytosanitary surveillance, seed tuber health certification, and the development of effective and sustainable nematode management strategies, including species-specific approaches for integrated nematode control (Swibawa et al., 2024).

MATERIALS AND METHODS

Research Site. This study was conducted at the Plant Nematology Laboratory, Faculty of Agriculture, IPB University, from January 2023 to December 2024.

Survey and Sample Collection. Field surveys were conducted in major potato-producing areas of Java Island, Indonesia, including West Java (Pangalengan: Sukamanah; Pasirjambu: Cisondari; Rancabali: Alam Endah; Cisurupan: Cidatar and Cisurupan; Cikajang: Cikandang and Cibodas; Cigedug: Cigedug), Central Java (Batur: Dieng Kulon, Karang Tengah, Pekasiran, and Batur), and East Java (Tosari: Ngadiwono and Mororejo; Bumiaji: Sumberbrantas; Plaosan: Singolangu).

Potato tubers showing symptoms suspected of root-knot nematode infection, including tuber malformation, surface galls, and other abnormal symptoms, were collected, individually labeled, and transported to the laboratory in sealed plastic containers. Sampling sites were grouped according to cultivation altitude: 1000–1250 m above sea level (asl), >1250–1500 m asl, and >1500 m asl. Each sample was divided into two portions. One portion was used for immediate morphological examination, whereas the remaining portion was stored under laboratory conditions for 3–24 months to evaluate nematode survival during storage. The occurrence of *Meloidogyne* spp. at each sampling location was subsequently used to construct a distribution map of PTBN on Java Island.

Nematode Extraction. Nematodes were extracted from stored potato tubers using a combination of the Baermann funnel and mist chamber techniques following Bridge & Starr (2007). Extracted second-stage juveniles (J2) were counted under a compound microscope and used for morphological and molecular

identification. To determine nematode abundance in relation to symptom severity, symptomatic tubers were cut into approximately 1 cm^3 pieces and carefully dissected under a stereomicroscope to observe different developmental stages, including eggs, juveniles, and females.

Morphological and Morphometric Identification. Morphological observations were conducted using a stereomicroscope (Olympus SZ-ST) and a compound microscope (Olympus CH30). Adult females obtained from infected tubers were used for preparation of perineal patterns according to the procedures described by Eisenback et al. (1980). Perineal patterns were examined at 400× magnification to evaluate the dorsal arch, lateral lines, and cuticular striations. Morphometric measurements of second-stage juveniles (J2), including body length, stylet length, tail length, and hyaline tail terminus, were compared with the diagnostic descriptions provided by Hunt & Handoo (2009), Karssen et al. (2013), and Eisenback & Triantaphyllou (1991). Morphological identification was subsequently confirmed by molecular characterization using species-specific SCAR markers (Marquez & Hajihassani, 2023).

Molecular Identification. Genomic DNA was extracted from individual second-stage juveniles using a modified protocol of Holterman et al. (2006). Species identification was performed by polymerase chain reaction (PCR) using species-specific primers. For *M. incognita*, the primer pair Mi-F (5′-GTGAGGATTCAGCTCCCCAG-3′) and Mi-R (5′-ACGAGGAACATACTTCTCCGTCC-3′) was used (Meng et al., 2004), whereas *M. javanica* was identified using the primer pair Fjav (5′-GGTGCGCCGATTGAACTGAGC-3′) and Rjav (5′-CAGGCCCTCAGTGGAACTATAC-3′) (Zijlstra et al., 2000).

Each 50-µL PCR reaction consisted of 25 µL of 2× MyTaq™ HS Red Mix, 2 µL each of forward and reverse primer (10 µM), 4 µL of DNA template, and nuclease-free water to the final volume. PCR amplification was performed using a Bio-Rad T100™ Thermal Cycler under the following conditions (Kurniawan, 2010): initial denaturation at 95 ºC for 3 min, 35 cycles of denaturation at 94 ºC for 30 s, annealing at 55–57 ºC for 45 s, and extension at 72 ºC for 60 s, followed by a final extension at 72 ºC for 7 min.

Amplified products were separated by electrophoresis on 1% agarose gel stained with GelRed® (Biotium, USA) in 0.5× TBE buffer at 100 V for 30–35 min. DNA fragments were visualized using a UV transilluminator with 100 bp and 1 kb DNA ladders (Geneaid) as molecular size markers.

DNA Sequencing and Phylogenetic Analysis. Representative PCR products were purified and sequenced commercially by PT Genetika Science Indonesia. Raw nucleotide sequences were edited and assembled using BioEdit. Consensus sequences were compared with reference sequences available in the GenBank database using BLASTn (National Center for Biotechnology Information, NCBI) to determine sequence identity.

Multiple sequence alignment was performed using the MUSCLE algorithm (Edgar, 2004). Phylogenetic relationships were reconstructed using MEGA XI (Tamura et al., 2021) with the Neighbor-Joining (NJ) method based on 1000 bootstrap replications. Sequence similarity and species demarcation were further evaluated using Species Demarcation Tool (SDT) version 1.2 (Muhire et al., 2014).

RESULTS AND DISCUSSION

Symptoms of *Meloidogyne* spp. Infection on Potato Tubers. Potato tubers collected from major production centers across Java exhibited a wide range of characteristic symptoms associated with root-knot nematode (*Meloidogyne* spp.) infection (Figure 1). The observed symptoms included branched tubers, daughter tubers, forked tubers, elongated tubers, russeted tubers, pimple-like swellings, and knobby tubers. These deformities represent distinct morphological abnormalities that substantially reduce both the marketability and seed quality of potato tubers. The diversity of symptom expression suggests differences in nematode population density, infection timing during tuber development, and environmental conditions among production sites. Similar tuber abnormalities have been reported in potato-growing regions worldwide, where Meloidogyne infection results in significant economic losses due to reduced tuber quality and rejection of seed tubers.

Among the observed symptoms, knobby tubers, russeted tubers, and pimple-like swellings were most frequently associated with severe nematode infestations and therefore may serve as reliable field indicators of high *Meloidogyne* populations within tuber tissues. Importantly, viable *Meloidogyne* individuals remained detectable in symptomatic tubers stored for up to nine

months at room temperature and for 3–24 months under low-temperature storage (10–15 ºC). The prolonged survival of nematodes within stored tubers highlights their capacity to persist during storage and supports the hypothesis that infected seed tubers constitute an important pathway for long-distance dissemination.

Population Density of *Meloidogyne* spp. in Symptomatic Potato Tubers. Symptomatic potato tubers were classified according to symptom severity and evaluated for nematode population density per cm³ of tuber tissue (Table 1). A clear positive relationship was observed between symptom severity and nematode population density. Tubers with symptom scores of 3–5, corresponding to 41–100% gall coverage, contained significantly higher populations of adult females, eggs, and juvenile stages (J2–J4), whereas asymptomatic tubers (score 0) were free of nematodes.

Adult females were consistently detected in infected tubers, ranging from 12.33 ± 2.89 to 25.33 ± 2.89 individuals per cm³. The high abundance of eggs together with multiple juvenile stages indicates that *Meloidogyne* spp. are capable of completing their life cycle within potato tuber tissues. This finding demonstrates that potato tubers function not only as feeding sites but also as reproductive habitats that support nematode development and long-term survival. Similar observations have been reported for stored potato tubers, in which viable *Meloidogyne* populations remained infective for several months under both ambient and refrigerated storage conditions. Consequently, infected tubers may serve as effective inoculum sources for subsequent planting seasons, further supporting the designation of *Meloidogyne* spp. as PTBN.

Morphological Identification of *Meloidogyne* spp. Morphological identification was conducted using permanent slide preparations representing different developmental stages (Figure 2). The examined specimens exhibited the diagnostic characteristics of the genus *Meloidogyne*, including body shape, stylet morphology, tail characteristics, and female perineal patterns. Second-stage juveniles (J2) were slender with tapering tails and well-developed stylets, whereas adult females were pear-shaped with rounded posterior

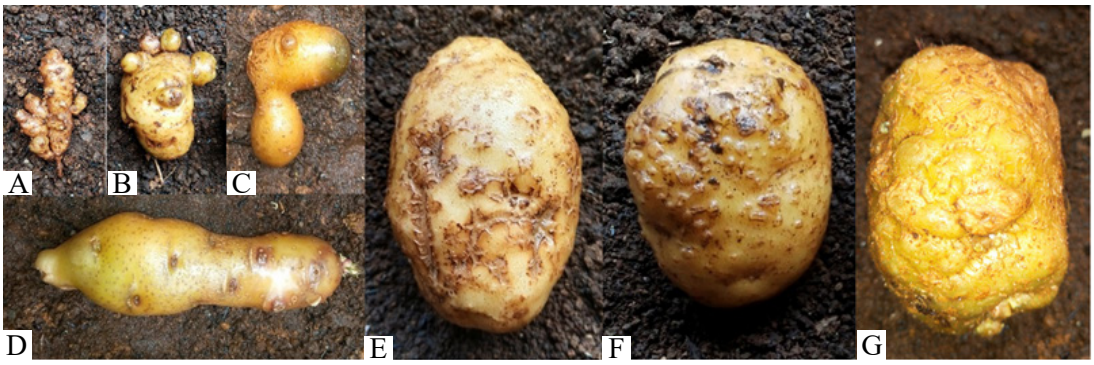

Figure 1. Symptoms of potato tubers infected by root-knot nematodes (*Meloidogyne* spp.). A. Tuber branching; B. Daughter tuber; C. Forked tuber; D. Elongated tuber; E. Russeted tuber; F. Pimple-like swelling; G. Knobby tuber.

Table 1. Numbers of *Meloidogyne* spp. at different developmental stages in 1 cm³ of symptomatic potato tuber tissue according to symptom severity score

Score	Total population of *Meloidogyne* spp. in 1 cm³ symptomatic potato tubers (nematodes/cm³)					
	Adult	Egg	Juv 1	Juv 2	Juv 3	Juv 4
5	16.00 ± 1.73	4.33 ± 1.15	0.00 ± 0.00	7.33 ± 0.58	25.33 ± 8.08	30.67 ± 2.31
4	24.67 ± 5.77	10.67 ± 0.58	9.33 ± 8.08	3.67 ± 0.58	48.67 ± 30.02	56.67 ± 10.97
3	25.33 ± 2.89	5.67 ± 0.58	9.33 ± 8.08	3.67 ± 2.31	45.00 ± 36.37	44.33 ± 25.40
2	12.33 ± 2.89	4.67 ± 0.58	7.33 ± 4.62	2.00 ± 1.73	34.33 ± 21.94	51.00 ± 32.91
1	13.33 ± 2.31	9.00 ± 5.20	3.00 ± 1.73	0.00 ± 0.00	14.33 ± 11.55	19.33 ± 13.28
0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0

Symptom severity score: 0 = No symptoms; 1 = Galls covering 1–20% of the tuber surface; 2 = Galls coversing 21–40% of the tuber surface; 3 = Galls covering 41–60% of the tuber surface; 4 = Galls covering 61–80% of the tuber surface; 5 = Galls covering 81–100% of the tuber surface.

regions. Eggs were enclosed within typical oval egg masses.

Species identification was primarily based on female perineal patterns. *M. incognita* exhibited a high dorsal arch with fine, wavy striations, whereas *M. javanica* was characterized by a lower dorsal arch with two distinct lateral lines (Eisenback et al., 1980; Hunt & Handoo, 2009). Based on these diagnostic characteristics, two predominant species, *M. incognita* and *M. javanica*, were identified from symptomatic potato tubers collected across the surveyed production areas.

These findings are consistent with those of Hamidi et al. (2022), who reported the occurrence of *M. incognita* and *M. javanica* in symptomatic potato tubers from major potato-producing regions of Sumatra, suggesting that tuber infestation by root-knot nematodes is widespread in Indonesia. The detection of both species within potato tubers further demonstrates their ability to colonize non-root tissues, including stolons and the tuber periderm, thereby facilitating dissemination through infected seed tubers (Scurrah et al., 2005; Sikora et al., 2018).

Although perineal pattern analysis remains a classical and widely accepted method for *Meloidogyne* species identification, considerable overlap in morphological characteristics among closely related species may result in ambiguous diagnoses, particularly in tropical populations (Eisenback & Triantaphyllou, 1991). Consequently, integrating morphological observations with species-specific molecular markers provides a more robust and reliable approach for species identification, especially in phytosanitary surveillance, quarantine, and seed certification programs (Marquez & Hajihassani, 2023; Wainer & Dinh, 2021).

Molecular Identification of *Meloidogyne* spp. Molecular identification using species-specific SCAR primers confirmed the morphological observations. Amplification with *M. incognita*-specific primers produced the expected 955-bp fragment in samples collected from most potato-growing regions across Java (Figure 3A). In contrast, amplification with *M. javanica*-specific primers generated a 434-bp fragment only in the isolate collected from Cikandang, Cikajang (Figure 3B), indicating a more restricted distribution of this species.

The predominance of *M. incognita* across the surveyed regions is consistent with previous reports identifying this species as the most widespread root-knot nematode in tropical potato production systems. The limited detection of *M. javanica* suggests that environmental conditions, host preference, and local agroecological factors may influence species distribution. The SCAR marker system provides rapid, highly specific, and reliable species identification without requiring adult females for morphological examination (Carneiro et al., 2024; Ju et al., 2019; Zijlstra et al., 2000). Therefore, integrating morphological, morphometric, and molecular approaches provides a robust framework for accurate identification of *Meloidogyne* species, as recommended by DemiRbaş et al. (2020), Jones et al. (2013), and Kurniawan (2010).

Phylogenetic Analysis of *Meloidogyne* spp. Phylogenetic analysis was conducted to confirm the molecular identification of *Meloidogyne* spp. based on SCAR sequence data and to determine the genetic relationships among populations collected from potato tubers in major potato-producing regions of Java. The

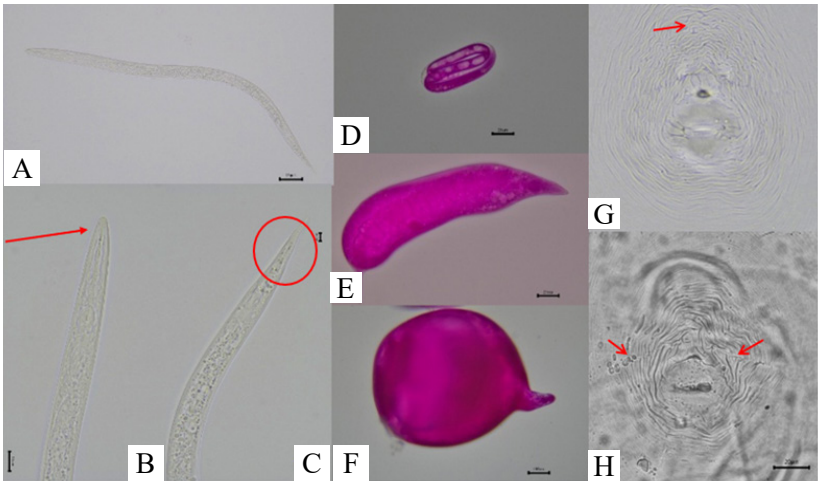

Figure 2. Morphology characteristics of potato tuber-borne root-knot nematodes *Meloidogyne* spp. A. Second-stage juvenile (J2); B. Head region; C. Tail region; D. Egg; E. Fourth-stage juvenile (J4); F. Adult female; G. Female perenial pattern of *M. incognita*; H. Female perenial pattern of *M. javanica*.

phylogenetic tree was constructed using the Neighbor-Joining (NJ) method implemented in MEGA version 11.0.13, with *Ditylenchus dipsaci* used as the outgroup (Figure 4).

The phylogenetic tree showed that all Indonesian *M. incognita* isolates (GenBank accession numbers

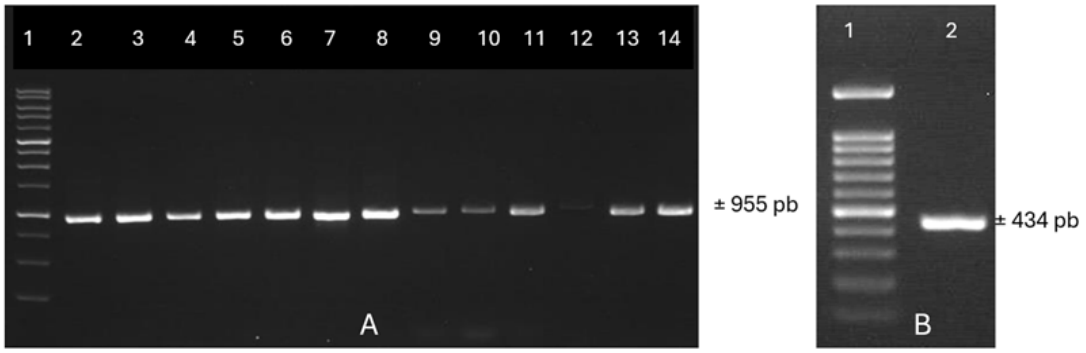

Figure 3. PCR amplification of species-specific SCAR markers for *Meloidogyne* spp. A. *Meloidogyne incognita* showing the expected amplicon of 955 bp. Lane 1 (M) = 1 kb DNA ladder (Thermo Scientific, USA); Lane 2 = Cisondari, Pasirjambu; Lane 3 = Alam Endah, Rancabali; Lane 4 = Cibodas, Cikajang; Lane 5 = Cikandang, Cikajang; Lane 6 = Cisurupan; Lane 7 = Cigedug; Lane 8 = Sukamanah, Pangalengan; Lane 9 = Dieng Kulon, Batur; Lane 10 = Karang Tengah, Batur; Lane 11 = Batur; Lane 12 = Ngadiwono, Tosari; Lane 13 = Sumberbrantas, Bumiaji; Lane 14 = Singolangu, Plaosan. B. *Meloidogyne javanica* showing the expected amplicon of 434 bp. Lane 1 (M): 100 bp DNA ladder (Thermo Scientific, USA); Lane 2 = Cikandang, Cikajang.

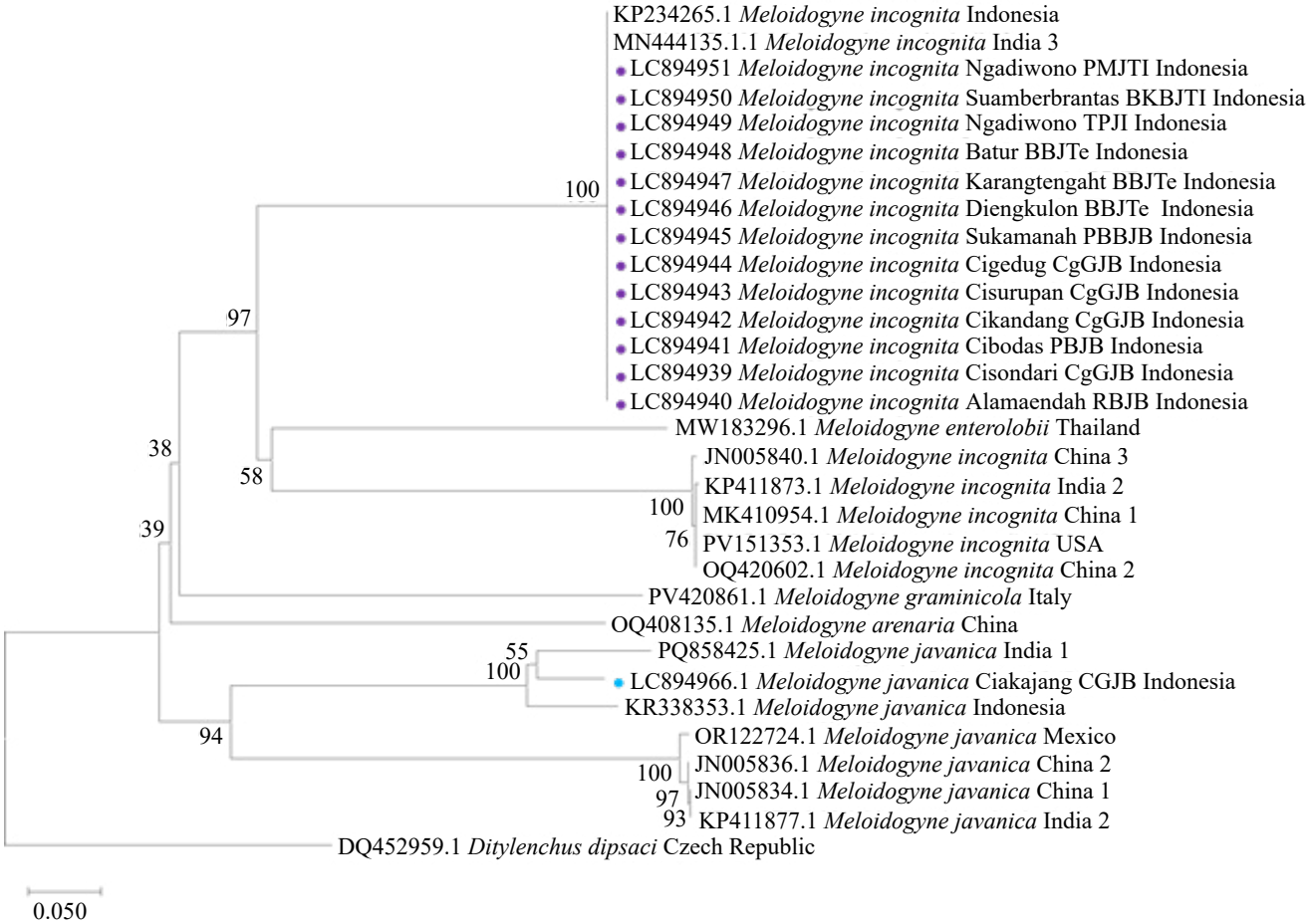

Figure 4. Neighbor-Joining phylogenetic tree of *Meloidogyne incognita* and *M. javanica* isolates from Java, Indonesia, together with reference sequences from other countries, constructed from SCAR marker sequences using MEGA version 11.0.13. Bootstrap values (%) are based on 1000 replicates. *Ditylenchus dipsaci* (GenBank accession no. Q452959) was used as the outgroup.

LC894939–LC894951), representing samples from West Java, Central Java, and East Java, clustered within a well-supported monophyletic clade together with reference isolates from China, India, and Thailand, with bootstrap values ≥97%. This clustering indicates a close genetic relationship among *M. incognita* populations across Java and suggests either a common evolutionary origin or similar adaptation to the agroecological conditions of highland potato production systems. In contrast, the *M. javanica* isolate (LC894966) from Cikandang, Cikajang formed a separate but closely related clade with reference isolates from India and Indonesia, supported by a bootstrap value of 100%. The observed clustering pattern is consistent with the findings of (Zijlstra et al., 2000), who demonstrated that SCAR markers provide reliable species discrimination and accurately reflect phylogenetic relationships among closely related *Meloidogyne* species.

Sequence Homology Analysis. Sequence homology analysis using the Sequence Demarcation Tool (SDT) further supported the phylogenetic results by revealing a high level of nucleotide similarity between the Indonesian isolates and reference sequences available in GenBank (Figure 5). Pairwise sequence comparisons showed nucleotide identities ranging from 94% to 100% among *M. incognita* and *M. javanica* isolates collected from different potato-growing regions of Java, indicating a high degree of genetic conservation within both species. The Indonesian *M. incognita* isolates exhibited the highest sequence similarity with isolates from India and China, whereas the *M. javanica* isolate was most closely related to isolates from India and Thailand.

The high nucleotide identity observed among geographically separated populations suggests limited genetic variation within the analyzed SCAR region and supports the hypothesis that the dissemination of these nematodes may have occurred through the movement of infested seed tubers or other vegetative planting materials, as previously reported by Adam et al. (2007).

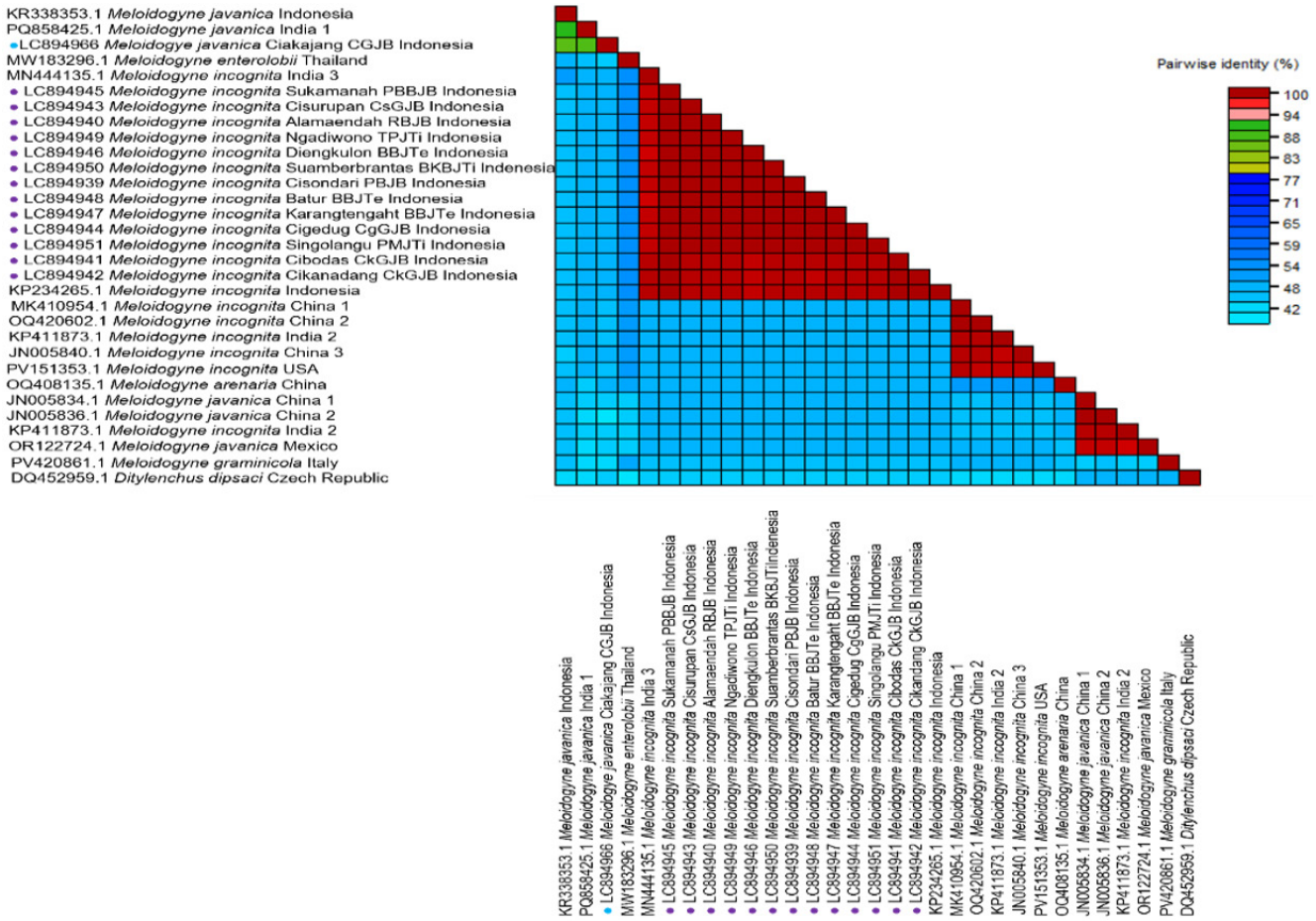

Figure 5. Pairwise nucleotide sequence identity matrix generated using the Sequence Demarcation Tool (SDT), showing the genetic similarity among Indonesian *Meloidogyne incognita* and *M. javanica* isolates and reference sequences from other countries. Pairwise sequence identities are presented as a color-coded matrix, with the corresponding identity scale indicated by the color key.

The relatively low genetic variation observed among the Indonesian isolates is also consistent with the biology of *Meloidogyne* spp., particularly *M. incognita* and *M. javanica*, which reproduce predominantly by mitotic parthenogenesis. This reproductive strategy contributes to high genetic stability while enabling successful adaptation to diverse host plants and environmental conditions (Abad et al., 2003; Castagnone-Sereno et al., 2013).

In contrast, substantially lower nucleotide identity values (≤77%) were observed when the Indonesian isolates were compared with other *Meloidogyne* species, including *M. enterolobii* and *M. graminicola*, as well as with the outgroup *Ditylenchus dipsaci* (Figure 5). These results further confirm the accuracy of the molecular identification and demonstrate that all isolates analyzed in this study belong to the *M. incognita* and *M. javanica* species complex.

Distribution of *Meloidogyne* spp. in Potato Production Centers of Java. Distribution mapping demonstrated that *M. incognita* and *M. javanica* occur throughout the principal potato production regions of West Java, Central Java, and East Java (Figure 6). These findings extend previous reports from Sumatra, where *M. incognita* and *M. javanica* were also identified from symptomatic potato tubers (Hamidi et al., 2022), suggesting that both species are widely distributed across the major potato-producing regions of Indonesia. *M. incognita* was the dominant species and was detected across highland production areas between approximately 1200 and 2100 m asl, whereas *M. javanica* was identified only in Cikandang, Cikajang. The occurrence of *M. javanica* in this location may be associated with its relatively warmer environmental conditions, which are considered favorable for the development of this species.

The widespread distribution of *M. incognita* indicates that this species is well established in the potato agroecosystems of Java. The movement of uncertified seed tubers among production areas is likely one of the major factors facilitating its dissemination, consistent with previous reports demonstrating that *Meloidogyne* spp. are readily spread through infected planting materials (Blok & Powers, 2009). These findings emphasize the importance of implementing certified nematode-free seed tubers and routine phytosanitary surveillance to reduce the risk of further geographical spread (Jones et al., 2013).

Collectively, the integration of symptom observation, population analysis, morphological characterization, molecular identification, phylogenetic reconstruction, and distribution mapping provides strong evidence that *M. incognita* and *M. javanica* function as PTBN in Indonesia. Their persistence within stored tubers, extensive distribution across Java Island, and close genetic relationship with

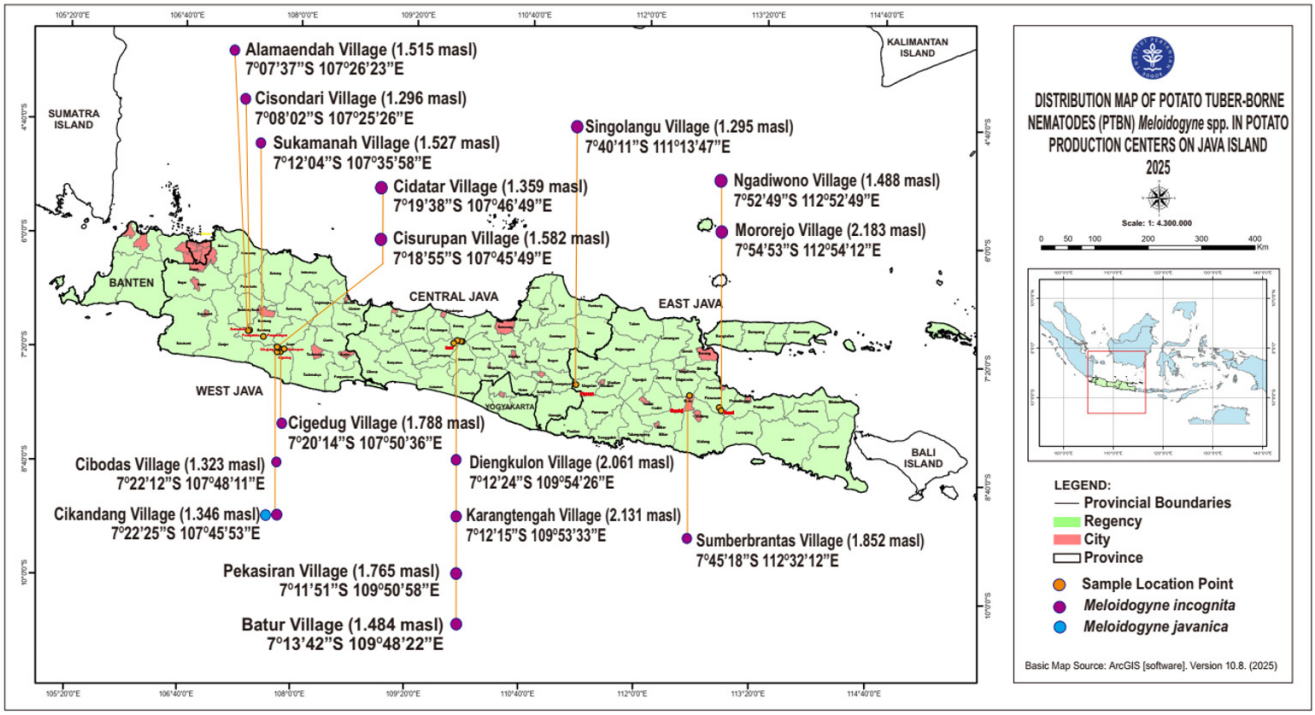

Figure 6. Distribution map of potato tuber-borne nematodes (PTBN) *Meloidogyne* spp. in the potato production centers of Java Island.

internationally reported populations highlight their phytosanitary significance and underscore the need for seed certification and molecular surveillance programs to minimize further dissemination.

Overall, the present study demonstrates that *M. incognita* and *M. javanica* associated with potato tubers in the major potato-producing regions of Java belong to globally distributed root-knot nematode species exhibiting high genetic conservation. The limited sequence divergence observed among Indonesian isolates is consistent with the predominantly mitotic parthenogenetic reproduction of tropical *Meloidogyne* species, which promotes genetic stability while maintaining broad host adaptability. These characteristics contribute to the successful establishment and dissemination of these nematodes through infected planting materials, including seed tubers (Castagnone-Sereno et al., 2013; Yadav et al., 2025). Consequently, the occurrence of *M. incognita* and *M. javanica* in potato tubers confirms their potential role as PTBN and highlights the urgent need for certification of nematode-free seed potatoes in Indonesia. Accurate species identification is therefore fundamental for designing effective management strategies, including the application of biological control agents. Previous studies have demonstrated that biological nematicides based on *Purpureocillium lilacinum* effectively suppress *Meloidogyne* populations and reduce root damage, highlighting the importance of integrating reliable diagnosis with sustainable nematode management programs (Swibawa et al., 2024).

CONCLUSION

This study demonstrated that potato tubers collected from major potato production centers across Java Island exhibited diverse symptoms associated with root-knot nematode infection, resulting in reduced tuber quality and potential yield losses. Integrated morphological, morphometric, and molecular analyses confirmed the presence of two root-knot nematode species, *Meloidogyne incognita* and *M. javanica*. Both species were able to survive in infected potato tubers for up to 24 months under storage conditions, confirming their potential as potato tuber-borne nematodes (PTBN). These findings provide the first comprehensive evidence of PTBN distribution in the major potato-producing regions of Java and highlight the importance of implementing nematode-free seed certification, routine phytosanitary surveillance, and strict quarantine measures to prevent the dissemination of root-knot nematodes through infected seed tubers.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the Indonesian Education Scholarship Program (Beasiswa Pendidikan Indonesia, BPI), administered by the Ministry of Higher Education, Science, and Technology of the Republic of Indonesia, for supporting this research. The authors also thank all collaborators and laboratory staff who contributed to the field surveys, laboratory analyses, and technical assistance throughout this study.

FUNDING

This research was partially supported by the Indonesian Education Scholarship Program (Beasiswa Pendidikan Indonesia, BPI) through the research project entitled “Identification of Parasitic Nematodes Carried by Potato Tubers in the Potato Production Centers of Java Island: Identification, Diversity, and Control.”

AUTHORS’ CONTRIBUTIONS

WK conceived and designed the study, conducted the field surveys and laboratory experiments, including morphological and molecular identification, DNA sequencing, and data collection, analyzed the data, and prepared the original manuscript draft. S contributed to the study design, supervised the research, and critically reviewed and edited the manuscript. AM provided expertise in nematode identification and statistical analysis and contributed to manuscript revision. G contributed to the study design, interpretation of the results, and critical revision of the manuscript. All authors read, revised, and approved the final manuscript and agree to be accountable for all aspects of the work.

COMPETING INTEREST

The authors declare that they have no competing interests.

REFERENCES

Abad P, Favery B, Rosso MN, & Castagnone-Sereno P. 2003. Root-knot nematode parasitism and host response: Molecular basis of a sophisticated interaction. *Mol. Plant Pathol.* 4(4): 217–224. https://doi.org/10.1046/j.1364-

3703.2003.00170.x

Adam MAM, Phillips MS, & Blok VC. 2007. Molecular diagnostic key for identification of single juveniles of seven common and economically important species of root-knot nematode (*Meloidogyne* spp.). *Plant Pathol*. 56(1): 190–197. https://doi.org/10.1111/j.1365-3059.2006.01455.x

Aprilyani, Supramana, & Suastika G. 2015. *Meloidogyne incognita* penyebab umbi berbintil pada kentang di beberapa sentra produksi kentang di Jawa [*Meloidogyne incognita* causing pimple-like knot on potatoes in several Provinces in Java]. *J. Fitopatol. Indones.* 11(5): 143–149. https://doi.org/10.14692/jfi.11.5.143

Blok VC & Powers TO. 2009. Biochemical and molecular identification. In: Perry RN, Moens M, Starr JL (Eds.). *Root-Knot Nematodes*. pp. 98–118. CABI. Wallingford, UK. https://doi.org/10.1079/9781845934927.0098

Bridge J & Starr J. 2007. Collection, extraction, and preservation of nematodes for diagnosis. In: Bridge J & Starr J (Eds.). *Plant Nematodes of Agricultural Importance*. pp. 135–144. CRC Press. London. https://doi.org/10.1201/B15142-10

Carneiro RMDG, Souza CFB, Mattos VS, & Correia VR. 2024. Molecular techniques for root-knot nematode identification. In: Molinari S (Ed.). *Plant-Nematode Interactions. Methods in Molecular Biology*. Vol. 2756. pp. 227–245. Humana, New York. https://doi.org/10.1007/978-1-0716-3638-1_5

Castagnone-Sereno P, Danchin EGJ, Perfus-Barbeoch L, & Abad P. 2013. Diversity and evolution of root-knot nematodes, genus *Meloidogyne*: New insights from the genomic era. *Annu. Rev. Phytopathol*. 51(1): 203–220. https://doi.org/10.1146/annurev-phyto-082712-102300

DemiRbaş Pehli VH, Kaşkavalci G, Kasapoğlu Uludamar EB, Toktay H, & Elekcioğlu H. 2020. Identification and prevalence of potato cyst nematodes and root-knot nematodes in the potato production areas of İzmir Province, Turkey. *Turk. Entomol. Derg.* 44(2): 259–272. https://doi.org/10.16970/entoted.683173

Edgar RC. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res*. 32(5): 1792–1797. https://doi.org/10.1093/nar/gkh340

Eisenback JD, Hirschmann H, & Triantaphyllou AC. 1980. Morphological comparison of Meloidogyne female head structures, perineal patterns, and stylets. *J. Nematol*. 12(4): 300–313.

Eisenback JD & Triantaphyllou HH. 1991. Root-knot nematodes: *Meloidogyne* species and races. In: Nickle WR (Ed.). *Manual of Agricultural Nematology*. pp. 191–274. CRC Press. Boca Raton. https://doi.org/10.1201/9781003066576-6

Hamidi I, Supramana, Mutaqin, KH, & Kurniawati F. 2022. Spesies Meloidogyne penyebab umbi berbintil kentang pada tiga sentra produksi di Sumatra [Species Meloidogyne cause pimple-like swelling on potato tuber in three production centers in Sumatra]. *Jurnal Fitopatologi Indonesia*. 18(2): 66–74. https://doi.org/10.14692/jfi.18.2.66-74

Holterman M, van der Wurff A, van den Elsen S, van Megen H, Bongers T, Holovachov O, Bakker J, & Helder J. 2006. Phylum-wide analysis of SSU rDNA reveals deep phylogenetic relationships among nematodes and accelerated evolution toward crown clades. *Mol. Biol. Evol*. 23(9): 1792–1800. https://doi.org/10.1093/molbev/msl044

Hunt DJ & Handoo ZA. 2009. Taxonomy, identification and principal species. In: Perry RN, Moens M, & Starr JL (Eds.). *Root-Knot Nematodes*. pp. 55–97. CABI. Wallingford, UK. https://doi.org/10.1079/9781845934927.0055

Jones JT, Haegeman A, Danchin EGJ, Gaur HS, Helder J, Jones MGK, Kikuchi T, Manzanilla-López R, Palomares-Rius JE, Wesemael WML, & Perry RN. 2013. Top 10 plant-parasitic nematodes in molecular plant pathology. *Mol. Plant Pathol*. 14(9): 946–961. https://doi.org/10.1111/mpp.12057

Ju Y, Lin Y, Yang G, Wu H, & Pan Y. 2019. Development of recombinase polymerase amplification assay for rapid detection of *Meloidogyne incognita, M. javanica, M. arenaria,* and *M. enterolobii. Eur. J. Plant Pathol.* 155(4): 1155–1163. https://doi.org/10.1007/s10658-019-01844-6

Karssen G, Wesemael W, & Moens M. 2013. Root-

knot nematodes. In: Perry RN & Moens M (Eds.). *Plant Nematology*. 2nd Edition. pp. 73–108. CABI. Wallingford, UK. https://doi.org/10.1079/9781780641515.0073

Kurniawan W. 2010. Identifikasi Penyakit Umbi Bercabang pada Wortel, *Daucus carota* (L.) di Indonesia [Identification of Forked Root Disease in Carrot, *Daucus carota* (L.), in Indonesia]. *Thesis*. Institut Pertanian Bogor. Bogor.

Marquez J & Hajihassani A. 2023. Identification and virulence of five isolates of root-knot nematode *Meloidogyne floridensis* on vegetables. *Plant Dis*. 107(5): 1522–1528. https://doi.org/10.1094/PDIS-06-22-1331-RE

Meng QP, Long H, & Xu JH. 2004. PCR assays for rapid and sensitive identification of three major root-knot nematodes, *Meloidogyne incognita, M. javanica,* and *M. arenaria. Acta Phytopathol. Sin*. 34: 204–210. https://eurekamag.com/research/004/260/004260581.php?srsltid=AfmBOooKm8vLk3jHc2_TCJMkyDbJom3uKJtA0nK_IXkTfaCoIiUnb-lz&__cf_chl_f_tk=KMocBPxQSdc.tyvjv_veOIIRWAbmUkPGI9fE6fP1Dtw-1783438742-1.0.1.1-bz1brNTcugS6ZKZ7tdNosK3J08n4dmDYLOdQw4Sy3xw

Moens M, Perry RN, & Starr JL. 2009. Meloidogyne species - a diverse group of novel and important plant parasites. In: In: Perry RN, Moens M, & Starr JL (Eds.). *Root-knot Nematodes*. pp. 1–17. CABI. Wallingford, UK. https://doi.org/10.1079/9781845934927.0001

Muhire BM, Varsani A, & Martin DP. 2014. SDT: A virus classification tool based on pairwise sequence alignment and identity calculation. *PLoS ONE*. 9(9): e108277. https://doi.org/10.1371/journal.pone.0108277

Mutala'liah, Indarti S, & Wibowo A. 2019. Short Communication: The prevalence and species of root-knot nematode which infect on potato seed in Central Java, Indonesia. *Biodiversitas*. 20(1): 11–16. https://doi.org/10.13057/biodiv/d200102

Patel B, Patel D, Tapre PV, Singh NK, & Patel R. 2019. Integrated management of root-knot nematode (*Meloidogyne incognita*) in potato (*Solanum tuberosum* L.) cv. Lady Rosetta. *Int. J. Bio-resource. Stress Manag.* 10(5): 561.

Patel B, Patel DB, Tapre PV, Singh NK, & Patel R. 2020. Pathogenicity of root-knot nematode (*Meloidogyne incognita*) and determination threshold level in potato (*Solanum tuberosum* L.) crop cv. Lady Rosseta. *Int. J. Bio-Resour. Stress Manag.* 11(1): 103–107. https://indianjournals.com/article/ijbsm-11-1-016

Przybylska A & Obrępalska-Stęplowska A. 2020. Plant defense responses in monocotyledonous and dicotyledonous host plants during root-knot nematode infection. *Plant Soil* 451: 239–260. https://doi.org/10.1007/s11104-020-04533-0

Scurrah MI, Niere B, & Bridge J 2005. Nematode parasites of solanum and sweet potatoes. In: Luc M, Sikora RA, & Bridge J (Eds.). *Plant Parasitic Nematodes in Subtropical and Tropical Agriculture: Second Edition*. pp. 193–219. CABI. Wallingford, UK. https://doi.org/10.1079/9780851997278.0193

Semblat JP, Bongiovanni M, Wajnberg E, Dalmasso A, Abad P, & Castagnone-sereno P. 2000. Virulence and molecular diversity of parthenogenetic root-knot nematodes, *Meloidogyne* spp. *Heredity*. 84(1): 81–89. https://doi.org/10.1046/j.1365-2540.2000.00633.x

Sikora RA, Coyne D, Hallmann J, & Timper P. 2018. Reflections and challenges: Nematology in subtropical and tropical agriculture. In: Sikora RA, Coyne D, Hallmann J, & Timper P (Eds.). *Plant Parasitic Nematodes in Subtropical and Tropical Agriculture*. 3rd Edition. pp. 1–19. CABI. Wallingford, UK. https://doi.org/10.1079/9781786391247.0001

Swibawa IG, Fitriana Y, Solikhin, Fiandani A, Suharjo R, Purnomo, Susilo FX. 2024. Effectiveness of bionematicide from *Purpureocillium lilacinum* in controlling root-knot nematodes (*Meloidogyne* spp.). *J. Trop. Plant Pests Dis*. 24(2): 181–189. https://doi.org/10.23960/jhptt.224181-189

Tamura K, Stecher G, & Kumar S. 2021. MEGA11: Molecular evolutionary genetics analysis version 11. *Mol. Biol. Evol*. 38(7): 3022–3027. https://doi.org/10.1093/molbev/msab120

Utami BS, Supramana S, & Giyanto G. 2017. Deteksi dan identifikasi spesies Meloidogyne penyebab umbi berbintil pada kentang asal Sulawesi Utara [Detection and identification of *Meloidogyne* species, pimple-like knot pathogen of potato tuber from North Sulawesi]. *Jurnal Fitopatologi Indonesia.* 13(3): 98–104. https://

doi.org/10.14692/jfi.13.3.98

Wainer J & Dinh Q. 2021. Taxonomy, morphological and molecular identification of the potato cyst nematodes, *Globodera pallida* and *G. rostochiensis*. *Plants*. 10(1): 184. https://doi.org/10.3390/plants10010184

Yadav H, Roberts P A, & Lopez-Arredondo D. 2025. Combating root-knot nematodes (*Meloidogyne* spp.): From molecular mechanisms to resistant crops. *Plants*. 14(9): 1321. https://doi.org/10.3390/plants14091321

Zijlstra C, Donkers-Venne DTHM, & Fargette M. 2000. Identification of *Meloidogyne incognita, M. javanica* and *M. arenaria* using sequence characterised amplified region (SCAR) based PCR assays. *Nematology*. 2(8): 847–853. https://doi.org/10.1163/156854100750112798