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Review Article

Biology, Taxonomy, and Management of the Root-Knot Nematode (*Meloidogyne incognita*) in Sweet Potato

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Sweet potato is the seventh-ranked food crop produced after wheat, rice, maize, potato, barley, and cassava in the world. It is the most important root tuber crop in temperate, subtropical, and tropical areas of the world. It is grown for food, income-generating, and jobs for farmers and retailers. The important nutritional substances of sweet potatoes are *ß*-carotene and anthocyanins. However, the production and its valuable products are limited due to root-knot nematode parasitism. One of the most important destructive species of root-knot nematode to this crop is *Meloidogyne incognita*. The most destructive stage to sweet potato is at its second juvenile stage (J2). At this stage, it invades the roots and tubers of sweet potato highly in warm sandy soil conditions. It is an obligate plant-parasitic nematode. *M. incognita* caused significant yield loss to sweet potato in terms of quality, quantity, disturbing the process of photosynthesis and nutrient uptake through the formation of galling, establishing of its feeding sites, or induced galls that contain giant-feeding cells, and cracking of tubers and roots directly. It also reduces the market values of the infected tuber of sweet potato by downgrading the production values. The problem of quality and quantity losses to sweet potato by this pest is one of the major problems nowadays. It caused this problem alone or interaction with other plant-parasitic pathogens or through synergistic of fungi, bacteria, viruses, and others. Therefore, this review paper is focused on the sweet potato *M. incognita* biology, taxonomy, geographical distribution, and management measures.

1. Introduction

Sweet potato is the seventh-ranked food crop produced after wheat, rice, maize, potato, barley, and cassava in the world [1]. China is the leading producer of sweet potatoes, followed by Nigeria, Tanzania, Ethiopia, Indonesia, and Uganda [2]. Continentally, Asia (86.5%) is the leading producer followed by Africa (10.6%) [3]. It is a root tuber crop that is mostly used for the human diet. Nutritionally, sweet potato is rich in fiber, potassium, vitamins, carbohydrates, proteins, and other essential nutrients [4, 5]. It is also used for income-generating in addition to its food value for the producers and retailers in the market channel. Eating sweet potato provides us the β-carotene which is used for eliminating the deficiency of vitamin A [5] and anthocyanin [6]. Anthocyanin is used as an antioxidant that offers humans protection from a variety of degenerative diseases and protects our bodies from free radicals [6], and serves as an anti-cancer, antidiabetic, and anti-inflammatory activity [7]. This is why sweet potato is considered as an excellent novel source of natural health-promoting compounds. In addition to nutritional values, its extraction could be used as coloring agents of food [8]. However, its production and valuable products are hindered by root-knot nematode species, especially at resource-poor farmers [9].

Root-knot nematodes (RKNs) are the most problematic and destructive in warm moist sandy soil conditions. Under these conditions, they highly caused a reduction in the yield, quality, and quantity of the sweet potato tubers [10–12]. The well-known RKN species are *Meloidogyne incognita* [9, 12] and *M. enterolobii* (guava root-knot nematode) [12]. Both of them are the most destructive nematodes of sweet potato compared to *M. javanica, M. hapla,* and *M. arenaria* in the US [13, 14]. The survey conducted in Kyushu and Okinawa

of Japan indicated that 96% of the sweet potato was attacked by *M. incognita* under field conditions [15]. This finding also indicated that *M. incognita* is a serious pest of sweet potato tubers than other species of RKN. It can attack alone or interact with other plant pathogens [16, 17]. However, in most cases, the impact of *M. incognita* on a sweet potato is grossly underestimated. In many countries, the loss caused by *M. incognita* to food crops is neglected for decades due to unknown mostly and its sign and symptoms of damage look like or related to other pests of crops. In fact, good management practices are required to reduce the quality and quantity losses of sweet potato tubers by *M. incognita*.

The reason behind the choice of *M. incognita* for this review is its cosmopolitan distribution, severity and emerging pests to sweet potato crops. Hence, this review focused on biology, taxonomy, geographical distribution, and management strategies, because understanding them plays a vital role in its management.

2. Biology and Taxonomy

M. incognita is the most economically important plant-parasitic nematode species in tropical, subtropical, and warmer regions of the world. It is widely spread in tropical and subtropical regions of all the continents of the world [18]. Ecologically, the moist sandy soil texture and its temperatures are important factors that affect the survival and pathogenicity rate of *M. incognita*. It prefers and causes the most damage in a low clay content soil textures [19]. Its population densities are increased in sandy soils than silt and clay [20, 21]. In light sandy soil, it moves and aerates easily and causes more damage to host plants [22]. Ma [23] reported that *M. incognita* had lower penetration rates in well-watered soil. Kim *et al.* [24] also reported that the number of gall, egg mass formations, and root penetration rates of *M. incognita* increased in the sandy soil than in other soil texture [25]. The works of Koenning *et al.* [19] and Prot and Van Gundy [26] agreed with this report in that *M. incognita* is highly reproduced in soil that contains 72 to 91% sandy than in the soil that contains 30% of clay. *M. incognita* prefers a range of temperature between 25 and 30°C [27, 28]. Zhao-hui et al. [29] reported that the optimum temperature for the hatching of *M. incognita* egg was 15–30°C. This report also indicated that J2 could survive at a range of 10–25°C. Tsai [30] also reported that the longest survival of J2 was 380 days at 15°C and the shortest after exposed for 3:30 hours at 45°C (98.8% mortality), which was followed by 40°C (100% mortality) after 6 days, 35°C (100% mortality) after 60 days, and 25°C (100% mortality) after 25 days. The mortality rate at 5°C was 99.3% after exposure for 20 days. This report generally indicated that the temperature range has a great impact on the life expectancy of *M. incognita*. The shelf life becomes decreased as the temperature increases above the normal range, but the hatching rate of J2 increased from eggs to some extent of temperature increments. The eggs became inhibited to hatch below 10°C [31]. Generally, the RKNs can complete their generation within three to four weeks under suitable environmental conditions. But this can be extended; for instance, Ibrahim and El-Saedy [32] reported that, at 21°C, the *M. incognita* could be taken 37 days to complete its life cycle on *Antirrhinum majus*. The J2 stage (J2) enters the roots of the sweet potato plant to lay eggs rapidly to form severe galling on the roots of sweet potato [12]. The gelatinous matrix covering the egg mass is used to protect from water loss and predators [33]. Some *Meloidogyne* species can enter a state of anhydrobiosis in dry soil during J2 stages to live for a long [28]. J2 requires soil moisture content between 10 and 30% to grow and develop to the next stages. However, the soil moisture content of more than 30% had a negative effect on the hatching and survival of J2 [29]. Hatching of the *M. incognita* occurs in wet sandy soil [34]. The first molt occurred within the egg. Newly hatched J2 has a short free-living stage in the soil near host plants (rhizosphere) before migrating in the soil towards their host plant in the region of root elongation. It migrates in the root until it becomes sedentary and form a parenchyma cell to become multinucleate near its head to form feeding cells known as giant cells. Giant cells are the feeding sites of juveniles and adults [35, 36]. The J2 penetrates the root tips of the host plants by using a protrusible stylet and secreting the cell wall degrading enzymes [37]. Under favorable conditions, the J2 stage molts to J3 and then to J4 and finally to the adult stage. J2 can survive in the soil as a quiescent state to extend the period of unfavorable conditions by feeding on the lipid reserved or stored in its intestine [38].

2.1. Taxonomic Classification. Description of the organism:

Domain: Eukaryota
Kingdom: Metazoa
Phylum: Nematoda
Class: Secernentea
Order Tylenchida
Family: Heteroderidae
Genus: *Meloidogyne*
Species: *Meloidogyne incognita* [39]

Until 1949, the binomial name of the root-knot nematode was *Heterodera marioni*. However, the genus name was changed to *Meloidogyne* because of its morphological differences from cyst nematodes which were described by Chitwood [40]. In appearance, *M. incognita* is similar to other free-living soil nematode species. But it has a unique natural gift to move along shallower temperature gradients (0.001 C/cm) than any other known organism [41]. This is the thermotaxis, or movement of an organism according to the gradient of temperature. This report also indicated that the newly hatched J2 migrated towards the higher temperatures when placed in shallow thermal gradients averaging 23°C. The response from the host plant is complicated, while they search for chemical cues that can guide them to move towards an appropriate level in the soil to get specific roots [42, 43]. *M. incognita's* secretome overlaps with the reported secretome of mammalian parasitic nematodes (e.g.,

Brugia malayi), suggesting a common parasitic behavior and possible conservation of function between metazoan parasites of plants and animals [44].

2.2. Methods of *M. incognita* Identification from Other Related Species

2.2.1. Morphological. The shape and visual aspects of the perineal region, dorsal arch, dorsal striae, lateral lines, and phasmids of the females are used for morphological characteristics. They are used for the identification of RKN species traditionally. This method is cheap but requires a full microscope adjustment, lactic acid, glycerin, personnel skills, and mature females for diagnosis [45]. The female of *M. incognita* is identified by having a white pear-shaped body and knob of a stylet that sets off rounded to transversely elongated and indented or divided at its anterior position. It has also a characteristic of the circular marking usually found in the perineal area [18, 46]. The distance of the dorsal esophageal glands to the base of the stylet is short (2–3 μm), has 10–20 annules, a high dorsal arch, squarish, and has forked striae often along with a lateral line.

The characteristics on the head of males (e.g., size and shape of stylet) are useful parts to identify *M. incognita, M. enterolobii, M. paranaensis*, and *M. javanica*. They have a taxonomical value. They help in viewing their lateral surfaces during the diagnostic of the specimens under the microscope [47]. The distance from the dorsal esophageal gland orifice (DGO) to the stylet base of the males has indicated the distinction between *M. enterolobii* and *M. incognita* [48, 49]. The male of *M. incognita* has a vermiform shape, no offset head, longer conus of stylet than the shaft, stylet knobs prominent, usually of greater width than length with flat and concave at the anterior margins, having 0–5 annules, 1 or 2 testes, tail bluntly rounded, terminus unstriated [18]. The male, on the other hand, appears long and thin with a cylindrical body [46].

2.2.2. Biochemical. Reliable isozyme electrophoresis methods are used for the identification of a single young egg-laid by *M. incognita* females. The method was originally developed by Esbenshade and Triantaphyllou [50]. It was modified and adapted to the system of phast (an automated electrophoretic apparatus) by Karssen et al. [51]. The isozymes of glucose six phosphate dehydrogenase (EC 1.1.1.49) are used for differentiating RKN species [52]. This method of identification is based on the relative mobility of extracting enzymes from mature females by using gel electrophoresis. In this method, the protein extracted from the *M. javanica* females is applied to the gel and it is used as a reference of the phenotype [53]. It takes three to four hours to complete the whole procedure from sample processing to gel revelation.

2.2.3. Molecular. This method was applied by sequencing the deoxyribonucleic acid (DNA) of ribosomal (18S-ITS-5.8S, 28S D2/*D*3) and mitochondrial fragment flanking cytochrome oxidase genes. It requires the combined analysis of DNA sequencing and polymerase chain reaction (PCR) for the species-specific primers to verify *M. incognita* [54]. *M. incognita*, *M. enterolobii*, and *M. javanica* could be identified by using three pairs of specific primers. In this case, the specific primers of *M. incognita*, *M. enterolobii,* and *M. javanica* were approximately 1000, 200, and 700 bp, respectively [55]. The *M. incognita* is the most abundant species identified when compared with other studied species (95%) by this method [54]. A multiplex assay can also be used to identify tropical species of *M. incognita*, *M. javanica,* and *M. arenaria* [56]. The PCR tests can be performed on all developmental stages of *M. incognita* and the multiplex PCR method allows the detection of one or more species in a nematode mixture by a single PCR. EPPO [52] recommended the seven PCR molecular tests in detail. The sequences of the characterized amplified regions (SCARs) are used to identify the DNA of egg masses, J2, and female after extracted from the infested plant material [57].

2.2.4. Real-Time PCR (qPCR). It is a qualitative method that allows the identification of the target sequences, which is faster and more sensitive. It does not require the preparation of gels, because it can detect and quantify DNA based on the emission of fluorescence. In this method, the data are processed by using a computer. However, the method requires high costs in terms of equipment and reagents [47].

The nucleotide sequences of parasitic nematodes are varied among species. Its restriction sites differ in their locations along the genome and results in fragments of different sizes. Their restriction products are separated by gel electrophoresis [45]. This technique allows the identification of *M. hapla, M. incognita,* and *M. arenaria* [58]. First, the PCR reaction is carried out by using primers that amplify the region between cytochrome c oxidase subunit 2 (COII) and LrRNA of mitochondrial DNA. *M. hapla* sample will result in a 500 bp band, while a 1.7 kb band is formed for *M. incognita* and *M. arenaria* DNA [58].

2.3. Loop-Mediated Isothermal Amplification (LAMP). This method amplifies the DNA specifically with the highest sensitivity compared to PCR under isothermal conditions [59]. It is reported that this technique has been used for identifying *M. enterolobii, M. incognita, M. arenaria, M. javanica, M. hapla, M. chitwoodi*, and *M. fallax* [60–63]. However, the finding of [64] was a contrast to this previous report since it indicated that only *M. partityla* resulted in positive amplification, while no amplification was observed in case of *M. hapla*, *M. javanica*, *M. incognita*, and *M. arenaria* by the LAMP assay after being detected by agarose gel doc image analysis, SYBR™ green-based UV image, and Genie III amplification curve analysis. Niu et al. [63] reported that a universal RKN-LAMP can be used to identify the *M. incognita*, *M. arenaria*, *M. javanica*, and *M. hapla*.

LAMP method employs a DNA polymerase and it is a novel nucleotide amplification technique [65]. It sets the inner forwarding and backwarding of the outer primers with the possibility of one or two additional primers to increase

the amplification efficiency by forwarding and backwarding the loop of its primers. Particularly, its primers are designed for recognizing the six distinct sequences of the target DNA: its *Bacillus stearothermophilus* (Bst) which is used to facilitate a nonquantitative PCR method based on auto cycling strand displacement activity of DNA synthesis [65]. An inner primer contains the sequence of the sense and antisense of the target DNA strands. This could be initiated by LAMP, while the outer primer releases a single-stranded DNA. This served as a template for DNA synthesis. It was primed by the second inner and outer primers to hybridize the other end of the target which produces a stem-loop of the DNA structure. Subsequently, in the LAMP cycling, one inner primer hybridizes to the loop on the products and initiates the displacement of DNA synthesis to yield both its original and new stem-loop. The new stem-loop DNA stranded is two times longer than the original. The cycling reaction can accumulate 10^9 copies of the target DNA stem-loop. The final products are inverted repeatedly and look like a cauliflower structure with multiple DNA stem-loops. Generally, the LAMP recognizes and amplifies the target by six distinct sequences initially [59].

Amplification can be detected through visualization with the naked eye, due to the formation of the white precipitate of magnesium pyrophosphate (a byproduct of the amplification) [66] or the change of color of the solution by using dyes such as SYBR Green, calcein, HNB, and pico green [47].

2.4. Geographical Distribution. RKNs are widely distributed throughout the irrigated agricultural areas in many countries of the world. They occur mainly in tropics, subtropics, and warmer regions of the world [67]. The RKN is a roundworm plant-parasitic [68]. *M. arenaria, M. hapla, M. incognita*, and *M. javanica* are made up of 99% of all species identified in over 660 isolates from 65 countries [69]. *M. incognita* is widely distributed in many Asian, African, European, Oceania, and American countries [18]. *M. incognita* is distributed worldwide where sweet potatoes are grown (https://keys.lucidcentral.org).

2.5. Means of Dispersal. M. incognita is dispersed mostly by the infected sweet potato tuber seed [10], root materials, soil debris, and poorly sanitized bare-root of propagative plant materials [70]. It is also spread over a short distance by water and wind. The most likely method of introducing *M. incognita* into a new geographical area is through the movement of infected or contaminated planting material and *M. incognita* has limited potential for natural movement at the J2 stage in the soil at most, only a few tens of centimeters. Infected tubers can easily transport the eggs, J2, and females of *M. incognita*. However, sweet potato seed is a primary challenge that needs to be met [71]. The long-distance spread is also facilitated by the exchange of contaminated soil, rootstocks, and tubers. *M. incognita* is a quarantine pest of sweet potato. This means the tuber seeds must be certified before being introduced to new places. It is essential to keep in mind that, in the case of its low infection, the symptoms on the tubers of sweet potato are not visible easily. These nematodes are quite undetectable. This also means that rootstocks, ornamental species, etc. could infest from contaminated soil. This situation could enable the undetected spread of the species to new uninfected areas [72]. The invading process of *M. incognita* in the plant root starts from the development of an embryo in a proteinaceous matrix secreted especially by the adult female, which hatched to second-stage larvae (J2) which later travelled to sweet potato in the soil to initiate a fight with a crop to open gateway and establish a dwelling place [73].

2.6. Host Plant Range. M. incognita is the most economically damaging plant-parasitic nematode on horticultural and field crops. It is a polyphagous endoparasite of plants that causes serious problems on the growing plants [74]. It is an obligate parasite of the roots of thousands of plant species, including monocotyledonous and dicotyledonous, herbaceous, and woody plants. It can attack the annual, biennial, and perennial plants. Generally, it causes significant damage to a broad range of host plants [44] and severely damages sweet potato, potato, tomato, carrot, pepper, okra, watermelon, cantaloupe, onion, pumpkin, squash, sweet corn, eggplant, bean, pea, celery, garden pea, broccoli, cabbage, mustard, radish, and lettuce [75], perennial crops such as coffee, banana, grape, and nut trees [38], ornamental plants [76], and numerous grasses, sedges, and broad-leafed weed plants [77–79]. Ramadan [80] reported that RKN could be affecting more than 31 plant species belonging to 19 different plant families in Jordan alone.

Based on the degree of damage seriousness they cause, the sweet potato parasitic nematodes are categorized into major and minor pests. For instance, the root-knot *(Meloidogyne incognita),* Reniform (*Rotylenchulus reniformis*) [81], lesion (*Pratylenchus* spp.: *P. brachyurus, P. coffeae,* and *P. flakkensis*) [81], and stem and tuber rot (*Ditylenchus dipsaci* and *D. destructor*) are the major nematode pests of sweet potato [82] while burrowing (*Radopholus similis*), spiral (*Helicotylenchus dihystera*), sting (*Belonolaimus longicaudatus*), and stubby root (*Paratrichodorus minor* and *Trichodorus* spp.) nematodes are the minor nematode pests of sweet potato [12]. Among this entire group, the sweet potato is highly attacked and damaged by the root-knot nematodes in general and *M. incognita* species in particular. *M. incognita* attacked the diverse genotypes of sweet potato roots and tubers. Its attacking of sweet crops begins from J2 and continues to all of its next life cycles in obligate.

2.7. Symptoms on Sweet Potato. M. incognita causes severe changes in the physiology and morphology of the sweet potato plant. The sweet potato infected by *M. incognita* has resulted in the reduction of growth, loss of its vigorous, and they might get dried permanently.. The symptoms formed by *M. incognita* on the sweet potato plants are used as an indication and identification of a problem but often cannot be used as a diagnostic purpose because it may indicate similar symptoms that can be imposed by other causal agents. The damaged symptoms that occurred on the sweet potato plant

occurred both above and below the ground. The above-ground symptoms can be stunted growth, yellowing of leaves, leaf chlorosis, plant death, wilting of leaves, and poor shoot growth [83, 84]. The below-ground symptoms are tubers deformed and cracked, knotted roots, gall formation or swelling on the roots, and blistering or bumpiness [12, 81]. The presence of galls in the sweet potato roots limits the water supply and disrupts their physiology. The most distinctive symptom of *M. incognita* infestation is the appearance of galls on primary and secondary roots, which become swollen and distorted with heavy infestations. The galls formed on the host plant are varied in size and can be reached up to 15 mm in diameter [38]. It feeds inside of the sweet potato tubers by moving in it and leading it to surface cracks, small white lesions, rots and dries beneath of its skin without any indication of symptoms until the tubers are harvested or stored. The anatomical studies of the *M. incognita* indicated that giant cells are formed from a parenchyma cell in the stele region accompanied by crushed and deformed xylem and vessel elements to become multinucleate near its head to form feeding cells or feeding sites of J2, and later juvenile to adults [85].

3. Economic Impacts

M. incognita is economically the most damaging nematode of sweet potato plant worldwide [81, 86]. In sweet potato, an estimated annual yield loss of 10% was reported in California [87]. The varieties susceptibility and pathogenicity of *M. incognita* reported showed that a 50% storage root reduction at a population density of 20,000/cm^3 (https://keys.lucidcentral.org). Aside from yield loss, *M. incognita* exhibits cracking of the storage roots, predispose the roots to crack when soil moisture levels fluctuate during the development of the storage roots indirectly and pinpoint necrotic spots [88], reducing quality by causing internal necrosis and external galling, which reduces the market value of the storage roots to make it unmarketable [81, 89]. However, in most cases, the impact of *M. incognita* on a sweet potato is grossly underestimated and in many countries; the loss caused to food crops because of it is neglected for decades relative to other pests such as noxious weeds, insect pests, and pathogens specifically. Globally, in other cases, the annual yield loss of crop caused by *Meloidogyne* species is estimated to be $157 billion [90]. Berlitz et al. [91] reported that the economic loss caused by nematode has direct and indirect dimensions, for instance, it caused 100% and 14% of food crop and citrus fruit damage, respectively, that could be estimated financially to be $100 billion per annum.

The yield loss caused by RKN is high, though significant knowledge gaps persist between developed and developing countries of the world [92]. The quality or quantity losses of sweet potato by *M. incognita* could be alone or associated with other plant pests. This is why sweet potato is susceptible to many soilborne pathogens of different species [93–96], insect pests such as coleopteran (e.g. beetles like species of weevils such as *Cylas formicarius* (Fabricius) and *Euscepes postfasciatus* (Fairmaure)), and Lepidoptera (e.g. *Aedia* (Aediinae), *Helcystogramma (Spodoptera litura*) worldwide [93]. There is an additive, synergistic, and antagonistic interaction among the plant pathogens to cause severe damage. Sweet potato *M. incognita* is the primary pathogens that favor the establishment of secondary pathogens like bacteria, fungi, and viruses on its important parts which otherwise cannot infect the plant under normal conditions by inducing changes leading to the synergistic association for disease development through merely colonizing the dead cells. The quality and quantity losses of sweet potato caused by fungi, bacteria, viruses, and insect pests may occur at any point in the production cycle [93].

The black rot plant bed (*Ceratocystis fimbriata*), soil rot (*Streptomyces ipomoeae*), stem rot (*Fusarium oxysporum f.* sp. *batatas*) and different viral diseases such as feathery mottle virus, chlorotic stunt virus, leaf curl virus, crinkle leaf curl virus, latent virus, and symptomless virus were among the sweet potato pathogenic pests in alone, or followed by the damage of *M. incognita* [93].

The infection of the tuber is easily susceptible to soil fungal attack if present [72]. *M. incognita* is an ectoparasitic nematode that could interact with other RKNs species and migratory endoparasite nematodes. An economic damage threshold and intensity of damage by *M. incognita* depend on the susceptibility of the cultivar, population density, and environmental conditions, such as soil type and its fertility, moisture, temperature, and presence of other pathogenic organisms. The wounded sweet potato roots by *M. incognita* can easily be affected by with the other phytopathogenic organisms. Interaction between these two groups on the same fields and host's root system may also depend on the sequence of their infection. The damaged parts of sweet potato provide the entry sites for the other pests. However, more specific associations, which can result in additive, synergistic, or antagonistic responses by the host plant, demonstrated that more complex interactions have evolved. Most investigations on the inter-relationships of cyst nematodes and other plant parasites are focused on those with fungi, especially those causing wilt and root rot. Generally, these interactions are synergistic in relation to disease development but often result in restriction of nematode reproduction because of the associated root damage [97].

4. Management Measures

4.1. Cultural Practices. Cultural practices such as crop rotation, fallowing, flooding, sanitation, plowing 2–3 times, mulching, adding organic manure, optimizing the planting space in the field, time of sowing, and cover crops can reduce the severity and intensity of *M. incognita* [98, 99]. A fallow method is very effective in warm climates [79]. Removal of the primary infected sweet potato and other alternate host plants in each cropping system can reduce *M. incognita* intensity in the field. For instance, in South Africa, the farmers uproot and expose the tobacco residues to sunlight after harvested [100] or burnt them in situ [101]. In Zimbabwe, the early planting of tobacco on plowed ridges was reported as a key management tactic for RKNs [101].

Synchronizing the date of planting during low soil temperatures was effective for the management of *Meloidogyne* species [102]. *M. incognita, M. javanica*, and *M. arenaria* do not penetrate roots at soil temperatures below 59–64°F. Prolonged flooding periods might be effective to successfully manage crops like paddy because RKNs are highly populous where water moisture is limited [103]. Khan et al. [104] also reported that the application of the decomposed leaves of the *Tagetes erecta* to soil can reduce the numbers of J2 in the soil, the number of root galls, egg-masses, and its multiplication greatly. This report also indicated that adding poultry manure can significantly reduce both the number of root galling and nematode populations. Adding organic matter to the soil can also suppress the number and diversity of plant-parasitic nematodes in soil [105]. Chicken manure is very effective in reducing *M. incognita* egg masses by 56%. The finding of Osunlola and Fawole [106] also indicated that poultry dung at 10 to 20 t/ha was highly effective against *M. incognita* under the field conditions of sweet potato farms compared to the dung of cow, horse, and goat at 10 to 20 t/ha. Pedroche et al. [107] also reported that the crop residues of broccoli (*Brassica oleracea*) and the species of fungi like *Trichoderma inoculants* could decrease the *M. incognita* population from the host plants. The use of trap crops and antagonistic crops such as the planting of Mexican marigold (*Tagetes erecta)* and Rattlebox (*Crotolaria spectabilis)* in nematode-infested soil is effective against the RKN. Marigold, chrysanthemum, castor bean, partridge pea, velvet bean, vetch, rapeseed, and sesame have also the capability to suppress nematode populations in the soil [108].

Intercropping of the host with non-host plants can potentially reduce yield losses due to nematodes [79]. However, there is no literature finding that recommended a crop to be sown with sweet potato to reduce the infection of *M. incognita* to cite. But there was a report of the best performed intercrop from other host plants of *M. incognita*. For instance, intercropping of sesame with okra resulted in a decrease in the penetration of *M. incognita* during the J2 stage by delaying its maturation; it favored the development of *M. incognita* males and increased yields of okra and chickpea in the tested farm field. The intercropping of sesame with okra by distancing 15–30 cm from each other in sandy loam soil could reduce the intensity of damage when compared with clay soil [109]. The evidence from the Bulgaria greenhouse experiment also indicated that intercropping of different tomato varieties with the marigold plant has the potential of reducing the intensity of galling, egg masses, and population density of *M. incognita* [110].

The principal role of crop rotation lies in the distancing of the growth of the susceptible host crops in space and time from the targeted population to bring its damage below the economic threshold levels by planting the non-host plants [105]. But it is usually not very effective because *M. incognita* has wide host ranges. Therefore, strategies of cultural management such as crop rotations are less well developed and are difficult to design [18]. A five-year rotation with a non-host crop is recommended [12]. This system is one of the promising management measures that can suppress the RKN species population in potato crop production [111]. Non-host crops or resistant crops can be planted when the nematode of the population is high. Rotation of cotton with the potato was found to decrease population densities of *Belonolaimus longicaudatus* and *M. incognita* in comparison with continuous potato plantings [112], garden egg marigolds varieties such as Tangerine, Petite Gold, Petite Harmony, Single Gold (sold as Nema-Gone), and Lemon Drop were also suppressed the *M. incognita* populations in soils [113]. The combined application of poultry manure at a rate of 5 to 15 t/ha and rapeseed cake at 200 kg/ha on tomato seed variety of Marglobe can be used to knock down the number of *M. incognita* during the J2 stage, number of egg mass, and root galling index by improving the fruit yield [114].

4.2. Biological. Paecilomyces lilacinus is an egg parasitic fungal of *M. incognita*. Its effectiveness against *M. incognita* was found sound in the sweet potato plant. It could be reducing the egg masses by 50% by attacking its fatty acid and retinol-binding proteins (Mi-FAR-1). It increased its endospores attachment to the surfaces of the J4 cuticle before becoming adult to reduce their fecundity [115, 116]. The fungi of the genus *Trichoderma* are also known to suppress many soilborne diseases from sweet potato plants. It penetrates the nematode egg mass matrix and decreases its hatching [117]. Furthermore, its toxic metabolites directly inhibit nematode penetration and development [118]. Among the *Trichoderma* species, it was revealed that *T. harzianum* has a greater toxicity level against *M. incognita* than *T. viride* [119]. Tomato plants treated with Streptomyces antibiotics strain M7 and actinomycins were also safe nematicidal agents in reducing and suppressing the potential of RKNs [120].

Pasteuria penetrans are also used for knockdown of J2 infestation [121–123]. This parasitism is secreted from esophageal glands. Its role is to reduce the potential of *M. incognita* effector (MiISE5) in order to destroy the intended death of the cell [16].

Utilizing of both *Paecilomyces lilacinus* and *Pasteuria penetrans* was considered as good management practice of *M. incognita*. According to Manakau [124], natural soil bacteria (*Bacillus penetrans*) could manage the RKNs effectively. Biopesticides formulated from bacteria, viruses, and filamentous fungi could also destroy plant-parasitic nematodes. In line with this, Nagachandrabos [125] reported that *Pseudomonas fluorescens, P. lilacinus*, and *T. viride* liquid formulations can be reduced the *M. hapla* juvenile (J2) population in the soil. It reduced the infection of the female population to roots, and egg numbers per gram of host plant roots at various field conditions. The *M. incognita* is a sedentary endoparasite in various crops such as pulses [126], reducing the quantity and quality of harvested vegetables by 40% [25]. It could be managed by *Purpureocillium lilacinum* (biocontrol agent) [127]. The resistance ability of hybrid watermelon cultivars to F*usarium oxysporum f.* sp. *Niveum* can simultaneously reduce its attack by *M. incognita* [128].

4.3. Host Plant Resistance. Resistant sweet potato varieties will reduce the production costs and reliance of farmers on nematicides. Furthermore, they can increase the yields and marketability values of the products. Commercially, the available varieties of sweet potatoes, such as Covington [129] and Evangeline [130], have the ability to resist themselves from *M. incognita*. Bernard et al. [131] also reported that the cultivar of Nugget showed the highest degree of resistance and manifested in lower necrosis, galling formation, and had high fresh root weights, while having low number of eggs counted unlike the cultivars of Georgia Jet and DMO1. This report also indicated that the cultivars of TUO2 and Whatley Loretan resulted in intermediate resistance. In addition, the cultivars of W-86, L4-89, BPA4, Sinibastian, Jasper, Jewel, Miracle, Georgia Red, Garcia Yellow, and Travis also have the ability to be resistant against RKNs. However, *M. incognita* can infect even some of the resistant cultivars. Resistance varieties of soybean against the elucidated *M. incognita* have a maximum amount of phenol, salicylic acid, chlorogenic acid, and ascorbic acid as compared to susceptible plants [54, 132]. But the case of resistance in sweet potato plants is not yet described. Artemisia is a large and diverse genus of plants belonging to the daisy family or Asteraceae has an effective nematicidal character [126]. Izuogu et al. [133] also reported that the cowpea variety, IT89KD-288, was highly resistant to *M. incognita* in nematode-prone areas of agricultural soils. The fecundity and reproductive factor of the nematode were low in resistant cultivars of cucumbers (Long Green) and high in susceptible ones [134].

Complex mixtures of volatile compounds, α-pinene, limonene, 2-methoxy-3-(1-methyl propyl)-pyrazine, methyl salicylate (MeSA), tridecane and 4,5-di-epi-aristolochene, were emitted by pepper roots that detect thymol in one of the accessions (AVDRC PP0237) in Kenya [135].

4.4. Botanical. Bharadwaj and Sharma [136] reported that holy basil (*Ocimum sanctum*) aqueous extracts have high potential against the *M. incognita (*J2 hatching) when compared to neem (*Azadirachta indica),* papaya *(Carica papaya),* ricinus *(Ricinus communis),* French marigold (*Tagetes patula)*, and untreated control. Jumaah [137] also reported that *A. indica* and Carry leaf (*Murrage koenigi*) show the best performance in reducing the number of *M. incognita*. Plant root exudates affected root-knot nematode's egg hatching. Chemicals in root exudates can attract or repel nematodes via motility inhibition, or even cause death [138]. This report also indicated that the tomato root exudates can suppress *M. incognita* egg hatch, survival, and chemotaxis of the J2 by repelling due to increment of 2,6-Di-tertbutyl-p-cresol, L-ascorbyl 2,6 dipalmitate, dibutyl phthalate, and dimethyl phthalate after inoculation. The nematicide extracted from tobacco (*Nicotiana tabacum*), clove (*Syzygium aromaticum*), betel vine (*Piper betle*), and sweet flag (*Acorus calamus*) were effective in killing the nematodes under laboratory condition [139]. The extracts of the leaves of Mexican marigold (*T. erecta),* bitter (*Vernonia amygdalina*), lantana (*Lantana camara*), and seeds of baker tree (*Cupressus bakeri*) were the most efficacious (above 95% hatching inhibition) against the juveniles hatching in the laboratory, especially at 5% concentration [140]. Vinodhini et al. [141] also reported that the leaf extracts of asparagus indicated a promising direction to reduce RKN in tomato production.

4.5. Chemical. Treating soil with chemical fumigants prior to planting the sweet potato is a helpful, reliable, and effective way of managing *M. incognita*. There are several nematicides that have been very effective against the *M. incognita* in sweet potato farmlands. For example, Nemagon, Mocap, Dasanit, Nemacur, Furadan, Temik, and Vydate were effective for managing *M. incognita* in sweet potato farming. Early application of furfural was also recommended for the reduction of the J2`s of *M. incognita* infestation [121]. Similarly, root galling of both crops and inoculum levels of the nematode was increased proportionally in the glasshouse [142]. Typically, soil fumigants are used to manage *M. incognita* both in nursery hotbeds and in production fields. In contrast to this finding, Noling [143] reported that fumigating the soils with the multipurpose fumigant nematicides was effective against RKN in the soil. Non-fumigant nematicides need to be applied uniformly and incorporated into the soil pre- and post-planting for suppression of RKN [108]. According to Noling [144], the use of soil fumigants has been more consistently effective than non-fumigants for managing RKN in Florida. These fumigants need to be applied at least 3 weeks before planting of the crops because they cause phytotoxic to plants. The fumigant chemical nematicides such as Metam-sodium (Vapam, Sectagon), 1,3-dichloropropene (Telone) [9, 108], and metam-potassium were effective against RKN in a sweet potato field [9]. However, the utilization of synthetic pesticides alone is highly detrimental to man and the environment. But they are the principal means of nematode control. Therefore, it is suggested that the utilization of nematicides with other non-environmental detrimental methods such as organic amendments of animal wastes and other RKN management practices is better in an integrated form [145]. The combinations of termidust, worm force, and basudyne [146], methyl bromide, 1,3-chloropicrin, chloropicrin-proprietary solvent, and 1, 3-D-metam sodium [147] are used to suppress the population of plant-parasitic nematodes in the infested soil. Spraying of metam-sodium can also be used for managing the RKNs for a short period of time under high population pressure [147]. The farmers mostly rely on carbofuran to manage nematodes [146]. The insecticide (e.g., Emamectin benzoate) has also the potential for the control of *M. incognita*. VTo (fluensulfone drench; tradename: Nimitz, ADAMA Agricultural Solutions Ltd., Raleigh, NC) is a non-fumigant nematicide that is registered for use in fruit and vegetable crops in California at 1.96 kg/ha and is also helpful in managing the *M. incognita* damage than other nematicides in sweet potato production [9]. But they are hazards to the environment and health due to the emission of volatile organic compounds and their toxicity. Nevertheless, the environmentally sound, effective, and

economically viable alternatives methods against nematodes are not available, and this has been an important factor in the continued use of soil fumigants [148, 149].

4.6. Integrated Management. Among others, the integrated use of different *Bacillus* species and some biopesticides [such as Bioarc®, Bio Zeid®, and *Ascophyllum nodosum* (Algaefol®)] has prominent value for environmental safety and high effectiveness against nematodes [91]. Early application of biopesticides such as furfural and *P. penetrans* Lilacinum could have the ability to reduce the J2 of *M. incognita* infestation [121]. Utilizing both bacteria and fungi that parasitize or trap nematodes can be considered as a good control method. *Bacillus penetrans* are also found effective to manage RKN. Biopesticides can be formulated with bacteria, viruses, or filamentous fungi, which can destroy and feed on plant-parasitic nematodes. Nagachandrabos [125] reported that *P. fluorescens*, *P. lilacinus,* and *T. viride* liquid formulations might be good in reducing the J2 in the soil, root infection of females, and egg numbers.

The principal management method used for RKNs is the use of resistant or non-host crop plants. In addition, fallowing of the farmland, flooding infested land, disinfestations or protections of planting material, application of amendments or nematicides, and the use of microbial antagonists and biocontrol agents as an alternative can reduce the number, density, and intensity of *M. incognita* in the soil and then from the sweet potato. The use of any single management tool, perhaps with the exception of nematicides, rarely results in an effective strategy to alleviate nematode problems in resource-poor areas. Hence, nematode management might benefit greatly from the use of alternative control methods employing IPM strategies. Generally, the nematode exposed to unsuitable or suppressive soil can live longer than that was applied by bio and environmentally safe nematicide chemicals [105]. Applying chemical fumigants and non-fumigant nematicides alone or in combination with cultural practices like crop rotation with non-host crops are the most effective methods of managing RKNs [12].

The integration of *Pacecilomyces lilacinus* at 1.50% WP (Liquid) bio-formulations with farmyard manure (FYM) and neem cake was the most effective in reducing root galling by 44.52% and 50.60% under the net house and field conditions, respectively [150]. Rao et al. [151] reported that integration of neem with fungal biocontrol agents (*Paecilomyces lilacinus* and *Verticillium lecanii*) could reduce the *M. incognita*. *P. lilacinus* and *Trichoderma viride alone* or in combination with mustard oil cake and carbofuran group nematicide promoted the plant growth that could have the ability to reduce or suppress the number of galls and egg masses of *M. incognita* [152].

Integration of *Pasteuri apenetrans*, nematicides (carbofuran), and systemic insecticide (e.g., phorate) resulted in a higher rate of *M. incognita* parasitization [153–155].

5. Conclusion

Sweet potato is an important root tuber crop that is used for the human diet and has great value in health. However, its production and valuable products are hindered by *M. incognita* highly in the moist sandy soils. Therefore, this review paper presents *M. incognita*'s biology, taxonomy, geographical distribution, and management strategies. *Meloidogyne incognita* is the most economically damaging plant-parasitic nematodes on horticultural and field crops. It is an obligate parasite of the roots of thousands of plant species of monocotyledonous and dicotyledonous. It can attack the annual, biennial, and perennial plants which could be estimated to more than 31 plant species belonging to 19 different plant families. Moreover, this paper provides some of the updated information available on the management of *M. incognita*. Ecologically, the optimum temperature for its hatching was 15-30°C in wet sandy soil and J2 could survive at a range of 10–25°C and grow and develop well in the soil moisture content between 10 and 30%. The first molt occurred within the egg. The newly hatched J2 has a short free-living stage in the soil near the rhizosphere of the host plants and then migrated in the soil towards their host plant to invade the host roots in the region of root elongation. The J2 penetrates the root tips of the host plants by using a protrusible stylet and secreting the cell wall degrading enzymes to form a parenchyma cell near its head known as giant cells or feeding sites of juveniles and adults. It can be identified by different techniques like morphological, biochemical, molecular, real-time PCR (qPCR), and loop-mediated isothermal amplification (LAMP). It is dispersed from one place to another through the infected sweet potato tuber seed with eggs and females, soil debris, and poorly sanitized bare-root, water, and wind. Economically, *M. incognita* is important because it causes crack in the storage roots and reduces quality and the values of the sweet potato tuber market. The damage caused by the nematode has various dimensions of food crop losses up to 100% which could be estimated to be about $100 billion per annum. *Meloidogyne incognita* is the primary pathogen that favors the establishment of secondary pathogens like bacteria, fungi, and viruses on their important parts. These problems can be tackled by cultural practices, biological ways, using resistance varieties of sweet potato, botanical extracts, chemical, and their integration. To sum up, sweet potato nematode management might be a benefit greatly from the use of alternative control methods employing IPM strategies. In addition, agricultural policy planners should include this economically important unsegmented roundworm pest by making farmers aware of the ways of managing them for sustainable agricultural crop production in general, and small-scale farmers, in particular, are suggested in the future.

Data Availability

The data supporting this review are from previously reported studies and are cited within the article.

Disclosure

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

Conflicts of Interest

The author declares that there are no conflicts of interest.

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