Meloidogyne graminicola

Subjects: Pathology

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Rice (*Oryza sativa* L.) is one of the main cultivated crops worldwide and represents a staple food for more than half of the world population. Root-knot nematodes (RKNs), *Meloidogyne* spp., and particularly *M. graminicola*, are serious pests of rice, being, probably, the most economically important plant-parasitic nematode in this crop. *M. graminicola* is an obligate sedentary endoparasite adapted to flooded conditions. Until recently, *M. graminicola* was present mainly in irrigated rice fields in Asia, parts of the Americas, and South Africa. However, in July 2016, it was found in Europe, in northern Italy in the Piedmont region and in May 2018 in the Lombardy region in the province of Pavia.

Keywords: damage ; hosts ; life cycle ; plant-parasitic nematode ; rice root-knot nematode

1. Introduction

Rice (*Oryza sativa* L.) is the third most important cereal crop in the world, just behind wheat and maize, playing a strategic role in solving food security issues. New risks to plant health are constantly emerging. Many nematodes in rice have been detected and described, but only a few have harmful effects on rice production, such is the case of the rice root-knot nematode (RKN) *Meloidogyne graminicola* Golden and Birchfield, 1965 (*Mg*) [1], recently detected in Italy and added to the European and Mediterranean Plant Protection Organization (EPPO) Alert List [2]. *Mg* is considered a major threat to rice production, particularly in Asia. Projections by the Intergovernmental Panel for Climate Change indicate that there will be an increase in mean annual temperature and rainfall in South Asia, West Africa, and Europe. The elevated temperature and moisture may result in an increasing rate of infection, development, and reproduction, causing shifts in *Mg* abundance and geographic distribution. Such effects may have a detrimental impact on rice in temperate regions. Furthermore, *Mg* is a clear example of how alterations in rice production (shortage of water due to socioeconomic pressure and climate change) contributed to changes in its status as the major plant-parasitic nematode (PPN) in rice. An effort has been made to gather all the information regarding several aspects of *Mg* to present it as a comprehensive review on rice RKN.

2. Origin and Distribution

The rice RKN, *Mg*, was first isolated in India by Israel et al. [3], but it was only described in 1965 when it was found on the roots of barnyard grass (*Echinochloa colonum*) in Baton Rouge, Louisiana, USA [4]. Since then, this nematode has been reported from the USA on rice and weeds in Louisiana, on grass in Georgia and Mississippi, and on sandbur (*Cenchrus* spp.) in Florida [5][6][7][8]. Its occurrence has been widely accounted in rice fields in several Asian countries [9][10][11] and also in South Africa, Colombia, Brazil, and Italy [12][13][14].

Mg has been reported to parasitize primarily in irrigated and rainfed rice in South and Southeast Asian countries, such as China, India, the Philippines, Burma (Myanmar), Bangladesh, Pakistan, Laos, Thailand, Vietnam, and Nepal [15][16][17]. In China, it was first found on *Allium tistulosum* in the Hainan province by Zhao et al. [18]. More than a decade later, it was detected associated with rice and other hosts including weeds in the provinces of Anhui, Fujian, Hainan, Hunan, Hubei, Zhejiang, Jiangxi, and Sichuan, causing a severe incidence in the Hunan province [19][20][21][22].

In India, this nematode was first isolated in the county of Orissa from upland rice soils by Israel et al. [3]. Since then, it has been found infecting rice in the provinces of Andaman and Nicobar Islands, Assam, Andhra Pradesh, Bihar, Gujarat, Himachal Pradesh, Jammu and Kashmi, Karnataka, Kerala, Madhya Pradesh, Manipur, Orissa, Tamil Nadu, Tripura, and West Bengal [23][24]. In 1971, its presence was referred in Thailand, causing typical root galls in entire rice-growing areas and in nursery seedbeds [25], and in Bangladesh, where it has been often associated with deepwater and pre-monsoon upland rice systems [26][27][28]. Minor infestations were reported in lowland rainfed rice areas [28]. Nonetheless, in the northwest of Bangladesh, where the dominant cropping system is lowland rainfed alternated with wheat, severe infestations of *Mg* were observed [29].

Later, in the 1990s, *Mg* was reported infesting rice fields in Sri Lanka, where it is now dispersed into major rice-growing areas of the country [30][31][32]. In a study performed in Vietnam, in 1992, to determine the PPN in deepwater rice systems, *Mg* was identified for the first time as one of the main causes of high yield losses of rice [33]. In Pakistan, during a survey in rice fields of Sheikhupura (Punjab), Munir and Bridge [34] reported its presence for the first time in the country and in 2007, *Mg* was detected in Nepal [35].

The occurrence of *Mg* in Africa was recorded on grass roots of *Paspalum* sp. in the South East region of Antsirabe, and its identification was based on morphological traits [36]. Later, in 2014, during a survey carried out in 14 sites distributed along a NW/SE axis between the towns of Marovovay and Manakara, *Mg* was found [37].

The first report of *Mg* in South America was by Monteiro et al. [38] in cyperaceas collected in Presidente Prudente, São Paulo, Brazil. However, only in 1991, Sperandio and Monteiro [39] first reported and described the species in the municipality of Palmares do Sul (Rio Grande do Sul) and, in 1994, Sperandio and Amaral [40] found *Mg* in other municipalities in the south of Rio Grande do Sul. The latest reports confirm the presence of the rice RKN in the region [41][42].

In Ecuador, *Mg* was first identified in 1987, in the “Sausalito” village located in the corner of Puerto Inca, province of Guayas, in a field planted with the cultivar Oryzica 1. In surveys conducted in the Provinces of Manabí, Guayas, and Los Ríos, *Mg* was not found in any other field planted with rice. Nevertheless, by 2000, it had already been disseminated to all rice fields of the Province of Guayas and, in 2002, it was present in the Province of Los Ríos [43]. In a new survey conducted in 2015 in the provinces of Guayas and Los Ríos, the rice RKN was found to be the most widespread, occurring in both rainfed lowland and irrigated areas in high densities [13].

In Colombia, Goméz et al. [44] reported the presence of galls in the roots of rice plants in the county of Tolima, Ibague. Thirteen years later, in a survey programme established by the Colombian rice federation “FEDEARROZ”, Bastidas and Montealegre [45] described the symptoms of a new rice disease denominated as “Entorchamiento” and concluded that it was caused by nematodes of the *Meloidogyne* genus. The species *Mg* was later identified, on the basis of morphological and biometrical characters, in other counties and its presence confirmed in other rice production zones, corroborating its spread throughout the country [46][47].

In Europe, *Mg* was detected, in July 2016, in several rice fields of northern Italy in the Piedmont region, being the first report of its presence in the EPPO region [14]. Due to this detection, the EPPO decided to include *Mg* in the Alert List A2 in 2017. Following the first report, it was detected in the Lombardy region, province of Pavia [2].

This *Meloidogyne* species is present almost in every continent (**Table 1**. **Figure 1**). Such occurrence and increase detection draws attention to its potential to affect temperate rice agro-systems adversely.

Figure 1. Geographical distribution of *Meloidogyne graminicola*.

Table 1. Distribution of *Meloidogyne graminicola* in Africa, America, Asia, and Europe.

Distribution	Year	References
	Africa	
Madagascar	**2014**	[37]
South Africa	**1991**	[36]
	America (North-USA)	
Florida	**2003**	[8]
Georgia	**1984**	[6]
Louisiana	**1965**	[4]
Mississippi	**1990**	[7]
	America (South)	
Brazil	**1988, 1991, 1994, 2017, 2019**	[38][39][40][41][42][48]

Distribution	Year	References
Colombia	1994, 2001, 2010	[45][46][47]
Ecuador	1987, 2002, 2016	[13][43]
		Asia
Bangladesh	1971, 1978, 1979, 1983, 1990	[49][50][51][52]
China	2001, 2015, 2017, 2019, 2020, 2021	[18][19][20][21][22][53]
Indonesia	1993, 2015, 2018	[54][55][56]
India	1963, 1979, 1985, 1987, 1989, 1993, 1994, 2000, 2004, 2005, 2006, 2007, 2010, 2011, 2017	[3][23][57][58][59][60][61][62][63][64][65][66][67][68][69]
Laos	1968	[70][71]
Malaysia	1994	[72]
Myanmar	1981, 2011	[73][74]
Nepal	2007, 2009	[16][35]
Pakistan	2003	[34]
Philippines	1994, 2001	[75][76]
Singapore	2001	[77]
Sri-Lanka	1997, 2001	[30][31]
Thailand	1971	[25]
Vietnam	1992, 1994	[33][78]
		Europe
Italy	2016, 2018	[2][14]

3. Damage/Crop Losses in Rice

Mg is the most prevalent PPN on rice and considered a major threat to rice as yield losses can reach up to 70% [12][79][80]. *Mg* densities of 120, 250, and 600 eggs/plant in seedlings 10, 30, and 60 days after planting were reported by Rao et al. [81], causing 10% losses. In a later study, Cuc and Prot [65] stated that a density of 100 J2/g root could be considered as high infestation. Most recently, Win et al. [73] found that population densities could exceed 1000 J2/g root with 12–16 galls/plant, contributing to a 65% yield reduction. It has also been found that there is a decline in yield when more than 75% of the roots are affected by nematodes [32]. Additionally, the water regime is an important environmental factor that influences the development and population dynamics of *Mg*, and the damage and yield loss that it can cause to rice.

Soriano et al. [82] showed that rice cultivar tolerance to *Mg* varies with the water regime and that yield losses may be prevented or minimized when the rice crop is flooded early and maintain inundated until harvesting. For example, losses in lowland rainfed rice in Bangladesh can range between 16 and 20%, while in India, losses range between 16 and 32% under irrigated conditions and between 11 and 73% under flooded conditions [83][84]. In China, the highest incidence of the disease is in the Hunan provinces, exceeding 85% in infested paddy fields [19]. Furthermore, reports of *Mg* infestations in rice–wheat agroecosystem of India, Nepal, and Pakistan suggest that the damage caused by the rice RKN may be responsible for the poor productivity in this cropping system [10][11][35][85].

Changes in agricultural policy and adoption of new rice production technologies in South East Asian countries have influenced the status of the rice RKN problem [64]. For instance, in the Philippines, *Mg* became a major constrain due to the intensification of rice cropping and shortage of water supply. This situation forced the farmers to grow direct wet seeding, and intermittent irrigation, providing favorable conditions for *Mg* infestation and increasing the economic losses [9][64]. In India, the system of rice cultivation shifted to the so-called “system of rice intensification practice”, where a new ecological condition is being developed through modification of rice cultivation practices that includes planting younger and tender seedlings, the creation of greater aeration in soil, and regulation in irrigation. All these conditions provide a suitable environment to increase the infestation levels of the rice RKN [80][85][86].

Spatio-temporal studies have also demonstrated that densities of *Mg* J2 in the soil fluctuate throughout the year [87]. Moreover, *Mg*’s ability to survive and reproduce in off-seasons on weeds and forage crops contributes to increase the population levels in the soil, and rice infection in the next season [35]. Besides alternative hosts and irrigation, the soil type influenced the tolerance of plants to *Mg* and showed differences in the multiplication of the nematode [82]. Studies have also revealed that infestation levels depend on the rice cultivar [88][89], and the aggressiveness differs between populations, suggesting intraspecific variability [35][90]. It was also found that *Mg* consists of more than one race. In fact, populations from Florida have shown less aggressiveness and difference on the host infection and reproduction patterns than the Asian populations, and populations from Vietnam are not able to reproduce on tomato (*Solanum lycopersicum*), soy (*Glycyne max*), or green beans (*Phaseolus vulgaris*), despite these species being reported as a host of *Mg* [16][90][91].

4. Host Plants

In addition to the main host, rice, *Mg* has a wide range of alternative hosts, including cereals and grasses, as well as dicotyledonous plants [15][91][92] (**Table 2**). Forty-six weeds commonly growing in or around rice fields were assessed for host suitability and were found to be moderate to good hosts of *Mg* [93]. Khan et al. [94] reported 17 weed species and, in 2009, Rich et al. [15] reported 24, which supported the survival and multiplication of *Mg* in the field, acting as a reservoir of nematodes when rice is not present during crop rotations [15] (**Table 3**). Furthermore, it was believed that *Mg* caused yield losses only in rice; however, a reduction of the root length of onion (*Allium cepa*) was observed, with yield losses of 16–35% in the Philippines [76]. In Nepal, India, Pakistan, and Bangladesh, it is considered a threat to wheat crops and to vegetables, such as aubergine (*S. melongena)*, tomato, and okra (*Abelmoschus esculentus*) [10][93][95][96][97].

Table 2. Cultivated hosts of *Meloidogyne graminicola*.

Family	Species (Common Name)	Reference	Family	Species (Common Nam
Amaranthaceae	*Beta vulgaris* (Beetroot)	[98]	Musaceae	
	Spinacia oleracea (Spinach)	[12]		
Amaryllidaceae	*Allium cepa* (Onion)	[76]		
	A. tuberosum (Chive)	[101]		
	A. fitsulosum (welsh onion)	[101]		
Apiaceae	*Coriandrum sativum* (Coriander)	[98]	Poaceae	
Asteraceae	*Lactuca sativa* (Lettuce)	[12]		
Brassicaceae	*Brassica oleracea* (Cabbage)	[12]		
	B. oleracea var. botrytis (Cauliflower)	[100]		
Cucurbitaceae	*Cucumis sativus* (Cucumber)	[12]		*Zea mays (Maize)*

Family	Species (Common Name)	Reference	Family	Species (Common Nam
Fabaceae	***Glycine max* (Soybean)**	[93]	Solanaceae	***Capsicum frutescens* (C**
	***Phaseolus vulgaris* (Common bean)**	[5]		***C. annuum (Pepper)***
	***Vigna adiate* (Green gram)**	[12]		***Solanum lycopersicum***
	***V. unguiculata* (Cowpea)**	[12]		***S. melongena (Aubergi***
Malvaceae	***Abelmoschus esculentus* (Okra)**	[96]		

Table 3. Weeds hosts of *Meloidogyne graminicola*.

Family	Species (Common Name)	Reference	Family
Alismataceae	***Alisma plantago* (Common water- plantain)**	[14]	Oxalidaceae
	***Alternanthera sessilis* (Sessile joy weed)**	[94]	Papillionaceae
Amaranthaceae	***Amaranthus spinosus* (Spiny amaranth)**	[40]	Plantaginaceae

Family	Species (Common Name)	Reference	Family
	A. viridis (Slender amaranth)	[93]	
Acanthaceae	*Rungia parviflora*	[100]	
Apiaceae	*Centella asiatica* (Spade leaf)	[100]	
Apocynaceae	*Catharanthus roseus* (Periwinkle)	[12]	
Asteraceae	*Ageratum conyzoides* (Billy-goat- weed)	[94]	
	Blumea sp.	[102]	
	Eclipta alba (False Daisy)	[102]	
	E. prostrata (Eclipta alba)	[103]	
	Grangea ceruanoides	[102]	
	G. madraspatensis	[102]	
	Sphaeranthus sp.	[98]	
	Sphaeranthus senegalensis	[100]	
	Vernonia cinerea	[100]	
Balsaminaceae	*Impatiens balsamina* (Garden balsam)	[12]	
Brassicaceae	*Brassica juncea* (Brown mustard)	[12]	
	Brassica sp.	[12]	
Caryophyllaceae	*Spergula arvensis* (Corn spurry)	[23]	
	Stellaria media (Chickweed)	[93]	
Commelinaceae	*Cyanotis cucullata* (Roth)	[104]	
	Commelina benghalensis	[104]	Poaceae
	Murdannia keisak (Marsh dew flower)	[14]	
Compositae	*Gnaphalium coarctatum*	[105]	
Cyperaceae	*Cyperus brevifolius* (Kyllinga)	[98]	
	C. compressus (Annual sedge)	[106]	
	C. difformis (Variable Flatsedge)	[108]	
	C. imbricatus	[98]	
	C. odoratus (Flats edge)	[109]	
	C. pilosus (Fuzzy flats edge)	[100]	
	C. procerus	[98]	
	C. pulcherrimus (Elegant s edge)	[98]	
	C. rotundus (Purple nutsedge)	[94]	
	Fimbristylis complanata	[98]	
	F. dichotoma	[98]	
	F. littoralis (Lesser fimbristylis)	[98]	
	F. miliacea	[102]	
	Fuirena ciliaris	[98]	
	F. glomerata	[98]	
	Schoenoplectus articulatus	[100]	
Euphorbiaceae	*Chamaesyce hirta* (Asthma herb)	[136]	Polemoniaceae
	Phyllanthus urinaria	[102]	Pontederiaceae
Fabaceae	*Desmodium triflorum*	[93]	
	Pisum sativum (Garden pea)	[12]	Portulacaceae

Family	Species (Common Name)	Reference	Family
	Trifolium repens **(White clover)**	[12]	
	Trigonella polyceratia	[23]	
Hydrocharitaceae	***Hydrilla*** **sp.**	[104]	**Solanaceae**
Juncaceae	***Juncus microcephalus***	[137]	
Lamiaceae	***Leucas lavandulifolia***	[100]	
	Bonnaya brachiata	[93][98]	**Sphenocleaceae**
Linderniaceae	***Lindernia*** **sp.**	[134]	**Ranunculaceae**
	Vandellia **sp.**	[102]	**Rubiaceae**
Lythraceae	***Ammannia pentandra***	[98]	
Onagraceae	***Jussieua repens***	[102]	
	Ludwigia adscendens **(Primrose)**	[134]	

5. Management

The best strategy for management of *Mg* is to prevent the movement of plant and soil that in some cases may adhere to machinery or tools. In a recent pest risk analysis for *Mg* in Italy, it was concluded that the main ways of dispersion of this nematode are likely to be through the movement of infected plants and infested soil, non-host plants that may have grown near areas infested with *Mg*, and floating roots or plant material in the water [92]. Migrant waterbirds, machinery, and travelers were considered a secondary source of entrance. On the other hand, changes in the water regime (intermittent irrigation or water shortages) in many parts of the world are also contributing to the spread and infectivity of the nematode.

To minimize the losses resulting from *Mg*, management strategies are of extreme importance, and studies have shown that a combination of methods is the best approach to control this nematode in rice fields. The methods that have been applied to control *Mg* include the use of synthetic nematicides, known as the most efficient strategy, cultural methods, biological agents, and natural nematicides.

Some synthetic nematicides were, recently, strictly regulated or banned from the market, due to the adverse impacts on the environment and human health, reducing the alternatives for RKN control. Cultural methods (fallowing, soil solarization, crop diversification and rotation, etc.) also appeared to have some efficacy. For instance, crop rotation studies with non-host crops, like sweet potato (*Ipomoea batatas*), cowpea (*Vigna unguiculata*), sesame (*Sesamum indicum*), castor (*Ricinus communis*), sunflower (*Helianthus annuus*), soybean (*Glycine max*), turnip (*Brassica rapa* subsp. *rapa*), and cauliflower (*Brassica oleracea* var. *botrytis*), showed to prevent *Mg* development [81][104][111]. Nonetheless, none of these practices have gained importance among farmers, because of the high cost and unsatisfactory results. Furthermore, as many weeds found in rice fields are hosts for *Mg*, serving as nematode reservoirs for the next crops, a weed management programmme must be implemented to maintain a low nematode population in infested fields.

Alternative strategies, such as the “rice field flooding technique”, used by the Italian National Plant Protection Organization (Ministerial Decree of 6 July 2017) to control *Mg*, had some effect on the nematode population densities. *Mg* can still propagate under flooding conditions, but the damage induced by this nematode is lower than in shallow intermittently flooded fields [112][113]. Nevertheless, this method of control also has some limitations, as there are areas where this practice is not applicable due to the soil structure, characterized by a low water retention capacity, or restriction in water use. Another approach explored by Sacchi et al. [113] was the use of rice plants as trap crops. Preliminary results indicate that trap cropping for the management of the rice RKN is efficient in most rice-growing areas, especially those with water shortages. However, additional studies are required to establish the most effective number of trap crop cycles that are necessary to reduce *Mg* population density. Additionally, this technique, in our opinion, could be highly influenced by climate in northern latitudes in order to sow rice in advance and the cost of machinery and water.

The use of biological control agents, such as the fungi *Paecilomyces lilacinus*, *Trichoderma harzianum, T. viride*, and other *Trichoderma* spp.; the bacteria *Bacillus subtilis*; and the rhizobacterium *Pseudomonas fluorescence*, have shown promising results against *Mg* [114][115][116][117]. Studies by Amarasinghe and Hemachandra [117], in Sri Lanka, revealed that *T. viride* reduces gall formation and production of egg masses, which represents a potential strategy to be included in integrated pest management programs.

Similarly, the use of essential oils (EOs) has been explored to control RKN, as an alternative to the synthetic nematicides. The nematicidal effects of EO from spices and medicinal plants on RKN have been widely reported. The high effect of *Cymbopogon* spp. EO (*C. martini motia*, *C. flexuosusand*, and *C. winterianus*) on J2 mortality has been described [118][119][120]. Chavan et al. [121] stated that basil (*Ocimum basilicum*), peppermint (*Mentha*×*piperita*), and lemongrass

(*Cymbopogon citratus*) EOs have nematicidal properties against *Mg*. In order to confirm the efficacy of these EOs, the in vitro tests must be complemented by in vivo soil-based experiments.

Host plant resistance is an environmentally friendly and cost-effective strategy to mitigate damage caused by *Mg*. A promising alternative for the control of *Mg* is the screening of germplasm for genotypes that are resistant/tolerant and the development of resistant/tolerant cultivars [112][122][123]. Resistance sources against *Mg* have been identified in African wild accessions of rice (*O. glaberrima* and *O. longistaminata* and *O. rufipogon*) [124], and variability to a certain extent has been perceived [125]. Wild accessions that are partially or fully resistant to *Mg* can therefore act as resistant donors for interspecific crosses with Asian cultivars of rice [124][126]. Introgression of *O. glaberrima* into *O. sativa* has led, for example, to the new rice for Africa, NERICA cultivars [127], but the introgression has not been very successful [128]. Therefore, natural resistance in *O. sativa* cultivars is potentially very important. In Asian rice, using the Bala and Azucena mapping population, chromosomes 1, 2, 6, 7, 9, and 11 have been reported as having quantitative trait loci (QTL) for partial resistance to *Mg* [129]. Mapping of *Mg* resistance on chromosome 10 in Asian rice (cv. Abhishek), using bulk segregant analysis, was reported by Mhatre et al. [130]. A hypersensitivity-like reaction to *Mg* infection found in the Asian rice cv. Zhonghua 11 suggests that resistance to *Mg* was qualitative rather than quantitative, involving (a) major gene(s) [131]. Galeng-Lawilao et al. [132] reported the main effect QTL for field resistance in Asian rice on chromosomes 4, 7, and 9 plus two epistatic interactions (between loci on chromosome 3 and 11, and between 4 and 8).

Few studies have used genome-wide association studies (GWASs) as a viable strategy to identify novel QTLs for PPN resistance or susceptibility in different plants [133][134]. For example, Dimkpa et al. [133] confirmed the robustness of GWAS to screen for rice–nematode interactions and identified two resistant accessions (Khao Pahk Maw and LD 24). Studies carried out, in India, by Hada et al. [135] allowed the identification of 40 highly resistant accessions. Alternatively, the profiling of the defense response of 36 rice cultivars to *Mg* infection revealed a variation in the expression of plant defense genes [136]. Among all the selected plant defense genes, the expression of mitogen-activated protein kinases (MAPK20), isochorismate synthase genes (ICS1), nonexpressor of pathogenicity expression genes1 (NPR1), phytoalexin-deficient 4 (PAD4), allene oxidase synthase (AOS2), jasmonic acid-inducible rice myb gene (JAMYB), and 1-aminocyclopropane-1-carboxylic acid oxidase (ACO7) was upregulated, possibly providing resistance against *Mg*. This observation matches the insignificant expression in the susceptible genotypes. These outcomes are significant and can be exploited for breeding purposes.

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