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Genetic inheritance of resistance to root knot nematode (*Meloidogyne incognita*) in eggplant F_2 generation (*Solanum melongena*)

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Abstract

Eggplant (*Solanum melongena* L.) is one of the most widely consumed vegetables in Malaysia. However, root knot nematode (RKN) scientifically known as *Meloidogyne incognita* causes severe eggplant yield loss as high as 37%. The information on genetic diversity and its resistance to RKN is essential for eggplant improvement in Malaysia. This study investigated the inheritance of RKN resistance caused by *M. incognita* in eggplant progeny. Susceptible eggplant varieties (MTe-02) were crossed with two resistant accessions (DINO 03-0200 and DINO 03-0056) against RKN to produce the seed parent, including the F1 and F2 generations. After 60 days of *M. incognita* inoculation, the numbers of root knots and egg masses per plant root system were counted using a dissecting microscope. A chi-square ($\chi2$) test of the frequency distribution based on the root knot index (RKI) of the F2 progenies of the two crosses (susceptible × resistant) revealed a 1:3 (susceptible: resistant) ratio. These results confirmed that the resistance gene against *M. incognita* can be inherited from the resistant parent, which can be used to develop a new eggplant hybrid resistance to *M. incognita* infection. This model system could also be utilised as a basis to develop new resistance varieties against RKN for other crops.

Keywords: eggplant, inheritance, *Meloidogyne incognita*, resistance, root knot nematode

Introduction

Eggplant (*Solanum melongena*) belongs to the Solanaceae family and is one of the most important horticultural crops worldwide with an estimated harvested area and gross production value of 1,961,799 ha and US$24.77 billion, respectively in 2021 (FAOSTAT 2021). Eggplant cultivation can be found especially in tropical and subtropical regions, as well as in greenhouses and open fields (Motti 2021). Eggplant is mainly produced for fresh market and food processing. It contains a variety of minerals and vitamins, which contribute to a healthy diet for daily consumption (Naeem and Ugur 2019; Motti 2021). Despite its economic value, eggplant is known to be susceptible to a variety of pests and pathogens including fruit and shoot borers, wilt disease, as well as various abiotic stress conditions that significantly limit crop productivity. One of the main factors affecting eggplant production in the field is its susceptibility to soil-borne diseases, especially plant parasitic nematodes (Elling 2013; Philbrick et al. 2020).

Plant parasitic nematodes have been reported to cause annual yield loss in the agriculture sector at an estimated value of $230 billion worldwide (Atolani and Fabiyi 2020). Root-knot nematodes (RKNs), *Meloidogyne* spp., are one of the most serious diseases in eggplant production, accounting for 11.67% to 46.67% of global eggplant crop losses, especially in tropical and subtropical regions (Hallmann and Meressa 2018). Among the numerous existing RKN species, *M. incognita*, *M. javanica*, *M. arenaria* and *M. hapla* are the most damaging species with worldwide distribution and a wide range of host plants (Banerjee et al. 2017). They are widespread in most eggplant growing areas, particularly on sandy soils with warm climatic conditions and can survive in the soil for long periods as eggs or infective second

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juvenile stages in the absence of a suitable host (Greco and Vito 2009; Miyashita et al. 2014)). The infested root cells usually surround the vascular cells that control water and nutrient distribution in plants, resulting in sudden plant wilting, chlorosis, irregular growth, stunting and yield reduction (Ali et al. 2015, 2019). The extent of crop damage depends on several factors, such as the initial population of nematodes, plant susceptibility, plant growth stage, cultivation practices and introduction of other pathogens (Greco and Vito 2009; Asghar et al. 2020). In susceptible eggplant cultivars, root knot nematodes cause a delay in flowering, a reduction in fresh weight and dry weight of roots, stems and leaves and a reduction in fruit yield (Ali et al. 2015). In addition, seed production per fruit is drastically reduced and severe infestations can result in no seeds being produced per fruit (Anuar et al. 2020). This pathogen is considered a global threat to eggplant production as there is no known resistance to the various RKN species in commercially accepted cultivars (Banerjee et al. 2017).

To date, nematicides that are fumigant and non fumigant have been primarily used to manage RKN (Watson and Desaeger 2020). Nevertheless, chemical application induces adverse effects on human health and the ecosystem (Nyczepir and Thomas 2009). Other methods such as soil sterilisation and utilising resistant grafted plants have been demonstrated to partially suppress plant parasitic nematodes (Forghani and Hajihassani 2020). Resistance variety has been proven to be an efficient, affordable, environmentally and human health friendly approach to controlling RKN that could potentially be implemented in integrated nematode management approaches (Ali et al. 2017; Forghani and Hajihassani 2020). A previous study on crop rotation involving resistant tomato variety revealed a 90% reduction in nematode population following a trial over four cropping seasons and increased yield production (Da Silva et al. 2019). The stimulation of numerous plant genes suppresses giant cell growth and induces cell death, which could impact nematode development and reproduction, resulting in an unfavourable plant-RKN interaction (Shukla et al. 2018). Several plant varieties with RKN resistance have been identified and exploited as rootstocks or employed in plant breeding programs (Ali et al. 2019). Tomato, peanut, cucumber, mung bean, guava, plum, peach and sweet potato have been linked to sources of potential genetic and non-host resistance against *Meloidogyne* spp. (Chiamolera et al. 2018; Cheng et al. 2019; Da Silva et al. 2019; Expósito et al. 2020; Hajihassani et al. 2020; Singh et al. 2020). As a result of extensive studies, a few RKN-resistant rootstocks for tomato, pepper, cucumber and eggplant have been commercialised in some countries (Ros-Ibáñez et al. 2014; Baidya et al. 2017; Wubie and Temesgen 2019; Mukhtar and Kayani 2020).

Under natural conditions, some plants may become incompatible with plant parasitic nematodes, thereby leading to resistance ability. This plant may prevent the establishment of the nematode as early as in the egg stage and later in the nematode maturing stage. The results of these resistance mechanisms may show in terms of infertility egg, entry blocking of J2 or delay/incomplete development into full adult (Papolu et al. 2016; Mukhtar and Kayani 2020). Resistance towards RKN has been reported on some local native *S. melongena* varieties and in related eggplant species, including *S. torvum*, *S. aethiopicum*, *S. incanum* and *S. sisymbriifolium* (Anuar 2020; Anuar et al. 2021). A previous study highlighted that the resistance inheritance towards RKN in wild relatives' species of Solanum eggplant is determined by monogenic dominant genes (Ali et al. 2017, 2019). An earlier research by Nazarudin (2021) identified a few Malaysian eggplant germplasm candidates that could be employed as rootstocks or in upcoming breeding programs. In order to elucidate the transmission of resistance to *M. incognita*, susceptible eggplant cultivars MTe-02 were crossed with resistant types of DINO 03-0200 and DINO 03-0056 in this study. The objectives of this study were to evaluate the inheritance of RKN resistance in two local native *S. melongena* accession DINO 03-0200 and DINO 03-0056 through the analysis of resistance response against *M. incognita* infection between parents, F_1 and F_2 generation. Through this study, eggplant breeders will better comprehend the nematode resistance mechanism and the capacity to target RKN.

Materials and method

Plant material

This study was conducted at the Malaysian Agricultural Research and Development Institute (MARDI), Serdang, Selangor, Malaysia from 2020 to 2021. The plant materials included two *S. melongena* accessions (DINO 03-0200 and DINO 03-0056) and the commercial *S. melongena* cultivar MTe-02. All the accessions were deposited at the germplasm bank of the MARDI (Serdang, Malaysia) and were used as initial plant material. Eggplant seeds were sowed in a germinating tray containing peat moss for germination. Seedlings were transplanted into pots containing a mixture of sterile peat and perlite in a ratio of 1:1 (v/v) and maintained in a greenhouse at 20 °C night and 27 °C day temperatures.

Development of F_1 , F_2 and BC Population

The seed of the nematode-resistant lines, DINO 03-0200 and DINO 03-0056, and the nematode-susceptible line, MTe-02 (i.e., as a control), were used in the experiment. The MTe-02 was characterised as a round purple eggplant with a high yield and good quality attributes. Plants were crossed in a greenhouse between 2019 to 2020. Flowers were emasculated one or two days before anthesis (except in the case of self pollination) and pollinated as soon as they opened. Fruits were harvested six weeks after pollination. The resistant genotypes DINO 03-0200 and DINO 03-0056 were crossed with the susceptible line MTe-02. The crosses were performed reciprocally to test for possible cytoplasmic inheritance. The F_1 plants of the two series of crosses using DINO 03-0200 and DINO 03-0056 were selfed and the F_2 populations were raised. In addition, BC progenies were produced by backcrossing F_1 with either susceptible or resistant parents. As a result of these crosses, 16 different populations of F_1, F_2 and BC progenies were produced (*Table 1*). The resistance level of the parental and hybrid genotypes was analysed in greenhouse experiments by nematode inoculation (Fassuliotis 1970).

Nematode inoculum

The inoculum of *Meloidogyne incognita* used in the experiments was obtained from the root area of a diseased eggplant plant collected in Serdang province, Malaysia. Nematode inoculum was purified by using a single egg isolation method and was maintained and multiplied on susceptible eggplant cv. GW302 (Green World Genetics) in the greenhouse. The inoculum used in these experiments consisted of individual eggs extracted from infected roots by maceration using a 5% commercial bleach solution (40 g L^{-1} NaOCl) for 10 minutes (Hussey and Barker, 1973). The pathogenicity of the inoculum was tested before it was used for the tests. For this purpose, a preliminary study was conducted using two susceptible *S. melongena* (MTe-01 and MTe-02) and one resistant *S. torvum* (NTH 08-0024) lines. Artificial inoculation tests were performed in a greenhouse in MARDI Serdang according to the hole inoculation method. Parent seed, F_1, F_2 and BC populations were grown in plastic trays containing sterile peat medium in which plants were developed to the second third of the broadleaf stage. The eggs were resuspended in sterilised water and egg density was adjusted to 1 × 500 egg/ml. For the inoculation process, four holes were created in the surrounding eggplant seedling before inoculation suspension was injected into the holes. The roots of the control plants were inoculated with sterile tap water. The roots of each plant were inoculated with 5,000 eggs (Pi) surrounding the vicinity of the root zone (Hadisoeganda and Sasser 1982).

Resistance tests

About 50 plants from the parents, 100 plants from the F_1 and 300 plants from the segregated hybrid generations (F_2 and BC) were used in the tests. Plants were arranged in a randomised complete block design (RBD). The plants were watered daily to field capacity and fertilised with NPK green (15:15:15) (Nitrophoska) once a week throughout the experiments. Approximately three weeks after transplanting, plants were inoculated with 5,000 eggs of *M. incognita*. The plants were harvested 45 days after inoculation (DAI), roots were carefully cleaned of soil and the weight of fresh roots and shoots was documented before counting the number of egg masses on each seedling after staining with Phloxin B (Whitehead and Hemming 1965). Nematode symptoms were scored based on the infected roots and were rated on a gall index from 0 (no galls) to 10 (100% galled) scale (Bridge and Page 1980). The number of galls, egg masses and eggs per egg mass in each root system were also recorded.

To determine the effect of the nematode reproductive potential, the multiplication factor (MF) ratio of *M. incognita* was calculated ((number of egg masses × number of eggs per egg mass) / nematode inoculum level) for each line. Reproductive index (RI) was calculated as the percentage of eggs produced in the rootstock variety compared to that of the eggplant variety. The response of the plant host was categorised according to the RI as highly resistant (RI <1%), resistant (1 %≤RI<10%), moderately resistant (10%≤RI<25%), slightly resistant (25% ≤RI <50%) or susceptible (RI ≥50%) (Hadisoeganda and Sasser 1982).

Table 1. Parents and crosses populations used in the tests.

Code	Parents/hybrid	No. of plant
P	DINO 03-0200 (R)	50
P	DINO 03-0056 (R)	50
P	MTE-02 (S)	50
F_1	DINO 03-0200 × MTE-02	100
F_1	MTE-02 × DINO 03-0200	100
BC	(DINO 03-0200× MTE-02) × DINO 03-0200	300
BC	(DINO 03-0200×MTE-02) × MTE-02	300
BC	(MTE-02×DINO 03-0200) × DINO 03-0200	300
BC	(MTE-02×DINO 03-0200) × MTE-02	300
F_2	DINO 03-0200 × MTE-02	300
F_2	MTE-02 × DINO 03-0200	300
F_1	DINO 03-0056 × MTE-02	100
F_1	MTE-02 × DINO 03-0056	100
BC	(DINO 03-0056 × MTE-02) × DINO 03-0056	300
BC	(DINO 03-0056 × MTE-02) × MTE-02	300
BC	(MTE-02 × DINO 03-0056) × DINO 03-0056	300
BC	(MTE-02 × DINO 03-0056) × MTE-02	300
F_2	DINO 03-0056 × MTE-02	300
F_2	MTE-02 × DINO 03-0056	300
F_2	DINO 03-0200 × MTE-02	300
F_2	MTE-02 × DINO 03-0200	300
F_1	DINO 03-0056 × MTE-02	100
F_1	MTE-02 × DINO 03-0056	100
BC	(DINO 03-0056 × MTE-02) × DINO 03-0056	300
BC	(DINO 03-0056 × MTE-02) × MTE-02	300
BC	(MTE-02 × DINO 03-0056) × DINO 03-0056	300
BC	(MTE-02 × DINO 03-0056) × MTE-02	300
F_2	DINO 03-0056 × MTE-02	300
F_2	MTE-02 × DINO 03-0056	300

P: parent; F_1: filial 1; F_2: filial 2; BC: backcross; R: resistant; S: susceptible

Statistical analysis

Data from the bioassay experiments were normalised using the generalised linear model and subjected to one-way analysis of variance (ANOVA) in SAS software (version 14.1). Different parameters in control and transgenic events were compared via post-hoc Tukey's honest significant difference test (HSD) at p <0.01. Segregation ratios obtained by phenotypic observations (resistant or susceptible) were compared with theoretical segregation ratios using $\chi 2$ analysis. The goodness of fit test was performed using Microsoft Excel spreadsheet software for the segregation ratios 3:1 (resistant: susceptible) for the F_2 and 1:1 (resistant: susceptible) for the BC (Kranz 1988).

Results and discussion

Root knot nematode infestation is one of the major soilborne pathogen problems in the Solanum group that can cause significant yield losses for multiple crops (Nicol et al. 2011; Hallmann and Meressa 2018). Preventive measures are pertinent as most eggplant cultivars have high susceptibility that can result in significant crop losses if these cultivars are grown in areas with a history of RKN infestations (Nicol et al. 2011). Knowledge of the cause of resistance and its inheritance is necessary to develop a better and more comprehensive breeding technique, which could facilitate the production of a new resistant hybrid. In a previous study, we found that a few local eggplant accessions can overcome RKN infection, whereas most of the other eggplant cultivars were infected and demonstrated disease symptoms. Anuar (2020) also conducted a study among Malaysian local eggplant cultivars and found that there was a genetic potential in resistance towards RKN infection, and suggested using it in eggplant selection and breeding programs. Two of the resistant Malaysian eggplants, namely DINO 03-0200 and DINO 03-0056, were used in this study as parents to analyse the possibility of resistant inheritance to these progenies. Furthermore, an intraspecific reciprocal cross between the two extremes of symptoms (susceptible vs. resistant) in cultivated eggplant depicted that both genotypes were compatible with one dominant and one recessive gene controlling resistance (Daunay et al. 2019). These cross schemes may produce a superior progeny compared to parents as shown in this study.

Susceptible genotype MTe-02 exhibited clear visible gall symptoms on the roots 45 days after inoculation (*Figure 1*). However, inoculated plants of the two resistant genotypes showed a few gall symptoms and were barely visible compared to susceptible genotypes (*Figure 2*). This result is consistent with a previous finding by Anuar (2020) and Anuar et al. (2021) in which eggplant genotypes, DINO 03-0200 and DINO 03-0056, were able to resist RKN infection with a few gall related symptoms. Dewi and Indarti (2022) also reported that several accessions of eggplant were resistant to RKN infection. The researchers documented that the root of these eggplants produced secondary metabolites that were

Figure 1. Gall symptom on eggplant cv. MTe-02 45 days after inoculation

Figure 2. Root system of resistant eggplant showed a few galls symptom and barely visible

capable of preventing egg hatching and dissolving the nematode eggs. All F_1 progenies were resistant, regardless of whether susceptible or resistant genotypes were used as female or male parent (*Table 2*).

In all F_2 populations, the segregation ratio of resistant and susceptible plants corresponded to 3:1, as confirmed by chi-square analyses. Accordingly, the segregation ratios of resistant and susceptible plants in the backcross populations were consistent with the dominant monogenic inheritance model. All plants of the backcross progeny obtained by crossing F_1 with DINO 03-0200 and DINO 03-0056 were resistant, whereas plants obtained by crossing F_1 with the susceptible genotype MTE-02 segregated at a ratio of 1:1, which was confirmed by the chi-square analyses at a confidence level of 1% (*Table 2*). Assuming a disomic inheritance, the observed segregation patterns can be explained by a single dominantly inherited gene that would be present in homozygous form in the resistant parental genotypes. In addition, these genotypes have several advantages for their potential use in the breeding programme: They belong to cultivated eggplant species (*S. melongena*) and can be easily crossed with cultivated varieties that produce fruit bearing progeny; although the resistant genotypes produce small fruit bearing plants, they have plant characteristics that do not differ from those of cultivated eggplant (*Figure 3*).

The results clearly demonstrated that the resistance traits of DINO 03-0200 and DINO 03-0056 follow a simple inheritance pattern of a monogenic dominant trait. It also reveals that some eggplant materials are resistant to RKN and that sources of resistance without infection symptoms in eggplant are present in both the cultivated species *S. melongena* and wild relatives. Several resistance genes in multiple crops have been reported as a source of resistance against *Meloidogyne* spp. infection where only two have successfully been validated. Resistance gene *Ma* has been reported to produce a broad-spectrum resistance to multiple Meloidogyne species in Myrobalan plum while resistance gene *Mi* was reported to be resistant against *M. incognita*, *M. javanica* and *M. arenaria* in solanum crops (Kaloshian and Teixeira, 2019; Nguyen et al. 2022). These resistance genes may induce a hypersensitive reaction in which the plant's root produces a substance that prevents the infection of the nematode juvenile, thus causing death by starvation (Joshi et al. 2020; Somvanshi et al. 2020). These resistance mechanisms also involve an accumulation of reactive oxygen species (ROS) and a complex phytohormones pathway produced by the resistant plant (Shukla et al. 2018; Kaloshian and Teixeira, 2019).

Table 2. Results of chi-square tests for segregation responses of parents, F_1, F_2 and BC progeny against *Meloidogyne incognita*

Parents/cross population	Resistant	Susceptible	χ^2	P value
P (MTE-02) (S)		50		
P (DINO 03-0200) (R)	50			
P (DINO 03-0056) (R)	50			
F_1 (DINO 03-0200 × MTE-02)	100			
F_1 (MTE-02 × DINO 03-0200)	100			
F_2 (MTE-02 × DINO 03-0200)	177	123	1.45	0.32
F_2 (DINO 03-0200 × MTE-02)	180	120	2.38	0.13
BC (DINO 03-0200×MTE-02) × MTE-02	145	155	1.12	0.27
BC (MTE-02×DINO 03-0200) × MTE-02	151	149	1.53	0.34
BC (DINO 03-0200× MTE-02) × DINO 03-0200	300			
BC (MTE-02×DINO 03-0200) × DINO 03-0200	300			
F_1 (DINO 03-0056 × MTE-02)	100			
F_1 (MTE-02 × DINO 03-0056)	100			
F_2 (MTE-02 × DINO 03-0056)	173	127	1.65	0.42
F_2 (DINO 03-0056 × MTE-02)	181	119	0.13	0.61
BC (DINO 03-0056 × MTE-02) × DINO 03-0056	300			
BC (MTE-02 × DINO 03-0056) × DINO 03-0056	300			
BC (MTE-02 × DINO 03-0056) × MTE-02	151	139	1.86	0.21
BC (DINO 03-0056 × MTE-02) × MTE-02	142	158	0.43	0.51

P: parent; F_1: filial 1; F_2: filial 2; BC: backcross; R: resistant; S: susceptible

Figure 3. Plant morphology of three parent use in the experiment. From left, eggplant cv MTe-02, followed by DINO-0059 and DINO-0200

The marker assisted selection was an efficient approach to introgress the RKN resistance genes into susceptible cultivars given the oligogenic and epistatic nature of RKN resistance in eggplant, thus decreasing the time and selection in developing a new RKN-resistant eggplant cultivars (Shukla et al. 2018; Wubie and Temesgen 2019; Bali et al. 2019; Gabriel et al. 2020). A few breeding studies have been successful in producing a new high yielding and root knot nematode resistant hybrid by utilising and introducing the RKN-resistant genes *Mi-1* into commercial cultivars (Kiewnick et al. 2009; Shukla et al. 2018; Wubie and Temesgen 2019). Other resistant genes such as *Mi-2, Me-3* and *N* have also been successfully introduced into commercial solanaceous crops, such as pepper and tomato crops (El-Sappah et al. 2019; García Mendívil, 2019). Nonetheless, the cultivation of eggplant variety with resistance genes may expose the resistant plant to virulent nematodes (García-Mendívil et al. 2019; Saini and Kaushik 2019; Expósito et al. 2020). Crop management such as rotation with susceptible varieties using two different resistant crop species or using crops with different resistant gene action was proposed to reduce RKN virulence selection incidence that could lead to higher yield loss (Chitambo 2019; Van Esse et al. 2020; Sharma and Kaushik 2021).

This study provides better information on the approach of genetic control of resistance to *M. incognita* by a resistant gene in eggplant. Although resistance is controlled by nuclear factors, cytoplasmic factors are not effective. The genotypes, DINO 03-0200 and DINO 03-0056, provide a good source of resistance in a breeding program as these genotypes belong to *S. melongena* and can be easily crossed with other cultivated eggplants. The resistance gene is dominant where it only needs to be introduced into one parent to produce a new hybrid with a resistance inheritance gene. Despite the effectiveness of resistance varieties against RKN, a virulent nematode generation can overcome plant defence mechanisms if continuous cultivation of resistant plants bearing the same R-gene is implemented (Expósito et al. 2020). Hence, resistance varieties will only be efficient and long lasting if it is properly applied, such as in rotation sequences with several varieties with different types of resistance genes.

Conclusion

In this study, a better understanding of the inheritance of resistance genes to RKN in eggplant was evaluated. Although F_1 hybrids were resistant, the presence of susceptible BC hybrids indicated the need to conduct pathological and genetic RKN resistance studies in eggplant. The resistant materials can be used for the development of consistent resistant F_1 hybrids and the development of new materials with RKN resistance. Future research needs to focus on the identification of genomic positions of resistant genes and the development of markers that could facilitate marker assisted selection for resistance to RKN in eggplant and to introduce resistance genes into commercial eggplant hybrids.

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References

Ali, M. A., Abbas, A., Azeem, Javed, F. N. & Bohlmann, H. (2015). Plant-nematode interactions: From genomics to metabolomics. *Int. J. Agric. Biol.* 17. 1071–1082

Ali, M. A., Azeem, F., Abbas, A., Joyia, F. A., Li, H. & Dababat, A. A. (2017). Transgenic strategies for enhancement of nematode resistance in plants. *Frontiers in Plant Science* 8, 750

Ali, M. A., Shahzadi, M., Zahoor, A., Dababat, A. A., Toktay, H. & Bakhsh, A. (2019). Resistance to cereal cyst nematodes in wheat and barley: an emphasis on classical and modern approaches. *Int. J. Mol. Sci.* 20, 432

Anuar, M. N. (2020). Genetic diversity, resistance against root knot nematode *Meloidogyne incognita* and performance of F_1 generation in crossed population of eggplant [Master's thesis, Universiti Kebangsaan Malaysia]. Universiti Kebangsaan Malaysia Thesis Repository

Anuar, M.N., Shamsudin, N. A. A., Said, T., Suherman, F. H. S. & Baharom, N. A. (2021). Genetic diversity studies of twenty eggplant (*Solanum* spp.) accessions and their performance against root-knot nematode (*Meloidogyne incognita*) infestation. *Intl J Agric Biol. 2021* 26, 625–634

Asghar, A., Mukhtar, T., Raja, M. U. & Gulzar, A. (2020). Interaction between *Meloidogyne javanica* and *Ralstonia solanacearum* in chili. *Pakistan Journal of Zoology* 52

Baidya, S., Timila, R. D., Bahadur, K. C. R., Manandhar, H. K. & Manandhar, C. (2017). Management of root-knot nematode on tomato through grafting rootstock of *Solanum sisymbriifolium*. *J. Nepal Agric. Res. Counc.* 3, 27–31. doi: 10.3126/jnarc.v3i1.17272

Bali, S., Vining, K., Gleason, C., Majtahedi, H., Brown, C. R. & Sathuvalli, V. (2019). Transcriptome profiling of resistance response to *Meloidogyne chitwoodi* introgressed from wild species *Solanum bulbocastanum* into cultivated potato. *BMC genomics 20*, 1–18

Banerjee, S., Banerjee, A., Gill, S. S., Gupta, O. P., Dahuja, A. & Jain, P. K. (2017). RNA Interference: a novel source of resistance to combat plant-parasitic nematodes. *Front. Plant Sci.*

Boerma, H. R. & Hussey, R.S. (1992). Breeding plant for resistance to nematodes. *J. Nematol.* 24, 242–252

Bridge, J. & Page, S. L. J. (1980). Estimation of root-knot nematode infestation levels on roots using a rating chart. *Tropical Pest Management* 26(3), 296–298

Chaudhary, S., Dutta, T. K., Tyagi, N., Shivakumara, T. N., Papolu, P. K., Chobhe, K. A. & Rao, U. (2019). Host induced silencing of Mi-msp-1 confers resistance to root-knot nematode *Meloidogyne incognita* in eggplant. *Transgenic research*, *28*, 327–340

Chiamolera, F. M., Martins, A. B. G., Soares, P. L. M. & Cunha-Chiamolera, T. P. L. D. (2018). Reaction of potential guava rootstocks to *Meloidogyne enterolobii*. *Revista Ceres*, *65*, 291–295

Cheng, C., Wang, X., Liu, X., Yang, S., Yu, X. & Qian, C. (2019). Candidate genes underlying the quantitative trait loci for root-knot nematode resistance in a *Cucumis hystrix* introgression line of cucumber based on population sequencing. *J. Plant Res.* 132, 813–823

Chitambo, O. 2019. African nightshade and African spinach: A neglected and underutilised resource with significant potential to manage plant-parasitic nematodes.

Da Silva, A. J., de Oliveira, G. H. F., Pastoriza, R. J. G., Maranhao, E. H. A., Pedrosa, E. M. R. & Maranhao, S. R. V. L. (2019). Search for sources of resistance to *Meloidogyne enterolobii* in commercial and wild tomatoes. *Hortic. Bras.* 37, 188–198

Daunay, M. C., Salinier, J. & Aubriot, X. (2019). Crossability and diversity of eggplants and their wild relatives. *The eggplant genome*, 135–191

Dewi, A. & Indarti, S. (2022). Screening Resistance of Several Accessions Eggplant (*Solanum melongena* L.) Against Root-Knot Nematodes (*Meloidogyne incognita*). In *2nd International Conference on Smart and Innovative Agriculture (ICoSIA 2021)*, 180–190

Elling, A. A. (2013). Major emerging problems with minor *Meloidogyne* species. *Phytopathology*, *103*(11), 1092 – 1102

El-Sappah, A. H., Islam, M. M., El-Awady, H. H., Yan, S., Qi, S. & Liu, J. (2019). Tomato natural resistance genes in controlling the root-knot nematode. *Genes* 10:925

Expósito, A., Pujolà, M., Achaerandio, I., Giné, A., Escudero, N., Fullana, A. M. & Sorribas, F.J. (2020). Tomato and melon Meloidogyne resistant rootstocks improve crop yield but melon fruit quality is influenced by the cropping season. *Frontiers in Plant Science*, *11*, 560024

FAOSTAT. (2021). Food and Agriculture Organisation of the United Nations. Statistics Division. Available online at: www.fao.org/faostat (accessed on March 21, 2023)

Fassuliotis, G. (1970). Resistance of *Cucumis* spp. to the root-knot nematode, *Meloidogyne incognita* acrita. *J. Nematol. 2*, 174–178

Forghani, F. & Hajihassani, A. (2020). Recent advances in the development of environmentally benign treatments to control root-knot nematodes. *Front. Plant Sci.* 11, 1125

Gabriel, M., Kulczynski, S. M., Muniz, M. F. B., Boiteux, L. S. & Carneiro, R. M. D. G. (2020). Resistance of 'Debora Plus' tomato bearing Mi-1.2 gene/locus against fifteen *Meloidogyne* species. *Plant Pathol.* 69, 944–952

García-Mendívil, H. A., Sorribas, F. J. 2019. Fitness cost but no selection for virulence in *Meloidogyne incognita* after two consecutive crops of eggplant grafted onto *Solanum torvum*. *Plant Pathol.* 68, 1602–1606

Greco, N. & Vito, M. D. (2009). Population dynamics and damage levels. In *Root-knot nematodes*, 246–274. Wallingford UK: CABI

Hadisoeganda, W. W. & Sasser, J. N. (1982). Resistance of tomato, bean, southern pea, and garden pea cultivars to root-knot nematodes based on host suitability. *Plant Disease* 66, 145 – 50

Hajihassani, A., Rutter, W. B., Schwarz, T., Woldemeskel, M., Ali, M. E. & Hamidi, N. (2020). Characterization of resistance to major tropical root-knot nematodes (*Meloidogyne* spp.) in *Solanum sisymbriifolium*. *Phytopathology* 110(3), 666–673

Hallmann, J. & Meressa, B. H. (2018). Nematode parasites of vegetables. In *Plant parasitic nematodes in subtropical and tropical agriculture*, 346–410. Wallingford UK: CAB International

Hussey, R. S. & Barker, K. R. (1973). Comparison of methods of collecting inocula of *Meloidogyne* spp., including a new technique. *Pl. Dis. Rep.* 57, 1025–1028

Kaloshian, I. & Teixeira, M. (2019). Advances in plant-nematode interactions with emphasis on the notorious nematode genus Meloidogyne. *Phytopathology* 109, 1988–1996

Kiewnick, S., Dessimoz, M. & Franck, L. (2009). Effects of the Mi-1 and the N root-knot, nematode-resistance gene on infection and reproduction of *Meloidogyne enterolobii* on tomato and pepper cultivars. *J. Nematol. 41*, 134–139

Kranz, J. (1988). Measuring plant disease. *Experimental techniques in plant disease epidemiology*, 35–50

Miyashita, N., Yabu, T., Kurihara, T. & Koga, H. (2014). The feeding behavior of adult root-knot nematodes (*Meloidogyne incognita*) in rose balsam and tomato. *Journal of nematology* 46(3), 296–301

Motti, R. (2021). The Solanaceae family: Botanical features and diversity. *The wild solanums genomes*, 1–9

Mukhtar, T. & Kayani, M. Z. (2020). Comparison of the damaging effects of *Meloidogyne incognita* on a resistant and susceptible cultivar of cucumber. *Bragantia 79*, 83–93

Naeem, M. Y. & Ugur, S. (2019). Nutritional content and health benefits of eggplant. *Turkish Journal of Agriculture-Food Science and Technology*, *7*(sp3), 31–36

Nguyen, H. T., Mantelin, S., Ha, C. V., Lorieux, M., Jones, J. T., Mai, C. D. & Bellafiore, S. (2022). Insights into the genetics of the Zhonghua 11 resistance to *Meloidogyne graminicola* and its molecular determinism in rice. *Frontiers in plant science, 13,* 854961

Nicol, J. M., Turner, S. J., Coyne, D. L., Nijs, L. D., Hockland, S. & Maafi, Z. T. (2011). Current nematode threats to world agriculture. *Genomics and molecular genetics of plant-nematode interactions*, 21–43

Nyczepir, A. P. & Thomas, S. H. (2009). Current and future management strategies in intensive crop production systems. In *Root-knot nematodes*, 412–443. Wallingford UK: CABI

Papolu, P. K., Dutta, T. K., Tyagi, N., Urwin, P. E., Lilley, C. J. & Rao, U. (2016). Expression of a cystatin transgene in eggplant provides resistance to root-knot nematode, *Meloidogyne incognita*. *Frontiers in Plant Science* 7(July), 1–9

Philbrick, A. N., Adhikari, T. B., Louws, F. J. & Gorny, A. M. (2020). *Meloidogyne enterolobii*, a major threat to tomato production: current status and future prospects for its management. *Frontiers in Plant Science* 11, 606395

Ros-Ibáñez, C., Robertson, L., Martínez-Lluch, M., Cano-García, A. & Lacasa-Plasencia, A. (2014). Development of virulence to *Meloidogyne incognita* on resistant pepper rootstocks. *Span. J. Agric. Res.* 12, 225–232

Saini D.K. & Kaushik P. (2019): Visiting eggplant from a biotechnological perspective: A review. *Scientia Horticulturae 253*: 327–340

Sharma, M. & Kaushik, P. 2021. Breeding for root-knot nematode resistance in eggplant: progress and prospects.

Shukla, N., Yadav, R., Kaur, P., Rasmussen, S., Goel, S. & Agarwal, M. (2018). Transcriptome analysis of root-knot nematode (*Meloidogyne incognita*)-infected tomato (*Solanum lycopersicum*) roots reveals complex gene expression profiles and metabolic networks of both host and nematode during susceptible and resistance responses. *Mol. Plant Pathol*. 19, 615–633

Singh, B., Das, A., Parihar, A. K., Bhagawati, B., Singh, D., Pathak, K. N. & Gupta, S. (2020). Delineation of genotype-by-environment interactions for identification and validation of resistant genotypes in mungbean to root-knot nematode (*Meloidogyne incognita*) using GGE biplot. *Scientific reports* 10(1), 1–14

Somvanshi, V. S., Phani, V., Banakar, P., Chatterjee, M., Budhwar, R., Shukla, R. N. and Rao, U. (2020). Transcriptomic changes in the pre-parasitic juveniles of *Meloidogyne incognita* induced by silencing of effectors *Mi-msp-1* and *Mi-msp-20*. *Biotech* 10, 1–11

Van Esse, H. P., Reuber, T. L. & van der Does, D. (2020). Genetic modification to improve disease resistance in crops. *New Phytologist* 225, 70–86

Watson, T. T. & Desaeger, J. (2020). Non-Fumigant Nematicides Registered for Vegetable Crop: ENY-033/NG033, 4/2019. *EDIS*, *2020*(1), 1–4

Whitehead, A. G. & Hemming, J. R. (1965). A comparison of some quantitative methods of extracting small vermiform nematodes from soil. *Ann. App. Biol. 55*, 25–38

Wubie, M. & Temesgen, Z. (2019). Resistance mechanisms of tomato (*Solanum lycopersicum*) to root-knot nematodes (Meloidogyne species). *Journal of Plant Breeding and Crop Science* 11 (2), 33–40

Ye, D. Y., Qi, Y. H., Cao, S. F., Wei, B. Q. & Zhang, H. S. (2017). Histopathology combined with transcriptome analyses reveals the mechanism of resistance to *Meloidogyne incognita* in *Cucumis metuliferus*. *J. Plant Physiol. 212*, 115–124