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Identification of Promising Eggplant Genotypes for Root-knot Nematode (*Meloidogyne incognita*) Resistance

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Abstract. **Parasitic *Meloidogyne incognita* root-knot nematodes (RKNs) represent one of the most serious eggplant (*Solanum melongena*) biotic stress problems. We evaluated 47 eggplant genotypes, including three cultivated eggplant, 13 wild accessions, and 31 eggplant prebreeding materials (*S. melongena* introgressed with wild relatives), to determine their resistance to *M. incognita* based on disease severity (%), gall number/plant, and egg mass number/plant. Wide variability in resistance was noticed among the tested genotypes. *Solanum sisymbriifolium* SIS1 and the eggplant line F2-10, which has introgressions from *S. incanum* INC1, had the highest resistance to nematode infestation, with the lowest disease severity (1.43% and 8.86%, respectively), gall number, gall index, egg mass index, and number of egg masses. Additionally, accession *S. anguivi* ANG1 displayed moderate resistance. Interestingly, *S. sisymbriifolium* SIS1 had the highest root, shoot, and total fresh weights. *S. anguivi* ANG1 had the next highest root and total fresh weights. This study provides novel sources of resistance to nematodes, and these resistant materials could be used in breeding programs to develop RKN-resistant eggplant cultivars or as resistant rootstocks for eggplant and tomato crops.**

Vegetable crops play a substantial role in human diet and nutrition as sources of essential element minerals, fiber, antioxidants, and other bioactive compounds. Furthermore, eggplant (*Solanum melongena* L.) is considered one of the healthiest vegetables and is a good source of many important nutrients and phytochemicals associated with several human health benefits (Docimo et al. 2016). Eggplant is one of the most important members of the *Solanaceae* family, which includes more than 3000 species distributed in approximately 90 genera with large variability in fruit shape, color, size, and composition (Sadilova et al. 2006; Vorontsova and Knapp 2016). Eggplant is a crop that is well-adapted to tropical and subtropical climate conditions. Apart from *S. melongena*, in sub-Saharan Africa, there are two important species of cultivated eggplants: scarlet eggplant (*S. aethiopicum* L.) and gboma eggplant (*S. macrocarpon* L.) (Daunay and Hazra 2012; Taher et al. 2019). Globally, eggplant productivity exceeds 58 million tons from an area of approximately 1.9 million ha (FAOSTAT 2021). At present, the top five producing countries are China (37.4 million tons; 63.8% of the world's total), India (12.9 million tons; 21.9% of the world's total), Egypt (1.3 million tons), Turkey (0.83 million tons), and Indonesia (0.68 million tons) (FAOSTAT 2021).

Eggplant suffers from various biotic and abiotic stresses, including insects, bacteria, virus, fungi, and plant-parasitic nematodes as well as drought and salinity (Abdelaziz et al. 2022; Albalawi et al. 2022; Alkhatib et al. 2021; Hannachi et al. 2022; Taher et al. 2020). Therefore, eggplant productivity is adversely affected by root-knot nematodes (RKNs) caused by the soil-borne endoparasite *Meloidogyne incognita* (Kofoid and White) Chitwood, which affects a wide range of plant species (Jones et al. 2013; Manzanilla-Lopez and Starr 2009). Root-knot nematodes are sedentary, obligate plant parasites that are considered a major pest of vegetables worldwide. The economic global losses associated with RKNs were estimated at approximately \$157 billion/year, thus threatening food security (Zhang et al. 2021). Remarkably, under optimum environmental conditions for their development, RKNs can cause severe infestations with huge yield losses to the eggplant crop. Plants infected by RKNs display a reduction in the root system with extensive galling and root structure damage (Anwar and Mckenry 2010). Furthermore, root deformation and overall plant growth reduction as well as root lesions are additional symptoms of RKN. Moreover, RKNs induce the development of specialized feeding positions (galls) in infested plant roots. *Meloidogyne incognita* causes infestation of a broad range of host vegetables, including eggplant, carrot, tomato, potato, cucumber, watermelon, and others (Williamson and Kumar 2006). The second-stage juveniles (J2s) of *M. incognita* infect the normal root system of host species, resulting in the formation of giant cells, which are differentiated by hypertrophy and the hyperplasia effect (Yamaguchi et al. 2017). Moreover, nematode invasion may increase the severity of fungal infections such as fusarium wilt or bacterial diseases such as *Ralstonia solanacearum* species complex (Khan and Sharma 2020). Integrated management strategies for RKNs include cultural practices, biological control, nematicide applications, and resistant cultivars and rootstocks (Devran et al. 2010). Although nematicides may effectively control RKNs, its use has substantial human health and environmental risks (Devran et al. 2013). In contrast, the implementation of resistant cultivars can serve as an eco-friendly alternative for controlling RKNs (Rahman et al. 2002).

Nematode resistance has been identified in the cultivated genepool and/or wild-types in major crops such as tomato, cotton, and pepper (Chen et al. 2007; Milligan et al. 1998; Niu et al. 2007). Therefore, the tomato resistance gene *Mi-1*, which confers resistance to the most serious RKNs *M. arenaria*, *M. incognita*, and *M. javanica*, has been used

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in tomato breeding programs (Nombela et al. 2003). In eggplant, resistance to *M. incognita* in some wild-types such as *S. torvum* and *S. aculeatissimum* (Garcia-Mendivil et al. 2019; Öçal et al. 2018; Sargın and Devran 2021; Uehara et al. 2017; Zhou et al. 2018) has been reported. However, cross-incompatibility and the difficulty of obtaining backcrosses of eggplant with wild species have hampered breeding for RKN resistance in eggplant (Bagnaresi et al. 2013). Therefore, the identification of new sources of resistance to RKNs in cultivated eggplants and its introgression lines is extremely necessary for the development of new RKN-resistant cultivars (Johnson et al. 2014). The objective of this research was to evaluate close wild relatives of cultivated eggplant and unique prebreeding materials with introgressions from wild species for resistance to RKNs that may contribute to breeding new RKN-resistant cultivars or that may be used as rootstocks against *M. incognita*.

Materials and Methods

Plant materials and growth conditions. A total of 47 eggplant genotypes, including 13 wild accessions, three cultivated accessions, and 31 prebreeding lines with introgressions from wild relatives, were screened to detect *M. incognita* (Table 1). Eggplant line MEL4 was used as susceptible *M. incognita* control. Seeds of all tested accessions and the control were sown in 209-cell seedling trays for 4 weeks. Thereafter, seedlings were transplanted into plastic pots (diameter, 15 cm) filled with 2 kg of mixed substrate comprising sterilized soil, sand, and peatmoss with a volumetric proportion of 1:1:1 per pot. Plants were watered with tap water and fertilized with a nitrogen (N):phosphorus (P):potassium (K) 19–19–19 fertilizer based on the recommendation of the Egyptian Ministry of Agriculture and Land Reclamation.

Preparation of nematode inoculum. The trial was performed at the Faculty of Agriculture, Kafrelsheikh University, Kafrelsheikh governorate (Egypt). A *M. incognita* nematode colony was isolated from infected tomato plants grown in the Baltim region at Kafrelsheikh governorate, Egypt. The inoculum of *M. incognita* was prepared from cultures established from single egg masses of identified females and reared as a definite population on tomato plants. The RKN eggs were extracted from infected tomato roots using 0.5% NaOCl solution. The root system was cut into 2- to 4-cm pieces placed in a 1-L flask containing 200 mL of 0.25% NaOCl, shaken vigorously for 3 min, poured through a 400-mesh (32 µm) sieve, and rinsed with tap water to wash eggs through the upper sieve. Nematode identification was performed based on the morphology of adult and juvenile forms (Siddiqui 1986). After removal of the 20-mesh sieve, gentle and thorough rinsing of the eggs collected on the 500-mesh (25 µm) sieve was performed to remove residual bleach. The latter sieve was quickly placed under a stream of tap water to remove any remaining bleach. However, samples of rhizosphere soil were used to extract a population of nematode juveniles using the sieving method of Hussey and Barker (1973).

Table 1. Eggplant materials, including wild species, *S. melongena* accessions (MEL codes) and *S. melongena* lines with introgressions with wild species (F2 codes; each genotype originating from a single BC2 plant) for root-knot nematode (*Meloidogyne incognita*) resistance evaluation under greenhouse conditions.

Genotype no.	Code	Scientific name	Name/pedigree
E1	INS2	*S. insanum*	SLKINS-2
E2	ANG1	*S. anguivi*	BBS119
E3	CAM5	*S. campylacanthum*	MM680
E4	CAM6	*S. campylacanthum*	MM700
E5	CAM8	*S. campylacanthum*	MM1426
E6	INC1	*S. incanum*	MM664
E7	LIC1	*S. lichtensteinii*	MM674
E8	LIC2	*S. lichtensteinii*	MM677
E9	LIN1	*S. linnaeanum*	JPT0028
E10	PYR1	*S. pyracanthos*	SOLN-66
E11	TOM1	*S. tomentosum*	MM992
E12	SIS1	*S. sisymbriifolium*	SOLN-78
E13	MEL3	*S. melongena*	BBS175
E14	MEL5	*S. melongena*	8104
E15	F2-5	*S. melongena*	[(MEL1) × (ANG1) × (MEL1)2 × (MEL1)] S2-5
E16	F2-28	*S. melongena*	[(MEL1 × ANG2) × MEL1)2 × MEL1)] S2-28
E17	F2-30	*S. melongena*	[MEL1 × ANG2) × MEL1)4 × MEL1)] S2-30
E18	F2-32	*S. amelongena*	[MEL1 × ANG2) × MEL 1)6 × MEL1)] S2-32
E19	F2-41	*S. melongena*	[MEL1 × DAS1) × MEL1)1 × MEL1)] S2-41
E20	F2-56	*S. melongena*	[MEL1 × DAS1) × MEL1)7 × MEL1)] S2-56
E21	F2-57	*S. melongena*	[MEL1 × DAS1) × MEL1)7 × MEL1)] S2-57
E22	F2-12	*S. melongena*	[MEL1 × LIC1) MEL1)2 × MEL1)] S2-12
E23	F2-14	*S. melongena*	[MEL1 × LIC1) MEL1)4 × MEL1)] S2-14
E24	F2-15	*S. melongena*	[MEL1 × LIC1) MEL1)5 × MEL1)] S2-15
E25	F2-40	*S. melongena*	[MEL2 × INS2) × MEL2)4 × MEL2)] S2-40
E26	F2-94	*S. melongena*	[MEL2 × INS2) × MEL2)6 × MEL2)]S2-94
E27	F2-97	*S. melongena*	[MEL2 × INS2) × MEL2)5 × MEL2)]S2-97
E28	F2-36	*S. melongena*	[MEL3 × INS3) × MEL3)3 × MEL3)]S2-36
E29	F2-37	*S. melongena*	[MEL3 × INS3) × MEL3)4 × MEL3)]S2-37
E30	F2-2	*S. melongena*	[MEL4 × INS1) × MEL4)2 × MEL4)]S2-2
E31	F2-3	*S. melongena*	[MEL4 × INS1) × MEL4)5 × MEL4)]S2-3
E32	F2-67	*S. melongena*	[INS1.2 × MEL5) × MEL5)16 × MEL5)]S2-67
E33	F2-70	*S. melongena*	[INS1 × MEL5) × MEL5)17 × MEL5)]S2-70
E34	F2-91	*S. melongena*	[INS1 × MEL5) × MEL5)184 × MEL5)]S2-91
E35	F2-18	*S. melongena*	[MEL5 × INS3) × MEL5)3 × MEL5)]S2-18
E36	F2-19	*S. melongena*	[MEL5 × INS3) × MEL5)4 × MEL5)]S2-19
E37	F2-20	*S. melongena*	[MEL5 × INS3) × MEL5)5 × MEL5)]S2-20
E38	F2-48	*S. melongena*	[MEL5 × INC1) × MEL5)2 × MEL5)]S2-48
E39	F2-51	*S. melongena*	[MEL5 × INC1) × MEL5)5 × MEL5)]S2-51
E40	F2-53	*S. melongena*	[MEL5 × INC1) × MEL5)6 × MEL5)]S2-53
E41	F2-9	*S. melongena*	[MEL6 × INC1) × MEL6)4 × MEL6)]S2-9
E42	F2-10	*S. melongena*	[MEL6 × INC1) × MEL6)5 × MEL6)]S2-10
E43	F2-11	*S. melongena*	[MEL6 × INC1) × MEL6)6 × MEL6)]S2-11
E44	F2-23	*S. melongena*	[MEL6 × LID2) × MEL6)2 × MEL6)]S2-23
E45	F2-26	*S. melongena*	[MEL6 × LID2) × MEL6)4 × MEL6)]S2-26
E46	F2-93	*S. melongena*	[MEL6 × LID2) × MEL6)5 × MEL6)]S2-93
E47	MEL4	*S. melongena*	7145

Screening process. Healthy seedlings of all tested accessions were inoculated under greenhouse conditions at 28 ± 2 °C (day), 20 ± 2 °C (night), 70% relative humidity, and pH of 6.5 to 7.5 during a 8-h/16-h light/dark photoperiod. All pots, with one plant per plot, were evaluated under the same irrigation, fertilization, and protection procedures until the end of the experiment. Between four and eight plants per genotype were evaluated. The resulting egg suspension was diluted with tap water and agitated for 3 d at 24 °C to induce juvenile hatching. The RKN (*M. incognita*) inoculum was applied by pipetting an aqueous suspension of approximately 5000 eggs, including some newly hatched second-stage juveniles, per pot. Active juveniles were separated from eggs, and the juveniles were suspended in tap water and inoculated in four 3-cm-deep holes around the stem base with light watering. The inoculated holes and plastic pots were watered instantly to keep the soil moist.

Disease assessment. Seven weeks after *M. incognita* inoculation, RKN parameters in terms of disease severity (%), gall number/plant, and egg mass number/plant were determined. Moreover, vegetative growth parameters of eggplants such as the total fresh weight (g), root fresh weight (g), and shoot fresh weight (g) were recorded. Furthermore, plants were gently uprooted, and the roots were carefully washed with tap water to remove all dusts and clay. Egg masses of *M. incognita* were stained by dipping the root system in 0.15 g/L of Phloxine B solution for 20 to 30 min, as described by Daykin and Hussey (1985); then, the stained roots were washed with tap water to remove the residual stain on the roots. Phloxin B primary stain was used to stain the gelatinous egg sac and naked viable eggs (Barker et al. 1985).

The gall index (GI) and egg mass index (EMI) were estimated according to the work of Taylor and Sasser (1978) using a scale of 0 to 5 (0 = no galls in the root system; 1 = presence of 1–2 galls; 2 = presence of 3–10 galls; 3 = presence of 11–30 galls; 4 = presence of 31–100 galls and 5 = presence of >100 galls). Furthermore, the root GI categories were determined according to Hadisoeganda and Sasser (1982) as follows: 0 to 1.0 = highly resistant; 1.1 to 3.0 = very resistant; 3.1 to 3.5 = moderately resistant; 3.6 to 4.0 = slightly resistant; and 4.1 to 5.0 = susceptible. Additionally, the galling severity and disease categories of eggplant root system were estimated according to a scale of 1 to 9 developed by Thies and Fery (1998) and Thies and Levi (2003) (Table 2).

Statistical analysis. The collected nematode resistance data as well as vegetative growth parameters were subjected to the analysis of variance using the Costat software, and significant means were separated using Duncan's multiple range test (Duncan 1955).

Results

Wide variability in *M. incognita* resistance was noticed among the 47 eggplant genotypes evaluated and within plants in the same genotype in some cases (Table 3). Among the 47 evaluated eggplant genotypes, 307 individual plants were classified as five categories, including 23 that were highly resistant, 34 that were moderately resistant, 36 with low resistance, 105 that were susceptible, and 109 that were highly susceptible according to the disease severity scale for the root system of eggplant (Fig. 1). More than one-third (109) of the evaluated individual plants were highly susceptible, with scores of 8 to 9, which indicated 66% to 100% galled root systems, followed by susceptible category scores of 6 and 7, which indicated 39% to 65% galled root systems. However, the highly resistant category had the lowest number of evaluated plants (23 plants), with scores of 1 to 3 (0% to 12% galled root system).

Susceptible control plants of MEL-4 were susceptible or highly susceptible (Table 3). The eggplant wild relative *S. sisymbriifolium* SIS1 (E12) had the highest resistance to *M. incognita*, with all the evaluated plants exhibiting high resistance. The genotype E42, which is a second selfing of a second backcross of *S. incanum* INC1 toward eggplant, ranked second in resistance, with five highly resistant individual plants and two moderately resistant plants. Furthermore, the *S. anguivi* ANG1 (E2) accession was moderately resistant. At the other extreme, the following 10 genotypes were highly susceptible to *M. incognita* infestation, with the individual plants exhibiting a high level of susceptibility: E5 (*S. campylacanthum* CAM8); E6 (*S. incanum* INC1); E8 (*S. lichtensteinii* LIC2); E47 (*S. melongena* MEL4); and lines E16, E23, E31, E39, E44, and E46 (second selfings of second backcrosses of several wild species of *S. melongena*).

Five parameters, disease severity, egg mass number/plant, EMI, gall number/plant, and GI, of the inoculated plants were measured (Table 4). No genotype was immune to *M. incognita* infestation. Additionally, eight resistant genotypes, ANG1, PYR1, SIS1, F2-5, F2-10,

Table 2. Disease severity scale used to assess root-knot nematode *Meloidogyne incognita* resistance on the root system of eggplant based on previous studies (Thies and Fery 1998; Thies and Levi 2003).

Disease rating grade	Galled root system (%)	Disease category
1	0	High resistance
2	1–3	
3	4–12	
4	13–25	Moderate resistance
5	26–38	Low resistance
6	39–50	Susceptible
7	51–65	
8	66–80	Highly susceptible
9	81–100	

Table 3. Performance of individual plants of eggplant materials at 7 weeks after inoculation with the root-knot nematode *Meloidogyne incognita*.

			Response to root-knot nematode				
Genotype no.	Code	No. of plants	HR	MR	LR	S	HS
E1	INS2	7		1	1	2	3
E2	ANG1	8	2	4	1	1	
E3	CAM5	7	1			2	4
E4	CAM6	7		1		4	2
E5	CAM8	4				2	2
E6	INC1	8				1	7
E7	LIC1	8	1			3	4
E8	LIC2	6					6
E9	LIN1	8		1	1	6	
E10	PYR1	6	1	2		2	1
E11	TOM1	6		3			3
E12	SIS1	6	6				
E13	MEL3	6			2	2	2
E14	MEL5	6		1	1	2	2
E15	F2-5	8	2	2	1	1	2
E16	F2-28	4					4
E17	F2-30	7		1		1	5
E18	F2-32	6			1		5
E19	F2-41	7	1	1	2	3	
E20	F2-56	7		1		6	
E21	F2-57	5		2	1	1	1
E22	F2-12	5				4	1
E23	F2-14	5				1	4
E24	F2-15	7	1		1		5
E25	F2-40	7		1	1		5
E26	F2-94	6		1	3	1	1
E27	F2-97	4			1	3	
E28	F2-36	8			4	3	1
E29	F2-37	6	1			5	
E30	F2-2	7		1	3	1	2
E31	F2-3	7				3	4
E32	F2-67	7		1		5	1
E33	F2-70	7			3	4	
E34	F2-91	7		1		3	3
E35	F2-18	6		2	1	3	
E36	F2-19	7	1	1	2	2	1
E37	F2-20	7		1	1	4	1
E38	F2-48	6	1			2	3
E39	F2-51	6				2	4
E40	F2-53	6		1	1	1	3
E41	F2-9	7		1	1	2	3
E42	F2-10	7	5	2			
E43	F2-11	7			2	4	1
E44	F2-23	7				3	4
E45	F2-26	8		1	1	5	1
E46	F2-93	6				1	5
E47	MEL4	7				4	3
Total	**47**	**307**	**23**	**34**	**36**	**105**	**109**

HR = highly resistant; HS = highly susceptible; LR = lower resistant, MR = moderately resistant; S = susceptible.

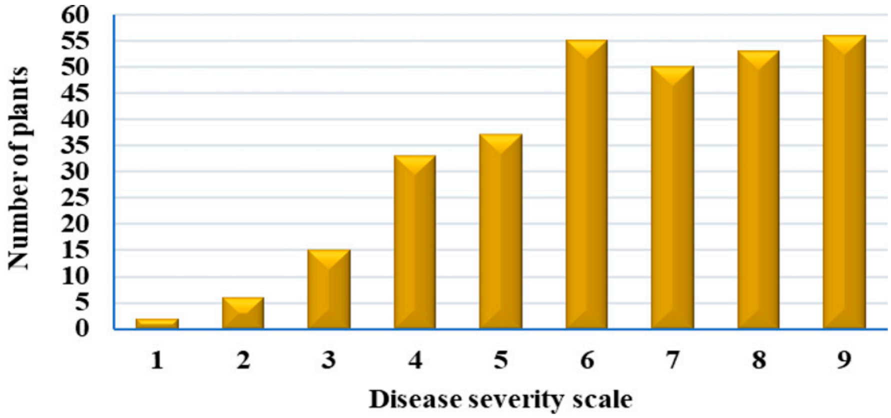

Fig. 1. Distribution of individual plants of the evaluated eggplant genotypes according to the disease severity scale (1 to 9) (Thies and Fery 1998) after 7 weeks of inoculation with the root-knot nematode *Meloidogyne incognita*.

F2-41, F2-57, and F2-94, showed different degrees of resistance to RKN. Two of eight genotypes (SIS1 and F2-10) were highly resistant to nematode infestation and had the lowest disease severity, gall number, GI, EMI, and number of egg mass.

Table 4. Disease severity, egg mass, egg mass index (EMI), galls per plant, and gall index (GI) of eggplant materials at 7 weeks after inoculation with the root-knot nematode *Meloidogyne incognita*.

Genotype no.	Code	Disease severity	Egg mass (no.)/plant	EMI	Galls (no.)/plant	GI
E1	INS2	56.14 d–j	65.57 h–n	4.17 b–h	89.86 k–s	4.14 b–f
E2	ANG1	18.75 kl	106.88 c–h	4.38 a–f	137.50 cl	4.63 abc
E3	CAM5	62.14 a–j	34.83 k–o	3.57 f–k	70.43 l–t	4.14 b–f
E4	CAM6	51.43 e–j	34.83 k–o	3.43 h–l	63.57 n–u	4.00 c–f
E5	CAM8	70.00 a–h	30.25 l–o	2.75 lm	49.75 q–u	3.50 f
E6	INC1	87.13 ab	34.83 k–o	3.50 g–l	66.13 m–u	4 c–f
E7	LIC1	57.38 c-j	82.75 f-l	4.13 b-h	109.00 f–r	4.38 a–e
E8	LIC2	81.50 a–d	89.00 e–k	4.33 a–f	107.33 f–r	4.50 a–d
E9	LIN1	41.88 h–k	21.75 m–o	3.13 j–l	38.25 s–u	3.50 f
E10	PYR1	35.17 jk	68.50 g–n	4.00 c–i	112.67 f–r	4.50 a–d
E11	TOM1	54.00 d–j	34.83 k–o	3.33 i–l	57.67 p–u	3.83 d–f
E12	SIS1	1.43 l	2.83 o	1.50 n	4.500 u	1.83 h
E13	MEL3	53.33 d–j	127.50 b–f	4.83 ab	172.00 a–f	5.00 a
E14	MEL5	57.17 c–j	138.00 a–e	4.67 a–d	193.00 a–d	5.00 a
E15	F2-5	37.75 i–k	75.88 f–m	4.13 b–h	102.13 h–s	4.13 b–f
E16	F2-28	88.00 a	139.00 a–e	5.00 a	189.50 a–e	5.00 a
E17	F2-30	69.71 a–h	104.86 c–h	4.43 a–e	135.29 d–l	4.57 a–d
E18	F2-32	74.33 a–g	69.33 g–n	4.17 b–h	104.17 g–s	4.50 a–d
E19	F2-41	37.86 i–k	86.71 e–k	4.43 a–e	121.71 f–p	4.71 a–c
E20	F2-56	48.57 e–j	101.57 d–h	4.29 a–g	160.14 b–j	4.86 ab
E21	F2-57	38.60 i–k	96.00 e–j	4.40 a–e	127.60 d–n	4.80 ab
E22	F2-12	52.00 e–j	181.20 a	5.00 a	210.00 ab	5.00 a
E23	F2-14	85.60 a–c	161.00 ab	5.00 a	170.60 a–g	4.80 ab
E24	F2-15	63.00 a–j	88.29 e–k	4.29 a–g	125.43 e–o	4.71 a–c
E25	F2-40	65.00 a–i	34.83 o	3.57 f–k	64.43 m–u	4.14 b–f
E26	F2-94	36.67 i–k	34.83 o	3.67 e–k	59.67 o–u	3.83 d–f
E27	F2-97	45.00 g–k	102.75 d–h	4.75 a–c	131.75 cm	4.75 a–c
E28	F2-36	48.50 e–j	63.38 h–n	3.88 d–j	85 l–s	4.25 a–e
E29	F2-37	45.83 f–k	31.33 l–o	3.17 j–l	46.50 r–u	3.67 ef
E30	F2-2	51.14 e–j	152.86 a–d	4.86 ab	162.86 b–i	5.00 a
E31	F2-3	69.86 a–h	100.43 d–h	4.43 a–e	129.00 d–n	4.71 a–c
E32	F2-67	59.29 a–j	64.29 h–n	3.86 e–j	94.00 j–s	4.29 a–e
E33	F2-70	42.14 h–k	113.86 b–h	4.57 a–d	167.43 b–h	4.86 ab
E34	F2-91	60.57 a–j	188.86 a	5.00 a	232.86 a	5.00 a
E35	F2-18	40.67 h–k	114.83 b–h	4.50 a–d	159.50 b–j	4.83 ab
E36	F2-19	41.71 h–k	121.86 b–g	4.43 a–e	157.14 bk	4.71 a–c
E37	F2-20	44.29 h–k	88.71 e–k	4.43 a–e	114.71 f–q	4.57 a–d
E38	F2-48	57.00 c–j	69.17 g–n	4.00 c–i	90.00 k–s	4 c–f
E39	F2-51	74.83 a–f	157.33 a–c	4.83 ab	195.67 a–c	4.83 ab
E40	F2-53	61.00 a–j	151.00 a–d	4.67 a–d	169.17 b–h	4.83 ab
E41	F2-9	55.29 d–j	74.57 f–n	4.14 b–h	96.57 i–s	4.43 a–d
E42	F2-10	8.86 l	10.14 o	2.29 m	16.29 tu	2.71 g
E43	F2-11	48.43 ej	104.29 d–h	4.43 a–e	122.29 f–p	4.86 ab
E44	F2-23	65.71 a–i	184.71 a	5.00 a	221.71 ab	5.00 a
E45	F2-26	49.38 e–j	96.88 e–i	4.50 a–d	120.50 f–p	4.63 a–c
E46	F2-93	75.83 a–e	72.67 g–n	4.00 c–i	109.17 f–r	4.67 a–c
E47	MEL4	65.71 a–i	21.14 n–o	3.00 kl	51.14 q–u	4 c–f

Means followed by the same letter within a column are not significantly different at the 5% level according to Duncan's multiple range test.

The genotype ANG1 was the only moderately resistant one, whereas the genotypes PYR1, F2-94, F2-5, F2-41, and F2-57 exhibited lower levels of resistance to infestation with *M. incognita*. However, 10 genotypes (CAM8, INC1, LIC2, F2-28, F2-30, F2-32, F2-14, F2-3, F2-51, and F2-93) were highly susceptible to nematode infestation. The eggplant genotype F2-28 had the highest disease severity (88%), followed by INC1 and F2-14 genotypes (87.13% and 85.60%, respectively). Additionally, *M. incognita* produced many galls and egg masses in these susceptible genotypes; therefore, the GI and EMI values increased. Moreover, the remaining 23 genotypes showed different degrees of susceptibility to RKNs.

As expected, resistant genotypes had the lowest EMI and GI category values; however, the susceptible eggplant genotypes had the highest values. Based on the EMI category and GI category, most evaluated genotypes were susceptible to RKN disease. The root system of the tested eggplant genotypes resulted in large differences according to the level of *M. incognita* infestation (Fig. 2A–2E). A noticeable increase in the gall number was observed in the susceptible genotypes (Fig. 2A–2C) when compared with the resistant genotypes (Fig. 2D and 2E).

Additionally, plant growth traits were negatively affected by RKN infestation (Table 5). Significant differences between the evaluated genotypes were recorded. The highly resistant genotype SIS1 displayed the highest root, shoot, and total dry weights (16.21, 33.08, and 49.29 g/plant, respectively) followed by the moderately resistant genotype ANG1, with root and total fresh weights of 12.43 and 28.29 g/plant, respectively, and a high shoot fresh weight (15.86 g/plant). However, the other highly resistant genotype, F2-10, displayed lower root, shoot, and the total dry weights (2.44, 4.31, and 6.75 g/plant, respectively). However, the susceptible genotype F2-19 ranked third for root and total dry weights, with 5.80 and 20.75 g/plant, respectively, and 14.95 g/plant for shoot weight. Moreover, the highly susceptible accession CAM8 had very low root, shoot, and total fresh weights (0.37, 0.68 and 1.05 g/plant, respectively), followed by accession LIC2.

Discussion

Eggplant is one of the most important horticultural crops for the enhancement of human health and nutrition. Eggplant productivity is adversely affected by various biotic and abiotic stresses, with plant parasitic nematodes being among the most damaging pathogens globally. *Meloidogyne incognita* is a soil-borne pest with a wide host range, which causes difficulty with control (Ocal and Devran 2019). Nematode infestation hinders the plant water intake and nutrient element intake from the rhizosphere and causes knots on its roots. In the case of severe infestation with nematodes, the economic losses of yield and quality may reach more than 80%, and there the possibility of a secondary pathogen attack exists (Pakeerathan et al. 2009).

Fig. 2. Root systems of different eggplant genotypes grown in infected plastic pots with root-knot nematode, *Meloidogyne incognita*, exhibiting severe root galling compared with resistant accessions. Line F_2-51 (*S. melongena* with introgressions of *S. incanum* INC1) (**A**); line F_2-28 (*S. melongena* with introgressions from *S. anguivi* ANG2) (**B**); accession LIC2 (*S. lichtensteinii* LIC2) (**C**); line F_2-10 (*S. melongena* with introgressions of *S. incanum* INC1) (**D**); and accession SIS1 (*S. sisymbriifolium*) (**E**).

Integrated management strategies are applied to control RKN, and the use of resistant cultivars is one of the most attractive approaches. Because the application of soil fumigation or nematicides is not ecofriendly and has significant environmental impacts, it became necessary to search for alternative and safe management strategies such as resistant cultivars (Begum et al. 2014; Montasser et al. 2019; Ocal and Devran 2019; Rahman et al. 2002).

During this study, the reactions of 47 eggplant genotypes to infestation with *M. incognita* varied not only in the different eggplant genotypes but also in individual plants of the same genotype. These findings may be attributable to the fact that the resistant genotypes possess unknown resistance genes (R-genes) and/or other biochemical or physiological resistance mechanisms that inhibit juvenile penetration of the cell wall of eggplant roots. These results are in agreement with those reported by Bakker et al. (2006), who indicated that if the host does not allow the nematode to create her feeding site, then the host is resistant to the RKN attack. Moreover, Begum et al. (2014) and Khan et al. (2019) pointed out that the susceptibility of a host to *M. incognita* is attributable to the capability of its juveniles (J_2) to penetrate the root system and construct giant cells, which are manifested as galls (knots) on the plant root. The adult female *M. incognita* remains inside the knots and continues to feed and generates egg masses. In the case of a resistant genotypes to RKN, the juveniles are either cannot penetrate the root system or die after penetration and, thus, are unable to complete their developmental stages. Additionally, *M. incognita* females cannot reproduce.

The diversity in the resistance degree among 47 genotypes was clarified. Two genotypes, SIS1 (*S. sisymbriifolium*) and F2-10 (*S. melongena* introgressed with *S. incanum* INC1), were categorized as highly resistant because all their individual plants had the lowest disease severity. Interestingly, *S. incanum* INC1 was susceptible, which indicated that the resistance of F2-10 must be caused by epistatic interaction. Genotypes with moderate and lower resistance had more resistant individual plants than those of the susceptible genotypes. These findings were in line with those reported by Ali et al. (2021), Anuar et al. (2021), and Begum et al. (2014), who mentioned that genotype resistance varied according to the presence of special genes, which are responsible for making plants less attractive or attractive to nematode attacks. Our data are in agreement with those of Boiteux and Charchar (1996), who found that SIS1 (*S. sisymbriifolium*) is considered a source of RKN resistance.

The highly resistant genotypes had the lowest disease-related parameters (disease severity, egg mass number per plant, EMI, gall number per plant, and GI), whereas the susceptible genotypes had the highest values for these traits. These results were in accordance with those of Haq et al. (2022). However, Dewi and Indarti (2022) reported that an increase in the gall number is not always followed by high egg mass numberss. Because the process of egg production depends on the interaction between the nematode and the host, the relationship between both the EMI and GI was also significant and highly correlated. This result was in agreement with the findings of Ali et al. (2021), who reported that the GI was linked to egg masses, adult females, and reproduction factors. On the contrary, the results reported by Anuar et al. (2021) and Aydinli et al. (2019) conflicted with ours because they found that an increase in the GI did not always reverse the higher egg number per gram root. Accordingly, our results also showed decreased values of the EMI and GI categories, respectively, of resistant and moderate genotypes compared with those of the susceptible ones. Although ANG1 was a moderately resistant genotype, it had higher egg mass number per plant, EMI, and gall number per plant values than those of the highly susceptible INC1. This may be attributed to its tolerance to infestation, especially because it ranked second in fresh root weight and total fresh weight after the highly resistant genotype (SIS1). This result was in line with those reported by Dewi and Indarti (2022) and Ali et al. (2021), who observed that the reactions of different tested eggplant accessions varied after infestation with RKNs and sometimes had no fixed rule. Wibowo (2015) found that RKNs differed in their penetrative power and propagation. Although susceptible plants could form a small gall, nematodes could proliferate properly. However, resistant plants could form many galls, but nematodes could not grow properly. Host plants differed in the structure of root tissues, secretion of chemical compounds that inhibit or encourage nematode attacks, and plant damage level.

The *M. incognita* RKN infestation had negative and significant effects on plant growth parameters of the evaluated genotypes. The highly resistant genotype SIS1 had the maximum fresh root, shoot, and total weights. On the contrary, the other highly resistant genotype F2-10 displayed lower weights. The moderately resistant genotype ANG1 exceeded F2-10 and followed the highly resistant genotype SIS1 in both root and total fresh weights, with high shoot fresh weights. However, the highly susceptible genotypes CAM8, LIC2, and F2-28 had lower plant growth trait values. These results are in agreement with those of Begum et al. (2014) and Khan et al. (2019). Therefore, resistant plant materials (cultivars, recombinant inbred lines, introgression lines, prebreeding lines, and others) and grafted seedlings are preferred because of their effectiveness, lower cost, and long-term and environmentally friendly defense approach compared with nematicides (Lopes et al. 2019). Moreover, new genetic sources of resistance played a crucial role in cultivation in the infested fields with RKNs.

Table 5. Effect of *Meloidogyne incognita* infection on some growth parameters of eggplant genotypes under greenhouse conditions. Root, shoot, and total fresh weights of eggplant materials at 7 weeks after inoculation with the root-knot nematode *Meloidogyne incognita*.

Genotype no.	Code	Root fresh wt (g/plant)	Shoot fresh wt (g/plant)	Total fresh wt (g/plant)
E1	INS2	2.60 d–m	6.05 f–o	8.65 e–m
E2	ANG1	12.43 b	15.86 bc	28.29 b
E3	CAM5	1.51 i–m	3.16 j–o	4.67 i–o
E4	CAM6	0.69 lm	1.34 no	2.03 m–o
E5	CAM8	0.37 m	0.68 o	1.05 o
E6	INC1	1.99 f–m	2.19 l–o	4.19 i–o
E7	LIC1	3.67 d–i	1.73 m–o	5.40 h–o
E8	LIC2	0.78 k–m	0.59 o	1.37 no
E9	LIN1	2.76 d–l	3.32 j–o	6.09 g–o
E10	PYR1	2.45 d–m	7.56 e–m	10.01 d–k
E11	TOM1	1.25 j–m	1.01 o	2.26 l–o
E12	SIS1	16.21 a	33.08 a	49.29 a
E13	MEL3	3.11 d–j	7.64 e–m	10.75 d–i
E14	MEL5	1.54 i–m	1.48 no	3.01 k–o
E15	F2-5	1.86 g–m	2.97 k–o	4.83 i–o
E16	F2-28	2.00 f–m	2.82 k–o	4.83 i–o
E17	F2-30	1.77 h–m	3.38 j–o	5.16 i–o
E18	F2-32	1.26 j–m	2.23 l–o	3.50 j-o
E19	F2-41	3.40 d–j	9.68 d–h	13.08 d–g
E20	F2-56	3.00 d–k	9.52 e–i	12.35 d–h
E21	F2-57	2.39 e–m	5.57 f–o	7.96 f–o
E22	F2-12	3.89 c–h	11.90 b–e	15.79 cd
E23	F2-14	3.13 d–j	5.17 g–o	8.31 e–n
E24	F2-15	2.07 f–m	6.08 f–o	8.15 f–o
E25	F2-40	4.21 c–f	8.61 e–k	12.83 d–g
E26	F2-94	2.57 d–m	8.01 e–l	10.58 d–j
E27	F2-97	2.44 d–m	6.52 e–o	8.97 d–m
E28	F2-36	4.02 c–g	8.93 e–j	12.96 d–g
E29	F2-37	1.22 j–m	0.93 o	2.15 m–o
E30	F2-2	3.95 c–h	11.26 c–f	15.22 c–e
E31	F2-3	1.43 i–m	2.61 l–o	4.03 i–o
E32	F2-67	3.21 d–j	7.94 e–l	11.15 d–i
E33	F2-70	4.62 cd	11.05 c–f	15.67 cd
E34	F2-91	4.39 c–e	10.40 d–g	14.79 c–f
E35	F2-18	No data	No data	No data
E36	F2-19	5.80 c	14.95 b–d	20.75 c
E37	F2-20	3.41 d–j	16.76 b	20.18 c
E38	F2-48	2.07 f–m	5.48 f–o	7.55 g–o
E39	F2-51	1.53 i–m	3.50 j–o	5.04 i–o
E40	F2-53	1.89 g–m	1.31 no	3.20 k–o
E41	F2-9	2.14 f–m	2.69 l–o	4.83 i–o
E42	F2-10	2.44 d–m	4.31 h–o	6.75 g–o
E43	F2-11	2.10 f–m	7.24 e–n	9.35 d–l
E44	F2-23	3.06 d–j	3.83 i–o	6.89 g–o
E45	F2-26	2.52 d–m	7.19 e-n	9.72 d–k
E46	F2-93	No data	No data	No data
E47	MEL4	2.29 e–m	2.90 k–o	5.18 i–o

Means followed by the same letter within a column are not significantly different at the 5% level according to Duncan's multiple range test.

The results of the current study revealed that *S. sisymbriifolium* and some eggplant materials introgressed with wild relatives such as F2-10 are promising materials that could be used as rootstocks for *Solanaceae* crops or for developing new and improved commercial cultivars of eggplant. Further studies are required to test the use of this wild-type and other *S. melongena* members in grafting technology and determine their production compared with susceptible commercial cultivars.

Conclusion

The identification of novel resistant genetic resources is of great relevance to developing eco-friendly control of *M. incognita* nematodes. Among 47 tested eggplant genotypes, including wild accessions and materials of *S. melongena* introgressed with wild species, three materials, SIS1, F2-10, and ANG1, were identified and selected as promising germplasm for nematode control management as a rootstock or use in breeding programs.

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