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Differences in parasitism of *Meloidogyne incognita* and two genotypes of *M. arenaria* on *Solanum torvum* in Japan

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Abstract

Two genotypes of root-knot nematode, *Meloidogyne arenaria* (A2-O and A2-J), are found in Japan. They were distinguished from each other based on mitochondrial DNA sequences. The primer set (C2F3/1108) amplified a 1.7-kb fragment from A2-J, whereas a 1.1-kb fragment was amplified from A2-O. *M. arenaria* (A2-O) was detected in local regions of southern Japan, whereas *M. arenaria* (A2-J) was widespread from the Kyushu region to the Tohoku region. The distribution of *M. arenaria* (A2-J) overlaps with the cultivation area of eggplant. *Solanum torvum* is used worldwide as a rootstock for eggplant cultivation, and it is resistant to *Meloidogyne* spp. In particular, it is reported that *S. torvum* is resistant to *M. arenaria* outside Japan. In this study, we inoculated *S. torvum* rootstock cultivars with *M. arenaria* (A2-J), *M. arenaria* (A2-O) and *Meloidogyne incognita* populations. Although *M. incognita* and *M. arenaria* (A2-O) produced only a few egg masses on *S. torvum*, thereby confirming its resistance, the four geographical populations of *M. arenaria* (A2-J) produced large numbers of egg masses on *S. torvum*. This study confirmed that *S. torvum* is resistant to *M. incognita* and *M. arenaria* (A2-O) populations, but susceptible to populations of *M. arenaria* (A2-J) in the eggplant production area of Japan.

KEYWORDS
eggplant, resistance, root-knot nematode, rootstock, susceptibility

1 | INTRODUCTION

Eggplant is widely cultivated and popular, particularly in Asian countries, such as India and China, and it has been one of the most important vegetable crops in Japan since long (Tachibana, 2006). Root-knot nematode (*Meloidogyne* spp.) is an important pathogen of eggplant (*Solanum melongena*) worldwide (Netcher & Sikora, 1990; Sasser, 1979). Approximately 17–29% of the total yield of eggplant is lost because of *Meloidogyne* spp. in the tropics (Sasser, 1979). Recently, Watanabe et al. (2013) reported that the yield of eggplant was decreased by an initial population of *Meloidogyne* spp. consisting of more than two-second-stage juveniles per 20 g soil. Using resistant cultivars is the most effective and environment-friendly method of reducing nematode-induced crop loss (Roberts, 2002). However, to the best of our knowledge, no eggplant cultivar resistant to *Meloidogyne* spp. has been found in Japan until date. Solanaceous crops such as tomato, pepper and eggplant are frequently cultivated by grafting onto disease- or pest-resistant rootstocks in order to prevent soil-borne diseases. In Japan, grafting of eggplants onto resistant rootstocks such as *Solanum torvum* "Torvum Vigor" is widely practiced to avoid soil-borne diseases by *Ralstonia solanacearum*, *Verticillium dahliae* and *Fusarium oxysporum* f.*melongenae* n. f. (Sakata, Monma, Narikawa, & Komochi, 1996; Yamaguchi et al., 2010). Even outside Japan, *S. torvum* is used as a rootstock for controlling wilt disease in eggplant (Gousset et al., 2005; Miceli, Sabatino, Moncada, Vetrano, & D'Anna, 2014). Moreover, several studies in Japan and elsewhere have shown that *S. torvum* is resistant to root-knot nematodes, including *Meloidogyne incognita*, *Meloidogyne javanica* and *Meloidogyne arenaria* (Ali, Matsuzoe, Okubo, & Fujieda, 1992; Boiteux & Charchar, 1996; Daunay & Dalmasso, 1985; Dhivya, Sadasakthi, & Sivakumar, 2014; Gonzalez et al., 2010; Hara, Momota, Kusakari, Abe, & Yamada, 1983; Ryu, 2012; Shetty & Reddy, 1985). Previously, we have demonstrated that *S. torvum* rootstock is

unlikely to cause sudden increases in *M. incognita* population density, in contrast to the other rootstock cultivars used for eggplant cultivation (Uehara et al., 2016).

Two genotypes of *M. arenaria* (A2-O and A2-J) are found in Japan (Narabu & Harada, 1997). They were distinguished from each other based on mitochondrial DNA (mtDNA) sequences and morphological characters. The primer set (C2F3/1108) (Powers & Harris, 1993) amplified a 1.7-kb fragment from A2-J, whereas a 1.1-kb fragment was amplified from A2-O. (Narabu & Harada, 1997). Moreover, these two types of *M. arenaria* are differentiated by their distribution area in Japan, depending on temperature. *M. arenaria* (A2-O) was detected in local regions of southern Japan, whereas *M. arenaria* (A2-J) was widespread from the Kyushu region to the Tohoku region (Narabu, 1995; Narabu & Harada, 1997; Orui, Nishi, & Matsuzawa, 1996). The distribution of *M. arenaria* (A2-J) overlaps with the cultivation area of eggplant, similar to that of *M. incognita*. However, to the best of our knowledge, no study has investigated the degree of resistance of *S. torvum* rootstock cultivars inoculated with *M. arenaria* (A2-J) populations. *M. arenaria* is one of the most variable species of the genus *Meloidogyne*. We consider that A2-J is not a typical *M. arenaria*. It is highly necessary to check the parasitism of A2-J, which inhabits widely in the cultivation area of eggplant, to *S. torvum* rootstock. Therefore, in this study, we inoculated *S. torvum* rootstock cultivars with *M. arenaria* (A2-J) populations to investigate whether *S. torvum* is resistant to *M. arenaria* (A2-J).

2 | MATERIALS AND METHODS

2.1 | Nematode species

Populations of *M. arenaria* and *M. incognita* were raised from one egg mass collected from each of the several regions of Japan (Table 1). The collection localities of the Gunma and Kumamoto populations of *M. arenaria* (A2-J) were geographically more than 850 km apart. Polymerase chain reaction–restriction fragment length polymorphism (PCR-RFLP) analysis of mtDNA was used for species identification (Orui, 1998; Powers & Harris, 1993). The primer set (C2F3/1108) amplified a 1.7-kb fragment from A2-J, whereas a 1.1-kb fragment was amplified from A2-O (Narabu, 2004; Narabu & Harada, 1997). Each nematode population was propagated on the tomato cultivar Kyouryoku-Beijyu, grown in pots (diameter 113 mm, depth 140 mm, ca. 1,000 m^3 soil), at a mean temperature of 25°C under greenhouse conditions. The egg masses were removed with tweezers from infected roots. Subsequently, the collected egg masses were incubated in a small volume of tap water and infective second-stage juveniles (J2) were collected from the suspension. The nematodes obtained were resuspended in a suitable volume of tap water and quantified by counting the number of nematodes in the aliquots of the sample under a light microscope.

2.2 | Plants

Plants used in the inoculation experiment included one *S. melongena* "Senryo 2gou," and rootstock cultivars *S. melongena* "Daitaro," *S. torvum* "Tonashimu," *S. torvum* "Torero" and *S. torvum* "Torvum Vigor". All seeds were purchased from a local supplier.

2.3 | Nematode infection assay

Seeds of eggplants and rootstock cultivars were planted in black polyethylene pots (diameter 9 cm, depth 7.6 cm, volume approximately 360 cm^3; Tokai Kasei Co., Ltd, Gifu, Japan) filled with horticultural soil (Nihon Hiryo Co., Ltd, Tokyo, Japan) and maintained at a mean temperature of 25–26.5°C for approximately 1 month. A glass pipette was used to inoculate each rootstock or eggplant cultivar at the rate of 500 or 1,000 J2 per pot. Subsequently, the pots were maintained at a mean temperature of 25–26.5°C for 60–75 days after inoculation. After removing the plants from the pots and rinsing the roots with water, the roots were stained with 0.02% phloxine B, and the number of egg masses on each root system was counted.

2.4 | Statistical analyses

Counts of egg masses were subjected to ANOVA and Tukey's HSD test using JMP 8 for Windows (SAS Institute).

3 | RESULTS

Seventy days after inoculation with 1,000 J2, many egg masses of the Saitama population of *M. arenaria* (A2-J) were observed on *S. torvum* "Tonashimu," whereas few egg masses of *M. incognita* were observed (Figure 1). When the number of egg masses on each root system was counted, although *M. incognita* produced only a few (under 1) egg masses on *S. torvum* "Tonashimu," a large number of egg masses were produced by the Saitama population of *M. arenaria* (A2-J) on *S. torvum* "Tonashimu". Either of the *Meloidogyne* species produced a

TABLE 1 Tested population of six *Meloiodgyne* spp. population

Species	Locality	Original host	Population
M. arenaria (A2-J)	Isesaki City in Gunma Pref.	*Amorphophallus konjac*	Gunma
M. arenaria (A2-J)	Fukaya City in Saitama Pref.	*Colocasia esculenta*	Saitama
M. arenaria (A2-J)	Matsue City in Shimane Pref.	*Glycine max*	Shimane
M. arenaria (A2-J)	Kikuyo Town in Kumamoto Pref.	*Colocasia esculenta*	Kumamoto
M. arenaria (A2-O)	Ohshima Town in Tokyo Pref.	*Bouvardia*	Izu-Ohshima
M. incognita	Kitakannbara Town in Nigata Pref.	*Solanum lycopersicum*	Nigata

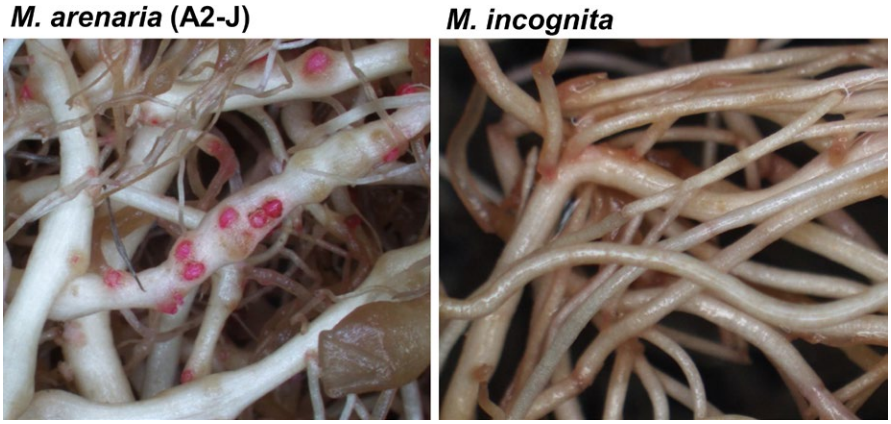

FIGURE 1 Tonashimu roots inoculated with *M. arenaria* (A2-J) and *M. incognita*. The root systems were inoculated with 1,000 J2 per pot. Egg masses were stained with phloxine B

TABLE 2 Number of egg masses produced by *Meloidogyne incognita* and *M. arenaria* (A2-J) (Saitama population) on *S. torvum* and *S. melongena*

Plant species	Cultivar	*M. incognita* Egg mass Mean ± *SE*	*M. arenaria* (A2-J) Egg mass Mean ± *SE*
S. torvum	Tonashimu	0.7 ± 0.7 c	201.7 ± 19.4 b
S. melongena	Senryo 2gou	380.7 ± 22.0 a	337.3 ± 6.4 a

Plants were cultivated for 60 days in a greenhouse after nematode inoculation.
Mean number of egg masses produced on root systems inoculated with 500 J2 per pot (n = 3).
Mean ± *SE* within a column followed by the same letters were not significantly different at $p < .05$ (Tukey's HSD test).

large number of egg masses on *S. melongena* "Senryo 2gou" (Table 2). *S. torvum* "Tonashimu" was susceptible to infection by the Saitama population of *M. arenaria* (A2-J), whereas it was resistant to *M. incognita*. Further, the Saitama population of *M. arenaria* (A2-J) produced a large number of egg masses on all three *S. torvum* rootstock cultivars (Tonashimu, Torero and Torvum Vigor) and on *S. melongena* "Daitaro." *M. arenaria* (A2-J) produced many egg masses on *S. melongena* "Senryo 2gou" (Table 3). Moreover, each of the three different geographical populations of *M. arenaria* (A2-J) produced many egg masses on *S. torvum* "Tonashimu." Several egg masses (<5) of *M. arenaria* (A2-O) were produced per root system in *S. torvum* "Tonashimu" (Table 4). When *S. torvum* "Tonashimu" was inoculated with *M. incognita*, 0–1 egg masses were produced per root system (Table 4). All infection experiments confirmed that *S. torvum* is resistant to *M. incognita* and *M. arenaria* (A2-O) populations, but susceptible to all four populations of *M. arenaria* (A2-J).

TABLE 3 Number of egg masses per root system of *M. arenaria* (A2-J) (Saitama population) on three *S. torvum* cultivars and two *S. melongena* cultivars

Plant species	Cultivar	Egg mass Mean ± *SE*
S. torvum	Tonashimu (n = 5)	108.6 ± 10.1 a
S. torvum	Torero (n = 5)	97.4 ± 13.0 a
S. torvum	Torvum Vigor (n = 5)	82.8 ± 15.0 a
S. melongena	Senryo 2gou (n = 3)	223.7 ± 2.9 b
S. melongena	Daitaro (n = 3)	61.3 ± 3.5 a

Plants were cultivated for 75 days in a greenhouse after nematode inoculation.
Mean number of egg masses produced on root systems inoculated with 500 J2 per pot (n = 3–5).
Mean ± *SE* within a column followed by the same letters were not significantly different at $p < .05$ (Tukey's HSD test).

TABLE 4 Number of egg masses per root system of five *Meloiodgyne* spp. populations on *S. torvum* "Tonashimu" rootstock

Nematode species	Nematode species	Egg mass Mean ± *SE*
M. arenaria (A2-J) (n = 6)	Gunma	204.8 ± 25.6 a
M. arenaria (A2-J) (n = 5)	Shimane	175.8 ± 25.8 a
M. arenaria (A2-J) (n = 6)	Kumamoto	136.3 ± 15.5 a
M. arenaria (A2-O (n = 5)	Izu-Ohshima	4.6 ± 1.2 b
M. incognita (n = 5)	Nigata	0.2 ± 0.2 b

Plants were cultivated for 70 days in a greenhouse after nematode inoculation.
Mean number of egg masses produced on root systems inoculated with 500 J2 per pot (n = 5–6).
Mean ± *SE* within a column followed by the same letters were not significantly different at $p < .05$ (Tukey's HSD test).

4 | DISCUSSION

Solanum torvum is used worldwide as rootstocks for eggplant cultivation, because of its resistance to the most serious soil-borne diseases, such as bacterial and fungal wilts (Gousset et al., 2005; Miceli et al., 2014). Several reports in Japan and abroad indicate that *S. torvum* is resistant to root-knot nematode (*Meloidogyne* spp.) (Ali et al., 1992; Boiteux & Charchar, 1996; Daunay & Dalmasso, 1985; Dhivya et al., 2014; Gonzalez et al., 2010; Hara et al., 1983; Ryu, 2012; Shetty & Reddy, 1985). In addition, our previous study showed that *S. torvum*

is resistant to *M. incognita* in Japan (Uehara et al., 2016). Moreover, *S. torvum* is resistant to *M. arenaria* in areas outside Japan (Daunay & Dalmasso, 1985; Gonzalez et al., 2010; Ryu, 2012). Two genotypes of *M. arenaria* (A2-O and A2-J) occur in Japan (Narabu, 2004; Narabu & Harada, 1997). The present study confirmed that *S. torvum* is resistant to *M. arenaria* (A2-O), but susceptible to *M. arenaria* (A2-J) in Japan. Although esterase phenotypes of both types of *M. arenaria* (A2-O and A2-J) is the two-isozyme (A2) phenotype, they were distinguished from each other based on the size of the amplified PCR products of mtDNA region and perineal patterns (Narabu & Harada, 1997). A 1.1-kb product is amplified for typical *M. arenaria* using the primer set C2F3/1108 (Blok & Powers, 2009; Powers & Harris, 1993; Williamson, Caswell-Chen, Wu, & Hanson, 1994). A2-O exhibited perineal patterns typical of *M. arenaria* and a 1.1-kb PCR product. A2-J had *M. javanica*-like perineal patterns and a 1.7-kb product (Narabu, 2004; Narabu & Harada, 1997; Orui, 1998). Blok, Wishart, Fargette, Berthier, and Phillips (2002) reported that two size classes of products, 1.7 and 1.1 kb, were produced by *M. arenaria* isolates. Further, a 1.7-kb amplicon was produced by the same primer set in the Korean *M. arenaria* populations (Oh et al., 2009). Based on various morphological features, Narabu (2004) suggested that A2-O occurring in Japan is the typical *M. arenaria*, whereas A2-J is similar to *M. arenaria* of East Asia (description by Rammah and Hirscman (1993). According to Rammah and Hirscman (1993), *M. arenaria* is one of the most variable species of the genus *Meloidogyne*, with complex morphology, host response, cytology and biochemistry. Consistent with the previous findings mentioned above, we consider that A2-J is not a typical *M. arenaria*; however, it is a member of the *M. arenaria* species complex.

In agricultural practice, nematodes are controlled by crop rotation and using nematicides and resistant plants. Non-chemical management strategies for enhancing root-knot nematode resistance in host plants are becoming increasingly crucial in agriculture for maximizing productivity. The results of the present study indicated that *S. torvum* is susceptible to *M. arenaria* (A2-J) infection. We consider that the use of *S. torvum* rootstocks for eggplant cultivation is not effective for the controlling *M. arenaria* (A2-J) populations. *M. arenaria* (A2-J), *M. arenaria* (A2-O) and *M. incognita* in Japan can be easily distinguished from each other by PCR-RFLP analysis. The success of nematode management programmes depends on accurate identification of nematodes. The present study demonstrates the need of accurate identification for selecting resistant rootstocks and applying nematicides.

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