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REVIEW

Suppression of Root-knot Nematode Damage to Next Crop by Prior Cultivation of Root-knot Nematode-resistant Sweet Potato Cultivars

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Abstract

Sweet potato (*Ipomoea batatas* (L.) Lam.) is a major crop in Japan and worldwide. The sweet potato cultivar 'Koganesengan' is susceptible to damage by the southern root-knot nematode *Meloidogyne incognita* in Japan. We investigated the effects of cropping new resistant cultivars on the suppression of nematode population density and subsequent damage to the succeeding 'Koganesengan' crops. 'Koganesengan' was cropped with two resistant cultivars ('Daichinoyume' and 'Konamizuki'). The tuberous roots of 'Daichinoyume' and 'Konamizuki' were seldom damaged, whereas 'Koganesengan' was heavily damaged. In the next spring, the nematode population density in the plow layer soil (10 cm-15 cm) was lower after 'Daichinoyume' and 'Konamizuki' cropping than after 'Koganesengan' cropping. Nematode damage to 'Koganesengan' tuberous roots after 'Daichinoyume' and 'Konamizuki' cropping was slightly suppressed compared to that after 'Koganesengan' cropping. Cropping of these cultivars is an effective method of suppressing nematode density and reducing damage to sweet potatoes. By clarifying the capability of resistant cultivars even overseas, it will be possible to use sweet potato as a nematode-suppressive crop.

Discipline: Agricultural Environment
Additional key words: cropping systems, *Ipomoea batatas*, *Meloidogyne incognita*, resistance, varieties

Introduction

Plant-parasitic nematodes are important pests for most of the world's crops. Estimates of crop loss usually range from 5% to 15%, but higher losses sometimes occur, and there are situations where nematodes are a major factor limiting the production of a particular crop (Stirling 2014). Root-knot nematodes (*Meloidogyne* spp.) are widespread and economically important plant parasitic nematodes with a worldwide distribution. *Meloidogyne incognita* is one of the major three tropical important species (Moens et al. 2009). In warm Japanese upland farming areas, *M. incognita* damages many crops, including important root vegetables such as sweet potato, carrot, and Japanese radish.

Sweet potato (*Ipomoea batatas*) is one of the world's most important crops and a major summer crop in Japanese upland farming. In 2015, the area of sweet potato cropping in Japan totaled 36,600 ha (Ministry of Agriculture, Forestry and Fisheries 2018a). Japan's main sweet potato producing area is the southern part of Kyushu (Miyazaki and Kagoshima prefectures), with a cropping area of 15,840 ha in 2015 (Ministry of Agriculture, Forestry and Fisheries 2018a). In sweet potato fields in the central and southern parts of Kyushu, root-knot nematodes were detected in almost all the fields, with 96% of the nematodes identified as *M. incognita* (Iwahori et al. 2000). The damage caused by root-knot nematodes includes a lower yield and degraded external appearance of the tuberous roots of sweet potatoes.

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Sweet potato is generally a suitable host for *M. incognita,* but resistance differs significantly between cultivars. Nematode resistance has been evaluated worldwide in various ways. The resistance does not necessarily mean that nematode propagation is suppressed. As the fluctuation in nematode densities in the soil has not always been evaluated, in many cases, the resistance is assessed by the investigation of plants. Actually, Cervantes-Flores et al. (2002a, 2002b) evaluated it by root necrosis, root galling, egg masses or eggs. Piedra-Buena et al. (2011) evaluated it by root galls. In Japan, Shibuya (1952) reported differences in nematode infection in sweet potato cultivars after the end of World War II. Field experiments were conducted from 1943 to 1953 on the varietal susceptibility differences of sweet potatoes to the root-knot nematode *M. incognita* by plant observation (e.g., root gall and female adults within roots) (Kondo et al. 1972). Some resistant cultivars suppress nematode propagation, and growing these cultivars can consequently reduce nematode population density (Kondo 1972, Inagaki & Momota 1983, Tabuchi & Sakamoto 1983, Ueda et al. 1986). Nematode damage to sweet potato was suppressed by the prior cultivation of resistant cultivars (Inagaki & Momota 1983, Fukunaga & Iwahori 2002, Suzuki et al. 2012). However, these previous studies did not account for the concept of nematode races, defined by their different pathogenicity to each sweet potato cultivar (as described below).

This review focuses on introducing sweet potato resistant cultivars as nematode-suppressive crops. First, we conducted an overview of the suppression of root-knot nematode damage to 'Koganesengan,' an important sweet potato cultivar for *shochu* production in Japan. Second, the cropping of nematode-resistant cultivars preceding the cropping of 'Koganesengan' is introduced as a useful technique for nematode suppression and the reduction of nematode damage to 'Koganesengan.' Third, we assess the future prospects for nematode control.

Root-knot nematode damage to 'Koganesengan' and actual control

As elsewhere in the world, sweet potato is cultivated in Japan for many purposes, such as for table use, *shochu* (a Japanese distilled spirit) and starch production, and food processing. Two cultivars—'Koganesengan' (mainly cultivated for *shochu* production) and 'Kokei-No.14' (mainly cultivated for table use)—are susceptible to *M. incognita* and suffer from nematode damage. However, these cultivars are largely cropped in the southern part of Kyushu, due to the high demand for their excellent traits for use. In 2015, the cultivation area of 'Koganesengan' totaled 7,389 ha, whereas that of 'Kokei-No.14' totaled 2,205 ha (Ministry of Agriculture, Forestry and Fisheries 2018a).

At the breeding stage, 'Koganesengan' was evaluated as slightly susceptible (Kumagai et al. 2002, Ishiguro et al. 2003, Katayama et al. 2004) to intermediate (Ide et al. 1982), whereas 'Kokei-No.14' was evaluated as susceptible (Ide et al. 1982) to slightly susceptible (Ishiguro et al. 2003, Kai et al. 2010). However, these reports did not directly evaluate nematode propagation and the damage to tuberous roots.

Nematode density was slightly lower or almost the same in 'Koganesengan' cultivation as compared to that in 'Kokei-No.14' cultivation, with a high population density recorded for both cultivars (Tabuchi & Sakamoto 1983, Torigoe 1996, Suzuki & Adachi 2008).

Araki et al. (1983) compared the damage to these two cultivars and found that more cracks and browning were caused in 'Koganesengan,' although the appearance of this cultivar was better than that of 'Kokei-No.14. The damage from nematodes is expected to be slightly less severe in 'Koganesengan' than in 'Kokei-No.14,' presumably due to the results mentioned above and in our field experiment (Suzuki & Adachi 2008). We also assessed this damage using a pot experiment, in which nematode population density could be controlled (Suzuki 2012). The relationship between nematode density in the rose balsam plant assay and the damage to tuberous roots was evaluated. The nematode density and nematode damage to tuberous roots in 'Kokei-No.14' and 'Koganesengan' were positively correlated (Fig. 1). The intercept of this linear equation was approximately zero. The inclination of the equation was smaller in 'Koganesengan' than in 'Kokei-No.14.' This result demonstrates that nematode damage to tuberous roots is less severe in 'Koganesengan' than in 'Kokei-No.14,' although there is some damage.

Perfect nematode control is required for table use cultivars in Japan, as desirable appearance attributes lead directly to a high product price in markets (Ueda 1995). However, the importance of nematode control does not differ considerably in 'Koganesengan' for products used in *shochu* production, despite not being consumed directly and with less severe damage. The nematode causes vertical cracks and abnormal shape that often hold soil on tuberous roots, in addition to a lower tuberous root yield. The parts that hold soil need to be trimmed before *shochu* production, thereby increasing the time required for processing. Therefore, nematode control is necessary to some extent in the cultivation of 'Koganesengan.'

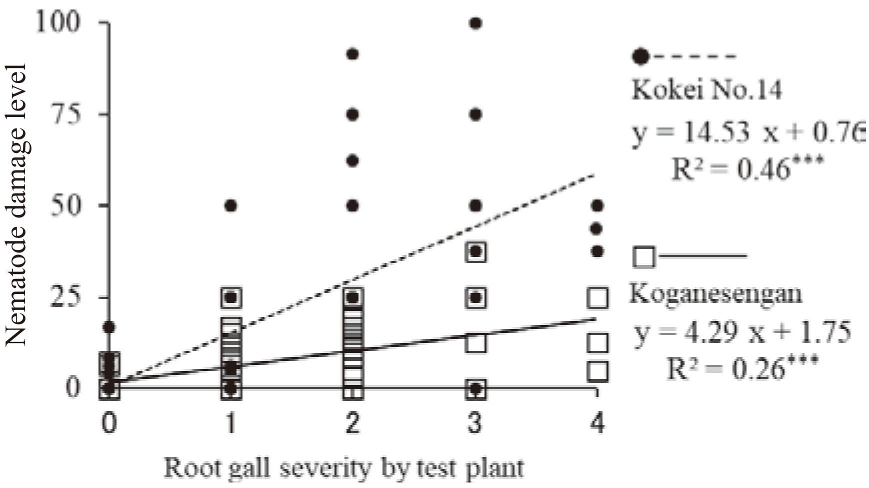

Fig. 1. Relationships between the severities of root gall in the rose balsam assay and damage to the tuberous roots of 'Kokei-No.14' and 'Koganesengan'
***: $P < 0.001$

For 'Koganesengan' production, nematode management largely depends on nematicide, a relatively low cost substance that is easy to apply. Although fumigants are often used, there had been a recent increase in the use of granules, which are applied just before planting and have benefits when the fallow period is short. In recent years, many kinds of granule nematicides have become commercially available in Japan. Fukuda & Hayashikawa (2016) reported the effects of some granule nematicides. However, the dependence on nematicide for nematode management causes some problems in farming. Although reducing costs is important for 'Koganesengan' production, and many attempts (e.g., before planting, planting, harvesting) have been made to do so (Tobimatsu 2010), the cost of nematicide application accounts for a large proportion of the expenses, and may also increase in the future. The total production cost of sweet potato was calculated in 2015 at 138,091 yen/10a (Ministry of Agriculture, Forestry and Fisheries 2018a), 54% of which accounts for the cost of labor; however, it should be noted that this was a trial calculation for sweet potato production for starch rather than *shochu*. The cost of the nematicide fosthiazate (1.5%) is 14,356 yen/10a (Ministry of Agriculture, Forestry and Fisheries 2018b: average price when applied at 20 kg/10a). This corresponds to more than 10% of the total production cost (in case the total production costs of sweet potato for starch and *shochu* production are the same). Moreover, chemical control treatment is usually required every season to maintain low nematode density. Increases in decomposition caused by the continuous use of nematicides have also been reported (Chung et al. 1999, Karpouzas et al. 2004, Osborn et al. 2009). This may reduce the controlling effect of nematicides. Given these situations, studies on alternative nematode control methods are required. Moreover, avoiding the use of unnecessary chemicals maintains the sustainability of agricultural environments.

One alternative nematode control method is the introduction of nematode-suppressive crops. Some crops are known to have nematode-suppressive effects in Japan, such as crotalaria (Kitagami et al. 1992) and hybrid sorghum (*Sorghum bicolor* × *Sorghum sudanense*) (Yamada et al. 2000). Cultivated as green manure, these crops are effective for improving the soil, but are not profitable. As the southern part of Kyushu is a vast feed production area, guinea grass (*Panicum maximum*) (Araki et al. 1991, Tateishi et al. 2003) can also be proposed as a nematode-suppressive forage crop. However, sweet potato farmers tend to lack the equipment necessary for feed production. Consequently, these nematode-suppressive crops have not been put to practical use.

Some resistant sweet potato cultivars have a nematode-suppressive effect (as described above and later). Therefore, cultivar rotation using these nematode-suppressive sweet potato cultivars and 'Koganesengan' would solve the aforementioned problems. Nematode-suppressive cultivars for starch production have recently been developed. Sweet potatoes for *shochu* and starch production are cultivated in the southern part of Kyushu; thus, combining these cultivations is an easy adaptation for farmers.

Suppression effects on nematode population density caused by cropping newly bred *M. incognita*-resistant sweet potato cultivars and reducing damage to succeeding 'Koganesengan' crops

Here, we investigate the suppression effects on the nematode population density caused by the cropping of newly bred resistant cultivars and reducing the damage to succeeding 'Koganesengan' crops in the southern part of Kyushu.

M. incognita has many races (Sano & Iwahori 2005, Tabuchi et al. 2017) that are identified based on their differing pathogenicity to several sweet potato cultivars. This has been investigated in Japanese cultivars (Sano et al. 2002, Tabuchi et al. 2015). SP2 is a dominant race in Miyazaki and Kagoshima prefectures in the southern area of Kyushu (Sano & Iwahori 2005). Some new cultivars have recently been found to exhibit a strong resistance to SP2 by evaluating the number of egg masses (Tabuchi et al. 2015). The cultivation of such SP2-resistant cultivars could suppress the nematode population in this area. Therefore, fluctuations in nematode population density and damage to the succeeding crop were investigated in an SP2 infested field (Suzuki et al. 2017).

Two SP2-resistant cultivars ('Daichinoyume' and 'Konamizuki') and one susceptible cultivar ('Koganesengan') were cropped. 'Murasakimasari,' another SP2 susceptible cultivar (Sano et al. 2002), was cropped at the same time. Custom plots of 'Koganesengan' with nematicide (1,3-dichloropropene) application every year ('Koganesengan + N') were also created. The field used for the experiment was located at the Kyushu Okinawa Agricultural Research Center, Miyakonojo, Miyazaki, Japan. The soil type was Andosol and the distinction results of inhabited *M. incognita* populations coincide with the reaction of SP2. Prior to sweet potato cultivation, the nematodes were extracted using the Baermann funnel method and population density was investigated.

The numbers of second-stage root-knot nematode juveniles were approximately the same between 'Koganesengan' and the other treatments (Table 1). Vine cuttings of each cultivar were planted in the spring. In the fall, the plants were uprooted and the damage was evaluated. The tuberous roots of 'Daichinoyume,' 'Konamizuki,' and 'Murasakimasari' were seldom damaged, whereas 'Koganesengan' was heavily damaged (Table 2). The tuberous roots of 'Koganesengan + N' were slightly damaged; thus, the weight of non-damaged and marketable grade tuberous roots was higher in 'Koganesengan + N' than in 'Koganesengan' (Table 2). The root gall indexes were lower in 'Daichinoyume,' 'Konamizuki,' 'Murasakimasari,' and 'Koganesengan + N' than in 'Koganesengan' (Table 2).

In the next spring, the nematode population density in the plow layer soil (10 cm-15 cm) was lower after the cropping of 'Daichinoyume' and 'Konamizuki' than after that of 'Koganesengan' (Table 1). The pattern of nematode density in the subsoil (25 cm-35 cm) was similar to that in the plow layer soil, although the overall nematode density was considerably higher in the subsoil than in the plow layer soil (Table 1). The densities in

Table 1. Effects of cropping on the numbers of root-knot nematode second-stage juveniles[1]

Treatments (n = 3)	Sampling date and depth (cm)			
	On March 17 in 2011		On March 12 or 13 in 2012	
	10-15	30-35	10-15	25-35
Daichinoyume	61 ± 30 NS	42 ± 17 NS	0 ± 0 *	14 ± 9 *
Konamizuki	60 ± 13 NS	25 ± 9 NS	0 ± 0 *	25 ± 20 NS
Murasakimasari	54 ± 45 NS	21 ± 15 NS	32 ± 9 NS	96 ± 81 NS
Koganesengan+N[2]	47 ± 20 NS	42 ± 15 NS	20 ± 11 NS	61 ± 32 NS
Koganesengan	76 ± 52	34 ± 19	29 ± 12	104 ± 31

The values are the mean ± standard deviation.
*Significant difference from the treatment of 'Koganesengan' on each date and at each depth (Dunnett's test, $P < 0.05$); NS: not significant. Data were statistically analyzed after $\log_e (X + 0.5)$ transformation.
[1] The number of juveniles per 20 g of soil.
[2] Nematicide treatment.
Reprint of Suzuki et al. (2017), courtesy of the editor-in-chief of *Nematological Research*.

both soils were approximately the same after the cropping of 'Murasakimasari' and 'Koganesengan + N' as compared with after the cropping of 'Koganesengan' (Table 1).

Then vine cuttings of 'Koganesengan' were planted in all plots and the damage was evaluated. The weight of non-damaged 'Koganesengan' tuberous roots after the cropping of 'Daichinoyume' was significantly higher than that of 'Koganesengan' (Table 3). Root gall indexes after the cropping of 'Daichinoyume' and 'Konamizuki' were significantly lower than that of 'Koganesengan' (Table 3). As a result, the nematode damage to 'Koganesengan' after the cropping of 'Daichinoyume' and 'Konamizuki' was slightly suppressed as compared with that following the cropping of 'Koganesengan' (Fig. 2).

The prior cropping of 'Daichinoyume' and 'Konamizuki' is therefore an effective method of suppressing nematode density and reducing nematode damage in sweet potatoes, without the use of soil fumigants or other nematicides.

Table 2. Effects of the cultivars and nematicide treatment on the damage to sweet potatoes caused by root-knot nematodes

Treatments (n = 3)	Weight of each grade of tuberous roots (g/m^2)			Root gall index[1]
	Non-damaged	Marketable	Total	(0-100)
Daichinoyume	2,430 ± 84 NA	2,461 ± 36 NA	2,472 ± 55 NA	13 ± 6 *
Konamizuki	2,912 ± 312 NA	2,912 ± 312 NA	2,912 ± 312 NA	14 ± 9 *
Murasakimasari	1,765 ± 178 NA	1,765 ± 178 NA	1,765 ± 178 NA	19 ± 4 *
Koganesengan+N[2]	2,029 ± 440 *	2,725 ± 458 *	2,825 ± 560 NS	59 ± 7 *
Koganesengan	357 ± 42	1,432 ± 185	2,404 ± 181	81 ± 7

The values are the mean ± standard deviation.
* Significant difference from the treatment of 'Koganesengan' ($P < 0.05$); NS: not significant; Welch's t-test was applied for the weights of non-damaged tuberous roots, Student's t-test was used for the weights of marketable and total tuberous roots, and Dunnett's test was utilized for the root gall indexes; NA: data were not statistically analyzed.
[1] Data were statistically analyzed after arcsine transformation.
[2] Nematicide treatment.
Reprint of Suzuki et al. (2017), courtesy of the editor-in-chief of *Nematological Research*.

Table 3. Effects of preceding cropping at the site on root-knot nematode damage to 'Koganesengan'

Treatments (Preceding cropping) (n = 3)	Weight of each grade of tuberous roots (g/m^2)			Root gall index[1]
	Non-damaged	Marketable	Total	(0-100)
Daichinoyume	2,746 ± 251 *	2,914 ± 40 NS	3,022 ± 140 NS	36 ± 4 *
Konamizuki	2,134 ± 187 NS	2,454 ± 78 NS	2,713 ± 140 NS	39 ± 14 *
Murasakimasari	1,249 ± 584 NS	1,929 ± 711 NS	2,346 ± 570 NS	60 ± 13 NS
Koganesengan+N[2]	2,574 ± 771 NS	2,870 ± 481 NS	2,947 ± 386 NS	47 ± 3 NS
Koganesengan	1,380 ± 533	2,315 ± 469	2,831 ± 172	63 ± 4

The values are the mean ± standard deviation.
* Significant difference from the treatment 'Koganesengan' in each treatment ($P < 0.05$); NS: not significant; Dunnett's test was applied for the weights of non-damaged and total tuberous roots, and root gall indexes; Dunnett's T3 test was used for the weights of marketable tuberous roots.
[1] Data were statistically analyzed after arcsine transformation.
[2] Nematicide treatment.
Reprint of Suzuki et al. (2017), courtesy of the editor-in-chief of *Nematological Research*.

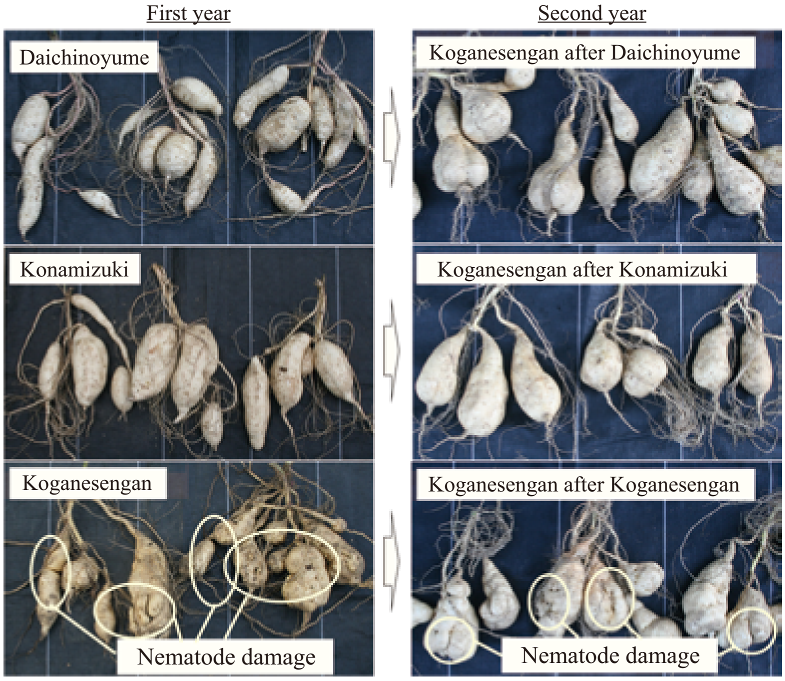

Fig. 2. Root-knot nematode damage to the tuberous roots of 'Koganesengan' after cropping of each cultivar

Future prospects for nematode control

One of the major problems in the worldwide production of sweet potatoes is the damage caused by plant-parasitic nematodes (Jatala 1991). Even in recent years, *M. incognita* has damaged sweet potato, including in such developing countries as Indonesia (Tuminem et al. 2015). In Japan, the nematode control strategy for sweet potato cropping has not changed over the last few decades, but some alternatives have been tested, such as soil solarization (Niimi et al. 2005) and *Pasteuria* application (Tateishi 1998, Tateishi et al. 2007). However, nematode control largely depends on chemical control methods, whereas cultural control methods are not commonly used, according to a survey conducted in 2012 (Mizukubo 2017). And in a questionnaire survey by Abe (2016), 55% of farmers responded that they would still use a nematicide even if the results of nematode diagnosis suggested no need for nematicides. These studies reflect the difficulty of changing a sweet potato production system dependent on chemical control in Japan; nevertheless, a new nematode control system might be required by farmers in other countries, such as small-scale farmers in Africa who feel that nematicides are too expensive (Onkendi et al. 2014). Regardless, the potential of the nematode-suppressive cultivar is the same in these developing countries.

A high demand for nematode-suppressive cultivars will be beneficial for the profitability and sustainability of practical cropping systems. 'Daichinoyume' (Katayama et al. 2004) and 'Konamizuki' (Katayama et al. 2011) are relatively new sweet potato cultivars for starch production, which earn income for farmers. 'Daichinoyume' is a recommended cultivar in Kagoshima Prefecture (Ministry of Agriculture, Forestry and Fisheries 2018a) and was grown on 325 ha in 2015. 'Konamizuki' contains starch that is gelatinized at low temperature and has highly desirable properties as a food material for starchy products (Tokimura et al. 2017). In Japan, nematode-suppressive sweet potato cultivars are not yet in high commercial demand. 'Shiroyutaka' (registered in 1985) is still the main cultivar used for starch production. It was cultivated on 3,518 ha in 2015 (Ministry of Agriculture Forestry and Fisheries 2018a), and propagates the nematode SP2 (Sano et al. 2002). By developing nematode-suppressive resistant cultivars that have practical characteristics comparable to those of 'Shiroyutaka,' such cultivars could easily replace 'Shiroyutaka' and thereby result in nematode suppression by resistant cultivars in the southern part of Kyushu.

The suggested nematode management strategy must still consider several factors, such as the differences in the races of *M. incognita* in different areas of Japan. The dominant races in the field are only reported in Kyushu (Sano & Iwahori 2005). In Kyushu, the dominant race varies in each area. In the sweet potato breeding program, most cultivars that have been recently registered have a strong resistance to root-knot nematodes (Katayama et al. 2017). However, this does not necessarily mean that all nematode races are suppressed by these resistant cultivars. It has been shown that cultivars whose nematode resistance is evaluated as "strong" or "slightly strong" may propagate some nematodes (Sano et al. 2002). In our study, no damage occurred in the tuberous roots of 'Murasakimasari,' but the population density increased to the same level as that of 'Koganesengan.' 'Murasakimasari' is regarded as resistant to root-knot nematodes (Kumagai et al. 2002) during the breeding stage, but has been determined to be susceptible to SP2 (Sano et al. 2002). Breeding a multi-race-resistant line is an important goal in this regard (Okada et al. 2017). Although nematode reproduction can be estimated by root galls because a strong correlation is observed between root galling severity and the number of nematode eggs (Cervantes-Flores et al. 2002a, Karuri et al. 2017), clarifying the nematode-suppressive effect of each line under field conditions is also ultimately required.

Nematodes survive in the subsoil after these suppressive cultivars have been cropped, which is important to note for nematode management, although this is a common problem with many nematode control methods relative to fumigation and nematode-suppressive crops. If the nematode propagates during the nematode-susceptible crop growth period, the nematode density during autumn would consequently be high. And if deep root crops such as burdock and Chinese yam are cultivated, these crops would run the risk of nematode damage. This suggests that nematode control must be undertaken every year, which poses an obstacle to increasing the profitability of a practical cropping system. A good choice to address this concern is the cultivation of a nematode-tolerant crop after a nematode-suppressive crop. For example, combining the cropping of nematode-tolerant cultivar 'Beniharuka' and nematode-susceptible cultivar 'Beniazuma' after the introduction of antagonistic plant guinea grass has been proposed (Chigira et al. 2013).

We have outlined a method of optimizing nematode control for the sweet potato 'Koganesengan' cultivar as an example of nematode control by preceding the cropping of nematode-suppressive sweet potato cultivars. By clarifying the nematode-suppressive capability of resistant cultivars even overseas, it will be possible to use sweet potato as a nematode-suppressive crop. For the optimization of nematode control, however, we developed and implemented individual nematode control techniques as an integrated pest management system. And the damage threshold for 'Koganesengan' has not been suggested, as it is complicated by such factors as cropping type (Suzuki et al. 2013). It is thus necessary to clarify the factors in production that could affect the damage. Moreover, the control of other pests (e.g., root-lesion nematodes, weevils, beetles) remains a difficult task. Therefore, a wider range of pest control methods adaptable for farmers must also be established.

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