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Expression of resistance to the root-knot nematodes, *Meloidogyne hapla* and *M. fallax*, in wild *Solanum* spp. under field conditions

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Abstract

In 1995 two fields in the Netherlands, naturally infested with *Meloidogyne hapla* (Wageningen) and *M. fallax* (Baexem), were used to evaluate resistant and susceptible *Solanum* genotypes under natural conditions. In April, genotypes were planted in circular microplots. Soil samples were taken and analyzed for the occurrence of second-stage juveniles every six weeks. From August onwards, large differences between resistant and susceptible genotypes in numbers of juveniles were found in the soil. For all resistant wild *Solanum* genotypes the level of infection in soil at the end of the growing season in October was equal to or lower than at the beginning. Glasshouse experiments were performed with the same genotypes and nematode populations (i.e. originally derived from these fields) and the results were comparable with the observations from the field. It is concluded that resistance, as selected in glasshouse trials, corresponds well with resistant behaviour in the field and that it is worthwhile to transfer the resistance from these *Solanum* sources to commercial potato cultivars for successful control of root-knot nematodes.

Introduction

In North-Western Europe root-knot nematodes, *Meloidogyne* spp., are expected to become a serious pest in agriculture. For potato, *M. hapla* Chitwood and *M. chitwoodi* Golden, O'Bannon, Santo and Finley are the predominant *Meloidogyne* species and can cause severe economic losses in terms of yield reduction and quality damage of tubers. Both species cause necrotic spots inside the tubers and, especially *M. chitwoodi*, gall formations visible on the outside of the tubers. In the Netherlands, a deviant type of *M. chitwoodi* has been characterized by its isozyme pattern and preliminary differences in host range (van Meggelen et al., 1994) and, very recently, this deviant type has been described as a new *Meloidogyne* species, *M. fallax* (Karssen, 1996). However *M. fallax* and *M. chitwoodi* are thought to be genetically closely related (Janssen et al., 1996) and *M. fallax* causes similar symptoms of infection on potato as *M. chitwoodi*.

Resistance to root-knot nematodes would be very effective against these pests, but has been shown to be lacking in currently used cultivars (Brown et al., 1994; Janssen et al., 1995). In recent years various *Solanum* species resistant to *Meloidogyne* spp. have been identified. In the USA research has been focused on resistance to *M. chitwoodi* races 1 and 2 and *M. hapla* and highly resistant genotypes of *S. bulbocastanum* and *S. hougasii* were selected (Brown et al., 1989, 1991). Races 1 and 2 of *M. chitwoodi* are distinguished by means of their differential reproductivity on carrot and lucerne (Santo and Pinkerton, 1985). In the Netherlands, screening trials in glasshouses have been performed with *M. chitwoodi, M. fallax* and *M. hapla* and have revealed numerous resistant *Solanum* species (Janssen et al., 1996). The populations of *M. chitwoodi* used for these screening trials resemble the

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originally described *M. chitwoodi* (race 1) (Golden et al., 1980). As a selection criterion for resistance an arbitrary chosen maximum number of 5 egg masses, representing 1% successful reproduction of the total number of inoculated juveniles, was used (Janssen et al., 1996).

To validate whether such resistance is effective under natural circumstances it is necessary to evaluate susceptibility and resistance in the field. Additionally, a field experiment will not only indicate whether the resistance selected in the glasshouse is effective under field cropping conditions, but growing plants in naturally infested soil will allow prolonged exposure of plants to the nematodes and demonstrate the effect of possible multiple generations during a growing season. This report describes the evaluation of wild *Solanum* genotypes, resistant to *M. hapla* or *M. fallax*, in naturally infested fields and compares the results with those from glasshouse experiments.

Materials and methods

Plant material

Extensive resistance screening trials in the glasshouse had revealed various *Solanum* species with resistance to *M. hapla, M. chitwoodi* and/or *M. fallax* (Janssen et al., 1995, 1996). For evaluation in the field *Solanum chacoense* 93-68-11, *S. gourlayi* 93-94-8, *S. hougasii* 93-71-5, *S. sparsipilum* 93-107-1 and the hybrid genotype *S. chacoense* × *S. tuberosum* 87-206-6 were selected for their resistance to *M. hapla*, while *S. sparsipilum* 93-107-8 was included as a susceptible wild genotype. For *M. fallax* the genotypes *S. fendleri* 93-114-12, *S. chacoense* 93-113-1, *S. bulbocastanum* 93-60-2, *S. stoloniferum* 93-STOL-4 were considered resistant and genotype *S. chacoense* 93-68-6 susceptible (Janssen et al., 1996). All tubers of selected and tested genotypes were obtained by growing plants under short day conditions in a glasshouse. Seed tubers of the cvs Nicola and Darwina, susceptible to *Meloidogyne* spp., were multiplied in a *Meloidogyne*-free field. All tubers were stored at 5 °C before use from March to September 1995.

Field experiments

Two fields in Wageningen and Baexem, both situated in the Netherlands and naturally infested with *M. hapla* and *M. fallax* respectively, were prepared for use in 1995. In Wageningen the first indication of infestation with *M. hapla* occurred in 1990 in a caraway crop. The following crops were wheat (1991), sugar beet (1992), potato (1993) and hemp (1994). In Baexem two successive years (1990 and 1991) of cultivation of evening primrose gave rise to a high infestation of *M. fallax*, although at that time it was still classified as *M. chitwoodi*. The following crops were black salsify (1992), sugar beet or potato (1993) and sugar beet (1994). Both fields consisted of sandy soil with approximately 2.9 and 1.9% organic matter, and a pH of 5.4 and 5.9 for Wageningen and Baexem respectively.

In April 1995 circular plastic containers (56 cm diameter × 35 cm deep) with no bottom were buried in the soil with a distance of 1.5 m between the centres of adjoining containers. The containers were used to prevent the growth of roots and stolons into neighbouring microplots. Genotypes were assigned to containers in four completely randomized complete blocks, in which each genotype was represented by three containers. Tubers were planted in pots in the glasshouse approximately three weeks before transplanting. Well-growing plants were selected and transplanted to the fields in Baexem and Wageningen on 21 and 24 April respectively. To avoid possible damage by night-frost, plants were twice covered with plastic for a few days during May. Weeds were regularly removed inside the containers and plants were protected against late blight, *Phytophthora infestans*, with commonly used agrochemicals following the suppliers' recommendations. Tubers, if present, were harvested after the last soil sampling and both field experiments were terminated in October 1995.

Soil samples for nematode assays were taken approximately every 6 weeks by sampling randomly 5 soil cores (1 cm diameter × 30 cm deep) from each container, starting before planting on 4 April. Soil from the three containers with the same genotype within the block were treated as one sample for analysis. To analyze the number of active juveniles in the soil two sub-samples of 100 cm^3 soil were taken and juveniles were extracted from the soil using an Oostenbrink elutriator (s'Jacob and van Bezooijen, 1984). The nematodes were allowed to move from a cotton filter into a water layer overnight and the numbers of *Meloidogyne* juveniles in the suspension were counted. At the beginning and end of the experiment 20 additional cores per container were taken to perform a bio-assay with lettuce (Zondervan and Huiskamp, 1987). For this essay, four-week-old lettuce plants (cv Norden) were transplanted in plastic pots, contain-

ing a sub-sample of 400 cm^3 soil. Each soil sample was represented in four replications and pots were randomly placed in a temperature-controlled glasshouse (18±2 °C). After five weeks the number of galls on the roots was counted and adjusted to numbers of infectious nematodes per 100 cm^3 soil.

For the statistical analysis square root transformation was used to obtain normal distribution of variance. The sampling dates and *Meloidogyne* spp. were separately analyzed with ANOVA using Genstat (Payne et al., 1987).

Glasshouse tests

Second-stage juveniles of *M. fallax* and *M. hapla*, extracted from infested soil taken from the fields in Baexem and Wageningen respectively, were maintained on tomato plants (Janssen et al., 1995). To prepare inoculum, eggs were harvested from the roots by dissolving egg masses with 0.5% NaOCl-solution (Hussey and Barker, 1973). Juveniles were hatched in water and stored at 4 °C up to one month until use as inoculum.

Tubers were planted in clay pots of 350 cm^3, filled with moist silver sand and slow release NPK fertilizer ('Osmocote', Sierra Chemical Company, Milpitas, USA). Pots were randomly placed in a temperature-controlled glasshouse (22 ± 2 °C). Inoculation with *M. fallax* or *M. hapla* followed two weeks after planting by supplying a water suspension of approximately 400 juveniles with an automatic syringe. Each genotype was tested in 16 replications. Eight weeks after inoculation egg masses on the roots were counted in eight of the replicates. The roots of the other eight were analyzed for the total number of eggs produced using 1.0% NaOCl-solution (Hussey and Barker, 1973). Each *Meloidogyne* species was treated as a separate experiment for the analysis of variance after square root transformation of the data. The experiment was carried out from September to December 1995.

Results

Resistance to *M. hapla* and *M. fallax* in the various wild *Solanum* genotypes was clearly expressed in the field. The number of juveniles in the soil was found to have increased significantly in the soil around the susceptible genotypes from August onwards in both the field in Wageningen (Figure 1) and in Baexem (Figure 2). The actual start of a new generation of juveniles is likely to have occurred some weeks earlier, but could not be visualised due to the fairly wide intervals between the chosen sampling dates. The vigour and duration of growth varied between *Solanum* genotypes, but it did not have a major effect on the final level of infection, as is shown with the susceptible wild genotypes and commercial cultivars in both fields. Figures 1 and 2 show that the numbers of juveniles in the soil around resistant genotypes did not increase or even decreased over time for most selected resistant genotypes.

The reproductive factor (RF = final population/initial population) (Oostenbrink, 1966) was analyzed and the results are in Tables 1 and 2 for *M. hapla* and *M. fallax* respectively. Of the resistant genotypes only *S. sparsipilum* 93-107-1 in Wageningen showed a slight but not significant increase in number of juveniles in October. For all other resistant genotypes the number of juveniles did not reach the infection level of the beginning of the season. It was noteworthy that *S. chacoense* 93-68-11 and to a lesser extent the hybrid 87-206-6 grew very vigorously in Wageningen during the season, resulting in enormous plants that were still green and flowering in October, but allowed hardly any reproduction of nematodes. The total of degree-days, measured at 10 cm depth with a base threshold temperature of 8.3 °C for *M. hapla* (Lahtinen et al., 1988) was 1530 day°, and this would have allowed at least 2 generations in Wageningen. With a total of 2100 day° and a base threshold temperature – supposedly similar to *M. chitwoodi* – of 5.0 °C (Pinkerton et al., 1991) *M. fallax* could have produced up to 3 generations in Baexem.

With the bio-assay comparable rankings of genotypes were obtained (Table 1 and 2). However the differences between high and low numbers of juveniles could not be expressed as well with the bio-assay due to the physical limitation to the maximum number of galls that a root system of lettuce can produce. Therefore, in the case of heavily infected soil, Rf-ratings estimated by the number of galls were much lower than Rf-ratings estimated by the number of juveniles.

The resistance observed in the field was very comparable to that observed in the glasshouse test (Tables 1 and 2). The results of the glasshouse tests are also in line with our earlier reported experiments with other nematode populations (Janssen et al., 1995, 1996). The only remarkable difference between the results of field and glasshouse tests was with *S. hougasii* 93-71-5. This genotype expressed a very high level of resistance to *M. hapla* in the field, while in the glasshouse test only a partial resistance was observed.

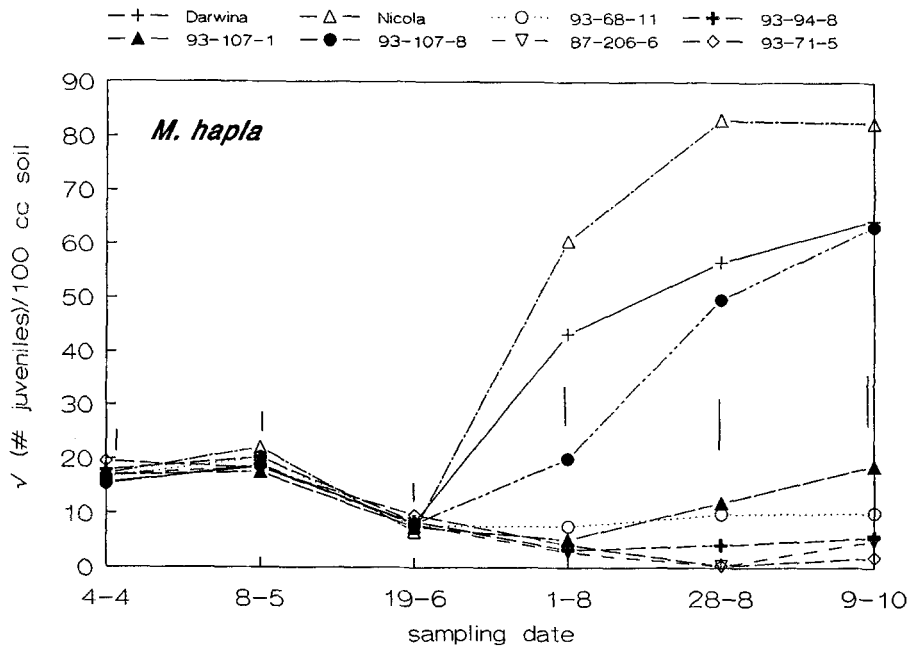

Figure 1. Number of juveniles of *M. hapla* per 100 cc soil in the field at Wageningen during growth of various *Solanum* genotypes. LSD-values per sampling date ($p < 0.05$) are indicated by vertical strokes.

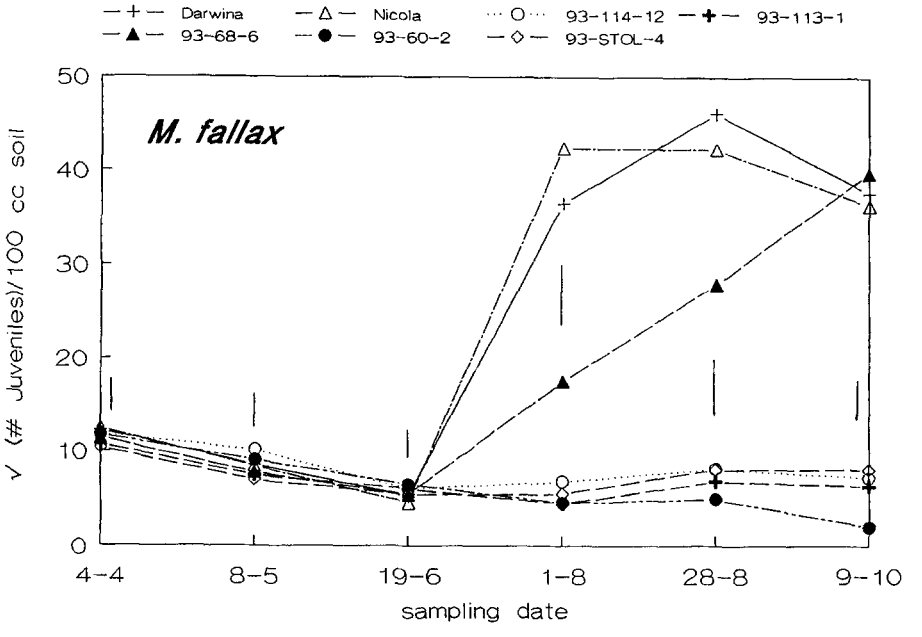

Figure 2. Number of juveniles of *M. fallax* per 100 cc soil in the field at Baexem during growth of various *Solanum* genotypes. LSD-values per sampling date ($p < 0.05$) are indicated by vertical strokes.

The various methods used to estimate differences in reproduction of root-knot nematodes in field and glasshouse experiments between resistant and susceptible genotypes gave mostly similar results. The coefficients of correlation are shown in Table 3. In the glasshouse test with *M. hapla* the plants of the cvs Nicola and Darwina were found to be in a rather poor condition and this is likely to have resulted in the

Table 1. Mean square root numbers of juveniles ($\sqrt{jv}$) and galls ($\sqrt{ga}$) in the lettuce bio-assay per 100 cc soil from the *M. hapla* infested field (Wageningen) before and after growing various *Solanum* genotypes and mean square root numbers of eggs ($\sqrt{eg}$) and egg masses ($\sqrt{em}$) in the glasshouse test. Reproductive factors (final population/initial population) were calculated using number of juveniles (Rf_{jv}) and galls (Rf_{ga}) in the field and number of eggs in the glasshouse (Rf_{eg})

		Field experiment							Glasshouse test		
			April		October						
Solanum sp.	Genotype	Vigour[a]	$\sqrt{jv}$	$\sqrt{ga}$	$\sqrt{jv}$	$\sqrt{ga}$	Rf_{jv}	Rf_{ga}	$\sqrt{em}$	$\sqrt{eg}$	Rf_{eg}[b]
S. tuberosum	Nicola	3	17.21	7.50	82.54	5.45	17.04	0.54	5.56[c]	46.2[c]	6.2
S. tuberosum	Darwina	3	15.60	7.08	64.48	5.85	22.54	0.68	6.48[c]	39.7[c]	4.1
S. sparsipilum	93-107-8	2	17.91	7.78	63.28	5.51	17.36	0.50	4.35	70.1	13.1
S. sparsipilum	93-107-1	2	16.97	7.50	18.79	3.33	1.22	0.21	1.20	10.4	0.3
S. chacoense	93-68-11	4	16.56	7.40	10.12	1.99	0.37	0.09	0.43	11.8	0.5
S. gourlayi	93-94-8	2	15.38	7.87	5.56	1.45	0.12	0.04	1.19	8.7	0.2
S. chac × *S. tub.*	87-206-6	4	16.99	7.81	4.95	1.25	0.11	0.04	0.13	1.3	0.0
S. hougasii	93-71-5	2	19.56	8.21	1.87	1.15	0.02	0.02	2.27	24.2	1.6
LSD ($p < 0.05$)			3.12	0.98	8.77	0.90	–	–	1.27	14.3	–

[a] The general vigour and duration of growth of plants in the field during the season is expressed on a scale from 1 to 4 representing poor to excellent growth respectively.
[b] As initial population the number of nematodes used for inoculation, 400 juveniles, is used.
[c] Plants were in poor condition.

Table 2. Mean square root numbers of juveniles ($\sqrt{jv}$) and galls ($\sqrt{ga}$) in the lettuce bio-assay per 100 cc soil from the *M. fallax* infested field (Baexem) before and after growing various *Solanum* genotypes and mean square root numbers of eggs ($\sqrt{eg}$) and egg masses ($\sqrt{em}$) in the glasshouse test. Reproductive factors (final population/initial population) were calculated using number of juveniles (Rf_{jv}) and galls (Rf_{ga}) in the field and number of eggs in the glasshouse (Rf_{eg})

		Field experiment							Glasshouse test		
			April		October						
Solanum sp.	Genotype	Vigour[a]	$\sqrt{jv}$	$\sqrt{ga}$	$\sqrt{jv}$	$\sqrt{ga}$	Rf_{jv}	Rf_{ga}	$\sqrt{em}$	$\sqrt{eg}$	Rf_{eg}[b]
S. tuberosum	Nicola	3	12.40	5.02	36.37	5.61	7.69	1.18	11.84	272.4	191.7
S. tuberosum	Darwina	3	12.16	5.27	37.68	6.45	8.92	1.49	8.40	161.4	69.3
S. chacoense	93-68-6	3	11.39	4.46	39.77	7.09	12.13	2.32	6.23	114.6	34.8
S. stoloniferum	93-STOL-4	3	10.34	4.88	8.07	2.68	0.60	0.27	0.14	5.3	0.2
S. chacoense	93-113-1	4	10.71	5.03	6.30	4.28	0.37	0.65	0.25	1.3	0.0
S. fendleri	93-114-12	2	11.75	4.91	7.19	4.93	0.41	0.95	0.18	1.7	0.0
S. bulbocastanum	93-60-2	3	11.65	5.22	1.98	1.59	0.04	0.13	0.13	1.1	0.0
LSD ($p < 0.05$)			3.65	3.08	3.95	2.18	–	–	1.11	30.0	–

[a] The general vigour and duration of growth of plants in the field during the season is expressed on a scale from 1 to 4 representing poor to excellent growth respectively.
[b] As initial population the number of nematodes used for inoculation, 400 juveniles, is used.

low production of eggs and the rather low correlation between this value and the numbers of egg masses ($r^2 = 0.50$). In the bio-assay with *M. fallax* relatively large variation between replicates was found and the results were found to be less comparable with counts of juveniles and the results from the glasshouse than those of the bio-assay of *M. hapla*.

The cvs Nicola and Darwina had produced tubers of reasonable size and quantity at the end of the growing season in Baexem, but several tubers were severely malformed by the characteristic galls caused by *M. fallax*. Underneath the surface of the tubers an average infection of 1.25 females per cm^2 was observed after examination of 16 tubers. Most wild *Solanum* genotypes had formed enormous amounts of stolons, which were effectively limited by the containers, but no or few very small tubers were found. In Wageningen not only the cultivars but also the hybrid *S. chacoense* × *S. tuberosum* 87-206-6 had produced a large number of tubers of reasonable size. None of the tubers showed

Table 3. Coefficients of correlation between data for multiplication in the fields, measured by extraction of juveniles ($\sqrt{jv}$) and bio-assay (ga), and in the glasshouse, measured by counting eggs ($\sqrt{eg}$) and egg masses (em)

	M. hapla				*M. fallax*			
	$\sqrt{jv}$	ga	$\sqrt{eg}$	em	$\sqrt{jv}$	ga	$\sqrt{eg}$	em
$\sqrt{jv}$	1.00				1.00			
ga	0.94	1.00			0.80	1.00		
$\sqrt{eg}$	0.71	0.70	1.00		0.75	0.45	1.00	
em	0.80	0.83	0.50	1.00	0.62	0.34	0.98	1.00

any visual symptoms of malformation. However, inside the tubers of the cultivars an average infection of 0.25 females per cm^2 was observed after examination of 12 tubers. Inside the tubers of the hybrid no females or egg masses were observed.

Discussion

The field experiments in Wageningen and Baexem demonstrated that resistance to *M. hapla* and *M. fallax* respectively, as selected in screening trials in the glasshouse, is also effective in suppressing the nematode populations under natural circumstances. Brown et al. (1994) also showed that resistance to *M. chitwoodi*, derived from *S. bulbocastanum*, was stable after a prolonged exposure to infection in microplots in the field. Although some nematodes may have reproduced on the resistant *Solanum* genotypes, this was not at a high enough level to lead to an increase of root-knot nematodes after the growing season. Consequently, in combination with the expected natural decrease of the nematode population during winter time, a very low infection level in the next spring will be the result.

The differences in level of infection in soil was better expressed by extracting and counting juveniles than by the lettuce bio-assay. The maximum number of galls on roots of lettuce is physically restricted by the size of the root system and therefore the bio-assay cannot demonstrate logarithmically higher infections. Even at the start of the growing period, the assessment of numbers of active juveniles in the soil by means of counting galls was approximately only 25% of the numbers of juveniles extracted directly. Nevertheless, this bio-assay is frequently used in the Netherlands, since for this method staff need not be experienced in the identification of *Meloidogyne* juveniles amongst other nematodes in natural soil samples. The bio-assay method also allows juveniles to hatch from eggs, thus supposedly giving a better estimate of the level of infectious nematodes (Zondervan and Huiskamp, 1987).

The field experiments were not suitable for detailed observations on tuber infection since the short day conditions necessary for tuberization of most wild *Solanum* genotypes were lacking. Only tubers of the hybrid *S. chacoense* × *S. tuberosum* could be investigated and these appeared to be free of egg masses. It has been reported that genotypes of *S. bulbocastanum* with resistance in the roots also exhibited tuber resistance (Brown et al., 1994, 1995; Mojtahedi et al., 1995). However, the low incidence of juveniles in soil around the resistant genotype in Wageningen during the formation of tubers makes it possible that tubers may have escaped infection. The tubers of the common cultivars were more severely infected by *M. fallax* than by *M. hapla*, but this might be caused by the earlier penetration and reproduction of *M. fallax* (Santo and O'Bannon, 1981).

The work reported here has shown that resistance from several different *Solanum* spp. is available to control root-knot nematodes in potato under field conditions. Although resistance to nematodes can remain effective after several consecutive years of exposure to infection (Roberts, 1992), examples are also known where the introduction of a single nematode resistance gene into cultivated crops can lead to a selection pressure towards virulent populations or related nematode species. In the Netherlands extensive use of cultivars with resistance to *Globodera rostochiensis*, based on the H1-gene from *S. tuberosum* ssp. *andigena*, has lead to an increase of *Globodera pallida* populations, whereas the use of the Mi-gene in tomato, which can suppress populations of *M. incognita, M. arenaria* and *M. javanica*, can lead to a rapid selection of virulent populations in glasshouses (Jarquin-Barberena et al., 1991). In order to avoid high selection pressures, it is now necessary to work on the durable management of resistance to *Meloidogyne* spp. in potato by introducing not a single but different resistance genes from various *Solanum* sources, such as those reported here, into the potato gene-pool.

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