Tropical Plant Pathology (2018) 43:230–241
https://doi.org/10.1007/s40858-018-0210-8

ORIGINAL ARTICLE

Evaluation of resistance and tolerance of rice genotypes from crosses of *Oryza glaberrima* and *O. sativa* to the rice root-knot nematode, *Meloidogyne graminicola*

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Received: 31 July 2017 / Accepted: 11 January 2018 / Published online: 8 February 2018

Abstract

Resistance and tolerance to *Meloidogyne graminicola* infection of introgressed rice genotypes derived from crosses between *M. graminicola*-resistant *Oryza glaberrima* genotype CG14 and -susceptible *O. sativa* genotype IR64 were evaluated in an indoor growth chamber and outdoor raised beds. None of the 44 introgressed genotypes: 24 first backcross F_2 generation (BC_1F_2) and 20 first backcross F_3 generation (BC_1F_3) evaluated did express the same level of resistance as the resistant *O. glaberrima* reference genotypes included in the experiments for comparison. Lower nematode multiplication factor on the BC_1F_3 genotypes suggests that *M. graminicola* resistance trait segregated among the 3rd generation progeny of the backcross population. The majority of the introgressed genotypes were susceptible and sensitive to *M. graminicola* infection, some genotypes were susceptible but tolerant and few were both resistant and tolerant to nematode infection. Several genotypes with resistance and/or tolerance to *M. graminicola* were identified that could either be further developed into advanced breeding lines to produce resistant and/or tolerant cultivars or in the short-term developed into *M. graminicola*-resistant and/or –tolerant cultivars for use by resource-poor farmers.

Keywords Plant traits · Resistance · Rice breeding · Susceptibility · Tolerance · Yield loss

Introduction

The rice root-knot nematode, *Meloidogyne graminicola* Golden and Birchfield, 1965, is considered one of the most important pathogen of rice in South and Southeast Asia and the major causal agent of yield loss in tropical aerobic rice (De Waele and Elsen 2007; Kreye et al. 2009; Jain et al. 2012; De Waele et al. 2013; Mantelin et al. 2017). Rice roots infected with this nematode develop galls, especially at the root tips where they are typical hook-like, while inside the root the permanent feeding sites (giant cells) induced by the nematodes disorganise the vascular cylinder affecting the transport and absorption of water and nutrients. Infected rice plants in a wide range of rice-based agro-ecosystems, including irrigated and rainfed rice, lowland and upland rice, and deepwater rice, showed considerable yield losses (Bridge and Page 1982; Arayarungsarit 1987; Plowright and Bridge 1990; Netscher and Erlan 1993; Tandingan et al. 1996; Soriano et al. 2000; Soriano and Reversat 2003; Padgham et al. 2004; Sharma-Poudyal et al. 2004; Win et al. 2015).

The options to manage *M. graminicola* are scarce because most practices, such as flooding, crop rotation and nematicides, have serious drawbacks limiting their use in rice fields (Mantelin et al. 2017). The use of rice varieties with resistance and/or tolerance to *M. graminicola* is considered a promising alternative for the management of this pathogen. Resistance to *M. graminicola* has been identified in *Oryza longistaminata*

Section Editor: Diana Fernandez

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s40858-018-0210-8) contains supplementary material, which is available to authorized users.

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A. Chev. and Roehrich (Soriano et al. 1999), *Oryza glaberrima* Steud. (Plowright et al. 1999; Soriano et al. 1999; Cabasan et al. 2012) and *Oryza sativa* L. (Jena and Rao 1977; Yik and Birchfield 1979; Sharma-Poudyal et al. 2004; Sabir and Gaur 2004; Prasad et al. 2006; Jena et al. 2012; Ravindra et al. 2015; Dimpka et al. 2015). However, few of these *O. sativa* genotypes are truly resistant (Bridge et al. 2005) and the majority of the germplasm is susceptible to *M. graminicola*.

Oryza glaberrima, originally domesticated in West Africa, is considered an important genetic resource to develop rice genotypes suitable for resource-poor farmers who are suffering from low yield due to multiple abiotic and biotic stresses in rice fields (Khush 1997; Futakuchi and Sié 2009). However, in contrast with *O. sativa*, *O. glaberrima* yield is low due to grain shattering and poor resistance to lodging (Linares 2002). The development of introgressed genotypes between *O. glaberrima* and *O. sativa* offers an opportunity to exploit the useful traits present in both rice species (Ghesquière et al. 1997). Although the transfer of useful genes from *O. glaberrima* into *O. sativa* is constrained by sterility in the early progenies of crosses (Second 1982), fertile progenies can be produced by backcrossing with the *O. sativa* parents (Jones et al. 1997a).

So far, efforts to introgress the resistance to *M. graminicola* from *O. glaberrima* into *O. sativa* has not been successful, as the interspecific progenies do not express the same degree of resistance observed in *O. glaberrima*. Plowright et al. (1999) identified four less susceptible progenies out of 14 progenies from a cross between *O. glaberrima* (CG14) and *O. sativa* (tropical *japonica* genotype WAB56-104) based on the low number of *M. graminicola* females/root system. In crosses of the *O. glaberrima* genotype TOG5681 and upland rice *O. sativa indica* genotype IR55423-01, Bimpong et al. (2010) identified two genotypes as resistant out of 15 introgressed progenies screened in outdoor raised beds and one genotype screened in a phytotron, based on the number of second-stage juveniles (J2)/root system.

Crossings carried out at the International Rice Research Institute (IRRI) in the Philippines have succeeded in producing fertile interspecific progenies from crosses between *O. glaberrima* genotype CG14 and *O. sativa* genotype IR64 through backcrossing the F_1 hybrids to the *O. sativa* parent. Backcross breeding aims to introgress one or more genes of interest from a donor parent into an elite crop genotype. The genotypes CG14 and IR64 were selected on the basis of their useful traits. CG14, an upland genotype of *O. glaberrima*, has weed competitiveness (Jones et al. 1997b), resistance to *M. graminicola* (Plowright et al. 1999; Cabasan et al. 2012), drought (Jones et al. 1997b) and water lodging (Futakuchi et al. 2001), adaptability to acidic soils with low phosphorus availability (Sahrawat et al. 2000) and strong resistance to iron toxicity (Sahrawat and Sika 2002). Resistance to multiple abiotic and biotic constraints is a highly desirable characteristic for rice cultivated by resource-poor farmers who are usually confronted with multiple problems in the fields. IR64 is an *O. sativa indica* rice genotype which is widely grown in irrigated lowland areas in tropical Asia and has been popular for many farmers because of its good yield potential and good eating quality (Khush 1987). However, it is only moderately susceptible to drought with drastic yield reduction when drought occurs around flowering (Wade et al. 1999).

The objective of this study was to evaluate the resistance and tolerance to *M. graminicola* of BC_1F_2 and BC_1F_3 backcrossed progenies of crosses between *M. graminicola*-resistant *O. glaberrima* genotype (CG14) and *M. graminicola*-susceptible *O. sativa* genotype (IR64).

Materials and Methods

Nematode inoculum

The *M. graminicola* isolate used in this study was obtained from naturally infected *O. sativa* plants (unidentified cultivar) collected in Batangas, Philippines, established and maintained on the susceptible and sensitive *O. sativa* upland genotype UPLRi-5, in pots in the glasshouse at 28±2°C under upland conditions. The nematode inoculum for the indoor growth chamber experiment was obtained by extraction of J2 from galled roots 24 h after incubation in a mist chamber (Seinhorst 1950); while for the raised beds experiment, galled roots were washed free of soil and cut into 1-cm-pieces. The initial population density in the soil was established by determining the number of J2 per g of infected roots inoculated in the known volume of sterilized soil.

Plant materials

Forty-four introgressed genotypes (24 BC_1F_2 and 20 BC_1F_3 genotypes) were randomly selected from the backcross populations. The introgressed genotypes were developed from a cross between *O. glaberrima* CG14 (IRGC 96717) and *O. sativa* IR64. Seeds from a single F_1 plant were backcrossed to IR64 to produce the F_1 generation of the first backcross (BC_1F_1) population. Random selection of introgressed genotypes was from 2nd (F_2) and 3rd (F_3) generations, which are partially and highly fertile, respectively. These populations were available as part of the wide hybridisation program of the Plant Breeding, Genetics and Biotechnology Division of IRRI. The *O. glaberrima*-resistant genotypes CG14, TOG5674 and TOG5675, and the *O. sativa*-susceptible genotypes IR64 and UPLRi-5 were included in the experiments as reference genotypes for comparison.

Host phenotype evaluation in an indoor growth chamber (IGC)

This experiment was conducted in an indoor growth chamber (IGC) at 26-29 °C (night-day temperatures) with a 12 h photoperiod and 70 % relative humidity. Seeds were pregerminated in Petri dishes at room temperature. The 5-days-old seedlings were transplanted into 2.6-cm-diameter x 21-cm-high polyvinyl chloride (PVC) tubes filled with 150 g of a heat-sterilised sandy-loam soil (52 % sand, 21 % loam, 27 % clay; pH 6.3; 0.14 % N, 1.06 % C). The soil was saturated (100 % of the soil volume filled with water) at planting and at field capacity (50 % of the soil volume filled with water) during nematode inoculation. The bottom of each tube was closed with a 0.25 mm mesh stainless steel sieve. The PVC tube was lined inside with a sheet of transparent polyethylene, slightly projected over the top of the PVC tube, to easily pull the cylinder of soil out of the tube without damaging the roots at the end of the experiment. Eight two-week-old plants from each introgressed genotype were inoculated with 75 *M. graminicola* J2. Nematode inoculation was repeated 2 days later to obtain a final pathogen pressure of 1 J2/g soil or 150 J2/tube. One day after nematode inoculation, the plants were watered at field capacity simulating upland conditions during the experiment and fertilized 3 times per week with Hoagland's nutrient solution. The pots were arranged in a completely randomized block design.

At 60 days after seed germination, *i.e.* 46 days after nematode inoculation, the plants were removed from the tubes and the root systems washed carefully and rated for galls according to a scale of 0-5 (Hussey and Janssen 2002). Fresh root system weights were recorded. The roots were cut into 1-cm-sections and placed in a mist chamber for 14 days to determine the final nematode population (Pf; Seinhorst 1950). The nematode multiplication factor (Mf) was calculated as Pf/initial population density (Pi = 150 J2). The Mf of each introgressed rice genotype was compared with that of the susceptible and resistant reference genotypes. Classification of the host phenotype as resistant, partially resistant, susceptible or inconclusive was according to the criteria used by (Dochez et al. 2005, Table 1). Resistance/susceptibility on the one hand and tolerance/sensitivity on the other hand are independent, relative qualities of a host plant based on comparison between genotypes. A host plant may either suppress (resistance) or allow (susceptibility) nematode development and reproduction; it may suffer either little injury (tolerance), even when heavily infected with nematodes, or much injury (sensitivity), even when relatively lightly infected with nematodes (Bos and Parlevliet 1995).

Host phenotype evaluation in an outdoor raised bed (ORB)

Concrete raised beds (3.6 m long x 1.08 m wide x 0.14 m deep) were filled with 600 kg of a heat-sterilised sandy-loam soil. For the *M. graminicola*-infected treatment, 450 g of finely chopped infected roots of the susceptible genotype UPLRi-5 were distributed evenly at 8 cm above the bed bottom and covered with sterilised soil. The Pi was equivalent to 2 J2/g soil. Non infested beds were included as control. The rice genotypes (5-days-old seedlings) were planted in rows, spaced 10 x 20 cm, in a split-plot arrangement in a randomized complete block design with eight replicates/genotype. Plants were watered occasionally as needed to maintain a field capacity water regime simulating upland conditions throughout the growing season and fertilised 3 times at planting, and at 30 and 60 days after planting (DAP) at a rate of 90-60-60 kg/ha of NPK. Insecticide was sprayed when needed to protect the plants from plant hopper infestation.

The number of tillers/plant was counted at 30 DAP. Shoot height was measured at maturity; at harvest, the number of panicles/plant and number of spikelets/panicle were counted and fresh root and shoot weights recorded. The % filled grains/panicle, weight of 100 grains/plant and filled grain weight/plant (adjusted to 14% moisture content) were also recorded. The yield/plant was measured based on the weight of the filled grains/plant, not including the unfilled and partially filled grains.

In the uninoculated treatment, the introgressed rice genotypes and the resistant *O. glaberrima* reference genotypes matured at 100 DAP and plants were harvested while the susceptible *O. sativa* reference genotypes matured and were harvested at 110 DAP. In the inoculated treatment, the introgressed rice genotypes started to mature from 110 DAP onwards and were harvested at 118 DAP. The resistant *O. glaberrima* reference

Table 1 Identification of the host phenotype of introgressed genotypes to *Meloidogyne graminicola* based on a comparison with the response of a susceptible and resistant reference genotypes

Comparison with susceptible reference genotype	Comparison with resistant reference genotype	Host phenotype of introgressed genotype
Significantly∗ different	Not significantly different	Resistant
Not significantly different	Significantly different	Susceptible
Significantly different	Significantly different	Partial resistant
Not significantly different	Not significantly different	Inconclusive

genotypes matured and were harvested at 104 DAP while the susceptible *O. sativa* at 118 DAP. Yield data was collected as soon as the plant matures to avoid grain shattering and tiller lodging which are typical for *O. glaberrima* genotypes and some of the introgressed genotypes. Plants were uprooted according to the maturity days of the genotypes in order to obtain the yield data and determine the tolerance/sensitivity of the genotypes to nematode infection.

Assessment of root galling severity and Mf were performed as referred before. Introgressed genotypes of the two different generations were evaluated in two batches, the first with the BC_1F_2 and the second with the BC_1F_3 populations. The same set of reference genotypes was included in the two batches and both were conducted during the dry season.

Statistical analysis

Statistical analyses were performed using STATISTICA 10.0 software. Data were subjected to $\log_{(x+1)}$ transformation prior to analysis to meet the assumptions of analysis of variance (ANOVA), *i.e.* normality and homogeneity of variances. One-way ANOVA was used to analyse significant differences between rice genotypes screened in the indoor growth chamber experiment. When a significant effect was found, mean comparison was done using Tukey´s HSD test ($P < 0.05$) and Dunnett´s test was used to compare the mean of the rice genotype to the mean of the susceptible and resistant reference rice genotypes. A factorial split-plot ANOVA was used to examine the effect of nematode inoculation (compared with uninoculated plants) on rice genotypes grown in the ORB experiments. In the case of absence of interaction between the two factors (rice genotype and nematode infection) for a specific vegetative growth or yield-contributing trait, the factor level means (*M. graminicola* inoculated and uninoculated plants) were compared by Tukey's HSD test and presented for all rice genotypes together. In the case of interaction between the two factors, individual comparisons were made between inoculated and uninoculated plants with the LSD t-test ($P<0.05$) and presented for each rice genotype separately.

Results

Host phenotype evaluation in an IGC

At 46 days after nematode inoculation, the fresh root weights of BC_1F_3 genotypes were 25 % lower compared to BC_1F_2 genotypes but no significant differences in J2/g roots, J2/root system, Mf and root galling were observed (Table 2). None of the 24 BC_1F_2 genotypes was classified as resistant to *M. graminicola*. Among the BC_1F_3 genotypes significant differences in numbers of J2 were observed. One out of the 20 BC_1F_3 genotypes was classified as resistant (IR87226-110-18-B) to *M. graminicola* and two (IR87226-106-6-B and IR87226-107-2) as partially resistant. The severity of root galling at 60 days after germination of the BC_1F_2 genotypes (on average 3.5) was higher compared to the BC_1F_3 genotypes (2.7) and comparable to the susceptible reference genotypes IR64 and UPLRi-5.

Host phenotype evaluation in an ORB

At plant maturity, the BC_1F_2 genotypes had about the same number of J2/g roots, J2/root system and root galling index compared to the susceptible reference genotypes, and about 15 and 9 times more ($P<0.05$) J2/g roots and J2/root system, respectively, compared to the resistant reference genotypes (Table 3). None of the BC_1F_2 genotypes was classified as resistant to *M. graminicola*.

No interaction between the BC_1F_2 genotypes and *M. graminicola* infection was observed for six out of the nine parameters examined. Hence, the effect of *M. graminicola* on these vegetative growth and yield-contributing parameters was measured for all introgressed genotypes combined (Supplement Table 1). *Meloidogyne graminicola* infection significantly ($P<0.05$) affected all these parameters, except number of panicles/plant and weight of 100 grains/plant. The highest ($P<0.05$) % reductions were observed in the number of spikelets/panicle and tillers/plant (-36 and -35.5 %, respectively). In about 75 % of the BC_1F_2 genotypes, *M. graminicola* infection significantly reduced the fresh shoot weight, % filled grains/panicle and filled grain weight/plant (Table 4). The highest reductions observed were 82.7% for fresh shoot weight, 68.3 % for % filled grains/panicle and 81.4 % for filled grain weight/plant for genotypes IR87226-41, IR87226-44 and IR87226-41, respectively. IR87226-63 and IR87226-35 appear to be tolerant: their yield decreased only 26 and 32.3 %, respectively, infected by as many as 63,750 and 61,564 J2/root system, respectively (on average) despite similar nematode levels to susceptible IR64.

At plant maturity, the BC_1F_3 genotypes had about the same number of J2/g roots compared to susceptible genotype UPLRi-5 but lower compared to IR64 (Table 5). The number of J2/root system of the BC_1F_3 genotypes was not significantly lower compared to both susceptible genotypes UPLRi-5 and IR64. The root galling index was comparable with both susceptible genotypes UPLRi-5 and IR64. Two of the 20 BC_1F_3 genotypes were classified as resistant (IR87226-110-15-B and IR87226-110-18-B) to *M. graminicola,* although they had, on average, 5.5 and 2.9 more J2/g roots, and 2.9 and 2.8 more J2/root system, respectively, compared to resistant genotype CG14.

No interaction between the 20 BC_1F_3 genotypes and *M. graminicola* infection was observed for the nine plant parameters analysed. Hence, the effect of *M. graminicola* on these vegetative growth and yield-contributing parameters was measured for all introgressed genotypes

Table 2 Reproduction of *Meloidogyne graminicola*, host phenotype and severity of root galling of 44 introgressed genotypes of *Oryza glaberrima* (CG14) and O. *sativa* (IR64), and of resistant (^{R}) and susceptible (^{S}) reference genotypes, grown in an indoor growth chamber, 46 days after inoculation with 150 second-stage juveniles (J2)/plant (Pi)

Rice Genotype	Fresh root weight (g)[1]		No. of J2/g roots[1]		No. of J2/root system[1]		Mf[1,2]		Host phenotype[3]	Root galling index[1]	
BC_1F_2											
IR87226-35	2.3±0.4	ab	1,175±238	bc	2,581±701	c	17.2±4.7	bc	S	3.9±0.5	cd
IR87226-38	2.8±0.4	bc	1,563±553	bc	3,541±963	c	23.6±6.4	bc	S	4.1±0.3	d
IR87226-41	2.5±0.2	ab	1,017±264	bc	2,325±598	c	15.5±4.0	b	S	3.5±0.3	cd
IR87226-44	2.2±0.3	ab	1,744±844	bc	3,413±1,422	c	22.8±9.5	bc	S	3.8±0.4	cd
IR87226-48	2.3±0.3	ab	1,411±464	bc	2,485±489	c	16.6±3.3	bc	S	3.7±0.4	cd
IR87226-52	2.8±0.4	bc	1,113±464	bc	2,836±335	c	18.9±2.2	bc	S	3.4±0.5	c
IR87226-55	2.2±0.5	ab	1,753±568	bc	2,145±471	c	14.3±3.1	b	S	3.3±0.5	c
IR87226-58	2.2±0.3	ab	1,402±416	bc	2,610±661	c	17.4±4.4	bc	S	4.0±0.0	d
IR87226-60	2.1±0.4	ab	1,220±258	bc	2,356±485	c	15.7±3.2	bc	S	3.6±0.5	cd
IR87226-63	1.9±0.5	ab	1,752±371	bc	3,035±1,792	c	11.7±2.5	b	S	3.6±0.4	cd
IR87226-66	2.1±0.2	ab	797±162	b	1,722±451	bc	11.5±3.0	b	S	2.9±0.3	bc
IR87226-69	2.2±0.3	ab	1,533±557	bc	2,493±616	c	16.6±4.1	bc	S	3.9±0.2	cd
IR87226-72	2.5±0.4	ab	1,902±598	bc	3,542±847	c	23.6±5.6	bc	S	4.3±0.3	d
IR87226-76	1.8±0.2	ab	821±183	b	1,336±266	bc	8.9±1.8	b	S	3.0±0.3	c
IR87226-78	1.9±0.3	ab	2,113±697	bc	3,449±920	c	23.0±6.1	bc	S	3.8±0.3	cd
IR87226-80	1.9±0.3	ab	1,592±428	bc	2,507±398	c	16.7±2.7	bc	S	3.8±0.2	cd
IR87226-82	1.5±0.2	ab	1,629±638	bc	2,003±562	c	13.4±3.7	b	S	3.9±0.4	cd
IR87226-87	1.5±0.3	ab	1,422±605	bc	1,829±518	bc	12.2±3.5	b	S	2.7±0.3	bc
IR87226-89	1.4±0.2	ab	1,297±338	bc	1,707±531	bc	11.4±3.5	b	S	3.4±0.5	c
IR87226-94	1.7±0.4	ab	1,162±293	bc	1,724±303	bc	11.5±2.0	b	S	2.6±0.5	bc
IR87226-96	1.6±0.2	ab	2,327±476	bc	3,673±701	c	24.5±4.7	bc	S	3.6±0.5	cd
IR87226-98	2.1±0.1	ab	1,846±603	bc	3,699±1,129	c	24.7±7.5	bc	S	3.3±0.5	c
IR87226-100	1.8±0.3	ab	1,825±789	bc	2,684±836	c	17.9±5.6	bc	S	3.7±0.4	cd
IR87226-103	1.5±0.3	ab	3,353±1,069	c	3,005±471	c	20.0±3.1	bc	S	3.1±0.3	c
BC_1F_3											
IR87226-104-11-B	1.1±0.2	ab	3,747±1,903	c	2,998±884	c	20.0±5.9	bc	S	2.7±0.6	bc
IR87226-104-15-B	1.8±0.2	ab	1,604±493	bc	2,506±580	c	16.7±3.9	bc	S	3.4±0.4	c
IR87226-104-17-B	0.9±0.2	a	3,180±614	c	2,827±677	c	18.8±4.5	bc	S	2.7±0.3	bc
IR87226-104-19-B	1.8±0.3	ab	1,159±301	bc	1,798±447	bc	12.0±3.0	b	S	3.0±0.2	c
IR87226-105-7	0.8±0.2	a	1,593±421	bc	1,124±154	bc	7.5±1.0	b	Inc	1.3±0.3	b
IR87226-105-10-B	1.8±0.6	ab	1,599±883	bc	1,852±262	bc	12.3±1.7	b	S	2.7±0.3	bc
IR87226-106-1-B	3.0±0.5	c	491±149	b	1,231±263	b	8.2±1.8	b	Inc	2.8±0.3	bc
IR87226-106-3-B	1.5±0.3	ab	2,106±889	bc	2,569±611	c	17.1±4.1	bc	S	3.8±0.4	cd
IR87226-106-5-B	1.6±0.4	ab	2,799±1,458	bc	2,071±528	c	13.8±3.5	b	S	2.6±0.4	bc

Table 2 (continued)

Rice Genotype	Fresh root weight (g)[1]		No. of J2/g roots[1]		No. of J2/root system[1]		Mf[1,2]		Host phenotype[3]	Root galling index[1]	
IR87226-106-6-B	1.5±0.3	ab	852±243	bc	942±141	b	6.3±0.9	b	PR	2.0±0.5	b
IR87226-107-2	2.2±0.3	ab	665±284	b	1,080±278	b	7.2±1.9	b	PR	3.4±0.5	c
IR87226-107-11-B	1.5±0.4	ab	2,723±1,646	bc	2,004±404	c	13.4±2.7	b	S	2.8±0.4	bc
IR87226-108-2-B	1.7±0.4	ab	893±261	bc	1,128±224	bc	7.5±1.5	b	Inc	2.7±0.3	bc
IR87226-108-3-B	1.8±0.8	ab	2,069±639	bc	2,446±933	c	16.3±6.2	bc	S	3.3±0.5	c
IR87226-110-15-B	1.2±0.2	ab	1,282±281	bc	1,290±195	bc	8.6±1.3	b	Inc	2.0±0.2	b
IR87226-110-18-B	1.1±0.4	ab	307±164	b	495±335	a	3.3±2.2	a	R	1.4±0.5	b
IR87226-110-23-B	0.8±0.3	a	3,222±750	c	5,009±1,659	cd	21.5±5.0	bc	S	3.0±0.4	bc
IR87226-111-5	1.1±0.2	ab	3,120±1,130	c	2,413±382	c	16.1±2.5	bc	S	3.0±0.3	bc
IR87226-111-10	0.9±0.2	a	3,445±451	c	2,977±395	c	19.8±2.6	bc	S	2.8±0.2	bc
IR87226-111-12	1.0±0.2	ab	2,085±877	bc	1,624±556	bc	10.8±3.7	b	S	2.5±0.3	bc
$CG14^{R}$	1.7±0.2	ab	129±24	a	195±32	a	1.3±0.2	a	R	0.9±0.1	a
$TOG5674^{R}$	0.9±0.1	a	272±92	a	187±49	a	1.2±0.3	a	R	0.6±0.2	a
$TOG5675^{R}$	1.3±0.3	ab	230±48	a	251±36	a	1.7±0.2	a	–	0.8±0.2	a
$IR64^{S}$	1.8±0.4	ab	5,831±2,853	cd	6,255±1,315	cd	41.7±8.8	cd	S	3.8±0.3	cd
$UPLRi\text{-}5^{S}$	1.3±0.1	ab	4,982±2,323	cd	5,825±2,629	cd	38.8±17.5	bc	–	3.5±0.2	cd
Average of BC_1F_2	2.0±0.3		1,627±544		2,559±627		17.1±4.2			3.5±0.4	
Average of BC_1F_3	1.5±0.3		2,036±737		1,930±450		12.9±3.0			2.7±0.4	

[1] Data are means ± standard deviation (n = 8). Means in the same column followed by the same letter are not significantly different according to Tukey's HSD test ($P<0.05$).

[2] Mf = multiplication factor = final nematode population/Pi.

[3] Host phenotype = R: Resistant; PR: Partially resistant; Inc: Inconclusive; S: Susceptible to *M. graminicola*. In comparison between the number of J2/root system of the introgressed rice genotypes and the susceptible reference UPLRi-5 and the resistant reference TOG5675.

–: reference genotype

Table 3 Reproduction of *Meloidogyne graminicola*, host phenotype and severity of root galling of 24 BC_1F_2 introgressed genotypes of *Oryza glaberrima* (CG14) and *O. sativa* (IR64), and of resistant (^{R}) and susceptible (^{S}) reference genotypes at harvest, grown under upland conditions in outdoor raised beds after inoculation with 2 second-stage juveniles (J2)/g soil

Genotype	No. of J2/g roots[1]		No. of J2/ root system[1]		Host phenotype [2]	Root galling index[1]	
IR87226-35	7,015±2,228	bc	61,564±23,062	bc	S	2.9±0.4	bc
IR87226-38	7,780±2,472	bc	57,474±19,151	bc	S	3.4±0.5	bc
IR87226-41	6,370±2,028	bc	35,911±9,917	bc	S	3.6±0.3	bc
IR87226-44	5,170±1,705	bc	95,936±45,227	c	S	3.4±0.5	bc
IR87226-48	4,900±1,243	bc	43,976±8,201	bc	S	2.9±0.3	bc
IR87226-52	6,978±3,061	bc	48,528±27,486	bc	S	4.2±0.5	c
IR87226-55	7,343±2,629	bc	49,731±14,426	bc	S	3.3±0.5	bc
IR87226-58	4,231±1,078	bc	60,274±29,975	bc	S	4.1±0.3	c
IR87226-60	5,635±1,905	bc	46,652±13,259	bc	S	3.6±0.4	bc
IR87226-63	7,484±2,366	bc	74,307±24,582	bc	S	4.5±0.2	c
IR87226-66	7,043±1,531	bc	83,005±31,980	c	S	3.3±0.5	bc
IR87226-69	6,040±887	bc	42,578±7,207	bc	S	4.3±0.4	c
IR87226-72	7,623±2,076	bc	58,943±8,767	c	S	4.1±0.4	c
IR87226-76	6,256±1,823	bc	61,613±31,147	bc	S	2.8±0.4	bc
IR87226-78	4,518±1,049	bc	43,274±14,241	bc	S	3.6±0.4	bc
IR87226-80	4,390±1,202	bc	54,896±18,820	bc	S	3.3±0.5	bc
IR87226-82	9,657±5,843	bc	38,006±10,697	bc	S	3.3±0.5	bc
IR87226-87	5,731±1,883	bc	46,320±13,024	bc	S	3.6±0.4	bc
IR87226-89	5,712±1,701	bc	25,933±7,630	bc	Inc	3.9±0.3	bc
IR87226-94	5,011±1,358	bc	40,262±14,575	bc	S	3.4±0.4	bc
IR87226-96	6,332±2,997	bc	79,439±40,697	bc	S	4.3±0.3	c
IR87226-98	2,964±1,131	b	34,429±13,047	bc	Inc	3.0±0.3	bc
IR87226-100	10,963±2,831	c	87,001±28,937	bc	S	4.4±0.3	c
IR87226-103	5,350±1,990	bc	35,390±18,742	bc	Inc	4.1±0.4	c
$CG14^R$	533±158	a	5,767±1,816	a	R	1.0±0.2	a
$TOG5674^R$	280±131	a	5,958±2,671	a	R	0.6±0.2	a
$TOG5675^R$	420±184	a	6,257±2,099	a	–	0.4±0.2	a
$IR64^S$	6,351±1,377	bc	56,186±12,143	bc	S	4.3±0.2	c
$UPLRi\text{-}5^S$	5,894±3,000	bc	45,742±21,195	bc	–	3.6±0.3	bc
Average of introgressed genotypes	6,271±2,042		54,393±19,783			3.6±0.4	

[1] Data are means ± standard deviation (n = 8). Means in the same column followed by the same letter are not significantly different according to Tukey's HSD test ($P<0.05$).

[2] Host phenotype = R: Resistant; Inc: Inconclusive; S: Susceptible to *M. graminicola.* In comparison between the number of J2/root system of the introgressed rice genotypes and the susceptible reference UPLRi-5 and the resistant reference TOG5675

–: reference genotype

combined (Supplement Table 2). *Meloidogyne graminicola* infection significantly affected the number of tillers/plant, % filled grain/panicle and filled grain weight/plant. The highest ($P<0.05$) % reductions were observed for filled grain weight/plant and number of tillers/plant (44.6 and 30.4 %, respectively).

BC_1F_3 genotypes showed a reduction in yield when inoculated with *M. graminicola* (Fig. 1). IR87226-106-3-B and IR87226-104-19-B had the highest reduction in yield with 76 and 67.7 %, respectively while IR87226-104-15-B, IR87226-110-23-B and IR87226-106-1-B had the lowest yield reduction (5.3, 16.9 and 17.1 %, respectively). IR87226-104-11-B also had the lowest yield reduction but also the genotype with the lowest yield, while IR87226-111-10 had the highest yield in both uninfected and infected treatments. Susceptible genotype IR64 had the second-highest yield only when uninoculated and its yield was reduced significantly ($P<0.05$) in the presence of *M. graminicola* (58.1 %). Resistant genotype TOG5674 showed no reduction in yield when infected with *M. graminicola*. IR87226-110-15-B and IR87226-111-12 appear to be highly sensitive genotypes: their yield decreased by 64.2 and 54.5 %, respectively, infected with 12,851 and 27,316

Table 4 Effect of *Meloidogyne graminicola* on fresh shoot weight, % filled grain/panicle and filled grain weight/plant of the 24 BC_1F_2 introgressed genotypes, and of the resistant (^{R}) and susceptible (^{S}) reference genotypes, grown under upland conditions in uninoculated and *M. graminicola*-inoculated outdoor raised beds

Genotype	Fresh shoot weight (g) [1]				% filled grain/panicle				Filled grain weight/plant (g)			
	UI[2]	I[2]		% change	UI[2]	I[2]		% change	UI[2]	I[2]		% change
IR87226-35	82.5	33.3	*	-59.6	66.7	40.0	*	-40.1	3.3	2.2	ns	-32.3
IR87226-38	113.8	52.9	*	-53.5	88.4	64.6	*	-26.9	11.9	3.4	*	-71.4
IR87226-41	119.3	20.6	*	-82.7	80.1	41.7	*	-48.0	10.5	2.0	*	-81.4
IR87226-44	118.0	63.3	*	-46.3	81.8	25.9	*	-68.3	9.3	2.0	*	-77.9
IR87226-48	46.7	38.4	ns	-17.8	68.4	42.9	*	-37.3	5.5	2.0	ns	-63.1
IR87226-52	100.5	37.7	*	-62.5	71.2	35.8	*	-49.7	9.3	2.5	*	-73.0
IR87226-55	89.6	48.6	ns	-45.8	83.3	50.5	*	-39.4	8.0	3.3	*	-58.9
IR87226-58	83.9	38.2	*	-54.5	57.9	46.5	ns	-19.7	6.1	1.9	*	-68.7
IR87226-60	102.6	38.8	*	-62.2	83.5	33.1	*	-60.4	9.9	2.4	*	-75.4
IR87226-63	97.6	35.4	*	-63.7	50.3	43.6	ns	-13.3	2.8	2.1	ns	-26.0
IR87226-66	94.2	58.4	ns	-38.0	78.9	36.8	*	-53.4	7.6	2.7	*	-64.9
IR87226-69	113.4	37.2	*	-67.2	87.8	41.3	*	-53.0	8.8	1.8	*	-79.3
IR87226-72	131.1	42.8	*	-67.4	71.5	54.9	ns	-23.3	5.6	3.0	ns	-46.7
IR87226-76	92.5	29.9	*	-67.7	90.2	43.8	*	-51.4	11.0	2.2	*	-79.6
IR87226-78	84.4	50.8	ns	-39.8	87.9	45.2	*	-48.6	6.2	2.9	ns	-53.8
IR87226-80	132.4	63.5	*	-52.0	82.9	43.3	*	-47.7	9.6	3.6	*	-62.0
IR87226-82	64.9	56.0	ns	-13.7	57.8	48.9	ns	-15.3	5.2	1.7	*	-68.1
IR87226-87	100.6	41.3	*	-59.0	74.3	69.0	ns	-7.1	8.3	3.9	*	-53.4
IR87226-89	82.8	52.8	ns	-36.3	77.5	38.6	*	-50.2	7.0	2.7	*	-61.1
IR87226-94	71.5	54.1	ns	-24.3	79.2	48.0	*	-39.3	7.1	2.5	*	-64.2
IR87226-96	124.1	57.1	*	-54.0	72.6	57.7	ns	-20.5	9.3	4.4	*	-53.0
IR87226-98	77.1	39.0	*	-49.4	79.5	30.3	*	-61.9	1.8	1.5	ns	-20.1
IR87226-100	112.1	44.0	*	-60.8	72.2	47.3	*	-34.5	7.1	2.9	*	-59.1
IR87226-103	93.3	48.7	*	-47.8	78.5	57.6	*	-26.6	7.2	2.8	*	-60.9
$CG14^R$	125.0	54.2	*	-56.6	96.4	75.4	ns	-21.8	19.1	13.8	ns	-27.6
$TOG5674^R$	150.5	113.8	ns	-24.4	67.6	60.5	ns	-10.5	13.8	9.6	ns	-30.3
$TOG5675^R$	118.7	130.7	ns	10.1	90.7	69.1	ns	-23.8	9.3	8.0	ns	-13.9
$IR64^S$	104.4	62.1	ns	-40.5	84.7	46.7	*	-44.9	20.6	3.0	*	-85.6
$UPLRi\text{-}5^S$	89.4	81.6	ns	-8.7	77.5	12.5	*	-83.9	10.3	1.0	*	-90.0
Average of introgressed genotypes	97.0	45.1	*	-48.0	75.9	45.3	*	-40.3	7.4	2.6	*	-65.0

[1] Means followed by * is significant and ns not significantly different between uninfected and infected plants according to LSD t-test ($P<0.05$) (n = 8).

[2] UI: Uninfected plants; I: Infected plants.

J2/root system, respectively. In contrast, IR87226-104-15-B and IR87226-106-1-B appear to be tolerant: their yield decreased with only 5.3 and 17.1 %, respectively, infected by as many as 44,893 and 42,040 J2/root system, respectively.

Discussion

The number of J2/g roots and J2/root system on the BC_1F_2 and BC_1F_3 genotypes were lower than on the two susceptible reference genotypes. However, the Mf of the BC_1F_3 genotypes was lower compared to the BC_1F_2 genotypes. This difference suggests that the *M. graminicola* resistance trait segregated among the F_3 generation progeny of the backcross population. In the IGC experiment low root galling severity observed in the BC_1F_3 genotypes can be explained by the presence of less nematodes in the roots. When defense response mechanisms were present, plant resistant to *M. graminicola* have a hypersensitive response in the early stage of infection resulting to a failure of feeding site establishment and a late sensitive response after induction of giant cells resulting to less number of nematodes that could reproduce in the roots; as observed in the resistant *O. glaberrima* CG14 (Cabasan et al. 2014). However, in the ORB experiment, the severity of root galling at plant maturity of the BC_1F_2 plants was comparable to the BC_1F_3 plants and

Table 5 Reproduction of *Meloidogyne graminicola*, host phenotype and severity of root galling of 20 BC_1F_3 introgressed genotypes of *Oryza glaberrima* (CG14) and *O. sativa* (IR64), and of resistant (^{R}) and susceptible (^{S}) reference genotypes at harvest, grown under upland conditions in outdoor raised beds after inoculation with 2 second-stage juveniles (J2)/g soil

Genotype	No. of J2/g roots[1]		No. of J2/root system[1]		Host phenotype[2]	Root galling index[1]	
IR87226-104-11-B	2,465±739	c	46,116±14,312	cd	S	4.1±0.1	c
IR87226-104-15-B	5,451±1,405	d	44,893±10,261	cd	S	3.4±0.3	bc
IR87226-104-17-B	2,697±706	c	30,216±8,481	cd	S	4.0±0.2	c
IR87226-104-19-B	4,469±508	d	37,005±10,776	cd	S	3.8±0.3	c
IR87226-105-7	2,977±839	c	26,794±7,137	cd	S	3.3±0.4	bc
IR87226-105-10-B	1,828±415	c	25,207±7,031	cd	Inc	3.5±0.3	bc
IR87226-106-1-B	3,909±943	cd	42,040±12,135	cd	S	3.6±0.3	bc
IR87226-106-3-B	2,113±560	c	30,279±6,086	cd	S	3.6±0.3	bc
IR87226-106-5-B	3,292±869	c	52,607±9,494	d	S	3.9±0.3	c
IR87226-106-6-B	4,663±1,843	cd	42,998±12,765	cd	S	3.9±0.4	c
IR87226-107-2	2,430±677	c	52,823±17,398	d	S	4.3±0.3	c
IR87226-107-11-B	1,446±505	c	28,891±11,248	cd	S	3.9±0.5	c
IR87226-108-2-B	3,376±1,106	c	36,851±11,003	cd	S	3.4±0.5	bc
IR87226-108-3-B	2,410±928	c	28,059±8,183	cd	S	3.4±0.4	bc
IR87226-110-15-B	2,093±799	c	12,851±3,695	ab	R	3.3±0.4	bc
IR87226-110-18-B	1,554±871	ab	12,013±3,963	ab	R	3.3±0.3	bc
IR87226-110-23-B	3,291±1,266	c	29,721±12,344	cd	S	4.3±0.3	c
IR87226-111-5	2,452±558	c	29,074±9,866	cd	S	3.5±0.4	bc
IR87226-111-10	1,640±598	c	33,813±10,076	cd	S	4.3±0.2	c
IR87226-111-12	3,201±867	c	27,316±6,696	cd	S	3.4±0.3	bc
CG14 ^{R}	382±226	ab	4,362±225	a	R	1.8±0.5	ab
TOG5674 ^{R}	259±48	a	4,800±951	a	R	1.1±0.1	a
TOG5675 ^{R}	315±184	a	5,683±1303	ab	–	1.3±0.2	a
IR64 ^{S}	5,408±1,182	d	56,206±7,307	d	–	3.9±0.4	c
UPLRi-5 ^{S}	2,563±564	c	60,556±18,234	d	S	3.5±0.3	bc
Average of introgressed genotypes	2,888±850		33,478±9,647			3.7±0.3	

[1] Data are means ± standard deviation (n = 8). Means in the same column followed by the same letter are not significantly different according to Tukey's HSD test ($P<0.05$).

[2] Host phenotype = R: Resistant; Inc: Inconclusive; S: Susceptible to *M. graminicola*. In comparison between the number of J2/root system of the introgressed rice genotypes and the susceptible reference IR64 and the resistant reference TOG5675.

–: reference genotype

susceptible reference genotypes. The difference in root galling severity between the two experiments could be due to the time of the experiments: raised beds experiment (110 days) could generate more nematodes (6 *vs* 3 life cycles) than the IGC experiment (60 days; Fernandez et al. 2013).

Resistance and tolerance of plants to nematode infection may differ between experiments due to differences in experimental conditions, type of inoculum or inoculum pressure. However inclusion of the same reference genotypes in both experiments will minimize this variation. Genotypes IR87226-106-6 and IR87226-107-2 were classified as partially resistant in the IGC experiment and susceptible in the ORB experiment. In contrast, the genotype IR87226-110-15-B was classified as susceptible in the IGC experiment and as resistant in the ORB experiment. This inconsistency in host phenotype also suggests segregation for *M. graminicola* resistance among F_3 plants and, also, that the F_3 plants are more heterozygous. Only the genotype IR87226-110-18-B was classified as resistant in both experiments.

Variability in sensitivity/tolerance to *M. graminicola* was observed within and between the two introgressed genotype populations. BC_1F_2 populations grown in *M. graminicola*-infested soil were more sensitive to nematode infection with a reduction on average of the yield/plant of 65 % *vs* 44.6 % in the BC_1F_3 populations. Higher yields in BC_1F_3 genotypes could be a result of an accumulation of alleles that favor the yield or a reduction of alleles for an undesirable trait, or both.

Some of the introgressed genotypes were both susceptible and sensitive to *M. graminicola* infection while some others

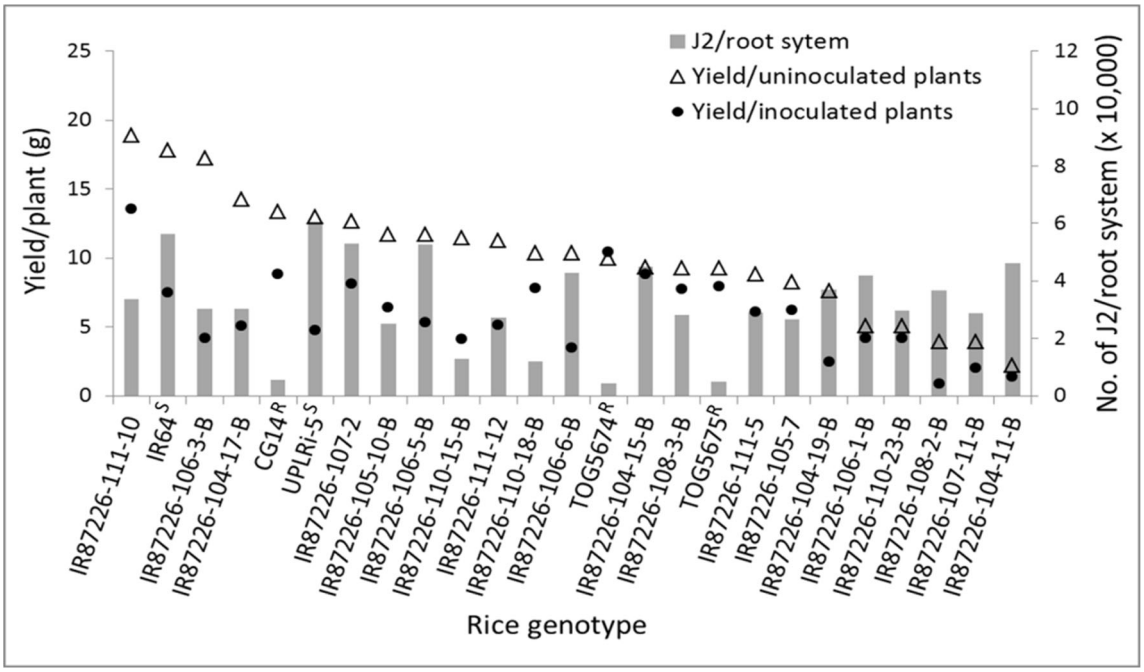

Fig. 1 Effect of *Meloidogyne graminicola* infection on the yield (filled grain weight/ plant) of 20 BC_1F_3 introgressed genotypes, and on resistant (^{R}) and susceptible (^{S}) reference genotypes grown in infested and uninfested soil (2 J2/g soil) under upland conditions in outdoor raised beds

were susceptible but tolerant. Resistance and tolerance to a nematode species can be independent attributes of a plant species (Trudgill 1991). The results of our study suggest that resistance and tolerance to *M. graminicola* infection are either independently or simultaneously expressed.

In our study, BC_1F_2 and BC_1F_3 genotypes identified as resistant or partially resistant to *M. graminicola* infection appeared to be tolerant, less sensitive or hypersensitive in terms of yield reduction when infected with *M. graminicola*. The BC_1F_2 genotypes IR87226-89 and IR87226-103 classified as susceptible (inconclusive in the ORB experiment) were both hypersensitive to nematode infection resulting in a high yield loss (61 %). The BC_1F_3 genotype IR87226-105-10-B was also classified as susceptible (inconclusive in the ORB experiment) and the yield decreased by 45 %. In contrast, the yield of the BC_1F_2 genotype IR87226-98, classified as susceptible in the IGC and as inconclusive in the ORB experiment, was only reduced by 20 %. IR87226-110-15-B was resistant (inconclusive in the IGC experiment) but hypersensitive to nematode infection resulting in a yield loss of 64 % while IR87226-110-18-B was resistant resulting in a yield loss of 25 %.

Although the majority of the susceptible BC_1F_2 and BC_1F_3 genotypes were sensitive to *M. graminicola* infection, some genotypes simultaneously expressed resistance and tolerance to nematode infection. This also suggests that resistance and tolerance to *M. graminicola* in rice may be expressed or inherited simultaneously or independently (Boerma and Hussey 1992; Barker 1993; Davis and May 2003). This variability in host phenotype indicates that numerous genes for tolerance are likely to be involved. Similar to nematode resistance, the trait for nematode tolerance may be quantitative in nature and controlled by more than one gene (Shrestha et al. 2007).

In conclusion, our results demonstrate the potential of genotypes derived of crosses between the resistant *O. glaberrima* genotype CG14 and the susceptible *O. sativa* genotype IR64 to improve resistance in *O. sativa* to *M. graminicola*. Promising genotypes with resistance and/or tolerance to *M. graminicola* infection were identified that could be further developed into advanced breeding lines and ultimately resistant and/or tolerant cultivars. Although it would require several years to develop a new rice genotype with superior phenotypes for nematode resistance and/or tolerance (Boerma and Hussey 1992), available resistant and tolerant rice genotypes could already alleviate the problem caused by *M. graminicola* and prevent yield reduction caused by this important nematode species (De Waele et al. 2013). This will in turn increase food security and cash income of farmers. Molecular technologies could enhance the efficiency of the breeding programs. Data on the genetic basis of resistance to *M. graminicola* in rice are limited. The identification of molecular markers that are closely associated with *M. graminicola* resistance and tolerance quantitative trait loci is currently underway.

Acknowledgements This research was supported by a Flemish Interuniversity Council (VLIR-UOS) Ph.D. scholarship to MTN Cabasan. The authors would like to thank the Plant Breeding, Genetics and Biotechnology Division (PBGB) and Crop and Environmental Sciences Division (CESD) of IRRI for the seeds, equipment, facilities and assistance in conducting the experiments.

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