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Host response of drought-tolerant aerobic Asian rice genotypes to infection of the rice root-knot nematode *Meloidogyne graminicola*

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Summary. Twenty-five progenies (either F_4 or F_6) derived from crosses between the drought-tolerant Indian upland rice cv. Vandana and the drought-sensitive Indonesian upland rice cv. Way Rarem (both Asian rice) were examined for their host response to *Meloidogyne graminicola* infection under aerobic conditions in a field experiment at IRRI, Los Baños, Philippines. The host response was compared with the host response of the susceptible references UPLRi-5 and IR64 (both Asian rice), and the resistant reference CG14 (African rice). None of the aerobic progenies was classified as resistant. Compared with UPLRi-5 on the basis of the number of second-stage juveniles (J2) (root system)$^{-1}$, 22 progenies were classified as partially resistant and three as susceptible. Based on the number of J2 (g roots)$^{-1}$, 13 progenies were classified as partially resistant and 12 as susceptible. Compared with IR64 and based on both J2 (root system)$^{-1}$ and J2 (g roots)$^{-1}$, 13 progenies were classified as partially resistant and 12 as susceptible. The aerobic progenies showed a wide variation in terms of tolerance to *M. graminicola* infection. Fresh root weight was the plant growth trait most affected and percentage filled grains per panicle the yield-contributing trait most affected. On the basis of percentage reduction in yield/plant, seven progenies were classified as tolerant (< 10% yield reduction), nine progenies as less sensitive (10-20% yield reduction), eight progenies as sensitive (21-30% yield reduction) and one genotype as highly sensitive (36% yield reduction). Of the eight progenies classified as tolerant, three progenies (IR84984-83-15-862-B, IR90019:6-86 and IR90020:22-265) were also partially resistant. Cultivar Vandana was partially resistant and less sensitive, whilst cv. Way Rarem was partially resistant/susceptible and tolerant to *M. graminicola* infection.

Key words: aerobic rice, breeding, damage potential, reproductive potential, plant traits, resistance, sensitivity, susceptibility, tolerance, yield loss.

Aerobic rice is a water-saving rice production system for water-short environments with favourable soils and adapted, potentially high-yielding varieties that are direct dry-seeded in well-drained, non-puddled and non-saturated soils without ponded water. Soils remain aerobic but supplementary irrigation is applied as necessary (Bouman, 2001; Bouman *et al.*, 2005). The rice varieties used in this system usually combine the drought resistance of upland varieties and the high-yielding ability of lowland varieties (Lafitte *et al.*, 2002).

Continuous cropping of aerobic rice in the same field can result in yield decline (Peng *et al.*, 2006), rapid yield losses (George *et al.*, 2002; Pinheiro *et al.*, 2006; Nie *et al.*, 2012) and even yield failure (Kreye *et al.*, 2009). The rice root-knot nematode *Meloidogyne graminicola* Golden & Birchfield, 1965 was identified as one of the soil-borne pathogens limiting yield of aerobic rice (Kreye *et al.*, 2009). During the past decades, this sedentary endoparasitic nematode species has emerged as one of the most important biotic constraints to rice production in Asia (De Waele & Elsen, 2007). It is present in all South Asian and Southeast Asian countries surveyed so far (Jain *et al.*, 2012) and can cause significant yield losses of Asian rice grown in all rice-based production systems: lowland as well as upland, irrigated as well as rainfed, and deepwater rice (Bridge & Page, 1982; Prot *et al.*, 1994; Padgham *et al.*, 2004; Bridge *et al.*, 2005; Win *et al.*, 2011). In upland conditions and shallow intermittently flooded land, *M. graminicola* is considered to be by far the most damaging *Meloidogyne* species on rice (De Waele & Elsen 2007). In *M. graminicola*-infested upland rice fields, nematicide application resulted in a yield increase of 12-33% in Thailand (Arayarungsit, 1987) and 28-87% in Indonesia (Netscher & Erlan, 1993).

Management options for *M. graminicola* include crop rotation, prolonged flooding and the use of nematicides (De Waele *et al.*, 2013). Crop rotation can be effective (Ventura *et al.*, 1981; Rahman, 1990) but is seldom adopted by farmers unless there is an additional benefit, such as a marketing-for-cash-income opportunity, beyond nematode management (Starr *et al.*, 2002). Also, *Echinocloa* spp., which are dominant weed species in aerobic rice fields, are good hosts of *M. graminicola* (Chauhan & Johnson, 2011). Prolonged or permanent flooding is not feasible in areas that are experiencing water scarcity. The use of nematicides is limited to smallholder farmers because of their high cost and toxicity to humans and the environment. In this context, the use of resistant or tolerant cultivars offers a promising alternative for the effective, economic and environment-friendly management of *M. graminicola*.

The objective of our study was to examine the host response to *M. graminicola* infection of aerobic Asian rice (*Oryza sativa* L.) genotypes with improved tolerance to drought. These aerobic genotypes were either F_4 or F_6 progenies of cvs Vandana × Way Rarem crosses. Cultivar Way Rarem is a drought-sensitive Indonesian upland rice cultivar, whilst cv. Vandana is a drought-tolerant Indian upland rice cultivar. Following the terminology of Bos & Parlevliet (1995), resistance/susceptibility and tolerance/sensitivity are defined as 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. Resistance/susceptibility can be determined by measuring the nematode population densities on and in the roots, whereas tolerance/sensitivity can be determined by measuring the effect of the nematode population on plant growth, yield-contributing traits and/or yield (Cook & Evans, 1987).

MATERIAL AND METHODS

Plant material. Twenty-five aerobic rice progenies and the two parents, cvs Vandana and Way Rarem, were included in our study (Table 1). These progenies have an improved tolerance to drought based on field drought screening done at the International Rice Research Institute (IRRI) in Los Baños, Philippines (Kumar, pers. comm.). CG14^R (African rice) was included as the resistant reference rice genotype while IR64^S and UPLRi-5^S (both Asian rice) were included as susceptible reference rice genotypes to *M. graminicola* infection.

Field experiment. The experiment was carried out in a nematode-infested field (a so-called 'hot spot') under aerobic rice growing conditions at IRRI, Los Baños, Philippines (14°11' N, 121°15' E, 21 m above sea level) during the 2012 dry season (January-May). The soil of the IRRI upland farm is a Maahas clay loam soil (isohyperthermic mixed Tropudalf) (Zhao *et al.*, 2006). The infested field has been developed as a so-called hotspot for experiments with *M. graminicola*. For 2 years, the field was continuously planted with UPLRi-5^S to build up the *M. graminicola* population densities. Prior to the commencement of the experiment, soil sampling was done to determine the nematode population densities. On average, the field was infested with 87 second-stage juveniles (J2) (200 ml soil)$^{-1}$. Despite continuous planting of the susceptible cultivar, the nematode density was not equally distributed throughout the field; thus, to ensure a more uniform distribution in half of the field, nematode-infected UPLRi-5^S roots were chopped in 1-cm-pieces and 180 g infected roots were incorporated (3-5 cm deep) along each 3-m single row plot just before seeding. On average, 180 g roots were infected with 34,000 J2 and 170 females. In the other half of the field, solarisation and nematicide application was applied to kill the nematodes. The soil was covered with a black plastic sheet for 15 days before seeding after which carbofuran (Furadan®, 10 g) was applied at 4.5 kg a.s. ha^{-1}.

In both field halfs, the experimental layout was a three-replicated alpha lattice design with 3-m single row plots. The rows were spaced 0.25 m apart. Seeds of each rice genotype were dry direct-seeded using a seeding density of 1.5 g per linear meter of row. Basal fertiliser applications equivalent to 40 P and 40 K kg ha^{-1} in the form of single super phosphate and potassium chloride, and 120 kg ha^{-1} of N in the form of ammonium sulphate were applied in three even splits around 21, 42, and 61 days after seeding. After seeding, irrigation through evenly placed sprinklers was done daily for 5 days to keep the field saturated to allow good germination of the seeds. After germination, the plants were grown under aerobic rice growing conditions (*i.e.*, in a well-drained, non-saturated soil) for the duration of the experiment. They were irrigated twice weekly until maximum tillering of the plants, then three times weekly until harvest. Irrigation was not applied during rainy days. Manual weeding was done when necessary.

Assessment of the severity of root galling and *M. graminicola* population densities. Eighteen sample plants of each rice genotype (six from each replicate) were carefully removed from the soil, washed with tap water to remove all adhering soil particles and the fresh root weight of each root system recorded. The severity of root galling (root galling index) was visually assessed for each up-rooted plant by rating the percentage of roots with root tip galls per root system on a 0-5 scale, according to the rice root-knot rating chart of Hussey & Janssen (2002). After recording so-called root gall indices, roots were cut into about 0.5 cm pieces and placed on a labelled sieve contained in a plastic cup (8 cm diam., 12 cm high). Cups were placed in a mistifier at 27°C that produced a fine mist of water for 90 s every 10 min (Seinhorst, 1950; Hooper *et al.*, 2005). The nematodes in water suspension were collected at 7 and 14 days after the roots were placed in the mistifier. The suspension was homogenised by gentle blowing and a 1 ml sub-sample was taken (pipetted) for counting the J2 in a counting dish using a stereomicroscope. The average of two counts was used to calculate the final nematode population density (Pf = J2 (root system)$^{-1}$). Pf divided by the root weight gave the number of J2 per root unit (*i.e.*, 1 g fresh roots).

To measure the level of resistance to *M. graminicola* infection of each progeny, the number of J2 per root system and per g roots of nematode-infected plants were compared to UPLRi-5^{S} and IR64^{S}, and CG14^{R} based on the method described by Dochez *et al.* (2005) (Table 1).

Assessment of plant growth and yield-contributing traits. The phenotype of eighteen sample plants from each genotype (six plants from each replicate) was recorded. Plant height was measured at the seedling stage, maximum tillering and at the mature grain stage (harvest) of the plants. Plant height at seedling and maximum tillering stage was measured from the soil surface to the tip of the tallest leaf. Plant height at harvest was measured from the soil surface to the tip of the panicle of the main tiller. Days to flowering was noted when 50% of the plants of each genotype in a plot had flowering tillers. At harvest, fresh shoot and root weight were recorded. Dry shoot and root weight were recorded after oven drying at 70°C for 72 h.

Grains were manually threshed. Filled and unfilled grains in one panicle of 18 plants per genotype were counted. On the basis of this count, the total number of spikelets per panicle was determined. Yield per plant was calculated by weighing the totally filled grains of each plant. Yield per plot was determined by measuring the weight of all filled grains of all plants in a plot. The weight of 100 filled seeds of each genotype was also noted. Grain yield is reported at 14% moisture content.

To measure the level of tolerance to *M. graminicola* infection of each genotype, the yield of nematode-infected plants was compared with the yield of non-infected plants and the percentage reduction

Table 1. Classification of the host response of 25 aerobic rice progenies derived from cvs Vandana × Way Rarem crosses to *Meloidogyne graminicola* infection based on a comparison with the host response of the susceptible parents UPLRi-5^{S} and IR64^{S}, and the resistant parent CG14^{R}.

Statistical difference with IR64^{S} or UPLRi-5^{S}	Statistical difference with CG14^{R}	Host response
Significant(*)	Not significant	Resistant (R)
Significant	Significant	Partially resistant (PR)
Not significant (ns)	Significant	Susceptible (S)
Not significant	Not significant	Inconclusive (I)

* Significant according to LSD ($P \leq 0.05$).

calculated. The scale in Table 2 was used to determine the level of tolerance. It is based on the outcome of experiments conducted during a decade at IRRI (De Waele, pers. comm.).

Table 2. Level of tolerance of rice genotypes to *Meloidogyne graminicola* infection based on the percentage yield reduction between nematode-infected and non-infected plants.

% yield reduction	Level of tolerance
< 10	Tolerant
10-20	Less sensitive
21-30	Sensitive
> 30	Highly sensitive

Data analysis. All data were analysed using the mixed model analysis in IRRI CropStat 7.2. Nematode population densities were $\log10_{(x+1)}$ transformed prior to analysis. Plant growth and yield-contributing traits, yield and nematode population densities were analysed by ANOVA. The progenies were considered as a fixed effect, while block and replicates were considered as a random effect. The model was genotype + replication + block (replication) + error. Combined analysis was used to determine the effect of nematode infection on the plant traits measured compared with the non-infected plants. The infested and non-infested field plots were treated as trial and the model was trial + trial (rep) + trial (rep) (block) + genotype + trial (genotype) + residuals. Trial (rep) and trial (rep) (block) were considered as random effect and trial (genotype) was considered as fixed effect. Least significance difference (LSD) was used to compare nematode population densities and plant traits of progenies in the nematode-infested and non-infested field plots. The percentage reduction of the plant growth and yield-contributing traits, and yield of nematode-infected plants compared with non-infected plants were computed using this formula:

$$\%\text{reduction} = \frac{\text{values of non-infected plants} - \text{values of infected plants}}{\text{values of non-infected plants}} \times 100$$

RESULTS

Severity of root galling. The 25 aerobic progenies had an average root gall rating of 3 (26-50% root tips with galls). Gall rating in CG14^R averaged 1, and in UPLRi-5^S and IR64^S 4 and 5, respectively (Table 3).

***Meloidogyne graminicola* population densities.** The host response of the aerobic progenies to infection of *M. graminicola* in terms of susceptibility is presented in Table 3. None of the progenies was classified as resistant. When compared with UPLRi-5^S and CG14^R, and based on the number of J2 (root system)$^{-1}$, 22 progenies were classified as partially resistant and three as susceptible. Based on the number of J2 (g roots)$^{-1}$, 13 progenies were classified as partially resistant and 12 as susceptible. When compared with IR64^S and CG14^R, 13 progenies were identified as partially resistant and 12 as susceptible based on J2 (root system)$^{-1}$ while also 13 progenies were classified as partially resistant and 12 as susceptible based on J2 (g roots)$^{-1}$. The susceptible and resistant reference genotypes showed the expected host response.

Nematode population densities in the progenies averaged 2,407 J2 (root system)$^{-1}$ and 314 J2 (g roots)$^{-1}$. Among the progenies, the lowest (936) number of J2 (root system)$^{-1}$ was observed in IR900: 16-3 and the highest (4,514) number of J2 (root system)$^{-1}$ in IR84984-21-19-41-B. In UPLRi-5^S and IR64^S, nematode reproduction was 15,470 and 9,524 J2 (root system)$^{-1}$ and 1,426 and 1,301 J2 (g roots)$^{-1}$, respectively. The lowest nematode reproduction was observed in CG14^R (184 J2 (root system)$^{-1}$ and 29 J2 (g roots)$^{-1}$).

Cultivar Vandana was classified as partially resistant based on both J2 (root system)$^{-1}$ and J2 (g roots)$^{-1}$. With the exception of CG14^R, cv. Vandana had the lowest number of J2 (root system)$^{-1}$ (839) and only 75 J2 (g roots)$^{-1}$ of all genotypes examined. Of the 25 progenies, 12 (44.4%) were consistently partially resistant in both comparisons. Cultivar Way Rarem was classified as partially resistant when compared with UPLRi-5^S on the basis of J2 (root system)$^{-1}$ but as susceptible on the basis of J2 (g roots)$^{-1}$. It was classified as susceptible when compared with IR64^S on the basis of both J2 (root system)$^{-1}$ and J2 (g roots)$^{-1}$.

Effect of *M. graminicola* infection on plant growth and yield-contributing traits, and yield. The effect of infection with *M. graminicola* on the plant traits measured is presented in Tables 4 and 5. Nematode infection did not significantly affect plant height (data not shown). Fresh and dry root and shoot weights of nematode-infected plants of the progenies combined were on average reduced with 43.1, 19.5, 15.8 and 14.0%, respectively. The percentage reduction in fresh root weight in most progenies (22) was significant ($P \leq 0.05$). The percentage reduction in dry shoot weight was significant ($P \leq 0.05$) in only two progenies. In cv. Vandana only fresh root weight was significantly

Table 3. Fresh root weight, root population densities of *Meloidogyne graminicola*, host response (in terms of susceptibility) and severity of root gall rating of drought-tolerant progenies derived from cvs Vandana × Way Rarem crosses at harvest.

No.	Progeny designation	Root wt. (g)	Per root system			Per g/roots			Root gall rating
			No. of J2	Host response* (IR64^S/ CG14^R)	Host response* (UPLRi-5^S/ CG14^R)	No. of J2	Host response* (IR64^S/ CG14^R)	Host response* (UPLRi-5^S/ CG14^R)	
1	IR 84984-83-15-828-B	8.0	2999	S	PR	373	S	S	3
2	IR 84984-21-19-78-B	6.9	1757	PR	PR	254	PR	PR	2
3	IR 84984-83-15-110-B	7.6	4346	S	PR	573	S	S	3
4	IR 84984-83-15-837-B	9.3	1808	PR	PR	195	PR	PR	3
5	IR 84984-83-15-862-B	8.8	1879	PR	PR	213	PR	PR	3
6	IR 84984-21-19-685-B	9.2	1692	PR	PR	183	PR	PR	2
7	IR 84984-83-15-330-B	7.0	1513	PR	PR	217	PR	PR	2
8	IR 84984-83-15-151-B	7.2	1629	PR	PR	226	PR	PR	2
9	IR 84984-83-15-608-B	8.2	3227	S	PR	395	S	S	3
10	IR 84984-21-19-41-B	8.0	4514	S	PR	566	S	S	4
11	IR 84984-83-15-481-B	6.3	2912	S	PR	460	S	S	3
12	IR 90019:6-86	12.2	1726	PR	PR	142	PR	PR	3
13	IR 90019:16-8	7.6	2536	S	S	335	PR	PR	3
14	IR 90018:19-97	7.0	2466	S	PR	352	S	S	3
15	IR 90019:17-15	10.7	4192	S	PR	391	S	S	3
16	IR 90018:19-171	11.4	3783	S	S	331	S	S	3
17	IR 90019:17-156	7.6	1513	PR	PR	198	PR	PR	2
18	IR 90019:17-159	5.3	2343	S	S	443	S	S	3
19	IR 90023:23-1	6.5	1744	PR	PR	267	PR	PR	3
20	IR 90023:23-181	8.4	1214	PR	PR	145	PR	PR	3
21	IR 90020:22-283	4.8	2039	PR	PR	425	S	S	4
22	IR 90019:16-34	7.2	2535	S	PR	350	S	S	3
23	IR 90020:22-81	5.7	3052	S	PR	535	S	S	3

Table 3 (continued). Fresh root weight, root population densities of *Meloidogyne graminicola*, host response (in terms of susceptibility) and severity of root gall rating of drought-tolerant progenies derived from Vandana × Way Rarem crosses at harvest.

No.	Progeny designation	Root wt. (g)	Per root system			Per g/root			Root gall rating
			No. of J2	Host response ($IR64^S$/ $CG14^R$)	Host response (UPLRi-5^S/ $CG14^R$)	No. of J2	Host response ($IR64^S$/ $CG14^R$)	Host response (UPLRi-5^S/ $CG14^R$)	
24	IR 90019:16-3	6.8	936	PR	PR	137	PR	PR	2
25	IR 90020:22-265	11.0	1,821	PR	PR	165	PR	PR	2
	Average	**8.0**	**2407**			**314**			**2.8**
27	Way Rarem	6.0	2461	S	PR	409	S	S	2
26	Vandana	11.2	839	PR	PR	75	PR	PR	3
28	$CG14^R$	6.4	184	R	R	29	R	R	1
29	UPLRi-5^S	10.8	1547	S	S	1,426	S	S	4
30	$IR64^S$	7.3	9524	S	S	1,301	S	S	5
	LSD (5%)		1			0.73			1.3

Data represent the average of 18 replicates.
J2 = second-stage juveniles.
* Host response based on a comparison with $IR64^S$ and CG^R, and UPLRi-5^S and $CG14^R$. R: resistant; PR: partially resistant; S: susceptible based on LSD ($P \leq 0.05$).
Root galling rated by 0 = no galls, 1 = 1 < 10% galls, 2 = 11-25% galls, 3 = 26-50% galls, 4 = 51-75% galls and 5 = > 70% of the root system galled.

Table 4. Fresh and dry root and shoot weight, and percentage reduction of drought-tolerant progenies derived from cvs Vandana × Way Rarem crosses at harvest grown in non-infested (U) and *Meloidogyne graminicola*-infested (I) fields.

Progenies designation	Fresh root wt.			Dry root wt.			Fresh shoot wt.			Dry shoot wt.		
	U	I	% Reduc-tion	U	I	% Reduc-tion	U	I	% Reduc-tion	U	I	% Reduc-tion
IR 84984-21-19-41-B	11.7	6.1	48.1 *	1.5	1.2	21.4 ns	39.0	38.7	0.7 ns	15.3	14.0	8.3 ns
IR 84984-21-19-685-B	10.2	5.6	44.8 *	1.4	1.0	29.9 ns	41.8	35.5	15.2 ns	13.6	12.5	7.9 ns
IR 84984-21-19-78-B	8.8	7.3	16.9 ns	1.4	1.3	6.7 ns	43.8	33.6	23.1 ns	16.4	15.4	6.3 ns
IR 84984-83-15-110-B	10.3	5.6	45.3 *	1.5	1.2	19.9 ns	41.2	36.4	11.8 ns	17.8	12.7	28.5 ns
IR 84984-83-15-151-B	9.7	5.3	45.1 *	1.5	1.2	18.6 ns	40.9	36.8	10.1 ns	18.5	13.5	27.3 ns
IR 84984-83-15-330-B	12.8	6.1	52.3 *	1.4	1.2	14.5 ns	46.8	37.0	20.9 ns	16.7	12.8	23.4 ns
IR 84984-83-15-481-B	9.2	4.8	47.7 *	1.4	1.2	13.4 ns	41.2	26.1	36.6 *	14.4	11.2	21.9 ns
IR 84984-83-15-608-B	14.2	5.9	58.8 *	1.3	1.1	13.3 ns	40.3	35.6	11.7 ns	16.6	16.1	2.7 ns
IR 84984-83-15-828-B	10.6	6.3	40.5 *	1.4	1.2	19.3 ns	45.2	36.8	18.6 ns	16.0	14.6	8.7 ns
IR 84984-83-15-837-B	9.1	5.9	35.0 *	1.6	1.2	25.5 ns	42.4	34.5	18.6 ns	19.2	15.7	18.6 ns
IR 84984-83-15-862-B	8.0	5.4	32.8 ns	1.4	1.1	19.1 ns	50.6	48.2	4.8 ns	19.8	18.6	6.1 ns
IR 90018:19-171	10.1	5.4	46.4 *	1.4	1.1	23.0 ns	39.5	35.9	9.3 ns	20.3	15.4	24.2 ns
IR 90018:19-97	9.9	5.0	49.1 *	1.4	1.0	29.0 ns	49.8	44.4	10.7 ns	26.3	20.7	21.1 ns
IR 90019:16-3	10.4	5.3	49.1 *	1.5	1.2	17.6 ns	39.3	35.1	10.8 ns	14.4	15.3	+6.3 ns
IR 90019:16-34	8.8	4.8	44.8 *	1.5	1.1	23.5 ns	33.5	28.8	14.0 ns	16.0	12.2	23.5 ns
IR 90019:16-8	10.1	4.9	51.3 *	1.4	1.1	18.7 ns	35.1	31.3	10.8 ns	15.4	15.5	+0.5 ns
IR 90019:17-15	9.9	5.5	44.2 *	1.5	1.2	23.7 ns	40.5	31.9	21.3 ns	17.9	16.7	6.9 ns
IR 90019:17-156	8.6	5.5	36.0 *	1.4	1.3	6.9 ns	33.0	25.3	23.4 ns	12.2	12.6	+2.7 ns
IR 90019:17-159	10.0	5.0	50.0 *	1.5	1.1	25.3 ns	39.0	37.4	4.3 ns	15.5	14.4	7.5 ns
IR 90019:6-86	8.2	5.5	33.2n s	1.5	1.1	23.2 ns	30.4	30.3	0.5 ns	11.9	12.1	+1.1 ns
IR 90020:22-265	10.7	5.5	48.2 *	1.4	1.1	21.9 ns	38.8	35.2	9.2 ns	12.3	11.8	3.7 ns
IR 90020:22-283	9.4	6.9	26.1 ns	1.5	1.1	26.3 ns	48.6	33.8	30.4 *	18.8	14.6	22.6 ns
IR 90020:22-81	9.0	5.3	41.3 *	1.4	1.2	14.8 ns	48.1	47.8	0.6 ns	20.6	13.7	33.5 *
IR 90023:23-1	9.7	5.8	40.0 *	1.5	1.3	11.9 ns	51.4	30.0	41.7 *	20.9	14.5	30.7 *
IR 90023:23-181	10.3	5.2	49.8 *	1.5	1.2	20.6 ns	43.9	27.9	36.5 *	18.8	13.6	27.7 ns

Table 4 (continued). Fresh and dry root and shoot weight, and percentage reduction of drought-tolerant progenies derived from Vandana × Way Rarem crosses at harvest grown in non-infested (U) and *Meloidogyne graminicola*-infested (I) fields.

Progenies designation	Fresh root wt.			Dry root wt.			Fresh shoot wt.			Dry shoot wt.		
	U	I	% Reduction	U	I	% Reduction	U	I	% Reduction	U	I	% Reduction
Average	**10.0**	**5.6**	**43.1**	**1.4**	**1.2**	**19.5**	**41.8**	**35.0**	**15.8**	**17.0**	**14.4**	**14.0**
cv. Vandana	10.1	5.4	47.1 *	1.2	1.2	2.9 ns	43.4	37.2	14.3 ns	14.4	10.3	28.5 ns
cv. Way Rarem	11.0	8.0	27.5 *	1.5	1.3	13.8 ns	58.4	31.4	46.2 *	13.4	10.1	24.9 ns
CG14^{R}	7.0	6.4	8.2	1.3	1.2	7.7 ns	44.1	41.8	5.2 ns	14.2	13.7	3.7 ns
UPLRi-5^{S}	15.0	10.8	27.7 *	**2.7**	1.2	55.6 *	31.8	20.3	36.2 *	8.8	5.5	37.5 *
IR64^{S}	12.0	7.3	39.0 *	2.3	1.1	52.2 *	47.4	22.0	53.6 *	10.4	4.2	59.4 *
LSD (0.05)	3.2			0.9			14.3			6.5		

Data represent the average of 18 replicates.

*: significantly different; ns: not significantly different between plants grown in non-infested (U) and nematode-infested (I) field according to LSD ($P \leq 0.05$).

"+" indicates an increase in dry shoot weight.

Table 5. Percentage filled grains/panicle, weight of 100 seeds, yield/plant, percentage reduction in yield/plant and host response (in terms of sensitivity) of 27 drought-tolerant progenies derived from cvs Vandana × Way Rarem crosses at harvest grown in non-infested (U) and *Meloidogyne graminicola*-infested (I) fields.

Progenies designation	**Percentage filled grains/ panicle**		**Wt. of 100 seeds**		**Yield/ plant**		**Percentage yield reduction**	**Host response**
	U	**I**	**U**	**I**	**U**	**I**		
IR 84984-21-19-41-B	84.2	78.4	2.4	2.3	8.2	7.3	11 ns	LS
IR 84984-21-19-78-B	85.1	82.4	2.5	2.4	9.0	7.5	17 ns	LS
IR 84984-21-19-685-B	81.5	85.9	2.5	2.4	9.0	7.7	14 ns	LS
IR 84984-83-15-110-B	79.4	78.8	2.4	2.4	8.8	7.1	19 ns	LS
IR 84984-83-15-151-B	85.4	79.1	2.5	2.4	10.1	7.4	27 *	S
IR 84984-83-15-330-B	81.5	77.4	2.3	2.3	8.6	6.8	21 ns	S
IR 84984-83-15-481-B	81.5	78.4	2.4	2.4	9.4	6.0	36 *	HS
IR 84984-83-15-608-B	85.7	77.0	2.5	2.4	9.4	7.4	21 ns	S
IR 84984-83-15-828-B	73.4	72.8	2.4	2.3	9.7	6.8	30 *	S
IR 84984-83-15-837-B	79.4	79.7	2.3	2.4	9.6	7.2	25 *	S
IR 84984-83-15-862-B	77.5	74.6	2.5	2.3	9.1	8.3	9 ns	T
IR 90018:19-97	80.6	74.4	2.5	2.4	9.2	9.2	0 ns	T
IR 90018:19-171	82.1	81.5	2.4	2.4	7.9	7.9	0 ns	T
IR 90019:6-86	77.1	72.4	2.5	2.5	7.7	7.0	9 ns	T
IR 90019:16-3	78.5	79.8	2.4	2.4	9.3	7.7	17 ns	LS
IR 90019:16-8	78.4	75.2	2.5	2.4	8.7	8.5	2 ns	T
IR 90019:16-34	80.3	76.7	2.4	2.3	8.1	7.3	10 ns	LS
IR 90019:17-15	80.4	72.0	2.4	2.3	8.3	7.0	15 ns	LS
IR 90019:17-156	87.3	78.1	2.5	2.4	7.8	6.3	20 ns	LS
IR 90019:17-159	80.3	78.7	2.4	2.3	9.2	7.9	14 ns	LS
IR 90020:22-81	77.6	70.8	2.5	2.4	8.3	8.4	+2	T
IR 90020:22-265	80.8	65.9	2.6	2.5	7.8	8.0	+3	T
IR 90020:22-283	80.4	75.2	2.5	2.5	9.8	6.9	30*	S
IR 90023:23-1	79.5	79.7	2.5	2.5	9.9	7.0	30*	S
IR 90023:23-181	82.5	73.3	2.6	2.5	10.0	7.0	30*	S
Average	**80.8**	**76.7**	**2.5**	**2.4**	**8.9**	**7.4**	**16**	
Vandana	81.3	78.9	2.5	2.4	8.4	7.0	18 ns	LS
Way Rarem	78.7	66.0	2.5	2.5	6.6	6.1	7 ns	T
CG14^{R}	92.7	84.0	2.5	2.4	8.3	7.2	13 ns	LS
UPLRi-5^{S}	43.0	39.3	2.3	2.3	11.0	3.0	72 *	HS
IR64^{S}	67.2	62.8	2.4	2.4	14.4	4.1	72 *	HS
LSD(0.05)					2.3			

Data represent the average of 18 replicates.

*: significantly different; ns: not significantly different between plants grown in non-infested (U) and nematode-infested (I) field according to LSD ($P \leq 0.05$).

+: indicates an increase in yield.

T: tolerant (< 10% yield reduction); LS: less sensitive (10-20% yield reduction); S: sensitive (21-30% yield reduction) and HS: highly sensitive (> 30% yield reduction).

($P \leq 0.05$) reduced, while in cv. Way Rarem fresh root and shoot weight were significantly ($P \leq 0.05$) reduced. In nematode-infected plants of UPLRi-5^S and IR64^S, the percentage reduction in fresh and dry root and shoot weight was always significant ($P \leq 0.05$) but never in CG14^R.

Yield reduction in the progenies ranged from 0 to 30% and averaged 16% (Table 5). Of the 25 progenies, seven progenies were classified as tolerant, nine progenies as less sensitive, eight progenies as sensitive and one progeny as highly sensitive to *M. graminicola* infection. Cultivars Vandana and Way Rarem were classified as less sensitive and tolerant, respectively. CG14^R was classified as less sensitive and both UPLRi-5^S and IR64^S as highly sensitive. The highest percentage yield reduction (72%) was observed in both UPLRi-5^S and IR64^S.

Of the eight progenies identified as tolerant, three progenies were partially resistant, whilst five were susceptible to *M. graminicola* infection. Of the nine less sensitive genotypes, four were partially resistant and five were susceptible to *M. graminicola* infection. Four of the tolerant progenies (IR90018:19-97, IR90019:16-8, IR90020:22-81 and IR84984-83-15-862-B) were high-yielding in both the non-infested and the infested field halfs.

DISCUSSION

The host response of the susceptible and resistant parents included in our study in terms of nematode infection levels at harvest shows that the establishment of the field as a 'hot spot' was successful and that the results obtained are reliable. These results show a variation in host response to *M. graminicola* infection among the aerobic progenies examined, as well in susceptibility as in sensitivity.

No resistance comparable to the resistance of CG14^R was found but many of the aerobic progenies were found to be partially resistant, *i.e.*, less susceptible compared with either IR64^S or UPLRi-5^S or both. The number of J2 (root system)$^{-1}$ recovered from the aerobic progenies was 4.0 and 6.4 times lower compared with the average number of J2 (root system)$^{-1}$ recovered from IR64^S and UPLRi-5^S, respectively. This observation also suggests that the partial resistance, especially of the parent cv. Vandana, was inherited by the progenies and that the reproductive potential of *M. graminicola* on the aerobic progenies is lower. The number of partially resistant progenies was higher when UPLRi-5^S was used as the susceptible reference genotype (both based on J2 (root system)$^{-1}$ and J2 (g roots)$^{-1}$) than when IR64^S was used as the susceptible reference genotype. This difference is due to the difference in degree of susceptibility between the two susceptible reference genotypes. Using IR64^S is more rigorous in identifying resistant and partially resistant genotypes.

Among the plant growth traits examined, fresh root weight was the trait most affected. One should expect that drought-tolerant rice genotypes have a root system that allows them to withstand adverse soil conditions but our results show that as well the drought-tolerant parent cv. Vandana (–47.1%) as most of the aerobic progenies (–43.1% for all the progenies combined) suffered extremely high reductions in fresh root weight. Among the yield-contributing traits examined, percentage filled grains per panicle was the trait most affected.

Yield was significantly reduced in about 25% of the aerobic progenies. Recently, De Waele *et al.* (2013) reported yield losses ranging in some upland aerobic and Asian rice genotypes evaluated under aerobic conditions in outdoors raised beds. A reduction in root fresh weight is a typical damage caused by soil-borne plant-parasitic nematodes. Especially the disruption of sedentary endoparasitic root-knot nematodes such as *M. graminicola* is a major cause of root damage (Trudgill, 1991). The galls and the feeding sites (giant cells) induced by these nematodes disrupt the xylem and divert assimilates (Meon *et al.*, 1978; Wilcox-Lee & Loria, 1987). This type of damage directly reduces root growth and the uptake of water and nutrients from the soil (Evans *et al.*, 1977). It can also cause substantial reductions in the photosynthetic rate per unit area of leaf, which in turn can make the plants non-responsive to any inputs (Loveys & Bird, 1973; Arntzen & Schans, 1988). In rice, water is most crucial during the reproductive stage starting from panicle initiation to flowering. Root damage prior and during this stage will lead to unfilled grains that eventually result in yield reduction.

Interestingly, three genotypes (IR84984-83-15-862-B, IR90019:6-86 and IR90020:22-265) were at the same time partially resistant and tolerant to *M. graminicola* infection. These progenies can be grown in nematode-infested field under aerobic conditions because they will limit yield losses caused by the nematodes and might suppress the build-up of high nematode soil population densities. Five other progenies with partial resistance were either less sensitive or sensitive. This observation suggests that resistance and tolerance to *M. graminicola* infection in Asian rice are inherited and expressed independently, confirming previous observations (De Waele *et al.*, 2013). Progenies with partial resistance and which are less sensitive to *M. graminicola* (such as IR84984-21-19-685-B, IR84984-21-19-78-B, IR90019:16-3, IR90019:17-156 and cv. Vandana) might be utilised in crop rotation sequences with susceptible and sensitive Asian rice genotypes although their efficacy in managing *M. graminicola* below damage threshold levels should be investigated. Progenies that are susceptible but are less sensitive might be also useful in a crop rotation sequence following resistant genotypes as means of reducing the rate of selection for virulence. Five of the tolerant progenies (IR90019:16-8, IR90020:22-81, IR90018:19-97, IR84984-83-15-862-B and IR90020:22-265) were high-yielding even when infected with *M. graminicola* and these can also be directly grown in nematode-infested field under aerobic conditions. Susceptible and sensitive progenies (such as IR84984-83-15-608-B and IR84984-83-15-828-B) and susceptible and highly sensitive progenies (such as IR84984-83-15-481-B) should not be cultivated in the field to avoid substantial yield losses and even yield failure.

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REFERENCES

ARAYARUNGSARIT, L. 1987. Yield ability of rice varieties in fields infested with root-knot nematode. *International Rice Research Notes* 12: 14.

ARNTZEN, F.K. & SCHANS, J. 1988. The effect of density of potato cyst nematodes and plant genotype on photosynthesis and biomass production. *Nematologica* 34: 255.

BOS, L. & PARLEVLIET, J.E. 1995. Concepts and terminology on plant/pest relationships: toward consensus in plant pathology and crop protection. *Annual Review of Phytopathology* 33: 69-102.

BOUMAN, B.A.M. 2001. Water-efficient management strategies in rice production. *International Rice Research Notes* 26: 17-22.

BOUMAN, B.A.M., PENG S., CASTAÑEDA, A.R., VISPERAS, R.M. 2005. Yield and water use of irrigated tropical aerobic rice system. *Agricultural Water Management* 74: 87-105.

BRIDGE, J. & PAGE, S.L.J. 1982. The rice root-knot nematode, *Meloidogyne graminicola*, on deep water rice (*Oryza sativa* subsp. *indica*). *Revue de Nématologie* 5: 225-232.

BRIDGE, J., PLOWRIGHT, R.A. & PENG, D. 2005. Nematode parasites of rice. In: *Plant Parasitic Nematodes in Subtropical and Tropical Agriculture* (M. Luc, R.A. Sikora & J. Bridge Eds). pp. 87-130. Wallingford, UK, CAB International.

CHAUHAN, B.S. & JOHNSON, D. 2011. Row spacing and weed control timing affect yield of aerobic rice. *Field Crops Research* 121: 226-231.

COOK, R. & EVANS, K. 1987. Resistance and tolerance. In: *Principles and Practice of Nematode Control in Crops* (R.H. Brown & B.R. Kerry Eds). pp. 179-231. Sydney, Australia, Academic Press.

DE WAELE, D. & ELSEN, A. 2007. Challenges in tropical plant nematology. *Annual Review of Phytopathology* 45: 457-485.

DE WAELE, D., DAS, K., ZHAO, D., TIWARI, R.K.S., SHRIVASTAVA, D.K. VERA-CRUZ, C. & KUMAR, A. 2013. Host response of rice genotypes to the rice root-knot nematode (*Meloidogyne graminicola*) under aerobic soil conditions. *Archives of Phytopathology and Plant Protection* 46: 670-681.

DOCHEZ, C., WHYTE, J., TENKOUANO, A., ORTIZ, R. & DE WAELE, D. 2005. Response of East African highland bananas and hybrids to *Radopholus similis*. *Nematology* 7: 655-666.

EVANS, K., TRUDGILL, D.L. & BROWN, N.J. 1977. Effects of potato cyst-nematodes on potato plants. V. Root system development in lightly and heavily infested susceptible and resistant varieties, and its importance in nutrient and water uptake. *Nematologica* 23: 153-164.

GEORGE, T., MAGBANUA, R., GARRITY, D.P., TUBAÑA, B.S. & QUITON, J. 2002. Rapid yield loss of rice cropped successively in aerobic soil. *Agronomy Journal* 94: 981-989.

HOOPER, D.J., HALLMANN, J. & SUBBOTIN, S.A. 2005. Methods for the extraction, processing and detection of plant and soil nematodes. In: *Plant Parasitic Nematodes in Subtropical and Tropical Agriculture* (M. Luc, R.A. Sikora & J. Bridge Eds). pp. 53-86. Wallingford, UK, CAB International.

HUSSEY, H. & JANSSEN, G.J.W. 2002. Root-knot nematode: *Meloidogyne* species. In: *Plant Resistance to Parasitic Nematodes* (J.L. Starr, R. Cook & J.N. Carter Eds). pp. 43-70. Wallingford, UK, CAB International.

JAIN, R.K., KHAN, M.R & KUMAR, V. 2012. Rice root-knot nematode (*Meloidogyne graminicola*) infestation in rice. *Archives of Phytopathology and Plant Protection* 45: 635-645.

KREYE, C., BOUMAN, B.A.M., CASTAÑEDA, A.R., LAMPAYAN, R.M., FARONILO, J.E., LACTAOEN, A.T. & FERNANDEZ, L. 2009. Possible causes of yield failure in tropical aerobic rice. *Field Crops Research* 3: 197-206.

LAFITTE, R.H., COURTOIS, B. & ARRAUDEAU, M. 2002. Genetic improvement of rice in aerobic systems: progress from yield to genes. *Field Crops Research* 75: 171-190.

LOVEYS, B.R. & BIRD, A.F. 1973. The influence of nematodes on photosynthesis in tomato plants. *Physiological Plant Pathology* 3: 525-529.

MEON, S., WALLACE, H.R. & FISHER, J.M. 1978. Water relations of tomato (*Lycopersicon esculentum* Mill. cv. Early Dwarf Red) infected with *Meloidogyne javanica* (Treub), Chitwood. *Physiological Plant Pathology* 13: 275-281.

NETSCHER, C. & ERLAN, X. 1993. A root-knot nematode, *Meloidogyne graminicola*, parasitic on rice in Indonesia. *Afro-Asian Journal of Nematology* 3: 90-95.

NIE, L., PENG, S., CHEN, M., SHAH, F., HUANG, J., CUI, K. & XIANG, J. 2012. Aerobic rice for water-saving agriculture. A review. *Agronomy for Sustainable Development* 32: 411-418.

PADGHAM, J.L., DUXBURY, J.M., MAZID, A.M., ABAWI, G.S. & HOSSAIN, M. 2004. Yield losses caused by *Meloidogyne graminicola* on lowland rainfed rice in Bangladesh. *Journal of Nematology* 36: 42-48.

PENG, S., BOUMAN, B.A.M., VISPERAS, R.M., CASTAÑEDA, A.R., NIE, L. & PARK, H. 2006. Comparison between aerobic and flooded rice in the tropics: agronomic performance in an eight-season experiment. *Field Crops Research* 96: 252-259.

PINHEIRO, B.D.S., CASTRO, E.D.M.D. & GUIMARÃES, C.M. 2006. Sustainability and profitability of aerobic rice production in Brazil. *Field Crops Research* 97: 34-42.

PROT, J.-C., SORIANO, I.R. & MATIAS, D.M. 1994. Major root-parasitic nematodes associated with irrigated rice in the Philippines. *Fundamental and Applied Nematology* 17: 75-78.

RAHMAN, M.L. 1990. Effect of different cropping sequences on the root-knot nematode *Meloidogyne graminicola* and yield of deepwater rice. *Nematologia Mediterranea* 18: 213-217.

SEINHORST, J.W. 1950. De betekenis van de toestand van de grond voor het optreden van aantasting door het stengelaaltje (*Ditylenchus dipsaci* (Kühn) Filipjev). *Tijdschrift over Plantenziekten* 56: 289-348.

STARR, J.L., BRIDGE, J. & COOK, R. 2002. Resistance to plant parasitic nematodes. In: *Plant Resistance to Parasitic Nematodes* (J.L. Starr, R. Cook & J.N. Carter Eds). pp. 1-22. Wallingford, UK, CAB International.

TRUDGILL, D.L. 1991. Resistance to and tolerance of plant parasitic nematodes in plants. *Annual Review of Phytopathology* 29: 167-192.

VENTURA, W., WATANABE, I., CASTILLO, M.B. & DELA CRUZ, A. 1981. Involvement of nematodes in soil sickness of a dryland rice-based cropping system. *Soil Science and Plant Nutrition* 27: 305-315.

WILCOX-LEE, D.A. & LORIA, R. 1987. Effects of soil moisture and the root-knot nematode, *Meloidogyne hapla* (Chitwood), on water relations, growth, and yield in snap bean. *Journal of the American Society of Horticultural Science* 112: 629-633.

WIN, P.P., KYI, P.P. & DE WAELE, D. 2011. Effect of agro-ecosystem on the occurrence of the rice root-knot nematode *Meloidogyne graminicola* in Myanmar. *Australasian Plant Pathology* 40: 187-196.

ZHAO, D.L., ATLIN, G.N., BASTIAANS, L. & SPIERTZ, J.H.J. 2006. Cultivar weed-competitiveness in aerobic rice: heritability, correlated traits, and the potential for indirect selection in weed-free environments. *Crop Science* 46: 372-380.

Galeng-Lawilao, J., A. Kumar, D. De Waele. Реакция хозяина при заражении засухоустойчивых аэробных азиатских генотипов риса рисовой галлообразующей нематодой *Meloidogyne graminicola*.

Резюме. На 25 гибридах (F_4 или F_6), происходящих от скрещивания между засухоустойчивым индийским суходольным сортом cv. Vandana и засухоустойчивым индонезийским суходольным сортом cv. Way Rarem (Азиатские сорта), была исследована реакция на поражение нематодой *Meloidogyne graminicola* при аэробных условиях в полевом эксперименте на бае Международного института риса в Лос-Баньос, Филиппины. Реакцию растения-хозяина сравнивали с таковой у восприимчивых азиатских сортов UPLRi-5и IR64 и устойчивым африканским сортом CG14. Ни один из гибридов не был устойчивым. По числу личинок 2-й стадии на корневую систему 22 полученных гибрида оказались частично устойчивыми в сравнении с UPLRi-5, а три - чувствительными. По числу личинок 2-й стадии на грамм корней 13 гибридом оказались устойчивыми, а 12 – восприимчивыми. В сравнении с IR64по двум этим параметрам 13 гибридов оказались частично устойчивыми, а 12 – чувствительными. В аэробных условиях гибриды показывали значительную вариабельность в устойчивости к *M. graminicola*. Вес живых корней оказался наиболее восприимчивым к заражению физиологическим параметром, а процент налившихся зерен на метелку – самым восприимчивым производственным параметром. По показателю сокращения выхода зерен на растение семь гибридов рассматриваются как устойчивые (< 10% падения выхода), девять – как восприимчивые (10-20%), восемь как восприимчивые (21-30%), а один сорт – как сверхвосприимчивый (36%).