THE EFFECT OF TEMPERATURE ON RESISTANCE IN AFRICAN RICE (*ORYZA GLABERRIMA* STEUD.) GENOTYPES TO THE RICE ROOT-KNOT NEMATODE *MELOIDOGYNE GRAMINICOLA*

Ma. Teodora Nadong Cabasan [1,3,4,]*, Stéphane Bellafiore [5,6], Arvind Kumar[3], and Dirk De Waele[1,2,3]

[1]Laboratory of Tropical Crop Improvement, Department of Biosystems, Faculty of Bioscience Engineering, University of Leuven (KU Leuven), Willem De Croylaan 42, B-3001 Heverlee, Belgium; [2]Unit for Environmental Sciences and Management, North-West University, Private Bag X6001, 2520 Potchefstroom, South Africa; [3]International Rice Research Institute (IRRI), DAPO Box 7777, Metro Manila, Philippines; [4]Department of Biological Sciences, College of Arts and Sciences, University of Southern Mindanao, Kabacan 9407 Cotabato, Philippines; [5]IRD, LMI RICE, University of Science and Technology of Hanoi, Agricultural Genetics Institute, Hanoi, Vietnam; [6]IRD Institut de recherche pour le développement, UMR 186, 911, avenue Agropolis, BP 64501, 34394 Montpellier cedex 5, France. *Corresponding author: mtncabasan@usm.edu.ph

ABSTRACT

Cabasan, M. T. N., S. Bellafiore, A. Kumar, and D. De Waele. 2016. The effect of temperature on resistance in African rice (*Oryza glaberrima* Steud.) genotypes to the rice root-knot nematode, *Meloidogyne graminicola*. Nematropica 46:221-228.

The rice root-knot nematode, *Meloidogyne graminicola*, has emerged as a serious soilborne pathogen of rice in most Asian countries. The host response of the *M. graminicola*-resistant African (*Oryza glaberrima*) rice genotypes TOG5674, TOG5675, and CG14 was examined at two day/night temperature regimes, 29/26°C and 34/31°C. At the 34/31°C regime, second-stage juvenile population densities in roots of the African rice genotypes increased significantly compared to those of plants grown at the 29/26°C regime, suggesting that the resistance to *M. graminicola* became ineffective at the latter temperature regime. An increase in temperature also resulted in a significant reduction in all yield-contributing traits and yield of the three African rice genotypes. High variability was recorded in terms of percentage reduction of all traits measured among the genotypes examined at the 34/31°C, compared to the 29/26°C regime. However, the highest reduction was for yield.

Key words: damage potential, *Oryza*, reproductive potential, susceptible, yield loss.

RESUMEN

Cabasan, M. T. N., S. Bellafiore, A. Kumar, y D. De Waele. 2016. Efecto de la temperatura sobre la resistencia al nematodo de las agallas en la raíces del arroz, *Meloidogyne graminicola* en genotipos de arroz africano (*Oryza glaberrima* Steud.) genotypes to the rice root-knot nematode. Nematropica 46:221-228.

El nematodo de las agallas en las raíces del arroz, *Meloidogyne graminicola*, se ha mostrado como un serio patógeno del suelo para el arroz en la mayoría de paises asiaticos. La respuesta como hospedadores de los genotipos de arroz africano (*Oryza glaberrima*) TOG5674, TOG5675, y CG14, resistentes a *M. graminicola* se examinó en dos regímenes de temperatura dia/noche, 29/26°C y 34/31°C. En el régimen 34/31°C, las densidades de juveniles de segundo estadío en raíces de los genotipos de arroz africano aumentaron significativamente en comparación con aquellas plantas cultivadas en el régimen 29/26°C, sugiriendo que la resistencia a *M. graminicola* perdió su efectividad en este ultimo régimen de temperaturas. Un aumento en la temperatura también produjo una reducción significativa en todos los estimadores de producción en los tres genotipos de arroz africano. Se registró una alta variabilidad en términos de porcentaje de reducción de todas las características medidas entre los genotipos examnados a 34/31°C, comparados con el régimen a 29/26°C. No obstante, la mayor reducción fue para la cosecha.

Palavras chave: Potencial de daño, *Oryza*, potencial reproductor, susceptible, perdidas de cosecha.

INTRODUCTION

During the past decade, the rice root-knot nematode, *Meloidogyne graminicola* Golden and Birchfield, has emerged as one of the most common and important soilborne pathogens of Asian rice (*Oryza sativa* L.) in South and Southeast Asia (De Waele and Elsen, 2007; Jain *et al*., 2012). This sedentary endoparasite can occur in all rice-based production systems, lowland as well as upland, irrigated as well as rainfed, and deepwater rice (Bridge *et al*., 1982; Prot *et al*., 1994; Padgham *et al*., 2004; Bridge *et al*., 2005; Win *et al*., 2011). In lowland rainfed rice fields infested with *M. graminicola*, nematicide application resulted in a yield increase of 16 to 20% or about 1 t/ha in Bangladesh (Padgham *et al*., 2004) whereas in upland rice fields, nematicide application resulted in a yield increase of 12 to 33% in Thailand (Arayarungsarit, 1987) and 28 to 87% in Indonesia (Netscher and Erlan, 1993). Resistance to *M. graminicola* has been identified in some African rice (*Oryza glaberrima* Steud.) and Asian rice genotypes (Jena and Rao, 1976; Yik and Birchfield, 1979; Plowright *et al*., 1999; Soriano *et al*., 1999; Sharma-Poudyal *et al*., 2004; Prasad *et al*., 2006; Cabasan *et al*., 2012; De Waele *et al*., 2013; Dimpka *et al*., 2015), and efforts are now underway to introgress this resistance in new Asian rice varieties (De Waele, pers. communication). Expression of resistance is not only influenced by inherent characteristics of the pathogen and the host plant (such as the gene-for-gene interaction) but also by the environment. Thus, one of the potential limitations of the use of nematode-resistant plant genotypes is the loss of efficacy of the resistance trait caused by environmental factors such as high temperatures (Devran *et al*., 2010; Newton *et al*., 2012). Therefore, to optimise the use of these natural resistance sources in a management strategy, the stability of resistance to *M. graminicola* should be tested under different environmental conditions.

Temperature is not only a critical abiotic factor for the growth and yield of rice plants, it can also have an impact on nematode-host plant interactions by influencing the rate of hatching, development, and reproduction of nematode pests (Jatala and Russell, 1972; Noe, 1991; Sydenham *et al*., 1997). Temperature has also been identified as an abiotic factor that may affect the expression of resistance to plant-parasitic nematodes in plants. In root-knot nematode-resistant tomato (*Solanum lycopersicum* L.) genotypes, a soil temperature higher than 28°C can alter the expression of the Mi-gene resistance to many populations of various *Meloidogyne* species such as *M. incognita*, *M. arenaria*, and *M. javanica* (Williamson, 1998). However, in some genotypes of wild tomato (*L. peruvianum* (L.) Mill.), resistance

to *M. incognita* race 2 was stable even at 32°C (Devran *et al*., 2010). The resistance of pepper plants infected with *M. incognita* was compromised at 28 to 32°C, indicating a partial loss of resistance conditioned by the N gene (Thies and Fery, 2000), while the expression of resistance to *M. incognita* in cotton became ineffective at 35°C (Carter, 1982). An increase in severity of root galling was also observed in resistant alfalfa (*Medicago sativa* L.) cultivars infected with *M. hapla* grown at 32°C compared to those cultivated at 28°C (Griffin and Elgin, 1977). In contrast, resistance of some common bean genotypes to *M. incognita* and *M. arenaria* was not reduced or lost at 32°C (Sydenham *et al*., 1997). Nonetheless, one bean genotype was resistant to *M. incognita* at 16 to 22°C but susceptible at 24°C and higher temperatures (Mullin *et al*., 1991). In cucumber, the resistance to *M. hapla* was effective at 30°C while it was partially compromised at 24°C (Cardin, 1979).

With the emergence of *M. graminicola* as a very important pathogen of rice in South and Southeast Asia (De Waele and Elsen, 2007), and the increased efforts to develop Asian rice varieties that are either resistant or tolerant to this nematode species (De Waele, pers. communication), it is essential to determine if the efficacy of the available natural *M. graminicola* resistant and tolerant sources can be influenced by temperature. The definitions for resistance and susceptibility, as well as tolerance and sensitivity as proposed by Bos and Parlevliet (1995), refers to a host plant which either suppresses (resistance) or allows nematode development and reproduction (susceptibility). The plant may suffer little injury even when heavily infected with nematodes (tolerance), or much injury even when relatively lightly infected with nematodes (sensitivity). Resistance and susceptibility can be determined by measuring the nematode population densities in and on the roots, whereas tolerance and sensitivity can be determined by measuring the effect of the nematode population on plant growth, yield-contributing traits and (or) yield (Cook and Evans, 1987).

The objective of our study was to examine the effect of temperature on the expression of resistance or susceptibility and tolerance or sensitivity to *M. graminicola* in selected *M. graminicola*-resistant African rice genotypes.

MATERIALS AND METHODS

Nematode inoculum

The *M. graminicola* population used in this study was isolated from naturally infected Asian rice plants collected in Batangas, Philippines. A

pure culture of the Batangas population originating from a single second-stage juvenile (J2) was maintained in the glasshouse on the susceptible and sensitive Asian upland rice genotype UPLRi-5. The population was maintained at about 28°C in a sandy loam soil (52% sand, 21% loam, 27% clay), that was typical of upland soils and subjected to moisture stress. Infected plants were irrigated with tap water only when needed, with no surface water accumulation (at field capacity = 50% of the soil volume filled with water).

The inoculum was prepared by extraction of J2 from galled roots using the mistifier technique (Seinhorst, 1950). Galled roots were carefully washed, cut into 0.5- to 1-cm-pieces and incubated in a mist chamber. The J2 extracted after 24 hr of incubation were used as inoculum.

Rice genotypes

Three African rice genotypes, TOG5674, TOG5675 and CG14, which are resistant to *M. graminicola* (Plowright *et al.*, 1999; Soriano *et al.*, 1999; Cabasan *et al.*, 2012) were included. TOG5674 and TOG5675 are traditional varieties from Nigeria while CG14 is from Senegal. Two *M. graminicola*-susceptible Asian rice genotypes, IR64 and UPLRi-5, were also included. The rice seeds were obtained from the seed bank of International Rice Research Institute (IRRI), based in the Philippines. Some characteristics of these genotypes have been described in Cabasan *et al.* (2012).

Rice seeds were pre-germinated in Petri dishes and two, 5-day-old seedlings were transplanted in 20-cm-diameter, 24-cm-high plastic pots. The pots were filled with 6 kg of a sterilised sandy loam soil (52% sand, 21% loam, 27% clay) with a pH of 6.3, containing 0.14% N and 1.06% organic C. Plants were grown in two phytotrons each with 8 blocks: one set at an optimal temperature for cultivation of rice crops using 12 hr day/night temperature regime (29/26°C) and the other at a high (34/31°C) regime. Relative humidity was maintained at 70% throughout the duration of the experiment. At planting the soil in the pots was saturated with tap water, while at nematode inoculation the soil-water levels in the pots was at field capacity. One week after transplanting, the seedling population was thinned to one plant per pot.

Roots of 2-week-old plants were inoculated with approximately 3,000 *M. graminicola* J2 by pipetting three aliquots, each containing 1,000 J2, in three 5-cm-deep holes around the base of the seedlings. Two days later, the nematode inoculation was repeated so that the initial population density (Pi) was about one J2/g soil (6,000 J2/plant). There were no uninoculated (control) plants.

The water levels in the soil in which the rice plants grew were maintained at field capacity up to plant maturity. The rice plants were fertilised 3 times (at transplanting, and at 30 and 60 days after transplanting) at a rate of 90-60-60 kg/ha (N-P-K). The experimental lay-out was a randomised complete block design (RCBD) with eight replications for each temperature regime.

At maturity, the plants were carefully uprooted, and the roots of each plant excised from its aerial parts. The African rice genotypes were harvested at 103 days after planting (DAP) while the Asian rice genotypes were harvested at 110 DAP. The roots were washed with tap water, and the severity of root galling was determined based on a rating scale of 0-5 (Hussey and Janssen, 2002). After the fresh root weight of each plant was recorded, the roots were cut into 1-cm-pieces and incubated for 2 wk in a mistifier for nematode extraction (Seinhorst, 1950). After 2 wk in the mistifier, the nematode suspension was collected and the number of J2 per root system (Pf) counted using a stereomicroscope (100× magnification). The nematode multiplication factor (Mf) was calculated as Pf/Pi (Greco and Di Vito, 2009) as a measure of the reproduction of *M. graminicola*.

At harvest, the following three plant growth and four yield-contributing traits were measured: fresh root and shoot weight, plant height (from the soil surface to the tip of the tallest panicle), number of panicles per plant (this number is equal to the number of productive tillers at maturity), number of spikelets per panicle, percent filled grains per panicle, weight of 100 grains per plant, and grain weight per plant (adjusted to 14% moisture content). The yield per plant was measured based on the weight of the filled grains produced per plant, not including the unfilled and partially filled grains. The number of tillers per plant was counted at 30 days after transplanting to examine the effect of temperature on tiller formation at a young plant-growth stage.

Data analysis

Analyses were performed using STATISTICA software. Prior to analysis, nematode counts were $\log_{(x + 1)}$-transformed to reduce the variance in the data. Data were statistically analysed by analysis of variance (ANOVA) when the assumptions of normal distribution and homogeneity of variances were met. Factorial analysis of ANOVA was used to examine the effect of the treatments on plant growth, yield-contributing traits and yield. When an interaction was observed between two factors (temperature regime and rice genotype),

individual comparisons were made for each rice genotype separately. Tukey´s HSD test ($P < 0.05$) was applied for comparisons of factor level means for specific plant growth, yield-contributing traits, and yield. Dunnett's test ($P < 0.05$) was applied to compare the means of nematode reproduction in the resistant African rice genotypes with the means in the susceptible Asian rice genotype UPLRi-5. Data from eight replicates were pooled and analysed.

RESULTS

Significant two-factor interactions, in terms of temperature regime and rice genotype, were observed for nematode reproduction, plant growth and yield parameters. Except for the number of J2/g roots observed at 34/31°C, the number of J2/g roots and J2/root system, as well as the Mf and the root gall index were lower ($P < 0.05$) in the resistant genotypes than in the susceptible reference genotypes IR64 and UPLRi-5 at both temperature regimes (Table 1).

An increase ($P < 0.05$) in number of J2/g roots and J2/root system, Mf, and root gall index was observed in TOG5674 and TOG5675 grown at 34/31°C compared with 29/26°C. In the case of TOG5674, the number of J2/g roots increased 23.3 times, the number of J2/root system 9.4 times and Mf 10 times while the root gall index increased by 1.8 times. In the case of TOG5675, the number of J2/g roots increased 14 times, the number of J2/root system 5.9 times and Mf 5.6 times while the root gall index increased by 1.5 times. In contrast, an increase in temperature did not have a significant effect on the number of J2 per g roots and per root system, and the root gall index of CG14. Only the Mf of this genotype increased ($P < 0.05$) by 2.8 times.

Significant ($P < 0.05$) increases in numbers of J2/g roots and per root system and Mf were not observed for the two susceptible genotypes IR64 and UPLRi-5 grown at either 29/26°C or 34/31°C. In fact, the Mf of UPLRi-5 decreased almost twofold with increasing temperature. An increase in temperature did not have a significant effect on the root gall index of UPLRi-5 but significantly ($P < 0.05$) increased the root gall index of IR64.

An increase in temperature decreased ($P < 0.05$) the fresh root weight of TOG5674 by 67% and TOG5675 by 58%. This was not the case for CG14 and the two susceptible Asian rice genotypes. An increase in temperature decreased the fresh shoot weight (ranging from 31 to 58%) and plant height (ranging from 30 to 43%) of all genotypes with the exception of the plant height of IR64 (Table 2).

An increase in temperature resulted in a reduction ($P < 0.05$) in all yield-contributing traits measured with the exception of the number of tillers per plant of TOG5674 and the number of panicles per plant of TOG5674, TOG5675, and IR64. Substantial differences in percent reduction were observed

Table 1. Effect of temperature on the reproduction of *Meloidogyne graminicola* (Batangas population) on resistant African and susceptible Asian rice genotypes, and on the severity of root galling at plant maturity.

Rice genotype[x]	Temperature regime	
	29/26°C	34/31°C
No. of J2/g roots		
TOG5674	50 ±81a[y]*	1,166 ±710b
TOG5675	111 ±101a*	1,559 ±25b
CG14	476 ±469a*	952 ±558a
IR64	3,392 ±1,618a	3,866 ±2,014a*
UPLRi-5	2,713 ±1,405	1,629 ±1,074
No. of J2/root system		
TOG5674	1,943 ±3,042a*	18,249 ±13,185b*
TOG5675	3,991 ±3,711a*	23,412 ±11,282b*
CG14	11,098 ±7,195a*	23,256 ±14,094a*
IR64	145,956 ±93,492a	120,352 ±47,774a
UPLRi-5	157,931 ±76,616	82,511 ±53,989
Multiplication factor (Mf)[z]		
TOG5674	0.3 ±0.5a*	3.0 ±2.2b*
TOG5675	0.7 ±0.6a*	3.9 ±1.9b*
CG14	1.8 ±1.2a*	3.9 ±2.3b*
IR64	24.3 ±15.6a	20.1 ±8.0a
UPLRi-5	26.3 ±12.8	13.8 ±9.0
Root galling index		
TOG5674	1.3 ±0.5a*	2.3 ±1.0b*
TOG5675	1.3 ±0.5a*	2.0 ±0.8b*
CG14	1.9 ±1.1a*	1.8 ±0.5a*
IR64	3.9 ±1.0a	4.9 ±0.4b
UPLRi-5	4.8 ±0.7	4.6 ±0.7

[x]African (*Oryza glaberrima*) genotypes - TOG5674, TOG5675, and CG14; Asian (*Oryza sativa*) genotypes - IR64 and UPLRi-5.
[y]Data are means ± standard deviation (n = 8); means followed by the same letter in a row are not significantly different according to Tukey's HSD test ($P < 0.05$). Means within columns followed by an * in a category are significantly different ($P < 0.05$) from the susceptible standard UPLRi-5 according to Dunnett's test.
[z]Multiplication factor = number of J2 extracted per root system (Pf)/initial infestation rate (Pi) of 6,000 J2/plant.

Table 2. Fresh root and shoot weight, and plant height (indicating the percentage decrease/increase) of resistant African and susceptible Asian rice genotypes inoculated with 6,000 *Meloidogyne graminicola* (Batangas population) grown under different temperature regimes.

Rice genotype[y]	Fresh root weight (g)			Fresh shoot weight (g)			Plant height at maturity (cm)		
	29/26°C	34/31°C	% change	29/26°C	34/31°C	% change	29/26°C	34/31°C	% change
TOG5674	50.1 a[z]	16.6 b	-66.7	289.7 a	122.8 b	-57.6	184.4 a	104.6 b	-43.3
TOG5675	37.9 a	15.9 b	-57.9	304.2 a	184.2 b	-39.5	197.6 a	112.1 b	-43.3
CG14	32.7 a	27.1 a	-17.2	258.8 a	120.8 b	-53.3	169.3 a	119.3 b	-29.5
IR64	41.4 a	32.5 a	-21.5	186.0 a	128.4 b	-31.0	91.7 a	79.4 a	-13.4
UPLRi-5	60.6 a	52.7 a	-13.0	211.9 a	107.4 b	-49.3	118.0 a	82.2 b	-30.4

[y]African (*Oryza glaberrima*) genotypes - TOG5674, TOG5675, and CG14; Asian (*Oryza sativa*) genotypes - IR64 and UPLRi-5.
[z]Data are means (n = 8); means followed by the same letter in a row are not significantly different according to Tukey's HSD test ($P < 0.05$).

Table 3. Yield-contributing traits, indicating the percentage decrease/increase, of resistant African[y] and susceptible Asian[y] rice genotypes inoculated with 6,000 *Meloidogyne graminicola* J2/plant and grown under different temperature regimes.

Rice genotype	Number of tillers per plant			Number of panicles per plant			Number of spikelets per panicle		
	29/26°C	34/31°C	% change	29/26°C	34/31°C	% change	29/26°C	34/31°C	% change
TOG5674	6.4[z]a	4.5 a	-29.4	23.8 a	30.4 a	27.9	112.0 a	49.4 b	-55.9
TOG5675	6.9 a	3.8 b	-45.5	26.1 a	20.4 a	-22.0	110.0 a	55.6 b	-49.5
CG14	6.1 a	4.0 b	-34.7	29.3 a	44.6 b	52.6	142.7 a	49.6 b	-65.2
IR64	10.5 a	8.1 b	-22.6	24.1 a	22.0 a	-8.8	101.1 a	72.3 b	-28.5
UPLRi-5	7.4 a	5.8 b	-22.0	15.1 a	11.1 b	-26.4	84.7 a	79.9 b	-5.6

[y]African (*Oryza glaberrima*) genotypes - TOG5674, TOG5675, and CG14; Asian (*Oryza sativa*) genotypes - IR64 and UPLRi-5
[z]Data are means (n = 8); means followed by the same letter in a row are not significantly different according to Tukey's HSD test ($P < 0.05$).

among the genotypes. For instance, the number of spikelets per panicle was reduced by only 6% in UPLRi-5 but 65% in CG14. In contrast, the percent-filled grain per panicle was reduced 37% in CG14 and 67% in UPLRi-5. Sometimes the reduction was higher in the resistant genotypes compared with the susceptible genotypes. For instance, the reduction in percent-filled grains per panicle ranged from 25 to 37% in the resistant genotypes, but 60 to 67% in the susceptible genotypes. Similarly, the reduction in the number of spikelets per panicle ranged from 49 to 65% in the resistant genotypes, but was only 6 to 29% in the susceptible genotypes (Table 3). The highest reduction for all genotypes was observed for filled grain weight per plant and was always higher than 80% (Table 4). An increase in temperature increased the number of panicles per plant of CG14 (Table 3), the only positive effect observed.

DISCUSSION

Temperature affected the efficacy of resistance to *M. graminicola* in all three African rice genotypes included in our study, and overall resistance appeared to be more pronounced in TOG5674 and TOG5675 than in CG14. This was demonstrated by the significant increase in numbers of J2 per g roots and per root system, as well as the Mf and severity of root galling of the TOG5674 and TOG5675 plants grown at 34/31°C relative to those grown at 29/26°C. At 34/31°C, the number of J2/g roots of both TOG5674 and TOG5675 was also not significantly different from those in roots of the susceptible genotype UPLRi-5. The high temperature, however, had a direct effect on the root growth of the rice plants, which was significantly reduced in both TOG5674 and TOG5675, but not

Table 4. Yield-contributing traits, indicating the percentage decrease/increase, and yield of resistant African and susceptible Asian rice genotypes inoculated with 6,000 *Meloidogyne graminicola* J2/plant and grown under different temperature regimes.

Rice genotype[y]	% filled grains/panicle			Weight of 100 grains/plant (g)			Filled grain weight/plant (g)		
	29/26°C	34/31°C	% change	29/26°C	34/31°C	% change	29/26°C	34/31°C	% change
TOG5674	87.0a[z]	60.4b	-30.6	2.8a	2.2b	-22.6	41.9a	6.2b	-85.1
TOG5675	86.5a	64.7b	-25.2	2.7a	2.1b	-21.8	42.2a	5.3b	-87.3
CG14	80.7a	51.1b	-36.7	2.4a	2.1b	-10.6	51.7a	5.5b	-89.3
IR64	70.6a	28.0b	-60.3	2.0a	1.3b	-38.5	17.0a	2.6b	-84.5
UPLRi-5	84.4a	27.5b	-67.4	2.4a	1.5b	-36.5	24.2a	2.8b	-88.6

[y]African (*Oryza glaberrima*) genotypes - TOG5674, TOG5675, and CG14; Asian (*Oryza sativa*) genotypes - IR64 and UPLRi-5

[z]Data are means (n = 8); means followed by the same letter in a row are not significantly different according to Tukey's HSD test ($P < 0.05$).

in CG14, or in either susceptible genotype. This decrease in fresh root weight is likely not the only explanation for the increase of J2 numbers/g roots in TOG5674 and TOG5675. Higher J2 numbers/g roots were not recorded for either IR64 and UPLRi-5, and these genotypes showed a reduction of 22 and 13%, respectively, in fresh root weight at 34/31°C compared to 29/26°C. Furthermore, the number of J2/root system in TOG5674 and TOG5675 was significantly higher at 34/31°C than at 29/26°C despite the significant reduction in fresh root weight at 34/31°C.

Our observations suggest that the resistance to *M. graminicola* in the three African rice genotypes became ineffective at 34/31°C. Similar observations on the resistance to *Meloidogyne* species have been made for several other agricultural crops, although the mechanisms involved are not clear. Temperature may have a direct effect on the host plant by affecting the plant morphology or physiology. Temperature may also have a direct adverse effect on the nematodes themselves, although in our study an adverse effect on *M. graminicola* seems unlikely. Fernandez *et al.* (2013) observed little difference (dependent upon non-flooded or flooded soil) in the life cycle duration of *M. graminicola* in the roots of UPLRi-5 plants grown under either 29/26 or 36/32°C. Moreover, at 36/32°C, fewer nematodes developed into second-generation J2 than those at 29/26°C while less J2 were observed at 34/31°C than at 29/26°C. These observations on UPLRi-5 are confirmed by our observation that at 29/26°C the Mf on UPLRi-5 was about twice as high compared with the Mf at 34/31°C (26.3 vs 13.8, respectively).

Resistance genes in plants mediate the plant-pathogen interactions including those of plant-parasitic nematodes (Martin *et al.*, 2003; Belkhadir *et al.*, 2004). The tomato Mi-1 gene is currently the best characterised nematode resistance gene. There are limitations to the resistant effects of Mi-1 since the gene is ineffective at soil temperatures > 28°C (Williamson, 1998). As proposed by Zhu *et al.* (2010), in general the receptor-like function of resistance genes might be the temperature-sensitive component of the plant defense responses.

In our study, both *M. graminicola*-infected African and Asian rice genotypes showed significant reduction in almost every plant growth and yield-contributing trait measured when they were grown at the higher temperature regime, and filled grain weight per plant was reduced by more than 80%. Plants weakened by abiotic stresses, are predisposed to infection by plant pathogens and likely to be more susceptible and sensitive to these pathogens (Boland *et al.*, 2004).

The number of panicles per plants increased with increasing temperatures in the African rice genotype CG14. However, it produced panicles with fewer and shorter branches (data not shown) containing less spikelets per panicle, which mostly were sterile and remained unfilled. This could indicate that, in this rice genotype at high temperatures, panicle production may either escape damage or produce more panicles as a mechanism to compensate for the high sterility.

In summary, a temperature regime of 29/26°C is within the range of the optimum temperature for the normal development of rice plants. Higher temperature can affect the resistance to *M. graminicola* in African rice genotypes. The resistance to *M. graminicola* in African rice genotypes included in our study became ineffective at a temperature regime

of 34/31°C. Sensitivity of the African rice genotypes to *M. graminicola* infection was similar to those for Asian rice genotypes at the higher temperature, and the role of temperature must be considered in the management of *M. graminicola*, especially in the major rice-growing regions in the Philippines and other tropical regions where temperatures often reach 34°C (Bebber *et al*., 2013).

ACKNOWLEDGMENT

LITERATURE CITED

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

Bebber, D. P., M. A. T. Ramotowski, and S. J. Gurr. 2013. Crop pests and pathogens move polewards in a warming world. Nature Climate Change 3:985-988.

Belkhadir, Y., R. Subramaniam, and J. L. Dangl. 2004. Plant disease resistance protein signaling: NBSLRR proteins and their partners. Current Opinion in Plant Biology 7:391-399.

Boland, G. J., M. S. Melzer, A. Hopkin, V. Higgins, and A. Nassuth. 2004. Climate change and plant diseases in Ontario. Canadian Journal of Plant Pathology 26:335-350.

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

Bridge, J., S. Page, and S. Jordan. 1982. An improved method for staining nematodes in roots. Rothamstead Experimental Station, Annual Report, p 171.

Bridge, J., R. A. Plowright, and D. Peng. 2005. Nematode parasites of rice. Pp. 87-130 *in* M. Luc, R.A. Sikora, and J. Bridge (eds.). Plant parasitic nematodes in subtropical and tropical agriculture. Wallingford, UK: CABI Publishing.

Cabasan, M. T. N., A. Kumar, and D. De Waele. 2012. Comparison of migration, penetration, development, and reproduction of *Meloidogyne graminicola* on susceptible and resistant rice genotypes. Nematology 14:405-415.

Cardin, M.-C. 1979. Influence of temperature on the relationships of *Meloidogyne hapla* with cucumber roots. Revue de Nématologie 2:169-175.

Carter, W. W. 1982. Influence of soil temperature on *Meloidogyne incognita* resistant and susceptible cotton, *Gossypium hirsutum*. Journal of Nematology 14:343-346.

Cook, R., and K. Evans. 1987. Resistance and tolerance. Pp. 179-239 *in* R. H. Brown, and B. R. Kerry (eds.). Principles and practice of nematode control in crops. Sydney, Australia: Academic Press.

Devran, Z., M. A. Sogut, and N. Mutlu. 2010. Response of tomato rootstocks with the Mi resistance gene to *Meloidogyne incognita* race 2 at different soil temperatures. Phytopathology Mediterranea 49:11-17.

De Waele, D., and A. Elsen. 2007. Challenges in tropical plant nematology. Annual Review of Phytopathology 45:457-485.

De Waele, D., K. Das, D. Zhao, R. K. S. Tiwari, D. K. Shrivastava, C. Vera-Cruz, and A. Kumar. 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.

Dimpka, S. O. N., Z. Lahari, R. Shrestha, A. Douglas, G. Gheysen, and A. H. Price. 2015. A genome-wide association study of a global rice panel reveals resistance to *Oryza sativa* to root-knot nematodes. Journal of Experimental Biology. Online. DOI:10.1093/jxb/erv470.

Fernandez, L., M. T. N. Cabasan, and D. De Waele. 2013. Life cycle of the rice root-knot nematode *Meloidogyne graminicola* at different temperatures under non-flooded and flooded conditions. Archives of Phytopathology and Plant Protection 47:1042-1049.

Greco, N., and M. Di Vito. 2009. Population dynamics and damage levels. Pp. 246-300 *in* R. N. Perry, M. Moens, and J. L. Starr (eds.). Root-knot nematodes. Wallingford, UK: CAB International.

Griffin, G. D., and J. H. Elgin. 1977. Penetration and development of *Meloidogyne hapla* in resistant and susceptible alfalfa under differing temperatures. Journal of Nematology 9:51-66.

Hussey, H. S., and G. J. W. Janssen. 2002. Root-knot Nematode: Meloidogyne Species. Pp. 43-70 *in* J. L. Starr, R. Cook, and J. Bridge (eds.). Plant resistance to parasitic nematodes. Wallingford, UK: CAB International.

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

Jatala, P., and C. C. Russell. 1972. Nature of sweet potato resistance to *Meloidogyne incognita* and the effects of temperature on parasitism. Journal of Nematology 4:1-7.

Jena, R. N., and Y. S. Rao. 1976. Nature of root-knot (*Meloidogyne graminicola*) resistance in rice (*Oryza sativa*). 1. Isolation of resistant genotypes. Proceedings of the Indian Academy of Science 83:77-184.

Martin, G. B., A. J. Bogdanove, and G. Sessa. 2003. Understanding the functions of plant disease resistance genes. Annual Review of Plant Biology 54:23-61.

Mullin, B. A., G. S. Abawi, and M. A. Pastor-Corrales. 1991. Modification of resistance expression of *Phaseolus vulgaris* to *Meloidogyne incognita* by elevated soil temperatures. Journal of Nematology 23:182-187.

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

Newton, A. C., L. Torrance, N. Holden, I. K. Toth, D. E. L. Cooke, V. Blok, and E. M. Gilroy. 2012. Climate Change and Defense against Pathogens in Plants. Pp. 89-132 *in* S. Sariaslani, and G. M. Gadd (eds.). Advances in Applied Microbiology. Oxford, UK: Academic Press.

Noe, J. P. 1991. Development of *Meloidogyne arenaria* on peanut and soybean under two temperature cycles. Journal of Nematology 23:468-476.

Padgham, J. L., J. M. Duxbury, A. M. Mazid, G. S. Abawi, and M. Hossain. 2004. Yield loss caused by *Meloidogyne graminicola* on lowland rainfed rice in Bangladesh. Journal of Nematology 36:42-48.

Plowright, R. A., D. L. Coyne, P. Nash, and M. P. Jones. 1999. Resistance to the rice nematodes *Heterodera sacchari*, *Meloidogyne graminicola*, and *M. incognita* in *Oryza glaberrima* and *O. glaberrima* x *O. sativa* interspecific hybrids. Nematology 1:745-751.

Prasad, J. S., C. H. M. Vijayakumar, M. Sankar, K. S. Varaprasad, M. S. Prasad, and Y. K. Rao. 2006. Root-knot nematode resistance in advanced back cross populations of rice developed for water stress conditions. Nematologia Mediterranea 34:3-8.

Prot, J.-C., I. R. Soriano, and D. M. Matias. 1994. Major root parasitic nematodes associated with irrigated rice in the Philippines. Fundamental and Applied Nematology 17:75-78.

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 56:288-348.

Sharma-Poudyal, D., R. R. Pokharel, S. M. Shrestha, and G. B. Khatri-chhetri. 2004. Evaluation of common Nepalese rice cultivars against rice root-knot nematode. Nepal Agricultural Research Journal 5:33-36.

Soriano, I. R., V. Schmit, D. S. Brar, J. Prot, and G. Reversat. 1999. Resistance to rice root-knot nematode *Meloidogyne graminicola* identified in *Oryza longistaminata* and *O. glaberrima*. Nematology 1:395-398.

Sydenham, G. M., R. Mcsorley, and R. A. Dunn. 1997. Effects of temperature on resistance in *Phaseolus vulgaris* genotypes and on development of *Meloidogyne* species. Journal of Nematology 29:90-103.

Thies, J. A., and R. L. Fery. 2000. Heat stability of resistance to *Meloidogyne incognita* in Scotch Bonnet peppers (*Capsicum chinense* Jacq.). Journal of Nematology 32:356-361.

Williamson, V. M. 1998. Root-knot nematode resistance genes in tomato and their potential for future use. Annual Review of Phytopathology 36:277-293.

Win, P. P, P. P. Kyi, and D. De Waele. 2011. Effect of agro-ecosystem on the occurrence of the rice root-knot nematode *Meloidogyne graminicola* on rice in Myanmar. Australasian Plant Pathology 40:187-196.

Yik, C. P., and W. Birchfield. 1979. Host studies and reactions of cultivars to *Meloidogyne graminicola*. Phytopathology 69:497-499.

Zhu, Y., W. Qian, and J. Hua. 2010. Temperature modulates plant defense responses through NB-LRR proteins. PLoS Pathogens 6:1-12.