Journal of Nematology 32(3):309–317. 2000.

Expression of Tolerance for *Meloidogyne graminicola* in Rice Cultivars as Affected by Soil Type and Flooding[1]

Imelda R. S. Soriano,[2] Jean-Claude Prot,[3] and Danilo M. Matias

Abstract: The effects of different water regimes on the pathogenicity of *Meloidogyne graminicola* on six rice cultivars were determined in two soil types in three greenhouse experiments. Two water regimes, simulating continuous flooding and intermittent flooding, were used with five of the cultivars. All cultivars were susceptible to the nematode, but IR72 and IR74 were more tolerant than IR20 and IR29 under intermittent flooding. All were tolerant under continuous flooding. UPLRi-5 was grown under multiple water regimes: no flooding; continuous flooding; flooding starting at maximum tillering, panicle initiation, or booting stage; and flooding from sowing until maximum tillering or booting. In sandy loam soil, *M. graminicola* reduced stem and leaf dry weight, root dry weight, and grain weight under all water regimes. In clay loam soil, the nematode reduced root weight when the soil was not flooded or flooded only for a short time, from panicle initiation, or booting to maturity, and from sowing to maximum tillering. In clay loam soil, stem and leaf dry weight, as well as grain weight, were reduced by the nematode under all water regimes except continuous flooding or when the soil was flooded from sowing to booting stage. These results indicate that rice cultivar tolerance of *M. graminicola* varies with water regime and that yield losses due to *M. graminicola* may be prevented or minimized when the rice crop is flooded early and kept flooded until a late stage of development.
Key words: Meloidogyne graminicola, pathogenicity, rice, tolerance, water regime.

The rice root-knot nematode, *Meloidogyne graminicola,* causes yield losses in upland rice and rainfed lowland rice (Jairajpuri and Baqri, 1991; Prot et al., 1994b; Rao et al., 1986). It is also frequently observed in irrigated rice (Netscher and Erlan, 1993; Pradham et al., 1973; Prot and Matias, 1995; Prot et al., 1994), but yield losses are limited under continuous flooding (Kinh et al., 1982; Prot et al. 1994a; Prot and Matias, 1995). However, in many areas, water is not available to keep rice fields continuously flooded during the dry season. Due to the decrease in water availability for agricultural use and the increase in labor costs for irrigation and transplanting, many farmers use wet-seeding, delayed flooding, and intermittent irrigation. Severe crop damage associated with high levels of infestation by *M. graminicola* has been observed in wet-seeded rice in the Philippines and in fields that were not continuously flooded in Myanmar and the Philippines (Prot, unpubl. data). At a time when new cultural practices are being developed to reduce the quantity of water used in irrigated rice, it is important to determine if the abandonment of continuous flooding can result in greater yield losses due to *M. graminicola*.

The objectives of this study were to determine the effects of (i) continuous and intermittent flooding on the pathogenicity of *M. graminicola* on rice cultivars IR20, IR29, IR36, IR72, and IR74; and (ii) delay in flooding after seeding, and flooding from seeding until beginning of crop maturity on pathogenicity of *M. graminicola* on rice cv. UPLRi-5 in two soil types.

Materials and Methods

Three greenhouse experiments were conducted using 20-cm-diam. × 35-cm-high polyvinyl pots. The two soils used were clay loam (44% clay, 37% silt, 19% sand, and 0.12% nitrogen) and sandy loam (9% clay, 20% silt, 71% sand, and 0.05% nitrogen). Nitrogen was applied in all experiments and all treatments at a rate of 90 kg/ha (2 g ammonium sulfate/pot) in three equal parts at sowing and at 30 and 60 days after sowing. The population of *M. graminicola* used in all experiments was originally collected from

Received for publication 28 February 2000.
[1] Supported by the International Rice Research Institute (IRRI) and the Institut de Recherche pour le Développement (IRD).
[2] Entomology and Plant Pathology Division, International Rice Research Institute, MCPO Box 3127, Makati City 1271, Philippines. Tel: (63-2)-845-0563; Fax: (63-2)-891-1292; E-mail: i.soriano@cgiar.org
[3] Institut de Recherche pour le Développement (IRD), Center de Montpellier, 911 avenue Agropolis, BP 5045, 34042 Montpellier cedex 1, France. Tel: (33) 67 61 74 00; Fax: (33) 67 54 78 00; E-mail: prot@mpl.ird.fr
This paper was edited by K. Evans.

Laurel, Batangas, Philippines, from irrigated rice and cultured in a greenhouse on cv. UPLRi-5 under upland conditions. Second-stage juveniles (J2) were extracted from infected roots with intermittent mist (Seinhorst, 1950). Only J2 collected after 24 hours were used as inoculum.

Continuous and intermittent flooding: The effect of continuous and intermittent flooding on the reproduction and pathogenicity of *M. graminicola* on rice cultivars IR20, IR29, IR36, IR72, and IR74 was studied in pots containing 8.5 kg (dry weight) of soil and 0 or 8,500 J2 of *M. graminicola* per pot. Three 5-day-old seedlings were transplanted into each pot after saturating the soil with water. Juveniles were added by pipet 5 cm below the soil surface adjacent to seedlings in three equal parts at transplanting and at 2 and 4 days after transplanting. Immediately after the final inoculation of nematodes, half of the pots were flooded and water levels were maintained at 5 cm above the soil surface throughout the experiment. Intermittent flooding was simulated by briefly flooding the pots to 5 cm above the soil surface twice a week until maximum tillering, and three times a week thereafter. All combinations of soil type, water regime, cultivar, and nematode inoculum level were arranged in a split-split-split plot design with seven replications. Soil type was considered as main plot, water regime as subplot, cultivar as sub-subplot, and inoculum level as sub-sub-subplot. At harvest, grain yield, stem and leaf dry weight, and root dry weight were recorded. Root galling was rated based on a scale of 0–5 where 0 = 0% galled roots; 1 = <10%, 2 = 10 – %, 3 = – , 4 = – 75%, and 5 = >75% galled roots. Juveniles were extracted from two 3-g root subsamples by placing them in an intermittent mist chamber for 5 days (Seinhorst, 1950). Data were analyzed using ANOVA and means separated by Duncan's multiple-range test (DMRT).

Delay in flooding and draining before maturity: The effects of delay in flooding the soil after seeding and draining of floodwater before crop maturity on pathogenicity of *M. graminicola* on rice cv. UPLRi-5 were studied in two experiments. Three-day-old pregerminated seeds were sown (three per pot) in 9 kg of dry soil saturated to maximum capacity. Two inoculum levels were used: 0 or 9,000 J2/pot. Juveniles were introduced to the soil adjacent to the seedlings in three equal parts at sowing and at 3 and 6 days after sowing. Soil was maintained saturated in all pots until completion of the third inoculation.

In the first experiment, four water regimes were used: continuous flooding from seedling stage to maturity, and flooding starting at maximum tillering, booting stage, or panicle initiation. The pots that were kept permanently flooded from seedling stage were flooded to 5 cm above the soil surface from 12 hours after the last inoculation until harvest. Pots flooded at a later stage were watered daily to simulate upland conditions until they were flooded to 5 cm above the soil surface. Pots flooded at maximum tillering, booting, or panicle initiation were flooded 35, 50, or 60 days after sowing, respectively.

In the second experiment, six water regimes were used: continuous upland conditions (watering only when necessary), continuous flooding, flooding at maximum tillering or booting, and flooding until maximum tillering or booting followed by upland conditions until harvest. Pots kept under simulated upland conditions were watered daily until harvest. Procedures identical to those used during the first experiment were followed for the pots continuously flooded and those flooded at maximum tillering or booting stage. Pots flooded until maximum tillering or booting were flooded 12 hours after the last inoculation and kept flooded until they were drained at maximum tillering or booting stage, 35 and 60 days after sowing, respectively. Thereafter, they were watered daily to simulate upland conditions until harvest.

In both experiments, all combinations of soil type, water regime, and nematode inoculum levels were arranged in a split-split plot design with six replications. Soil type was considered as main plot, water regime as subplot, and inoculum level as sub-subplot.

At harvest, grain yield, stem and leaf dry weight, and root dry weight were recorded. J2 were extracted from two 3-g root subsamples by placing them in an intermittent mist chamber for 5 days (Seinhorst, 1950). Data were analyzed using ANOVA and means separated by DMRT.

Results

Continuous and intermittent flooding: The nematode reproduced on all cultivars tested under both water regimes (Table 1). The numbers of J2 recovered per 3 g roots in IR36, IR72, and IR74 were higher in intermittently flooded clay soil than in sandy soil. Under continuously flooded soil, the numbers of J2 recovered per 3 g roots in IR29, IR72, and IR74 were significantly higher in clay soil than in sandy soil. On the contrary, the J2 count from 3 g roots of IR29 was higher in sandy than in clay soil. The number of J2 from IR36 was not affected by soil type. In sandy soil, water regime did not affect the number of J2 recovered from 3 g roots, except in IR72, which had significantly higher J2 populations when grown under intermittent flooding than under continuous flooding. In clay soil, IR29 and IR36 had greater J2 counts under intermittent flooding.

All cultivars had greater root galling under intermittent flooding than under continuous flooding (Table 1). IR72 consistently had the lowest gall ratings. IR20, IR29, and IR36 had more root galling than the other cultivars in both soils and under both water regimes. Root galling in IR20 was significantly reduced in clay soil under continuous flooding.

In the absence of *M. graminicola,* all cultivars had significantly greater shoot dry weight in clay than in sandy soil under both water regimes, except for IR20 under continuously flooded conditions (Table 2). When the nematode was present, shoot dry

TABLE 1. Effects of water regime on the numbers of second-stage juveniles (J2) of *M. graminicola* in roots and root galling of five rice cultivars grown in two soil types.

Rice cultivar	Number of J2 (per 3 g roots) Flooding: Intermittent	Number of J2 (per 3 g roots) Flooding: Continuous	Root galling Flooding: Intermittent	Root galling Flooding: Continuous
	Sandy soil (S1)			
IR20	22,067[a] A[b] ab[c]	45,682 A a	4.3 A a	3.7 B a
IR29	86,570 A a	32,751 A a	4.3 A a	3.0 B b
IR36	13,313 A b	11,513 A b	4.2 A a	2.8 B b
IR72	16,437 A ab	4,970 B c	3.5 A b	2.2 B c
IR74	11,349 A b	11,069 A b	3.8 A ab	2.5 B bc
	Clay soil (S2)			
IR20	22,758 A b	17,316 A b	4.0 A a	2.8 B ab
IR29	83,718 A a	65,101 B a	4.0 A a	3.0 B a
IR36	82,373 A a	12,492 B b	3.8 A ab	2.3 B b
IR72	91,142 A a	10,879 A b	3.3 A b	1.7 B c
IR74	115,620 A a	27,735 A a	3.3 A b	2.3 B b
	Difference (S1–S2)			
IR20	−691 ns	28,366*	0.3 ns	0.8**
IR29	2,852 ns	−32,350*	0.3 ns	0.0 ns
IR36	−69,060**	−979 ns	0.3 ns	0.5 ns
IR72	−74,705**	−5,909*	0.2 ns	0.5 ns
IR74	−104,271**	−16,666**	0.5 ns	0.2 ns

[a] Means of seven replications.
[b] Means followed by a common uppercase letter in a row, for intermittently and continuously flooded conditions, are not significantly different by DMRT ($P < 0.05$).
[c] Means followed by a common lowercase letter in a column, among the five rice cultivars in each soil type, are not significantly different by DMRT ($P < 0.05$).
ns, not significant
*, $P < 0.05$
**, $P < 0.01$

TABLE 2. Effects of *M. graminicola* on the shoot dry weight of five rice cultivars grown under two water regimes and two soil types.

Rice cultivar	Shoot dry weight (g)					
	Sandy soil (S1)		Clay soil (S2)		Difference (S1–S2)	
	J2 per kg soil		J2 per kg soil		J2 per kg soil	
	0	1,000	0	1,000	0	1,000
	Intermittently flooded (W1)					
IR20	23.0[a] A[b] b[c]	13.7 A b	40.5 A b	15.2 B b	−17.5**	−1.5 ns
IR29	23.2 A b	12.2 B b	35.2 A b	24.8 B b	−12.0*	−12.7*
IR36	22.5 A b	18.5 A b	35.0 A b	23.3 B b	−12.5*	−4.8 ns
IR72	32.5 A ab	33.7 A a	55.8 A a	50.0 A a	−23.3**	−16.3**
IR74	34.0 A a	31.2 A a	60.2 A a	46.7 B a	−26.2**	−15.5**
	Continuously flooded (W2)					
IR20	20.2 A ab	18.2 A b	26.7 A c	26.7 A c	−6.5 ns	−8.5 ns
IR29	18.5 A b	22.3 A b	33.5 A c	41.2 A b	−15.0**	−18.8**
IR36	14.8 A b	17.2 A b	28.2 A c	28.5 A c	−13.3*	−11.3*
IR72	24.2 A ab	24.0 A ab	45.3 A b	50.8 A a	−21.2**	−26.8**
IR74	28.7 A a	32.5 A a	66.7 A a	60.0 A a	−38.0**	−27.5**
	Difference (W1–W2)					
IR20	2.8 ns	−4.5 ns	13.8**	−11.5*		
IR29	4.7 ns	−10.2*	1.7 ns	−16.3**		
IR36	7.7 ns	1.3 ns	6.8 ns	−5.2 ns		
IR72	8.3 ns	9.7*	10.5*	−0.8 ns		
IR74	5.3 ns	−1.3 ns	−6.5 ns	−13.3**		

[a] Means of seven replications.
[b] Means followed by a common uppercase letter in a row, for the absence (0 J2) or presence (1,000 J2) of the nematode, are not significantly different by DMRT ($P < 0.05$).
[c] Means followed by a common lowercase letter in a column, among the five rice cultivars in each soil type, are not significantly different by DMRT ($P < 0.05$).
ns, not significant
*, $P < 0.05$
**, $P < 0.01$

weight of IR20 was not affected by soil type under either water regime. All other cultivars had greater shoot dry weight in clay than in sandy soil under both water regimes, except for IR36 under intermittent flooding. Without nematodes, water regime did not affect shoot dry weight, except for IR20 and IR72, which had greater shoot dry weight under intermittent flooding in clay soil. With nematodes, IR29 had greater shoot dry weight under continuous than under intermittent flooding in both soil types. Similar results were observed for IR20 and IR74 in clay soil. On the contrary, shoot dry weight of IR72 was greater in intermittently flooded soil. No nematode effect on shoot weight was observed in continuously flooded sandy or clay soil. However, except in IR72, shoot weight was greater in nematode-free clay soil than with nematodes under intermittent flooding. The same trend was observed in IR29 in sandy soil.

Root dry weights of IR74 and IR72 were influenced by soil type in intermittently and continuously flooded soil, respectively (Table 3). Heavier root systems were produced in clay soil, except in IR74 under intermittent flooding in the absence of the nematode. Without nematodes, water regime did not influence root dry weight, except for IR72 and IR74 in clay soil. When *M. graminicola* was present, all cultivars had heavier root systems when permanently flooded than when intermittently flooded in clay soil. In sandy soil under the same water regime, only the root weight of IR29 was reduced by the nematode. *Meloidogyne graminicola* did not affect root dry weight of cultivars in any of the treatment combinations, except in IR74 under intermittent flooding in sandy soil.

Grain yields of all cultivars, except IR20, were significantly greater in continuously flooded than intermittently flooded clay soil

TABLE 3. Effects of *M. graminicola* on the root dry weight of five rice cultivars grown under two water regimes and two soil types.

Rice cultivar	Root dry weight (g)					
	Sandy soil (S1)		Clay soil (S2)		Difference (S1–S2)	
	J2 per kg soil		J2 per kg soil		J2 per kg soil	
	0	1,000	0	1,000	0	1,000
			Intermittently flooded (W1)			
IR20	1.2[a] A[b] c[c]	0.5 A a	1.2 A b	0.5 A c	0.0 ns	0.0 ns
IR29	1.3 A c	0.5 A a	1.0 A b	0.7 A c	0.3 ns	−0.2 ns
IR36	1.8 A bc	1.0 A a	2.0 A ab	1.5 A bc	−0.2 ns	−0.5 ns
IR72	3.2 A ab	1.7 A a	2.8 A a	3.0 A ab	0.3 ns	−1.3 ns
IR74	4.7 A a	1.2 B a	3.0 A a	3.5 A a	1.7*	−2.3**
			Continuously flooded (W2)			
IR20	2.5 A b	1.5 A b	1.8 A b	2.2 A b	0.7 ns	−0.7 ns
IR29	1.7 A b	1.8 A b	2.2 A b	2.8 A b	−0.5 ns	−1.0 ns
IR36	1.5 A b	1.8 A b	2.8 A b	3.3 A b	−1.3 ns	−1.5 ns
IR72	2.8 A ab	2.7 A ab	5.8 A a	5.5 A a	−3.0**	−2.8**
IR74	4.3 A a	3.8 A a	6.3 A a	5.2 A a	−2.0 ns	−1.3 ns
			Difference (W1-W2)			
IR20	−1.3 ns	−1.0 ns	−0.7 ns	−1.7*		
IR29	−0.3 ns	−1.3 ns	−1.2 ns	−2.2**		
IR36	0.3 ns	−0.8 ns	−0.8 ns	−1.8*		
IR72	0.3 ns	−1.0 ns	−3.0**	−2.5**		
IR74	0.3 ns	−2.7**	−3.3**	−1.7*		

[a] Means of seven replications.
[b] Means followed by a common uppercase letter in a row, for the absence (0 J2) or presence (1,000 J2) of the nematode, are not significantly different by DMRT ($P < 0.05$).
[c] Means followed by a common lowercase letter in a column, among the five rice cultivars in each soil type, are not significantly different by DMRT ($P < 0.05$).
ns, not significant
*, $P < 0.05$
**, $P < 0.01$

in the absence or presence of the nematode (Table 4). In intermittently flooded soil, yields of all cultivars, except IR36 (without the nematode), were not affected by soil type with or without the nematodes. Yields of all cultivars were unaffected by water regime in either soil type in the absence of nematodes, except for IR72 and IR74 in clay soil, which had higher yields when continuously flooded. However, all cultivars planted in both soil types in the presence of the nematode had higher yields under permanent flooding, except for IR36 and IR72 in sandy soil. Under intermittent flooding, *M. graminicola* reduced the yield of IR20 and IR29 in both soils and the yield of IR36 in clay soil. Yields of IR72 and IR74 were not affected by the nematodes in any treatment combination.

Delay in flooding and draining before maturity: In neither experiment was the number of J2 recovered per 3 g roots at maturity influenced by soil type (Table 5). Nematode counts were influenced by water regime in the second experiment but not in the first experiment. In clay soil, the number of J2 recovered per 3 g of root was greater under continuous flooding than under all other water regimens. In sandy soil, nematode counts were lower when the soil was flooded only until maximum tillering or booting stage than when the soil was continuously flooded or flooded from maximum tillering until harvest.

In the first experiment, soil type, *M. graminicola,* and the interaction between *M. graminicola* and soil type influenced shoot dry weight, whereas water regime did not. Shoot dry weight was less in sandy soil than in clay soil (Table 6). The nematode had more influence on shoot dry weight in sandy soil than in clay soil. In sandy soil, shoot dry weight was reduced by the nematode under all water regimes. In clay soil, the nematode

TABLE 4. Effects of *M. graminicola* on the grain weight of five rice cultivars grown under two water regimes and two soil types.

Rice cultivar	Grain weight (g/hill)					
	Sandy soil (S1)		Clay soil (S2)		Difference (S1–S2)	
	J2 per kg soil		J2 per kg soil		J2 per kg soil	
	0	1,000	0	1,000	0	1,000
			Intermittently flooded (W1)			
IR20	22.5[a] A[b] a[c]	7.8 B b	26.3 A b	10.0 B b	−3.8 ns	−2.2 ns
IR29	19.0 A a	7.8 B b	24.8 A b	13.0 B b	−5.8 ns	−5.2 ns
IR36	24.5 A a	17.7 A a	35.8 A a	12.7 B b	−11.3*	5.0 ns
IR72	26.8 A a	25.3 A a	26.2 A b	24.2 A a	0.7 ns	1.2 ns
IR74	23.8 A a	18.7 A a	18.0 A b	17.8 A ab	5.8 ns	0.8 ns
			Continuously flooded (W2)			
IR20	24.3 A ab	22.8 A ab	32.7 A c	34.7 A c	−8.3 ns	−11.8*
IR29	15.3 A b	22.8 A ab	31.5 A c	38.3 A bc	−16.2**	−15.5**
IR36	26.7 A a	25.8 A ab	41.5 A b	42.3 A bc	−14.8**	−16.5**
IR72	24.0 A ab	21.2 A b	50.2 A ab	45.0 A b	−26.2**	−23.8**
IR74	25.3 A a	31.7 A a	53.3 A a	54.0 A a	−28.0**	−22.3**
			Difference (W1-W2)			
IR20	−1.8 ns	−15.0**	−6.3 ns	−24.7**		
IR29	3.7 ns	−15.9**	−6.7 ns	−25.3**		
IR36	−2.2 ns	−8.2 ns	−5.7 ns	−29.7**		
IR72	2.8 ns	4.2 ns	−24.0**	−20.8**		
IR74	−1.5 ns	−13.9**	−35.3**	−36.2**		

[a] Means of seven replications.
[b] Means followed by a common uppercase letter in a row, for the absence (0 J2) or presence (1,000 J2) of the nematode, are not significantly different by DMRT ($P < 0.05$).
[c] Means followed by a common lowercase letter in a column, among the five rice cultivars in each soil type, are not significantly different by DMRT ($P < 0.05$).
ns, not significant
*, $P < 0.05$
**, $P < 0.01$

reduced shoot dry weight when soil was flooded at maximum tillering, panicle initiation, and booting stage. Similar results were observed in the second experiment but, in addition, shoot dry weight was influenced by an interaction between the nematode and water regime. *Meloidogyne graminicola* reduced shoot dry weight in both soils in all water regimes, except under continuous flooding in sandy soil, and in the three treatments where flooding was applied just after nematode inoculation in clay soil.

In both experiments, root weights were affected by soil type at any time of flooding and water regime and *M. graminicola* also influenced root weight (Table 7). Root weight was less when plants were not flooded or were flooded for a short period of time than when they were continuously flooded or flooded for long periods of time. In sandy soil, the nematode reduced root weight under all water regimes, except in continuous flooding in experiment 2. In clay soil, the nematode reduced root weight in unflooded pots and when the duration of

TABLE 5. Number of second-stage juveniles (J2) of *M. graminicola,* recovered per 3 g roots at maturity of rice cultivar UPLR15 grown under different water regimes and in two different soils.

Flooding	Clay soil	Sandy soil
	Experiment 1	
Continuous	8,363[a] a[b]	8,532 a
At maximum tillering	86,408 a	21,962 a
At panicle initiation	79,661 a	52,911 a
At booting	68,532 a	51,290 a
	Experiment 2	
Not flooded	64,123 bc	84,803 bd
Continuous	170,163 a	147,991 ab
At maximum tillering	91,316 b	168,076 a
At booting	37,913 bc	113,370 ac
Until maximum tillering	4,786 c	44,500 cd
Until booting	9,190 c	21,683 d

[a] Mean of six replications.
[b] In a column, means followed by a common lowercase letter are not significantly different at the 5% level by DMRT.

TABLE 6. Combined effects of two different soils, water regimes, and *M. graminicola* on the shoot dry weight (g/hill) of rice cv. UPLR15.

Flooding	Clay soil: Number of J2 per kg of soil 0	1,000	Mean	Sandy soil: Number of J2 per kg of soil 0	1,000	Mean
			Experiment 1			
Continuous	51.8[a] A[b] a[c]	48.1 A a	49.9 α[d]	36.3 A a	21.9 B a	29.1 β
At maximum tillering	57.9 A a	49.8 B a	53.7 α	33.4 A a	18.4 B a	25.9 β
At panicle initiation	52.8 A ab	45.3 B a	49.9 α	34.0 A a	22.2 B a	28.1 β
At booting	42.7 A c	33.2 B b	38.0 α	26.6 A b	17.3 B a	22.0 β
			Experiment 2			
Not flooding	71.1 A a	44.0 B a	57.5 α	44.1 A a	17.1 B a	30.6 β
Continuous	65.0 A a	58.5 A a	61.7 α	31.6 A a	24.5 A a	28.1 β
At maximum tillering	78.4 A a	58.2 B a	68.3 α	35.0 A a	24.1 B a	29.5 β
At booting	69.8 A a	58.5 B a	64.1 α	41.0 A a	31.0 B a	36.0 β
Until maximum tillering	64.5 A a	55.5 A a	59.0 α	34.2 A a	17.0 B a	25.6 β
Until booting	60.1 A a	60.0 A a	60.1 α	31.4 A a	22.0 B a	26.7 β

[a] Mean of six replications.
[b] In a row under each soil, means followed by a common lowercase letter are not significantly different by DMRT ($P < 0.05$).
[c] In a column, means followed by a common lowercase letter are not significantly different by DMRT ($P < 0.05$).
[d] In a row, means averaged over all subplots followed by the same symbol are not significantly different by DMRT ($P < 0.05$).

flooding was short (i.e. those plants that were watered only when necessary or maintained under upland conditions, flooded only from booting to harvesting, and flooded only from sowing to maximum tillering).

In both experiments, soil type, water regime, and *M. graminicola* influenced grain yield (Table 8). Grain yield was less in sandy soil than in clay soil. Grain yield was lower when plants were not flooded or were flooded for a short period of time than when they were continuously flooded or flooded for most of the growth duration. In sandy soil, the nematode reduced grain yield under all water regimes, except when flooding was done from sowing until booting where a yield reduction of 23% was not statistically significant. In clay soil, the nematode reduced yield under all water regimes,

TABLE 7. Combined effects of two different soils types, water regimes, and *M. graminicola* on root dry weight (g/hill) of rice cv. UPLR15.

Flooding	Clay soil: Number of J2 per kg of soil 0	1,000	Mean	Sandy soil: Number of J2 per kg of soil 0	1,000	Mean
			Experiment 1			
Continuous	7.7[a] A[b] ab[c]	6.8 A a	7.3 α[d]	9.6 A a	3.4 B a	6.5 β
At maximum tillering	7.6 A ab	5.4 A ab	6.5 α	6.6 A a	2.2 B a	4.4 β
At panicle initiation	9.1 A a	4.1 B a	6.6 α	8.6 A ab	3.0 B a	5.8 β
At booting	6.6 A b	4.0 B b	5.3 α	6.6 A b	2.4 B a	4.5 β
			Experiment 2			
Not flooding	9.9 A ab	3.3 B c	6.6 α	8.0 A a	1.9 B a	4.9 β
Continuous	11.5 A ab	10.9 A a	11.2 α	6.8 A ab	4.2 A a	5.5 β
At maximum tillering	11.8 A ab	9.4 A ab	10.6 α	8.5 A a	3.2 B a	5.8 β
At booting	12.2 A a	7.3 B a	9.7 α	8.6 A a	3.7 B a	6.1 β
Until maximum tillering	9.6 A ab	3.6 B c	6.6 α	6.0 A ab	2.5 B a	4.2 β
Until booting	9.0 A b	7.3 A b	8.1 α	5.2 A ab	2.1 B a	3.6 β

[a] Mean of six replications.
[b] In a row under each soil, means followed by a common uppercase letter are not significantly different by DMRT ($P < 0.05$).
[c] In a column, means followed by a common lowercase letter are not significantly different by DMRT ($P < 0.05$).
[d] In a row, means averaged over all subplots followed by the same symbol are not significantly different by DMRT ($P < 0.05$).

TABLE 8. Combined effects of different soils types, water regimes, and *M. graminicola* on grain yield (g/hill) of rice cv. UPLR15.

	Clay soil			Sandy soil		
	Number of J2 per kg soil			Number of J2 per kg soil		
Flooding	0	1,000	Mean	0	1,000	Mean
			Experiment 1			
Continuous	51.8[a] A[b] a[c]	48.1 A a	49.9 α[d]	36.0 A a	21.9 B a	29.1 β
At maximum tillering	57.9 A a	49.8 B a	53.7 α	33.4 A a	18.4 B a	25.9 β
At panicle initiation	52.5 A ab	45.3 B a	49.0 α	34.0 A a	22.2 B a	28.1 β
At booting	42.7 A c	33.2 B b	38.0 α	26.6 A b	17.3 B a	22.0 β
			Experiment 2			
Not flooding	32.0 A ab	14.3 B d	23.2 α	12.5 A b	1.6 B c	7.1 β
Continuous	44.1 A a	41.2 A a	42.6 α	24.8 A a	19.0 B a	21.9 β
At maximum tillering	49.4 A a	39.3 B ab	44.4 α	24.8 A a	12.6 B a	18.7 β
At booting	49.3 A a	34.5 B b	41.9 α	23.7 A a	16.8 B ab	20.3 β
Until maximum tillering	35.7 A b	26.3 B c	31.0 α	22.5 A a	5.3 B c	13.9 β
Until booting	43.7 A a	39.1 A ab	41.4 α	22.2 A a	17.1 A ab	19.7 β

[a] Mean of six replications.
[b] In a row under each soil, means followed by a common uppercase letter are not significantly different by DMRT ($P < 0.05$).
[c] In a column, means followed by a common lowercase letter are not significantly different by DMRT ($P < 0.05$).
[d] In a row, means averaged over all subplots followed by the same symbol are not significantly different by DMRT ($P < 0.05$).

except under continuous flooding and when flooding was applied from sowing to booting. In both soils, maximum yield reduction was observed under upland conditions, 87% in sandy soil and 55% in clay soil. In clay soil, yield reduction due to *M. graminicola* increased when duration of flooding after sowing decreased. In both soils, the nematode reduced ($P < 0.05$) yield when soil was drained after it had been flooded from sowing to maximum tillering.

Discussion

All rice cultivars were susceptible to *M. graminicola* but they showed different degrees of tolerance (Trudgill, 1991), depending on water regime and soil type. All cultivars were more tolerant of the nematode under continuous flooding, regardless of soil type. For all cultivars, shoot dry weight and root dry weight were higher under continuous flooding than under intermittent flooding, especially in clay soil. Previous studies have indicated that rice plants grown under flooded conditions were heavier and had more profuse root systems compared with plants grown in saturated soil (Pradham et al., 1973) and that optimum rice grain yield was achieved under continuous shallow flooding (De Datta, 1981). In addition to direct effects on the nematode, continuous flooding may increase the tolerance of rice cultivars for *M. graminicola* by increasing their yield potential.

Under intermittent flooding, the yields of IR20 and IR29 were reduced by *M. graminicola* in both soil types and were rated as intolerant. On the other hand, IR72 and IR74 were tolerant under all water regimes and soil types, and had heavier root and shoot dry weights than IR20 and IR29 with or without nematodes in most treatment combinations. These character differences are genetically governed. A more profuse root system may result in the dilution of the effect of the nematode and may allow the plant to overcome root damage by the nematode.

The results obtained when flooding was delayed or the flood water was drained before maturity showed that the numbers of J2 recovered from permanently flooded plants were similar to or greater than under other water regimes. Netscher and Erlan (1993) reported that rice plants grown under continuous flooding were free of *M. graminicola* in experimental conditions, and virtually free of nematodes in farmers' fields. In their experiment, soil was flooded before transplanting, thus preventing nematode infestation. However, wet-seeded fields are usually flooded 6–10 days after seeding. In our experiments, to simulate the field situation, flooding was done 6 days after seeding and nematode inoculation. This delay may have allowed the nematode to invade the roots. These results confirm previous observations (Bridge and Page, 1982; Prot and Matias, 1995) that *M. graminicola* can survive under flooded conditions and that, once it is established within the roots, flooding does not affect its reproduction.

In clay soil, continuous flooding prevented yield loss due to *M. graminicola.* Moreover, the reduction in root development and grain yield loss due to the nematode decreased with duration of flooding applied after sowing and increased with the delay between sowing and flooding. In sandy soil and under all water regimes, including continuous flooding, *M. graminicola* reduced root development and grain yield. Sandy soils have been found to favor the development of the rice root-knot nematode (Prot et al., 1994a; Rao and Israel, 1972). However, in our experiments, it is possible that permanent flooding had no effect on yield loss caused by *M. graminicola* due to low fertility of the sandy soil. Low nitrogen content of the sandy soil could have rendered the plants more susceptible to nematode damage, even under continuous flooding.

The results from these experiments indicate that degrees of tolerance of *M. graminicola* exist among rice cultivars and that tolerance varies with environmental conditions. Among the environmental factors that affect rice cultivar tolerance of *M. graminicola,* flooding appears to play a key role. Early flooding immediately after sowing, to limit invasion of roots by the nematode and to promote good establishment of the rice crop, appears necessary to prevent or minimize yield losses due to *M. graminicola* in irrigated and in wet-seeded irrigated rice. In addition, continuous flooding until the later stage of rice growth appears to help defer increase in the nematode population. In areas where water supply is limited and continuous flooding of the rice crop is not possible, it could be more efficient to keep soil flooded at the beginning rather than later in the cropping season.

Literature Cited

Bridge, J., and S. L. J. Page. 1982. The rice root-knot nematode, *Meloidogyne graminicola,* on deep water rice (*Oryza sativa* subsp. *Indica*). Revue de Nématologie 5: 225–232.

De Datta, S. K. 1981. Principles and practices of rice production. New York: John Wiley & Sons.

Jairajpuri, M. S., and Q. H. Baqri, eds. 1991. Nematode pests of rice. New Delhi: Oxford and IBH.

Kinh, D-N, N. M. Huong, and N. U. Ut. 1982. Root-knot disease of rice in the Mekong Delta, Vietnam. International Rice Research Newsletter 7:15.

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

Pradham, S. K., S. B. Varada, and S. Kar. 1973. The influence of soil water conditions on growth and root porosity of rice. Plant and Soil 38:501–507.

Prot, J.-C, and D. M. Matias. 1995. Effects of water regime on the distribution of *Meloidogyne graminicola* and other root-parasitic nematodes in a rice field toposequence and pathogenicity of *M. graminicola* on rice cultivar UPL Ri5. Nematologica 41:219–228.

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

Prot, J.-C., L. M. Villanueva, and E. B. Gergon. 1994b. The potential of increased nitrogen supply to mitigate growth and yield reduction of upland rice cultivar UPL Ri5 caused by *Meloidogyne graminicola.* Fundamental and Applied Nematology 7:445–454.

Rao, Y. S., and P. Israel. 1972. Influence of soil type on the activity of the rice root-knot nematode, *Meloidogyne graminicola* Golden and Birchfield. Indian Journal of Agricultural Science 42:744–747.

Rao, Y. S., J. S. Prasad, and M. S. Panwar. 1986. Nematode problems in rice: Crop losses, symptomatology, and management. Pp. 179–299 *in* G. Swarup and D. R. Dasgupta, eds. Plant-parasitic nematodes of India. Problems and progress. New Delhi: Indian Agricultural Research Institute.

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.

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