Nematode ecology, economic importance, and management in rice ecosystems in South and Southeast Asia

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Rice is cultivated on about 140 million ha (IRRI 1991) in five major ecosystems: irrigated, upland, rainfed lowland, deepwater, and tidal wetlands. Nematodes are major pests on most crops. More than 35 genera and 130 species of plant parasitic nematodes are associated with rice (Gerber et al 1987). Some are ectoparasites of the root system of rice (*Criconemella* and *Paralongidorus*); others enter the rice roots and are migratory endoparasites (*Hirschmanniella* and *Pratylenchus*) or sedentary endoparasites (*Meloidogyne*). With the exception of the root knot nematodes (*Meloidogyne* spp.), which causes galls in the roots, most of the root nematodes do not cause diagnostic symptoms and remain unnoticed even if they are constraints to high yields. Two nematodes that are parasitic to rice, *Aphelenchoides besseyi*, the causal agent of the white tip disease, and *Ditylenchus angustus,* which causes the ufra disease, are well-recognized because they attack the aboveground parts of the plants and cause specific symptoms. Among the 130 species of plant parasitic nematodes associated with rice, only a limited number are of economic importance. There are discrepancies in estimates of their economic importance. Sasser and Freckman (1987) estimated yield loss due to plant parasitic nematodes to be 10%; whereas, Herdt (1991) estimated this loss to be 0.1% in Southeast Asia.

This paper reviews the available information on the ecology of nematodes that are parasitic to rice, their economic importance, and the methods available to control them in upland, irrigated, and deepwater rice ecosystems.

The ecosystem and the diversity of nematode populations

With the exception of *A. besseyi*, the "white tip" nematode that occurs in most rice environments (Bridge et al 1990), the plant parasitic nematode fauna are not homogeneous across all rice ecosystems.

The diversity of root parasitic nematode populations in upland rice ecosystems is very high (Table 1); 13 and 11 genera were detected in upland rice-growing areas in

Table 1. Parasitic nematodes of rice roots observed in different rice ecosystems.

Genus	Upland		Rainfed lowland	Deepwater		Irrigated
	Senegal (Fortuner 1975)	Philippines (Villanueva et al 1992)	Senegal (Fortuner 1975)	Bangladesh (Rahman, unpubl.)	Vietnam (Cuc and Prot 1992)	Philippines (Prot et al unpubl.)
Criconemella	+	+	+	+		+
Helicotylenchus	+	+	+			+
Hemicycliophora	+	+	+			
Hemicriconemoides		+				
Heterodera	+		+	+		
Hirschmanniella			+	+	+	+
Hoplolaimus		+	+			
Longidorus			+	+		
Meloidogyne		+	+	+	+	+
Paralongidorus				+		
Paratylenchus	+		+			
Peltamigratus	+		+			
Pratylenchus	+	+	+			
Rotylenchulus		+				
Rotylenchus		+				
Scutellonema	+		+			
Telotylenchus	+		+			
Trichodorus	+		+			
Trichotylenchus	+		+			
Tylenchorhynchus	+	+	+	+	+	+
Uliginotylenchus			+			
Xiphinema	+	+		+		

Senegal (Fortuner 1975) and in the Philippines (Villanueva et al 1992), respectively. However, the number of genera is much more limited in irrigated rice in the Philippines and in deepwater rice in Vietnam, where in most fields one irrigated rice crop is grown after the harvest of the deepwater rice. *Hirschmanniella oryzae* is the prevalent species in flooded rice ecosystems. High populations of this nematode were detected in 99% of the deepwater ricefields in Vietnam (Cuc and Prot 1992b) and in 94% of the irrigated ricefields in the Philippines (Prot et al 1994). The nematode population in the rainfed lowland rice ecosystem is even more diverse than that in upland ecosystems. All the genera observed in the upland rice ecosystem and those observed in the irrigated ecosystem are present in the lowland ecosystem. In addition to species diversity, the frequency and population density of each genus vary with different ecosystems. For example, in the Philippines, high numbers of *Pratylenchus* and *Helicotylenchus* are present in 95-100% of the upland ricefields; whereas, *Hirschmanniella* is not detected. In irrigated ricefields, high numbers of *Hirschmanniella* are omnipresent; whereas, very low populations of *Helicotylenchus* and *Tylenchorhynchus* are detected and *Pratylenchus* are absent.

The species diversity observed in upland and rainfed lowland ecosystems may reflect the diversity of crops grown in rotation or association with rice. It is not proven that all the species detected in these fields are rice parasites. In most irrigated rice, species diversity is low. Differences in the distribution of *Pratylenchus* and *Hirschmanniella* in the Philippines, both active rice parasites, can be explained by differences in submersion of the soil. *Pratylenchus* spp. do not survive in flooded soils; whereas, *Hirschmanniella* spp. are detected only in soils that are flooded at least for some time. The absence of *Hirschmanniella* spp. in the upland rice environment may indicate that submersion is necessary for completion of their life cycle or that under upland rice conditions, competition from other nematodes prevents their development. Hydrologic conditions, especially the duration of flooding of the soil, appear to be the major factors that affect the distribution of parasitic nematodes of rice roots. In soils exposed to long periods of flooding, only a limited number of species are able to survive under anaerobic conditions. In rainfed lowland and deepwater ecosystems, the composition of the nematode fauna usually depends on the duration of submersion.

The distribution of the ufra nematode, *Ditylenchus angustus*, also depends on the environment. *D. angustus* occurs mainly in deepwater rice areas in South and Southeast Asia (Bridge et al 1990). In the Mekong Delta in Vietnam, the development of supplemental irrigation facilities has allowed the progressive abandonment of low-yielding deepwater rice in favor of one or two high-yielding rice crops before and after the flood. This change in cultural practices has resulted in a drastic reduction in the occurrence of ufra disease (Cuc and Prot 1992a). The high-yielding varieties grown under irrigated conditions are susceptible to the nematode, but infestation is low. During the months of low rainfall, the development of *D. angustus,* which requires partial submersion of the plant and high atmospheric humidity to infest the stems (Cox and Rahman 1980, Cuc and Kinh 1981) may be limited in irrigated ricefields where the water level is controlled.

Aphelenchoides besseyi in all rice ecosystems

Aphelenchoides besseyi is present in all rice ecosystems and causes the white tip disease. It is not an obligate parasite of higher plants because it can feed and reproduce on fungi. It has a wide host range that includes chinese cabbage, onion, soybean, sugar cane, sweet corn, sweet potato, and yam. It is seedborne and has been reported from all rice-growing countries (Fortuner and Orton Williams 1975, Ou 1985). During tillering, it feeds ectoparasitically on apical stem meristems (Yoshii and Yamamoto 1950b). Later, it migrates to the developing panicle, enters the spikelets before anthesis, and feeds ectoparasitically on embryo, lodicules, ovary, and stamens (Huang and Huang 1972). After anthesis, reproduction ceases but the development of juveniles to adults continues (Huang and Huang 1972). During grain ripening, nematodes coil into a state of anabiosis. They can survive for up to 3 yr in the grains (Yoshii and Yamamoto 1950b).

Symptoms of attack by *A. besseyi* were described by Yoshii and Yamamoto (1950a) and Todd and Atkins (1958). During early growth, the most characteristic symptom is the whitening of the young leaf tips for a distance of approximately 5 cm. These leaf tips later dry and shred. Other symptoms include twisting of the flag leaf, which hinders emergence of the panicle, atrophied panicles, a reduction in the number of grains, sterile flowers, misshapen grains, and a reduction in 1000-grain weight. In infested fields, yield losses range from 0 to 70% and vary with variety, year, and country (Yamada and Shiomi 1950, Yoshii and Yamamoto 1950a, Atkins and Todd 1959, Tamura and Kagasawa 1959).

Aphelenchoides besseyi can be controlled by cultural practices, use of resistant cultivars, chemical control in the field, or elimination of the nematode from the seed using hot water treatment or chemical application. Yield loss could also be avoided by growing tolerant cultivars. Cultural practices include cleaning of weeds, stubbles, and debris from the precedent crop (Vuong 1969); early planting (Cralley 1949, Yoshii and Yamamoto 1951); and sowing in water (Cralley 1956). Numerous chemical treatments of seeds, seedlings, and soil control the nematode (Fortuner and Orton Williams 1975, Bridge et al 1990); however, the economics of these treatments has not been assessed. Hot water treatment of the seeds at 52-57 °C for 15 min after presoaking in cold water for 3 h efficiently controls the nematode, which is mostly seedborne. Resistant varieties have been reported from most rice-growing areas (Armstrong and Jensen 1978, Bridge et al 1990). In addition, many cultivars are symptomless or tolerant (Goto and Fukatsu 1956, Buangsuwon et al 1971).

Aphelenchoides besseyi may still cause yield losses in some rice-growing areas (Rahman and Miah 1989). However, the nematode can be effectively controlled by hot water treatment of the seeds and by growing resistant cultivars. For example, *A. besseyi* is no longer a rice pest in the United States because it has been controlled by seed treatment in association with the planting of resistant cultivars (Hollis and Keoboonrueng 1984). It will certainly be difficult to find safer, less expensive, and more efficient methods of control.

Nematode pests in upland rice ecosystems

Among the plant parasitic nematodes observed in upland rice, two genera, *Meloidogyne* and *Pratylenchus*, have the highest potential to cause economic damage.

Meloidogyne spp.

Four major species of root knot nematodes occur in upland rice ecosystems: *Meloidogyne graminicola*, *M. incognita*, *M. javanica*, and *M. arenaria*. *M. graminicola* is mainly distributed in South and Southeast Asia (Bridge et al 1990). Its host range includes many weeds common in ricefields. *M. incognita*, *M. javanica*, and *M. arenaria* occur in most of the upland rice-growing areas in Africa (Luc and de Guiran 1960, Babatola 1980, Fortuner 1981) and South America (Bridge et al 1990). They have an extremely wide host range that includes most food and cash crops. Root knot nematodes are sedentary root parasites. They induce hyperplasia and hypertrophy in root tissues and produce gall formations throughout the root system. Aboveground symptoms include chlorosis, reduction in growth, tillering, and panicle numbers, wilting, delay in flowering, and unfilled spikelets (Babatola 1984, Diomandé 1984). Symptom intensity varies according to the rice variety and the species of *Meloidogyne*.

In India, yield losses of 16-32% were reported with *M. graminicola* (Biswas and Rao 1971, Rao and Biswas 1973). The population level that caused a 10% reduction in yield was estimated at 120 nematode per 10-d-old plant (Rao et al 1986). In the same country, Jairajpuri and Baqri (1991) estimated that the average yield loss because of *M. graminicola* in upland rice was 10-20%. Losses were as high as 50% in the case of severe infestations. High soil populations of *M. incognita* or *M. javanica* at sowing are necessary to cause grain losses. Yield losses of 40% were observed with 8000 juveniles of *M. incognita* per dm^3 of soil (Babatola 1984). More than 1000 *M. javanica* eggs per plant were necessary to reduce yield (Sharma 1980).

Chemical treatments, soil amendments, and crop rotations have been tested to control root knot nematodes in upland rice. Soil treatments with carbofuran, 1,3-dichloropropane- 1,2-dichloropropene mixtures (DD), methylbromide, or oxamyl effectively control these nematodes (Rao et al 1986). However, their applicability has not been assessed. Incorporation of tea waste, neem leaf, mustard cake, and water hyacinth compost has been suggested (Roy 1976, Jairajpuri and Baqri 1991). Long rotations with resistant plants or poor hosts such as groundnut, maize, soybean, sweet potato, castor, sesame, and onion (Rao et al 1986) reduce populations to a low level.

Few upland rice cultivars are resistant to or tolerant of root knot nematodes. Diomandé (1984) observed that *Oryza glaberrima* cultivars were resistant to *M. incognita*; whereas, *Oryza sativa* cultivars were susceptible. However, some improved cultivars (IRAT109, IRAT112, IRAT106, and IRAT133) were tolerant. Ikong Pao, which is usually grown in a rainfed lowland environment but which can be grown in upland conditions, shows some resistance to *M. incognita* (Babatola 1980). Recently Sujamkuhi, Aus 196, and a breeding line (IR47686-09-2B) were found tolerant (Villanueva and Prot, IRRI, unpubl.).

Pratylenchus spp.

Root lesion nematodes are migratory endoparasites. Two species—*Pratylenchus indicus* found in India and Pakistan, and *P. zeae* found in Africa, North and South America, and South and Southeast Asia—cause yield losses in upland rice. The host range of *P. zeae* includes weeds (*Amaranthus spinosus*, *Cynodon dactylon*, *Digitaria sanguinalis*, and *Echinochloa* sp.) and food crops such as maize, groundnut, wheat, oat, and sorghum (Bridge et al 1990). They induce metabolic changes in the plant (Prasad et al 1982) and cause lesions in the root cortex, which become necrotic and coalesce. They do not produce any specific aboveground symptom but root size, plant growth, and numbers of tillers and panicles are reduced (Plowright et al 1990, Matias and Prot 1992). *P. zeae* is omnipresent in upland rice ecosystems in the Philippines (Villanueva et al 1992) and Sumatra (Prot et al 1992). Its control by chemical treatment (Plowright et al 1990) or two croppings with cowpea or mungbean (Aung and Prot 1990) resulted in 13-55% yield increase. Under field conditions, yields are not correlated with initial nematode populations, but they depend on the nematode population density at harvest (Prot 1990, Prot and Savary 1992). Yield increase after control of low populations of *P. zeae* (Plowright et al 1990) and the absence of correlation between initial population and yield both in pot experiments (Matias and Prot 1992) and under field conditions (Prot and Savary 1992) suggest that yield loss can occur when detectable populations of this parasite are present. Significant yield losses (34%) caused by low initial number of nematodes (30 per seedling) have been observed with *P. indicus* (Prasad and Rao 1978b). *P. indicus* can be controlled by crop rotations with nonhost crops such as barley, mungbean, and wheat (Prasad and Rao 1978a).

Because they are widely distributed in upland rice, the root lesion nematodes may be among the most important pests of this crop. Low populations of these nematodes at sowing time cause important yield losses; therefore, it will be difficult to increase rice yield by controlling them by crop rotation under farmers' field conditions. It would be useful to identify sources of resistance or tolerance.

Other nematodes

Three other plant parasitic nematodes damage upland rice. In Japan, *Heterodera oryzicola* (Kumari and Kuriyan 1981) and *Heterodera elachista* (Shimizu 1971) can decrease the yield by 17-42% and 7-19%, respectively. *Hoplolaimus indicus* is found only in India where initial population levels of 100-10,000 nematodes per plant can reduce yield by 10-20% (Ramana and Rao 1978). They are of local importance.

Nematode pests in irrigated rice ecosystems

The rice root nematodes, *Hirschmanniella* spp., are omnipresent in flooded rice ecosystems especially in irrigated rice. Seventeen species of *Hirschmanniella* have been recorded in ricefields and seven of them damage rice: *H. belli, H. gracilis, H. imamuri, H. mexicana, H. mucronata, H. oryzae,* and *H. spinicaudata* (Bridge et al 1990). *H. oryzae* is recorded in 94% of the irrigated ricefields in the Philippines (Prot et al 1994) and in 99% of the ricefields in the Mekong Delta in Vietnam (Cuc and Prot 1992b). It is the most commonly found nematode species in flooded rice environments. Another root parasitic nematode, the rice root knot nematode, *M. graminicola*, has been detected in 50% of the irrigated ricefields in Central Luzon, the major rice-producing area in the Philippines, and it is common in irrigated ricefields in the Mekong Delta (Prot and Cuc 1990).

Hirschmanniella spp.

The rice root nematodes, *Hirschmanniella* spp., have a large host range that includes numerous ricefield weeds and a few crops such as maize, tomato, and sugarcane (Bridge et al 1990). They are migratory endoparasites that produce cavities in the root cortex and brown lesions (Van der Vecht and Bergman 1952, Babatola and Bridge 1980, Hollis and Keoboonrueng 1984). *Hirschmanniella* spp. do not produce specific aboveground symptoms. They can cause yellowing of the plant, reduce the number of tillers, and delay flowering. Inoculation experiments, conducted in microplots, have established that *H. oryzae* can reduce yield by 23% when adequate fertilizers are applied and by 42% when fertilizers are not applied (Fortuner 1974, 1977). Similar results were obtained in inoculation experiments conducted in pots. At a population level of 1000 nematodes per plant, *H. imamuri, H. oryzae*, and *H. spinicaudata* reduced yields by 31-34% (Babatola and Bridge 1979). With *H. oryzae*, yield reductions of 27-39% were observed with inoculum levels of 1200 nematodes per plant (Yamsonrat 1967), 100 nematodes per plant (Mathur and Prasad 1972), and 1-10 nematodes per gram of soil (Jonathan and Velayuthan 1987). Panda and Rao (1971) observed a reduction of 51% in grain weight when 1-d-old seedling were inoculated with 5000 *H. mucronata*. In Vietnam, Khuong (1987) estimated that economic damage occurred at 40 nematodes per hill at transplanting. However, Thorne (1961) estimated that *H. oryzae* did not cause yield loss under favorable agronomic conditions.

Hirschmanniella spp. can be controlled by chemicals and cultural practices. Chemical control results in significant yield increase: 24-36% in Thailand (Taylor 1968) and 10-38% in Japan (Ichinohe 1972). Experiments in Japan indicated that chemical control of nematodes must be accompanied by a reduction of N input by 20-60% to avoid too rapid growth and lodging (Ichinohe 1972). In Ivory Coast, nematicide treatments increased yield by 20-53%, but the absence of significant correlation between number of nematodes and yield suggested that an unidentified factor was suppressing both nematode population and yields (Cadet and Quénéhervé 1982). In spite of the yield increases, chemical controls are seldom economical and practical (Ichinohe 1972). Crop rotations with nonhost dry season crops such as cotton, cowpea, groundnut, millet, onion, pigeon pea, sorghum, soybean, sweet potato, tobacco, and wheat (Mathur and Prasad 1973, Babatola 1979) can be used to reduce population levels. Three green manure crops that have different modes of action can be used to control *Hirschmanniella* spp. *Aeschynomene afraspera* and *Sesbania rostrata* act as trap plants. The nematodes infect the roots and appear to be killed inside the roots (Germani et al 1983, Pariselle 1987, Hendro et al 1992). *Sphenoclea zeylanica* produces toxic exudates (Mohandas et al 1981). In microplots, after *H. oryzae* was controlled by growing *S. rostrata*, the yield of rice was increased by 214% compared with continuous rice cropping (Germani et al 1983). Under field conditions, the control of *H. mucronata* and *H. oryzae* by the use of *A. afraspera* and *S. rostrata* as rotational crops (without incorporating them as green manure) resulted in yield increases of 27-164% (Prot et al 1992). Without nematode control, yield losses due to rice root nematodes can be reduced by increasing fertilizer inputs (Mathur and Prasad 1972).

Meloidogyne graminicola

The rice root knot nematode was not considered a pest in irrigated rice because it was believed that it could not invade rice roots under flooded conditions (Bridge and Page 1982). However, *M. graminicola* is able to invade the roots, cause galls, reproduce, and migrate from root to root under a permanent flooding depth of 10 cm (Tandigan and Prot, IRRI, unpubl.). It may be a pest of irrigated rice in some areas, especially where farmers use flash irrigation or where susceptible dry season crops are grown in rotation with rice. Yield losses caused by *M. graminicola* in irrigated rice have not been assessed. Numerous irrigated rice cultivars are resistant to this nematode (Bridge et al 1990).

Other nematodes

Criconemella onoensis decreases rice production by 15% in Louisiana (Hollis et al 1968). This nematode is seldom observed on irrigated rice in South and Southeast Asia. *Paralongidorus australis* caused poor growth in irrigated rice in Queensland, Australia (Stirling 1984, Stirling and Vawdrey 1985). These nematodes appear to be of of local importance.

Nematode pests in deepwater rice ecosystems

In addition to *A. besseyi*, two other nematodes may cause yield losses in deepwater rice: *Ditylenchus angustus* and *Meloidogyne graminicola.*

Ditylenchus angustus

The rice stem nematode, *D. angustus,* is the causal agent of ufra disease in Bangladesh, India, Myanmar, and Vietnam (Ou 1985). An ectoparasite, it feeds on the younger tissues of unemerged leaves, leaf sheaths, peduncles, and developing spikelets. It can survive in an active state on the living host throughout the year, but in absence of the host, it coils and survives on stubble and crop debris left in the field (Cox and Rahman 1979b). Plant infestation, disease development, and spread are favored by humidity above 80%, an air temperature of 30 °C, and flood and high rainfall (Butler 1913, 1919; Cox and Rahman 1980; Cuc and Kinh 1981; Rahman and Evans 1987). Several wild rices and weeds *Hygroryza aristata, Leersia hexandra, Sacciolepis interrupta,* and *Echinochloa colona* are alternative hosts (Hashioka 1963, Cuc 1982, Bridge et al 1990).

Splash-pattern chlorosis at the bases of young leaves is the diagnostic symptom at the vegetative stage of the crop. After heading, panicles and flag leaves are distorted and twisted. In severe infections, panicles may either remain enclosed within distorted sheaths or partially emerge. In all cases, spikelets are mostly unfilled. In infested fields, yield losses range from 5 to 100%: 5-50% in Uttar Pradesh (Singh 1953); 10-30% in West Bengal and Assam (Rao et al 1986), 40-100% in Bangladesh (Miah and Bakr 1977a), and 50-100% in Vietnam (Cuc and Kinh 1981). In Bangladesh, Catling et al (1979) estimated the annual yield loss caused by ufra in deepwater rice to be 4% (20% yield loss over 20% of the area).

Ditylenchus angustus can be controlled by cultural practices, crop rotations, and chemicals. In addition, sources of tolerance and resistance have been identified. Destruction of weeds and ratoons and burning of stubble and straw are efficient and have long been suggested to control ufra (Butler 1919). However, it is sometimes difficult to burn the stubble and straw because of standing water in the field, or because a large proportion of the straw is removed for cattle feeds and fuel, which leaves an insufficient amount for effective burning. Farmers' collaboration is also essential, otherwise nematodes from unburned fields will spread to fields in which the stubble has been burned. Delays in sowing and transplanting reduce disease incidence and increase yield considerably (McGeachie and Rahman 1983). They are difficult to apply in an agricultural system that is totally dependent on rain. The nematode is spread by water flow; therefore, improvements in river bunds and the construction of irrigation canals to control water flow may prevent spread of the nematode (Sein and Zan 1977). Application of zinc (Miah et al 1984) and calcium silicate (Rahman, IRRI, unpubl.) reduce ufra incidence and increase yield.

Nonhost crops such as jute (McGeachie and Rahman 1983) and mustard (Miah and Rahman 1985) grown in rotation reduce ufra incidence. In addition, ufra incidence was low in fields where the rotation deepwater rice - dry season irrigated rice - deepwater rice was practiced in Bangladesh.

Chemicals such as benomyl, carbofuran, fensulfothion, hexadrin, monocrotophos, and phenazine have been tested to control *D. angustus* (Miah and Bakr 1977a, Sein 1977b, Cox and Rahman 1979a, Rahman et al 1981, Miah and Rahman 1985). Chemical treatments efficiently control the nematode, but they are uneconomical and not feasible.

A large number of wild rices, rice varieties, and breeding lines have been screened for resistance to *D. angustus*. Khao Tah Ooh in Thailand (Hashioka 1963), B-69-1 in Myanmar (Sein 1977a), BKN 6986-8 in Vietnam (Kinh and Nghiem 1982), RD16-06 and *Oryza subulata* (Miah and Bakr 1977b) and nine Rayada lines (Rahman 1987) are resistant or moderately resistant. Several crosses were made to develop an ufra-resistant variety acceptable to farmers. These crosses showed resistance to moderate resistance both in F_2 and F_3 populations of IR59239, IR63188, IR63225, and IR63226 (Rahman, IRRI, unpubl.). In addition, the early-maturing cultivars Digha and Padmapani escaped postinfection damage (Mondal and Miah 1987, Rathaiah and Das 1987).

Meloidogyne graminicola

Meloidogyne graminicola have been recorded in deepwater rice in Bangladesh (Page and Bridge 1978), India (Prasad and Rao 1985), and Vietnam (Cuc and Prot 1992b). Symptoms are similar to those observed in upland rice. Infested plants usually fail to elongate and remain submerged as the flood rises. In infested fields, 40-50% of plants are drowned, which results in a poor stand and low yield (Rahman et al 1990). Yield reductions of 9-22% in Bangladesh (Rahman et al 1990) and up to 65% in Vietnam (Kinh et al 1982) have been reported. The control methods used in upland rice can be used in deepwater rice. In addition, breeding lines BR306-B-3-2, BR224-2B-2-5, and variety Gabura are resistant (Rahman 1990).

Other nematodes

Hirschmanniella spp. are omnipresent in deepwater rice in Vietnam (Cuc and Prot 1992b) and have been reported from deepwater rice in Bangladesh (Page and Bridge 1978). However, their importance, as well as the importance of other nematodes present in this ecosystem, have not been assessed.

Conclusion

Plant parasitic nematodes are present in all rice ecosystems, but the diversity of the nematode fauna and the distribution of genera and species depend on the ecosystem.

Some are found only in upland rice, others are observed only in soils that are flooded for some time. The rainfed lowland rice ecosystem appears to be a transition environment where the species observed in both upland and flooded environments can be present. Flooding seems to be the most important factor affecting the distribution of the different species of rice parasitic nematodes.

Aphelenchoides besseyi, the white tip nematode, and *D. angustus*, the ufra nematode, parasitizes the aboveground parts of the rice plant, cause diagnostic symptoms, and are well-recognized. Infestation by *A. besseyi* can be kept below the economic threshold by seed treatments and by planting resistant cultivars. *Ditylenchus angustus* is a major pest of deepwater rice in Assam (India) and Bangladesh. However, because deepwater rice accounts for only 3% of the total rice production in South and Southeast Asia, the ufra nematode has a limited and localized impact.

Root parasitic nematodes do not produce specific aboveground symptoms and, most of the time, remain unnoticed. The symptoms they produce (chlorosis, poor growth, and tillering) are attributed to other causes such as poor soil conditions or lack of fertilizer. However, because they are omnipresent and permanently present in ricefield soils, root parasitic nematodes can be major pests of rice. For example, *Pratylenchus* spp. and *Meloidogyne* spp. are widespread in upland rice ecosystems and *Hirschmanniella* spp., mainly *H. oryzae*, are omnipresent in flooded rice ecosystems. They cause significant damage and their control by chemicals or crop rotations always results in significant yield increases. Because irrigated rice accounts for 72% of total rice production, the rice root nematodes, *Hirschmanniella* spp., which are also present in rainfed lowland and deepwater rice ecosystems, are certainly the rice parasitic nematodes with the greatest potential for economic impact. *Pratylenchus* spp. and *Meloidogyne* spp., which can cause more than 30% loss of yield over large upland rice-growing areas, are also of major importance. Their importance may even increase if cultivation of upland environments is intensified and limits traditional slash-and-burn practices. *Meloidogyne graminicola,* which is already present in flooded ecosystems, may become a major pest of irrigated rice if flash irrigation becomes a common practice because of the increasing scarcity and cost of irrigation water.

Soilborne nematodes are difficult to control. Because rice is not a high-value cash crop and because of human health and environmental hazards, control of soilborne nematodes with chemicals is neither economical nor feasible. Long fallows or crop rotations are often not acceptable to poor farmers who cultivate their limited area of land and cannot afford to take their land out of rice production. Crop rotation is also of limited value because the nematodes are not in pure populations. A crop rotation that controls one nematode will increase the damage caused by another. For example, *Hirschmanniella* spp. can be controlled by a rotation with *S. rostrata,* but the legume crop is a good host for *M. graminicola* and yield loss caused by this nematode will increase. This failure of *S. rostrata* rotation has been observed in north Thailand where *M. graminicola* is common in both rainfed lowland and upland rice (D. Puckridge, IRRI, pers. commun.).

Resistance and tolerance are the most promising tools for economic control of rice parasitic nematodes. Identification and transfer of resistance to high-yielding cultivars that are acceptable to rice farmers and consumers will require cooperative research by geneticists, plant breeders, and nematologists. Biological control may be an alternative to chemical control. The development of biocontrol agents will require the participation of microbiologists, agronomists, and nematologists. It may also be possible to limit or compensate the losses caused by root parasitic nematodes by using better methods of crop management. The development of these methods will require a characterization of host-parasite relationships and collaboration between agronomists and nematologists.

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