Part II. Section 4. Rice nematodes or roundworms

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1. Introduction

Nematodes or roundworms form a biologically diverse phylum of unsegmented molting animals. They are the most numerous Metazoa on earth and occur in nearly all habitats as free-living or parasites of plants and animals. While only 23,000 different species have been described so far, there might be more than 1 million nematode species (Blaxter and Koutsovoulos 2015).

In contrast to their great range of size and diversity of life styles, nematodes display a relatively narrow morphology (Decraemer and Hunt 2013). They have a long thin tubular body consisting of an external cylinder (the body wall) and an internal cylinder (the digestive system) separated by the fluid-filled pseudocoelom. Typically, nematodes possess a cuticle that is a multi-layered proteinaceous cover secreted by the underlying hypodermis. To allow growth, nematodes undergo four molts from the first stage juvenile to the adult. During molting, the new cuticle is synthesized and the old one is shed. Development starts in the egg with embryogenesis forming the stage-1 juvenile, molting into stage 2 inside the egg. The stage-2 juvenile hatches from the egg and, in most plant-parasitic nematodes, this stage is infective, i.e., able to invade the host plant. Inside the plant, the stage-2 juvenile will then develop through consecutive molts into adult nematodes.

Nematodes are, in essence, aquatic animals. They depend on water films for their locomotion and their active life. Nevertheless, some species can withstand long periods of dehydration in an anhydrobiotic stage (Treonis and Wall 2005). The plant-parasitic *Globodera* and *Heterodera* species have evolved cysts protecting their eggs as a survival mechanism to adverse conditions.

In recent decades, nematode classification has been significantly influenced by molecular phylogenetic analyses. Increasingly wide-ranging analyses, including more species and even whole genomes, are gradually leading to a stable phylogeny (Blaxter and Koutsovoulos 2015). One of the particularities of the Nematoda is the multiple emergence of (animal and plant) parasitic lifestyles. The phylum Nematoda comprises three subclasses (Enoplia, Dorylaimia, and Chromadoria) and plant-parasitism has independently evolved in each of these subclasses.

Plant-parasitic nematodes are well equipped for infection of plants. Despite the fact that plant parasites are not always directly related in phylogenetic terms (Blaxter and Koutsovoulos 2015), convergent evolution has resulted in common structural features (Decraemer and Hunt 2013). All plant-parasitic nematodes have a needle-like structure that is used to pierce plant cells. This structure (stylet, onchiostyle or odontostylet in the various taxonomic groups) is used to introduce nematode secretions into plant tissues and to feed from plant cells. Stylets vary in shape and size according to the feeding strategy of the nematode; for example, ectoparasitic nematodes that feed on epidermal cells have shorter stylets than those feeding on cells deeper within the plant. In many plant-parasitic nematodes, the pharyngeal gland cells are enlarged in comparison to free-living nematodes such as the model species *Caenorhabditis elegans*. The secretions of these glands play important roles in the host parasite interaction.

The relationships between plant-parasitic nematodes and their hosts are diverse. Although some plant-parasitic nematodes ascent into the aerial plant parts, most are root dwellers. They may be sedentary or migratory and can be ectoparasites or endoparasites. For migratory ecto- and endoparasites, plant cells simply provide a temporary food source, and the interaction between the nematode and the plant is limited. They are called migratory because all stages from J2 (second-stage juvenile) to adult are vermiform, mobile, and infective. For other nematodes, the interactions are far more complex and long lasting; the sedentary endoparasitic nematodes are fundamentally biotrophic: the stage-2 juveniles induce sophisticated feeding sites in the roots of their hosts that serve to supply the nematode with a rich and continuous food source. Inside the roots, the stage-2 juveniles become sedentary and they lose their muscles and get a swollen body. The juveniles molt at the feeding site, all consequent stages being sedentary, except for the adult males that are mobile.

Nematode feeding sites are incredibly diverse but have some conserved features (Wyss 2002). All have structural characteristics of metabolically active cells including cytoplasm highly enriched in subcellular organelles. Many show signs of DNA replication and have multiple enlarged nuclei. Syncytia induced by cyst nematodes are large multinucleate cells formed by breakdown of plant cell walls and fusion of adjacent protoplasts. Giant cells of root-knot nematodes are formed through repeated rounds of nuclear division and cell growth in the absence of cytokinesis (Kyndt et al 2013). The nematodes that induce these complex feeding sites are among the most economically important plant-parasitic nematodes.

In the sedentary endoparasitic nematodes, there are clearly two subventral gland cells and one dorsal gland cell. The subventral gland cells are large and full of secretory granules in the invasive J2 and during the earliest stages of parasitism. By contrast, the dorsal gland cell increases in size throughout the life cycle, indicating a role later in the parasitic process. The secretions of the subventral glands contain a range of cell wall degrading enzymes to overcome the tough plant cell wall barrier during nematode penetration, migration, and feeding. Phylogenetic analysis of the encoding genes convincingly supports several independent events of horizontal gene transfer from rhizosphere fungi and bacteria into nematode genomes (Haegeman et al 2011).

Plant parasitic nematodes attacking crop plants can cause significant yield losses, estimated at USD 80 billion per year (Nicol et al 2011). Probably, this is an underestimation because plant-parasitic nematodes are microscopic, usually below ground and induce relatively nonspecific symptoms resembling nutrient deficiencies or abiotic stress. For rice, production losses of 10 to 25% have been estimated (Bridge et al 2005). Over 100 nematode species have been reported infesting rice (Fortuner and Merny 1979), but we will limit the descriptions in this chapter to the best studied species that are of economic importance.

Rice is grown in diverse cultivation systems that also modulate the prevalence of specific plant-parasitic nematode species. The foliar parasite, *Ditylenchus angustus*, also known as the rice stem nematode, is a major problem in deep water rice in India and Southeast Asia. *Aphelenchoides besseyi* (white tip) and *Hirschmanniella sp.* (root rot) are nematodes that cause frequent problems on shoots and roots, respectively, of lowland irrigated rice throughout the world. *Heterodera* spp. damage mainly lowland irrigated rice and have been identified as a major problem on rice in West Africa (Coyne and Plowright 2002). On the other hand,

upland rice is commonly infested by lesion nematodes, *Pratylenchus* and root-knot nematodes (*Meloidogyne* spp.). Root-knot nematodes, however, can occur in nearly every rice cultivation system, causing yield losses depending on the conditions and the species. They are most likely a major factor in the yield decline of aerobic rice, an evolving water-saving rice cultivation system (Kreye et al 2009).

Molecular analysis of rice-nematode interactions has emerged as a new research topic in the past decade (Kyndt et al 2014). The response of rice to different types of plant parasitic nematodes has been compared (Kyndt et al 2012) and a detailed analysis of nematode populations and their genetic diversity has been facilitated by molecular techniques, like in the case of the rice root-knot nematode (Bellafiore et al 2015). Haegeman et al (2013) and Petitot et al (2015) have investigated the transcriptome of *Meloidogyne graminicola* across several life stages of the nematode. To search for possible effectors, transcriptomes of *Hirschmanniella oryzae* (Bauters et al 2014), *Pratylenchus zeae* (Fosu-Nyarko et al 2016) and *Aphelenchoides besseyi* (Wang et al 2014) are available. Indeed, to get more insight into the molecular signal exchange, the analysis of effectors secreted by plant parasitic nematodes and their molecular plant targets has boomed (Haegeman et al 2013) and the first rice nematode effectors have recently been characterized (Chen et al 2017).

2. Root-knot nematodes, especially *Meloidogyne graminicola*

Root-knot nematodes (RKN) are considered a major threat to Asian rice cultivation, particularly under rainfed upland and lowland conditions (Prot and Rahman 1994). *Meloidogyne graminicola, M. tritocoryzae, M. oryzae, M. incognita, M. javanica*, and *M. arenaria* have been reported to attack rice.

The most damaging RKNs in rice-cultivation systems are *M. graminicola* and possibly *M. oryzae*, as they are the only known RKN species that can survive in flooded soil conditions (Bridge et al 1990). However, *M. oryzae* was only reported to survive in shallow-flooded (<10-cm) rice fields for relatively short periods (Bridge et al 1990), whereas *M. graminicola* can survive in soil flooded to a depth of 1 m for at least 5 months.

Presence of *M. graminicola* has been reported in rice-growing areas throughout South and South-East Asia as well as in the United States and Latin America (Mantelin et al 2017, Negretti et al 2017). This nematode was originally thought to be absent from Africa. However, Kleynhans (1991) reported its presence in South Africa. Recently, it was detected in Madagascar (Chapuis et al 2016), in the Italian Piemonte region (Fanelli et al 2017), and in China (Tian et al 2017).

Because of its widespread occurrence and the damage it causes to rice, *Meloidogyne graminicola* Golden & Birchfield 1965 is probably the best-studied RKN on rice.

2.1. Symptoms

Aboveground symptoms of *M. graminicola*-infected plants include stunting, chlorosis, and loss of vigor. However, exact diagnosis can only be done by examining the root systems where hook-shaped galls (root swellings) are formed on infected roots, mainly at the root tips. Infected seedlings fail to elongate and drown in flooded rice conditions (Bridge and Page 1982). In the field, yield losses may be exacerbated when RKN infestation is combined with other biotic or abiotic stresses such as drought.

2.2. Disease cycle

M. graminicola has a relatively short life cycle on rice (**Nem Figure 1**), taking 18 to 27 days, depending on soil temperature (Yik and Birchfield 1979; Bridge and Page 1982; Bellafiore et al 2015).
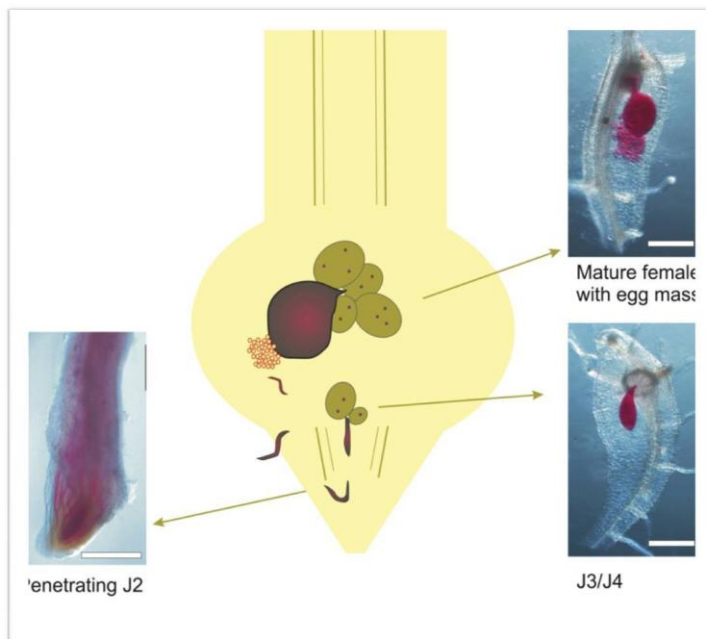
Nem Fig. 1. Schematic overview of the life cycle of *M. graminicola* in rice roots. After penetrating at the root elongation zone, the nematode migrates towards the root tip, where it makes a U-turn to induce a feeding site—*giant cells*—in the root vasculature. Inserts show microscopic observations of an infected root system stained with acid fuchsin, a pink dye which specifically stains the nematode and its feeding site. Microscopic photos courtesy of Zobaida Lahari. Scale bar: 400 µm.

Like other *Meloidogyne* spp., the first-stage juvenile molts in the egg to become a preparasitic J2. After hatching, if the nematodes are released in the soil, they locate roots by chemotaxis (Reynolds et al 2011) and invade the root elongation zone. Once inside the root, the J2 migrates intercellularly in the rice root cortex towards the root tip where it invades the vascular cylinder (**Nem Figure 1**). Signals from the J2 promote parenchyma cells near the head of the J2 to become multinucleate to form feeding cells, generally known as giant cells, from which the J2 and later the adults feed (Hussey and Grundler 1998; Jena and Rao 1977; Cabasan et al 2014).

The nematode reproduces by facultative meiotic parthenogenesis, although amphimixis may occur in rare cases (ca. 0.5%) (Triantaphyllou 1969).

It takes around 14 days from nematode invasion to maturation (**Nem Figure 1**), after which eggs are laid in the root cortex. From day 18 after infection, J1s are present in the eggs (Bellafiore et al 2015). After hatching, the juveniles either reinfect the same root system or leave to search for a new host plant.

2.3. Host range and agronomic importance

M. graminicola can infect most cereals, grass plants, and other monocots such as onion and garlic, as well as dicotyledonous plants such as some legumes (Long et al 2017, Win et al 2016). It is also infecting many weeds that are a major reservoir of nematodes (Rich et al 2009).

Yield losses in rice range from 10 to 80% (Netsher and Erlan 1993, Plowright and Bridge 1990, Soriano et al 2000, De Waele and Elsen 2007). Although most frequently reported from upland and/or aerobic rice cultivation systems (De Waele and Elsen 2007), its adaptation to flooded conditions makes *M. graminicola* a threat to all types of rice agrosystems. *M. graminicola* adult females remain inside the root where they are protected from the external environment, and release their eggs inside the root cortex. The next generation of nematodes is capable of making new feeding sites within the same root (Mantelin et al 2017).

2.4. Control measures

Constant immersion of rice in irrigated fields allows the best control of infection. Although *M. graminicola* can survive flooding and still propagate, it cannot penetrate new rice roots under flooded conditions (Bridge and Page 1982).

Crop rotation, a cropping system in which farmers introduce nonhost plants, such as mustard, sesame, millet (Rahman 1990), mung bean (Ventura et al 1981), or cowpea (Soriano and Reversat 2003) can reduce the occurrence of *M. graminicola* and therefore yield losses in rice. Addition of organic amendments to infested soil can partially reduce the nematode population and/or the root knot index (Sharma-Poudyal et al 2002, Dangal et al 2008). This effect can be enhanced by adding the fungal nematode-parasite *Nematoctonus robustus*, a potent biological control agent for *M. graminicola* (Singh et al 2017).

Lines of African rice from *O. glaberrima, O. longistaminata*, and *O. rufipogon* (Plowright et al 1999; Soriano et al 1999) as well as several *Oryza* landraces were described as fully or partially resistant (Gergon and Prot 1993; Plowright et al 1999; Soriano et al 1999) and have been used as resistance donors for interspecific crosses with *O. sativa* (Ghesquiere et al 1997). Reproducible and high resistances in *O. sativa* have been actively sought for several decades (Cabasan et al 2012, Bridge et al 2005) and were recently found in a number of *O. sativa* cultivars (Dimpka et al 2015, Mhatre et al 2017).
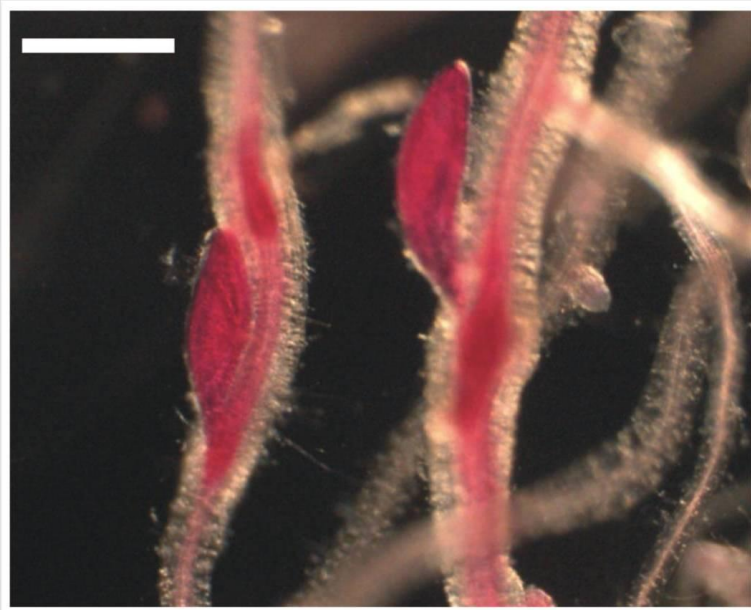
3. Cyst nematodes, especially *Heterodera sacchari*

Four cyst nematode species have been described as parasitizing rice roots: *Heterodera oryzicola, H. elachista, H. oryzae*, and *H. sacchari.*

H. oryzicola has been found only on upland rice in Kerala State India (Bridge et al 2005) while *H. oryzae* occurs on lowland rice in some parts of Ivory Coast and Senegal (Fortuner and Merny 1979) and in Bangladesh (Page and Bridge 1978). *H. elachista* was initially believed to be endemic to Japan (Oshima 1974), but has recently been reported on rice in China (Ding et al 2012).

On the other hand, *Heterodera sacchari* Luc & Merny, 1963 (sugarcane cyst nematode) occurs on rice under different rice cultivation conditions throughout West Africa (Babatola 1984, Lamberti et al 1991, Coyne et al 1996, Coyne and Plowright 2000). Due to its widespread occurrence and the damage that it causes on rice, *H. sacchari* warrants more study and so we describe it here in more detail.

3.1. Symptoms

H. sacchari-infected plants are wilted, chlorotic, and retarded in growth and their tiller number is reduced (Babatola 1983). Aboveground symptoms caused by this nematode can be confused with nitrogen deficiency or drought stress (Audebert et al 2000). Hence, diagnosis should be based on root examination. Lemon-shaped, swollen, white females (ca. 0.25 mm in diameter) can be observed on the root surface (see the pink-stained female in **NEM Figure 2**). When mature, the female body becomes dark brown in color. The root systems of heavily-infected plants become necrotic, dark brown, and twiggy (Akpheokhai et al 2015), and proliferation of lateral roots can be observed at the infection points (Babatola 1983).

A recent study on upland NERICA rice varieties showed a significant reduction in leaf chlorophyll content in *H. sacchari*-infected plants (Akpheokai et al 2014). In pot experiments, at inoculum density of >1 egg/2 ml soil, rice growth and development were reduced in susceptible cultivars NERICA1 (Akpheokai et al 2014) and IDSA6 (Coyne and Plowright 2000).

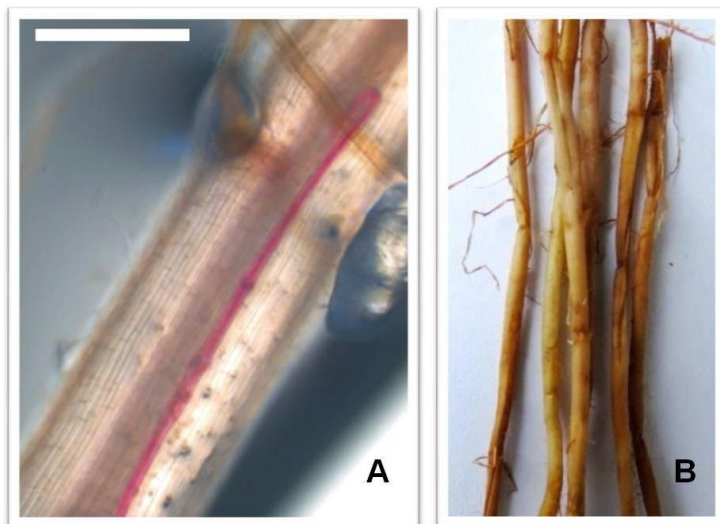Nem Fig. 2. Microscopic observation of an *Heterodera sacchari*-infected root system stained with acid fuchsin, a pink dye that specifically stains the nematode and its feeding site. Microscopic photos courtesy of Henok Zemene Yimer. Scale bar: 250 μm.

3.2. Disease cycle

Infective second-stage juveniles of *H. sacchari* penetrate the rice roots and migrate through the cells, where they develop and establish a multinucleate syncytium in the cortical or vascular regions of the root. Akpheokhai et al (2015) investigated the histopathological changes in *H. sacchari* infected NERICA 1 rice. At 14-21 days after inoculation (dai), extensive root damage and disorganization of epidermal, cortical, and vascular elements were observed. At 21 dai, mature white females were found aggregating along the root axis.This nematode reproduces by mitotic parthenogenesis. At 24 dai, large numbers of embryonated eggs were observed inside the female body. Unlike *H. oryzicola,* which is dependent on root exudates for egg hatching, *H. sacchari* requires only the presence of water (Ibrahim et al 1993).

3.3. Host range and agronomic importance

This nematode can infect sugarcane (*Saccharum officinale* L.), rice, and some wild grasses (Odihirin 1975). Coyne and Plowright (1999) reported that other cereal crops are also susceptible to *H. sacchari* infection, including maize, millet, and sorghum.

Field studies have shown a maximum rice yield loss of 70% in nematode-infested soil (Fademi 1984, Coyne and Plowright 2000). According to Bridge and Starr (2007), seedlings may be killed in heavily infested soils. *H. sacchari* reproduces under both upland and simulated swamp conditions, although symptoms of infection are more discernible in upland rice plants (Babatola 1983) and the nematode is more abundant in sandy soils than in clay soils (Jerath 1968). *H. sacchari* generally cannot withstand extended flooding (Bridge and Starr 2007).

3.4. Control measures

Control of this nematode can lead to yield increases of over 60% (Bridge and Starr 2007). Although applications with the nematicide carbofuran can reduce the preplant inoculum density, this product does not absolutely control *H. sacchari* as its efficacy decreases over time in the field (Akpheokai et al 2014). Moreover, many nematicides cause negative side-effects on the environment and human health (Haydock et al

2006). Coyne and Plowright (1998) have optimized a solarization technique to control cyst nematodes in the field. Pot experiments have shown that maize, millet, and sorghum, which are commonly cultivated in cropping systems with rice in West Africa, were hosts, albeit poor, of *H. sacchari*, and cysts can still survive in the soil (Coyne and Plowright 1999).

When evaluating different varieties of *O. sativa*, variation in female numbers was observed, but all were susceptible to *H. sacchari* (Babaola 1983, Plowright et al 1999). Nevertheless, the related African rice, *O. glaberrima,* is (partially) resistant to this nematode (Reversat and Destombes 1995, Coyne et al 1996). Similar numbers of cysts develop on *O. sativa* and *O. glaberrima*, but cysts from *O. glaberrima* are smaller and contain fewer eggs, resulting in significantly lower population densities of *H. sacchari* (Lorieux et al 2003). In a cross between *O. sativa* cv. WAB56-104 and *O. glaberrima* line CG14, some of the progenies were found to be resistant to *H. sacchari*. The expression of resistance in the interspecific progeny suggests that resistance to *H. sacchari* is qualitative, while against *M. graminicola,* it is quantitative (Plowright et al 1999). The resistance gene *Hsa*-1(Og) has been mapped on *O. glaberrima* chromosome 11 (Lorieux et al 2003).

Significantly higher population densities for *H. sacchari* have been observed in weed-free rice plots compared to rice plots with weeds, potentially because reduced interspecific competition in weed-free plots facilitated increased rice growth and increased multiplication of *H. sacchari* (Coyne et al 1999). Blouin et al (2005) have shown that rice is more tolerant to *H. sacchari* infection in the presence of earthworms, but the mechanism is unknown. Yield reduction was not observed although there was no corresponding reduction in cyst population in the presence of earthworms.

4. Migratory root nematodes, especially *Hirschmanniella oryzae*

Fifteen *Hirschmanniella* spp. have been found to be associated with rice, but *H. oryzae* (van Breda de Haan, 1902) Luc&Goodey, 1964, the rice root nematode (**Nem Figures 3A, B**), is the most widespread and damaging (Bridge et al 2005). It is a migratory root endoparasite adapted to anaerobic conditions with *Oryza sativa* as its main host. *H. oryzae* is the most common plant-parasitic nematode in flooded rice ecosystems worldwide (Bridge et al 2005). The nematode is long and slender with a mature body length of 0.9 to 1.6 mm (Pascual et al 2014).

Nem Fig. 3. (A) *Hirschmanniella oryzae* inside a rice root, stained with acid fuchsin. (B) Necrotic rice roots, caused by *H. oryzae* infection. Photos courtesy of Lander Bauters. Scale bar: 250 μm.

4.1. Symptoms

Symptoms due to *H. oryzae* are difficult to recognize in the field; some leaf chlorosis and growth reduction may occur but these can be attributed to many causes and very often no above ground symptoms are visible (Ichinohe 1988). Nevertheless, below-ground examinations reveal that infected roots display necrotic regions and these roots are prone to secondary infection by rot-inducing microorganisms, hence the name "root rot nematode" (Babatola and Bridge 1980).

4.2. Disease cycle

The nematodes enter the root mainly via lateral roots or root tips, often using the same entry point. They feed while migrating through the root parenchyma (**Nem Figure 3A**), which is well developed in flooded rice. Destruction of root cells along the nematode's path leads to a trace of necrotic tissue (**Nem Figure 3B**). This necrosis, together with the invasion by other microorganisms, causes browning of the rice roots (Babatola and Bridge 1980). All developmental stages of the nematode are infective and feed on the host and, after four molts, males and females develop from the juveniles (Karakas 2004).

Reproduction is through amphimixis and, after fertilization, female nematodes lay eggs that will hatch inside the roots within 4-5 days. A full life cycle may take about 33 days under ideal circumstances (Karakas 2004) but, in some cases, it may take much longer; between one and three generations per year are normal (Fortuner and Merny 1979). A soil temperature between 21 and 28°C is optimal for multiplication but this nematode can tolerate temperatures ranging from 8 to 45°C.

H. oryzae is well adapted to flooded rice fields and is one of the few nematodes able to survive in anaerobic conditions (Babatola 1981). The nematodes can persist for 7 months in wet soil without a host and can also persist by parasitizing several weeds from the Cyperaceae and Gramineae that are common in and around rice fields (Anwar et al 2011, Bridge et al 2005).

4.3. Host range and agronomic importance

Rice is the main host of *H. oryzae*, but alternate hosts that are therefore not to be used in crop rotation are cabbage, cotton, maize, okra, sugarcane, and wheat. *H. oryzae* is a problem in flooded rice fields all over the world, so not only in the rice-growing Asian countries but also in Africa, U.S., Latin America, and even Portugal. A survey of 539 rice fields in 12 regions of Myanmar revealed that 90% of the fields sampled were infested with *H. oryzae* (Maung et al 2010). In Luzon, Philippines, *Hirschmanniella* was ubiquitously present in lowland rice, but at a lower population density than *M. graminicola* (Pascual et al 2014).

Yield losses due to *H. oryzae* infection can be very variable depending on the cultivar, region, and population density. Under favorable environmental conditions, the injury caused by this nematode is less manifested due to the rapid formation of new roots (Edward et al 1985). On the other hand, losses of up to more than 30% have been reported (Babatola and Bridge 1979, Ichinohe 1988, Prot and Rahman 1994).

4.4. Control measures

Nematicides, such as carbofuran, can control *H. oryzae* with success, but they pose health risks and pollute the water. Nitrogen fertilization has been reported to reduce

grain weight loss due to *H. oryzae* infection, however, this resulted in the buildup of the nematode population thus increasing the problem for the next cropping season (Poussing et al 2015). Crop rotation with green manure crops, such as the legume *Sesbania rostrata*, reduced the nematode population in the field, however, this method appeared to be uneconomical (Prot et al 1992). Furthermore, *S. rostrata* increases the population of *M. graminicola* (Prot 1994). Cowpea, groundnut, mung bean, onion, sesame, sorghum, soybean, sweet potato, and tobacco are nonhosts for *H. oryzae* and can be used in a profitable rotation (Mathur and Prasad 1973, Babatola 1979, Edward et al 1985, Korayem 1993, Gao et al 1998, Bridge et al 2005, Maung 2011). Dissemination of *H. oryzae* can easily occur from infested nurseries to noninfested fields, indicating another point of attention for managing this nematode.

Use of organic amendments along with nematicides proved to be effective for managing *H. oryzae* in rice (Prasad et al 1986). Another option involves the combination of chitin amendments, neem cake, and *Pseudomonas fluorescens* (Swarnakumari et al 1999).

A lot of studies have been conducted to evaluate rice cultivars for resistance to *H. oryzae*, but most of the varieties tested were susceptible (Babatola 1979, Singh et al 1992, Pokharel 1995, Coyne et al 1999). In other evaluation trials, most of the tested cultivars appeared to be highly susceptible to *H. oryzae*, although some were moderately resistant (Dash et al 2008).

5. Root lesion nematodes, especially *Pratylenchus zeae*

Among the several species of root lesion nematodes (RLNs) that can infect rice, *Pratylenchus zeae* Graham 1951 is the most common and damaging (Castillo and Vovlas 2007). *P. zeae* is a problem in the cultivation of sugarcane and cereals worldwide. However, this nematode is mainly reported under upland rice cultivation conditions (Bridge et al 2005).
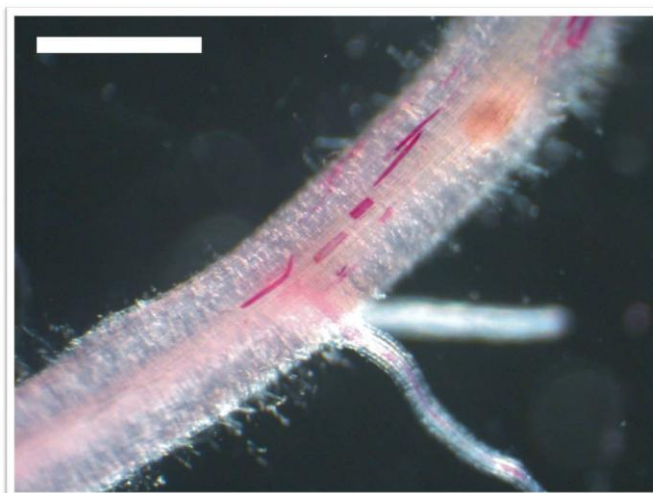
Nem Fig. 4. Rice roots infected by *Pratylenchus zeae*, stained with acid fuchsin. Photo courtesy of Njira Njira Pili. Scale bar: 400 μm.

5.1. Symptoms
P. zeae is a migratory nematode moving through and destroying root cortical cells (**Nem Figure 4**) (Stirling 1991). Its infection causes browning and root distortions with less branching; heavy infection can kill young plants. It is difficult to recognize *P. zeae* infection because the stunted growth and chlorosis are often mistaken for nutrient deficiency (Jones and Fosu-Nyarko 2014).

5.2. Disease cycle
The life cycle of *P. zeae* is typically completed in 30-40 days. However, this may be influenced by environmental conditions such as adequate temperature and moisture. The first-stage juveniles (J1) develop in the eggs, and then molt into J2, which hatch from the egg, J3, J4, and finally the adults. As a migratory nematode, all growth stages are vermiform and motile, and they feed on root cortex (**Nem Figure 4**).

They can leave the infested plant and move to new plants spreading the infection in the field (Jones and Fosu-Nyarko 2014). The initial wound inflicted on plant roots and other below ground parts by *P. zeae* may serve as entry points for other nematodes and pathogens possibly attracted by compounds released from the wounded tissue. Reproduction is usually parthenogenetic, the females (0.35 to 0.5 mm long) lay eggs either singly or in small clusters in the root cortex. After harvest, the nematodes can survive in decaying root material or in the soil and infect the next crop.

5.3. Host range and agronomic importance
P. zeae has a wide host range, which includes many cereal crops (e.g., maize), sugarcane, tobacco, apple, peach, and weeds such as *Dactylodenium aegyptium*, *Digitaria sanguinalis*, and *Echinochloa crusgalli* (Fortuner 1976, Riley and Kelly 2002).

In rice cultivation, RLNs mainly affect direct-seeded rain-fed rice in upland conditions in Africa but they have also been reported in the USA, Latin America, Southeast Asia, and Australia (Plowright et al 1990, Bridge et al 2005, Castillo and Vovlas 2007).

In a field trial conducted in the Philippines with low population densities of *P. zeae* (0-111 nematodes/100 ml soil) and no obvious symptoms of infection, nematicide application increased the yield of a susceptible cultivar by 13-29% (Plowright et al 1990). The yield reduction due to *Pratylenchus* infection is mainly based on lower grain weight and protein content (Rao and Prasad 1977).

5.4. Control measures
The nematicide carbofuran reduces root lesion nematode damage and yield losses but its use is not always cost-effective as the yield in upland rice cultivation is generally low (Prasad et al 1988).

Rotation of rice with mung bean or black gram is a good option to reduce *Pratylenchus* populations (Prasad et al 1983, Aung and Prot 1990). However, the common practice of rotating rice with maize in many African countries and in Brazil (Biela et al 2015) is not recommended as maize is an excellent host to *P. zeae*, which intensifies RLN problems. Soil addition of poultry litter has been shown to reduce *P. zeae* problems in rice (Khan and Haukat 2000).

Plowright et al (1990, 1999) found *O. glaberrima* Steud. and most *O. sativa* cultivars they tested to be susceptible to *P. zeae*, except for the cultivars Kinandang and IR36, which appeared relatively resistant. All 26 tested Brazilian rice cultivars were found to be susceptible to *P. zeae* although to varying degrees (Biela et al 2015). On the other hand, Pili et al (2016) classified the rice cultivars Basmati, known as Kenya Pishori, and Supa, which are commonly cultivated in Mwea (Kenya), as resistant to *P. zeae* because the Pi/Pf (an estimate of nematode reproduction) was <1 under controlled conditions. These potentially resistant cultivars warrant additional research as to their merit for the management of *Pratylenchus*.

6. Migratory shoot nematodes, especially *Ditylenchus angustus*
Ufra disease caused by the rice stem nematode, *Ditylenchus angustus,* Butler, (1913) Filipjev (1936) is one of the most devastating rice diseases in several South and Southeast Asian countries, with confirmed records from India, Bangladesh,

Thailand, Myanmar, and Vietnam. Although this nematode is predominant in deep water rice, it also infects irrigated and rainfed low land rice (Bridge et al 2005).

6.1. Symptoms

The disease caused by this nematode in rice (**Nem Figures 5** and **6**) is known as ufra disease, named after the farmer Uftur Rahman, the owner of the fields where the nematode was discovered. In Bangladesh, this disease is also called "dak pora", while in Myanmar, Vietnam, and Thailand, it is known as "akhet-pet "tiem dot san", and "yadngo", respectively.

Nem Fig. 5. Rice plant infected by *Ditylenchus angustus*: white patches at the leaf base. Photo courtesy of Shakhina Khanam.

During the vegetative stage of the crop, injury due to *D. angustus* is characterized by white patches or speckles at the leaf base (**Nem Figure 5**). Brown spots may develop on leaves and leaf sheaths, and the leaf margins become distorted. At the reproductive stage of the crop, the nematodes move upwards to feed on the ear primordia. When infection is severe, the panicles become twisted with empty spikelets or may not even emerge at all (Bridge et al 2005, Rahman 2003).

6.2. Disease cycle

The four juvenile stages (J1-J4) as well as the adult male and female *D. angustus* are vermiform and infective with the J4 stage (size 0.63 to 0.87 mm) showing the highest infectivity (Plowright and Gill 1994). The nematodes can actively swim to the plant and enter mainly at the collar region, migrating upward with the growth of the shoot. They accumulate in the leaf sheaths and the developing inflorescences. The nematode feeds mainly as ectoparasite but endoparasitic behaviour has also been observed (Singh et al 2013; **Nem Figure 6**). The nematode can also be cultured on fungi such as *Botrytis cinerea* (Ibrahim et al 1994).

Reproduction is amphimictic and the nematode completes its life cycle within 10-20 days at 27-30°C (Bridge and Starr 2007), allowing at least three generations to be completed within a growing season (Rahman 2003). The females (1.0-1.2mm long) lay 50 to 100 eggs in their lifetime. The J1 molts into J2 (0.28-0.43 mm) within the egg and hatches spontaneously in water without host stimuli (Ali and Ishibashi 1996). At rice harvest, the nematodes remain in a dormant state, mainly in the dried glumes of the lower panicle spikelets.

Although viable anhydrobiotic nematodes are present in and on the grains (Prasad and Varaprasad 2002), the chance of transmission by seed is unlikely when
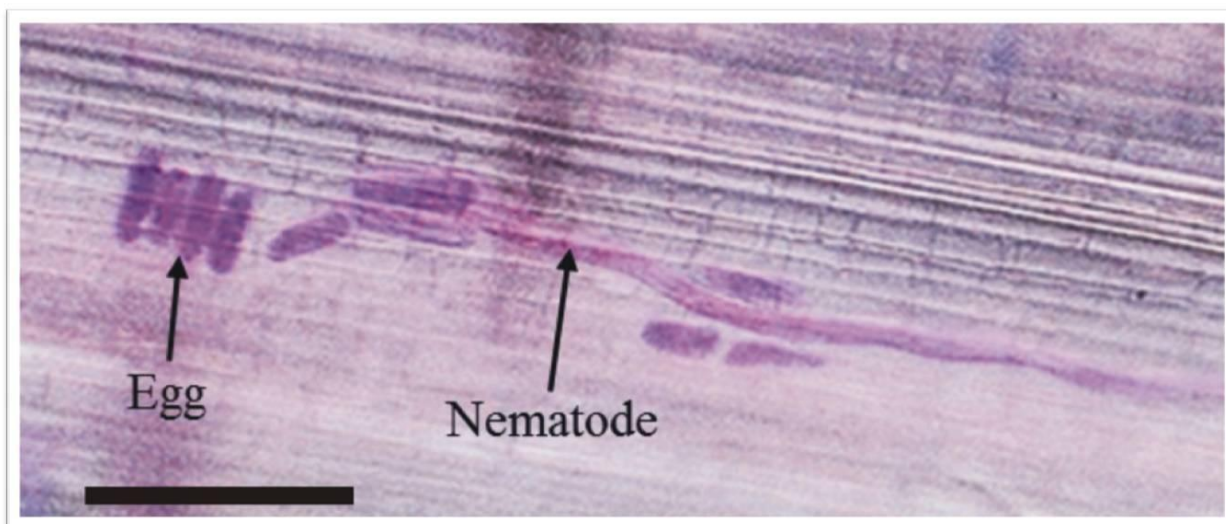
Nem Fig. 6. *D. angustus* and eggs in a rice leaf stained with acid fuchsin. Photo courtesy of Shakhina Khanam. Scale bar: 100 μm

the seeds are properly sun dried (Bridge and Starr 2007). Survival of nematodes from one season to another takes place in crop residues, soil and alternative hosts like weeds (Cox and Rahman 1979). The J4 especially can survive in desiccated conditions for many months in infected plant materials (Cox and Rahman 1979, Ibrahim and Perry 1993). Dissemination of nematodes from field to field is mainly through irrigation water and fresh water flooding in deep water rice (Rahman and Evans 1987).

6.3. Host range and agronomic importance

D. angustus infects cultivated and wild rice species (*Oryza sativa, O. alta, O. cubensis, O. eichingeri, O. glaberrima, O. latifolia, O. meyeriana, O. minuta, O. nivara, O. perennis, O. officinalis, O. rufipogon*) (McGeachie and Rahman 1983, Bridge et al 1990), and a few weed species (*Echinocloa colona, Hygroryza aristata, Leersia hexandra, Sacciolepsis interrupta*) (Vuong and Rabarijoela 1968, Cuc and Giang 1982).

Ufra disease mainly occurs in deep water rice (Butler 1919). However, together with the decline of deep water rice cultivation and increased area of irrigated and rainfed rice, *D. angustus* now also occurs in these cultivation systems (Prasad et al 2000). Because its distribution is limited, its global economic impact is relatively low (Bridge et al 2005). Nevertheless, if the nematode occurs, it can result in complete crop failure and even a low infection percentage in transplanted seedlings can cause substantial yield losses (Bridge and Starr 2007).

In Bangladesh, 40-49% or sporadically 90% yield losses have been reported (Latif et al 2011). In India, yield losses due to ufra were reported at 10-15% in West Bengal (Rao et al 1986) but up to 100% in certain areas in Assam. In Thailand, it was estimated that 500 ha of lowland rice had yield losses ranging from 20 to 90% due to *D. angustus* infestation (Hashioka 1963). Khuong (1983) reported a 50% yield loss in the Mekong Delta and Dong-Thap Province in Vietnam.

6.4. Control measures

Different management practices have been recommended to control nematode problems, such as stubble and straw burning, destruction of wild rice, regulation of irrigation water, use of organic amendments (Latif et al 2006) and crop rotation

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(Chakraborti 2000). However, implementation of many of these control measures is difficult due to socioeconomic reasons. Nematicide application, principally carbofuran, effectively controls *D. angustus* in rice fields, and is an important strategy of nematode management in Bangladesh and parts of India. Nonetheless, nematicides are hazardous to the environment and nontarget organisms, urging the search for alternative methods such as the use of resistant varieties (Haydock et al 2006). Proper sun drying of the seeds is a simple method to avoid the spread of the nematodes that are present on or in the seeds (Bridge and Starr 2007).

Although some rice genotypes have been identified as ufra resistant (Rahman 1987, Das and Sarmah 1995, Latif et al 2011), many of those resistant varieties are not popular due to their low yield potential. Therefore, Khanam et al (2016) screened 55 high-yielding varieties recently released by the Bangladesh Rice Research Institute (BRRI) for their resistance to ufra. Several local and deep water rice varieties were also included in the study. Unfortunately, most of the tested local varieties were (highly) susceptible, hence those varieties cannot be planted in ufra-infested areas.

One local variety (Manikpukha), which is cultivated in some parts of Bangladesh, was found to be highly resistant. Likewise, six high-yielding varieties were found to be resistant to *D. angustus* and could be recommended to farmers (Khanam et al 2016). The use of resistant varieties is necessary in rice breeding programs as well as in the development of a sustainable ufra management strategy.

7. Seedborne nematode, *Aphelenchoides besseyi*

White-tip disease of rice (**Nem Figure 7**) incited by the seedborne nematode,

Nem Fig. 7. Symptoms of white tip disease in rice caused by *A. besseyi.*

Aphelenchoides besseyi Christie 1942, was first described in Japan (Kakuta 1915). Since then, the disease has been reported in most rice-growing areas of the world. *A. besseyi* has two common names: white tip nematode of rice and summer crimp nematode of strawberry. The body of *A. besseyi*, at all stages, is slender and the mature females are 0.6 to 0.7 mm long.

7.1. Symptoms
A. besseyi infects rice in all rice-production environments. The ectoparasitic nematode feeds on above-ground young rice tissues. The most conspicuous symptom of infection is the emergence of white tips on new leaves from the leaf sheath. These diseased tips become dry, twisted, and wrinkled and then die off. An obvious irregular dark brown border is shown between white tip and the healthy part of the diseased leaves, whereas the rest of the leaves may appear normal (Todd and Atkins 1958a). The infected panicles are shorter than in healthy plants, and grains are deformed. Consequently, infection with *A. besseyi* affects both the quality and the quantity of rice yield (**Nem Figure 7**).

Some of the infected rice varieties do not have white tip symptoms, but only show the symptoms of "small grains" and "erect panicles" (Lin et al 2004). Moreover, some cultivars are symptomless, but lots of *A. besseyi* can be found in the panicles and grains, this is particularly true in japonica rice (H. Ji. unpubl. data).

7.2. Disease cycle
The life cycle of *A.besseyi,* on carrot discs takes 12.5 days at 26°C. Released eggs from adult females appear at day 2.5; J2s appear at day 5; J3/J4s appear at day 6; adults appear at day 9; the next generation eggs appear at day 15. *A. besseyi* is amphimictic and males are usually abundant (Huang et al 1979), however, parthenogenetic reproduction has also been found (Gokte-Narkhedkar et al 2001). *A. besseyi* is not only a parasite of higher plants but it can also feed on fungi.

When seeds infected with *A. besseyi* are soaked in water or planted, the nematodes become active. They migrate out of the seeds and start their ectoparasitic feeding on aboveground tissues. During early growth, *A. besseyi* is found in low numbers in all green tissues, although more abundant in shoots. A rapid increase in nematode numbers takes place at the flowering stage. At this stage, the nematodes are mainly found in the panicles (H. Ji, unpubl. data). Nematodes enter the spikelets before anthesis and feed ectoparasitically on the reproductive structures. As grain filling and maturation precede, reproduction of the nematode ceases. When kernel moisture is lost, nematodes become quiescent and are able to survive up to 3 years (Tenente et al 1994), but the number and infectivity of nematodes is reduced as seed age increases (Sivakumar 1987).

A. besseyi cannot survive long periods in soil between crops (Cralley and French 1952, Yamada et al 1953). Under northern Italian conditions, the nematode overwinters in rice straw but is unable to start a new infestation (Bergamo et al 2000). In the field, the nematodes are mainly spread by irrigation water and the long-distance transmission mainly relies on the transport of infected seeds, as well as in rice husks used as packaging material for goods (Uebayashi and Imamura 1972, Kobayashi and Sugiyama 1977).

7.3. Host range and agronomic importance
The main host plants of *A. besseyi* are rice and strawberry. In strawberry, it is causing the 'summer dwarf' or 'crimp' disease. Other host plants include numerous

ornamental plants and grasses. This nematode has also been reported to cause false angular leafspot of beans in Costa Rica (Salas and Vargas 1984). *A. besseyi* is included in the top 10 most destructive plant parasitic nematodes, making a significant contribution to the estimated USD 16 billion worth of damage caused by nematodes to rice crops (Jones et al 2013).

7.4. Control measures
Generally, indica varieties are more tolerant to *A. besseyi*, and nematode reproduction on this subspecies is lower (H. Ji, unpubl. data).

Contaminated seeds dispersed through irrigation water are a major source of *A. besseyi* infection. Therefore, control of the irrigation water will reduce nematode spread by water flow. Early planting and low seedbed planting densities can also effectively reduce the disease (Fortuner and Williams 1975). Preventing the dispersal of *A. besseyi*-infected seeds, use of nematode-free seeds, and planting in nematode-free fields will reduce or avoid *A. besseyi* infestation.

If seeds are known or suspected to be infested, the following treatments are recommended.

7.4.1. Hot-water treatment. The most effective treatment requires seeds to be presoaked in cold water for 18-24 hours, then immerse in water at 54-56°C for 15 minutes or directly soak at higher temperatures (58-60°C) for 10-15 minutes. After treatment, the seeds can be planted quickly, otherwise, they must be dried at 30-35°C or sun dried for long storage (Todd and Atkins 1958b).

7.4.2. Chemical treatment. Contaminated seeds can be soaked in various chemicals for control of *A. besseyi*. For example, in 8 ppm avermectin EC or in 70 ppm fosthiazate EC for 48 hours (H. Ji, unpubl. data). After soaking, seeds need to be rinsed with water to remove the pesticide residue.

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