Article bibliographique

ROOT-PARASITIC NEMATODES OF RICE

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Geographical distribution of nematodes associated with rice

More than one hundred species of nematodes have been reported from upland and paddy rice in many countries (Tab. 1). Their frequency and importance are very variable and, in most cases the existence of a parasitic relationship with rice is probable but has not been demonstrated.

Many species of root nematodes have been observed both in dry and irrigated fields but very few species are found in both situations. Several surveys made by the authors in West Africa have shown that a relatively low number of species are adapted to permanently flooded conditions. When the field is only temporarily flooded, the number of species present is higher and the nematode fauna tends to ressemble that observed in upland rice fields, which is composed of species also common in other crops. Unfortunately, in many papers, the authors fail to indicate with what kind of rice (paddy or upland rice) the parasite was associated.

Nematodes attacking roots can be divided into three categories.

MIGRATORY ENDOPARASITES

The most important migratory endoparasites associated with paddy belong to the genus *Hirschmanniella* of which several species have been observed associated with rice. *H. oryzae* is the most frequently encountered in all countries where rice is grown, except Europe. Another species, *H. spinicaudata*, is common in West Africa and has been observed once in South America. In West Africa a geographical gradient is observed in the distribution of both species : *H. spinicaudata* is highly prevalent in the humid countries like Ivory Coast whereas *H. oryzae* is found mostly in the Sahelian regions (North Senegal) ; a balanced mixture of both species is observed in intermediate geographical areas (Gambia).

Ten recognized species of *Pratylenchus* have been identified parasitizing rice. The most frequent is *P. brachyurus*, rather common in African upland rice fields, which has been observed once in South America ; *P. zeae* is a common parasite of paddy in Africa and South America ; *P. indicus* is common in India and a single species of *Pratylenchus (P. vulnus)* was observed in the Far East.

SEDENTARY ENDOPARASITES

Polyphagous populations of *Meloidogyne* belonging to the "*javanica-incognita-arenaria* group" have often been observed in the vicinity of rice roots in many countries. When they are found in irrigated paddy fields, their relation to

rice is doubtfull for they are known to be very susceptible to flooding and they are most probably associated with plants growing when the field is free of water. One species, *M. graminicola* is especially correlated with gramineae and, recently, *M. oryzae* has been discovered associated with irrigated rice.

Since 1961, four species of *Heterodera* have been found to be associated with rice : *H. oryzae* and *H. sacchari* are present in West African paddy, *H. graminophila* is associated with rice in the USA and *H. elachista* has been found parasitising upland rice in Japan.

ECTOPARASITES

The most frequently encountered ectoparasite belongs to the genus *Tylenchorhynchus*, several species of which have been observed in rice. The most wide-spread species is *T. martini* known to parasitise rice in the USA, the Middle and Far East and Africa. *T. mashhoodi*, which is perhaps a synonym of the former, is a frequent parasite of rice in West Africa.

Five species of *Criconemoides* have been reported from rice. One of them, *C. onoensis*, a polyphagous species, discovered in Africa but not associated with rice in this area, has been found in the U.S.A. where it seems to cause losses in paddy.

Ten species of *Helicotylenchus* were reported in various countries in the vicinity of rice, mostly upland. Their actual relationship with rice is not known.

Table 1

List and distribution of nematodes associated with rice roots

Species	*Records*
Aglenchus agricola (De Man, 1884) Meyl, 1961	USSR (MASLENNIKOVA, 1965 *b*)
A. costatus (De Man, 1921) Meyl, 1961	Côte d'Ivoire (MERNY, 1970)
A. bryophilus (Steiner, 1914) Meyl, 1961	USSR (MASLENNIKOVA, 1965 *b*)
Aphelenchoides asterocaudatus Das, 1960	USSR (MASLENNIKOVA, 1965 *b*), India (KHERA & CHATURVEDI, 1970)
A. bicaudatus (Imamura, 1931) Filipjev & Schuurmans Stekhoven, 1941	Japan (IMAMURA, 1931), Bengla Desh (TIMM & AMEEN, 1960), Côte d'Ivoire (MERNY, 1970), Brunei (ANON., 1972 *a*)
A. helophilus (De Man, 1880) Goodey, 1933	USSR (MASLENNIKOVA, 1963)
A. kuehnii Fischer, 1894	USSR (MASLENNIKOVA, 1963)
A. lagenoferrus Baranovskaya, 1963	USSR (MASLENNIKOVA, 1965 *b*)
A. limberi Steiner, 1936	Côte d'Ivoire (MERNY, 1970)
A. parietinus (Bastian, 1865) Steiner, 1932	USSR (MASLENNIKOVA, 1963)
A. subparietinus Sanwal, 1961	USSR (MASLENNIKOVA, 1965 *b*)
A. subtenuis (Cobb, 1926) Steiner & Buhrer, 1932	USSR (MASLENNIKOVA, 1963)
Aphelenchoides sp.	Venezuela (LOOF, 1964)
Aphelenchus avenae Bastian, 1865	Bengla Desh (TIMM, 1955) Côte d'Ivoire, Sénégal and Guinée (LUC & DE GUIRAN, 1960), Venezuela (LOOF, 1964) USSR (MASLENNIKOVA, 1965 *b*), Korea (CHOI, 1972), Cameroun (SAMSOEN & GERAERT, 1975)
Aphelenchus sp.	Guyana (ANON., 1971)
Basiria aberrans (Thorne, 1949) Siddiqi, 1963	USA (ATKINS *et al.*, 1955 *a*)
B. gracilis (Thorne, 1949) Siddiqi 1963	Côte d'Ivoire (MERNY, 1970)
B. graminophila Siddiqi, 1959	Iran (KHEIRI, 1972)

Species	*Records*
Boleodoroides oryzae Mathur, Khan & Prasad, 1966	India (MATHUR *et al.*, 1966)
Caloosia exilis Mathur, Khan, Nand & Prasad, 1969	India (MATHUR *et al.*, 1969)
C. paxi Mathur *et al.*, 1969	India (MATHUR *et al.*, 1969)
Criconemoides curvatus Raski, 1952	Guinée (LUC, 1959 *b*), Thailand (TAYLOR, 1968), Côte d'Ivoire (MERNY, 1970), Sénégal (FORTUNER & MERNY, 1973), Cameroun (SAMSOEN & GERAERT, 1975)
C. komabaensis (Imamura, 1931) Taylor, 1936 (species inquirenda)	Japan (IMAMURA, 1931)
C. onoensis Luc, 1959	USA (EMBABI, 1967), Côte d'Ivoire (LUC, 1970)
C. ornatus (Raski, 1952) Raski 1958	Sénégal (FORTUNER, 1975)
C. palustris Luc, 1970	Côte d'Ivoire (MERNY, 1970), Sénégal (FORTUNER & MERNY, 1973)
C. rusticus (Micoletzki, 1915) Taylor 1936	Bengla Desh (TIMM, 1955)
C. sphaerocephalus Taylor, 1936	Emp. Centre Africain (LUC, 1970) Japan (MOMOTA & OSHIMA, 1973)
Criconemoides sp.	Taiwan (LIN, 1970), El Salvador (INTERIANO MUÑOZ, 1970), Ghana (ADDOH, 1971), Guyana (ANON., 1971)
Ditylenchus intermedius (De Man, 1880) Filipjev, 1936	Japan (IMAMURA, 1931) USSR (MASLENNIKOVA, 1965 *b*)
Ditylenchus sp.	USA (ATKINS *et al.*, 1955), Bengla Desh (TIMM & AMEEN, 1960), Venezuela (LOOF, 1964), Panama (YEPEZ & MEREDITH, 1970), Cameroun (SAMSOEN & GERAERT, 1975)
Filenchus filiformis (Bütschlii, 1873) Meyl, 1961	Japan (IMAMURA, 1931), USSR (MASLENNIKOVA, 1965 *b*), India (KHERA & CHATURVEDI, 1970)
Helicotylenchus cavenessi Sher, 1966	Nigeria (CAVENESS, 1967), Iran (KHEIRI, 1972)
H. crenacauda Sher, 1966	Indonesia (SHER, 1966), Taiwan (LIN, 1970)
H. dihystera (Cobb, 1893) Sher, 1961 = *H. crenatus* Das, 1960	Madagascar (LUC, 1959 *a*), Venezuela (LOOF, 1964), Côte d'Ivoire (MERNY, 1970), India (NANDAKUMAR & RAO, 1974)
H. erythrinae (Zimmerman, 1904) Golden, 1956	Thailand (TAYLOR, 1968), USA (HOLLIS, 1969 *a*), Venezuela (YEPEZ & MEREDITH, 1970)
H. exallus Sher, 1966	Cameroun (SAMSOEN & GERAERT, 1975)
H. flatus Roman, 1965	Côte d'Ivoire (MERNY, 1970)
H. microcephalus Sher, 1966	Côte d'Ivoire (MERNY, 1970)
H. multicinctus (Cobb, 1893) Golden 1956	Bengla Desh (TIMM, 1955), Ghana (ADDOH, 1971)
H. pseudorobustus (Steiner, 1914) Golden, 1956	Nigeria (CAVENESS, 1967)
Helicotylenchus sp.	USA (ATKINS *et al.*, 1957), Sénégal and Guinée (LUC & DE GUIRAN, 1960) Emp. Centrafricain (LUC, MERNY & NETSCHER, 1964), USSR (IVANOVA, 1968), Guyana (ANON. 1971), Brunei (ANON., 1972 *a*), Gambia, (FORTUNER & MERNY, 1973), Rhodesia (ANON., 1973 *a*)
Hemicriconemoides cocophilus (Loos, 1949) Chitwood & Birchfield, 1957	Côte d'Ivoire (MERNY, 1970) Sénégal and Gambia (FORTUNER & MERNY, 1973)
H. intermedius Dasgupta Raski & Van Gundy, 1969	Korea (CHOI, 1972)

Species	Records
Hemicycliophora belemnis Germani & Luc, 1973	Sénégal (Fortuner, 1975)
H. diolaensis Germani & Luc, 1973	Sénégal (Germani & Luc, 1973)
H. nigeriensis Germani & Luc, 1973	Nigeria (Germani & Luc, 1973)
H. oostenbrinki Luc, 1958	Côte d'Ivoire (Merny, 1970), Ghana (Addoh, 1971)
H. paradoxa Luc, 1958	Côte d'Ivoire (Luc & de Guiran, 1960)
H. similis Thorne, 1955	Madagascar (Luc, 1959 *a*)
Hemicycliophora sp.	Guyana (Anon., 1971), Cameroun (Samsoen & Geraert, 1975)
Heterodera elachista Ohshima, 1974	Japan (Okada, 1955)
H. graminophila Golden & Birchfield, 1972	USA (Birchfield, 1973)
H. oryzae Luc & Berdon, 1961	Côte d'Ivoire (Luc & Berdon, 1961) Sénégal (Fortuner & Merny, 1973)
H. sacchari Luc & Merny, 1963	Côte d'Ivoire (Merny, 1970), Sénégal and Gambia (Fortuner & Merny, 1973)
Hirschmanniella belli Sher, 1968	USA (Sher, 1968)
H. caudacrena Sher, 1968	USA (Sher, 1968)
H. gracilis (De Man, 1880) Luc & Goodey 1963	Taiwan (Lin, 1970), India (Mathur & Prasad, 1971)
H. imamuri Sher 1968	Japan (Imamura, 1931), Korea (Choi, 1972)
H. mangaloriensis Mathur & Prasad, 1971	India (Mathur & Prasad, 1971)
H. mucronata (Das, 1960) Luc & Goodey, 1963	India (Das, 1960), Philippines, Thailand and Bengla Desh (Sher, 1968)
H. oryzae (Van Breda de Haan, 1902)	Indonesia (Van Breda de Haan, 1902), Japan (Imamura, 1931), Bengla Desh (Timm, 1955), USA (Atkins *et al.*, 1955 *a*), Sri Lanka & Malaysia (Johnston, A., 1958), Madagascar (Luc, 1959 *a*), Thailand and Philippines (Thorne, 1961), India (Birat, 1965), Sierra Leone & Nigeria (Sher, 1968), Venezuela (Sher, 1968), El Salvador (Sher, 1968), Taiwan (Sher, 1968), Korea (Park *et al.*, 1970), Ghana (Addoh, 1971), Sénégal and Gambia (Fortuner & Merny, 1973), Mauritanie (Fortuner, 1975).
H. spinicaudata (Schuurmans Stekhoven, 1944) Luc & Goodey, 1963	Cameroun (Luc, 1957), Venezuela (Loof, 1964), Nigeria (Sher, 1968), Côte d'Ivoire (Merny, 1970), Sénégal and Gambia (Fortuner & Merny, 1973)
H. thornei Sher, 1968	Indonesia (Sher, 1968)
Hirschmanniella spp.	Hong Kong & New Zeland (Sher, 1968)
Hoplolaimus clarissimus Fortuner 1973	Senegal (Fortuner & Merny, 1973)
H. tylenchiformis von Daday, 1905 = *H. coronatus* Cobb, 1923	Bengla Desh (Timm, 1955)
H. indicus Sher, 1963	India (Birat, 1965)
Hoplolaimus sp.	USA (Atkins *et al.*, 1957)
Hypsoperine sp.	Costa Rica (Figeroa & Jimenez, 1974)
Lelenchus discrepans (Andrassy, 1954) Meyl, 1961	Côte d'Ivoire (Merny, 1970)
L. infirmus (Andrassy, 1954), Meyl, 1961	USSR (Maslennikova, 1965 *b*)
L. leptosoma (De Man, 1880) Meyl, 1961	Japan (Imamura, 1931)

Species	*Records*
Longidorella parva Thorne, 1939	India (SURYAWANSHI, 1971)
Longidorus sp.	USA (ATKINS, FIELDING & HOLLIS, 1955 *a*), Emp. Centrafricain (LUC *et al.*, 1964), Senegal (FORTUNER, 1975)
Malenchus andrassyi Merny, 1970	Côte d'Ivoire (MERNY, 1970)
Meloidogyne arenaria thamesi Chitwood, 1952	South Africa (VAN DER LINDE, 1956)
M. exigua Goeldi, 1887	Thailand (KAŃJANASOON, 1964)
M. graminicola Golden & Birchfield, 1965	Laos (GOLDEN & BIRCHFIELD, 1968), India (PATNAIK, 1969), Thailand (BUANGSUWON *et al.*, 1971)
M. incognita (Kofoid & White, 1919) Chitwood, 1949	Egypt (IBRAHIM, IBRAHIM & REZK, 1972)
M. incognita acrita Chitwood & Oteifa 1952	Japan (ICHINOE, 1955), South Africa (VAN DER LINDE, 1956), Côte d'Ivoire and Guinée (LUC & DE GUIRAN, 1960)
M. javanica (Treub, 1885) Chitwood 1949	South Africa (VAN DER LINDE, 1956), Thailand (LEAUMSANG & KANJANASOON, 1961), Comores (VUONG, 1972), Egypt (IBRAHIM, IBRAHIM & REZK, 1972)
M. oryzae Maas, Sanders & Dede, 1978	Indonesia (MAAS, SANDERS & DEDE, 1978)
Meloidogyne sp.	USA (TULLIS, 1934, STEINER, 1934), Brasil (MONTEIRO, 1968), Taiwan (LIN, 1970), Ghana (ADDOH, 1971) Bengla Desh (OU, 1972) Sénégal (FORTUNER & MERNY, 1973)
Paralongidorus beryllus Siddiqi & Husain, 1965	India (SIDDIQI & HUSAIN, 1965)
P. citri (Siddiqi, 1959) Siddiqi, Hooper & Khan, 1963	India (BIRAT, 1965)
P. oryzae Verma, 1973	India (VERMA, 1973)
Paraphelenchus pseudoparietinus (Micoletzky, 1922) Micoletzky, 1925	Bengla Desh (TIMM, 1955), URSS (MASLENNIKOVA, 1965 *b*)
Paratylenchus aquaticus Merny, 1966	Côte d'Ivoire (MERNY, 1966)
Paratylenchus sp.	USA (ATKINS *et al.*, 1957), Sénégal and Gambia (FORTUNER & MERNY, 1973), Cameroun (SAMSOEN & GERAERT, 1975)
Peltamigratus nigeriensis Sher, 1963	Nigeria (CAVENESS, 1967), Sénégal (FORTUNER & MERNY, 1973)
Pratylenchus brachyurus Godfrey, 1929	Madagascar (LUC, 1959 *a*), Côte d'Ivoire (LUC & DE GUIRAN, 1960) Egypt (OTEIFA, 1962), Emp. Centrafricain & Congo (LUC, MERNY & NETSCHER, 1964), Brasil (MONTEIRO, 1968), Nigeria (BRIDGE, 1972), Senegal (FORTURNER, 1975)
P. delattrei Luc, 1958	Emp. Centrafricain & Congo (LUC, MERNY & NETSCHER, 1964)
P. goodeyi Sher & Allen, 1953	Egypt (OTEIFA, 1962)
P. minyus Sher & Allen, 1953	Egypt (OTEIFA, 1962), Korea (CHOI, 1972)
P. penetrans (Cobb, 1917) Chitwood & Oteifa, 1952	Egypt (OTEIFA, 1962)
P. pratensis (De Man, 1880) Filipjev, 1936	Egypt (OTEIFA, 1962)
P. sefaensis Fortuner, 1973	Senegal (FORTUNER, 1973)
P. thornei Sher & Allen, 1953	Egypt (OTEIFA, 1962)

Species	Records
P. vulnus Allen & Jensen, 1951	Korea (Choi, 1972)
P. zeae Graham, 1951	USA (Atkins *et al.*, 1957), Egypt (Oteifa, 1962), Venezuela (Loof, 1974), Brasil (Monteiro, 1968), Côte d'Ivoire (Merny, 1970), Cuba (Gateva & Penton, 1971), Rhodesia (Anon., 1972), Cameroun (Samsoen & Geraert, 1975), Sénégal (Fortuner, 1975)
Pratylenchus sp.	Sénégal and Guinée (Luc & de Guiran, 1960), Bengla Desh (Timm & Ameen, 1961), Taiwan (Lin, 1970)
Psilenchus hilarulus De Man, 1921	USA (Atkins *et al.*, 1955 *a*), Egypt (Elmiligy & Geraert, 1971)
Psilenchus sp.	Venezuela (Loof, 1964), Guyana (Anon., 1971)
Rotylenchulus borealis Loof & Oostenbrink, 1962	Côte d'Ivoire (Merny, 1970)
Rotylenchulus sp.	Emp. Centrafricain (Luc, Merny & Netscher, 1964), Sénégal (Fortuner & Merny, 1973)
Rotylenchus sp.	USA (Atkins *et al.*, 1957), Bengla Desh (Timm & Ameen, 1960), Guyana (Anon., 1971)
Seinura propora Siddiqi, Husain & Khan, 1967	India (Siddiqi, Husain & Khan, 1967)
S. diversa (Paesler, 1957) Goodey, 1960	USSR (Maslennikova, 1966)
S. oxura (Paesler, 1957) Goodey, 1960	USSR (Maslennikova, 1966)
S. speciosa (Andrassy, 1958) Goodey, 1960	USSR (Maslennikova, 1966)
Scutellonema cavenessi Sher, 1963	Gambia (Fortuner & Merny, 1973)
S. clathricaudatum Whitehead, 1959	Emp. Centrafricain (Luc, Merny & Netscher, 1964), Nigeria (Caveness, 1967), Côte d'Ivoire (Merny, 1970)
Scutellonema sp.	Cameroun (Samsoen & Geraert, 1975)
Telotylenchus sp.	Sénégal (Fortuner, 1975)
Triversus annulatus (Merny, 1964) Sher, 1973	Côte d'Ivoire (Merny, 1970)
Trichodorus christiei Allen, 1957	Brasil (Monteiro, 1968)
Trichodorus sp.	Taiwan (Lin, 1970), Ghana (Addoh, 1971), Sénégal (Fortuner & Merny, 1973)
Trichotylenchus falciformis Whitehead, 1959	Sénégal (Fortuner & Merny, 1973)
Tylenchorhynchus brassicae Siddiqi, 1961	India (Chhabra *et al.*, 1974)
T. clarus Allen, 1955	USSR (Ivanova, 1968), Egypt (Elmiligy & Geraert, 1971)
T. gladiolatus Fortuner & Amougou, 1973	Sénégal (Fortuner & Amougou, 1973)
T. martini Fielding, 1956	USA (Fielding, 1956), Bengla Desh (Timm & Ameen, 1960), Sierra Leone (Hooper & Merny, 1966), Taiwan (Lin, 1970), Iran (Kheiri, 1972)
T. mashhoodi Siddiqi & Basir, 1959 = *T. crassicaudatus* Williams, 1960 = *T. elegans* Siddiqi, 1961	India (Siddiqi, 1961), Thailand (Taylor, 1968), Côte d'Ivoire (Merny, 1970), Sénégal and Gambia (Fortuner & Merny, 1973), Mauritanie (Fortuner, 1975), Cameroun (Samsoen & Geraert, 1975)

Species	*Records*
T. phaseoli Sethi & Swarup, 1968	Cameroun (SAMSOEN & GERAERT, 1975)
T. sulcatus de Guiran, 1967	Nigeria (BRIDGE, 1972)
Tylenchorhynchus sp.	Guinée (LUC & DE GUIRAN, 1960), Venezuela (YEPEZ & MEREDITH, 1970), Guyana (ANON., 1971)
Tylenchus baloghi Andrassy, 1958	Côte d'Ivoire (MERNY, 1970)
T. kirjanovae Andrassy, 1954	USSR (MASLENNIKOVA, 1965 *b*)
T. parvus Siddiqi, 1963	Côte d'Ivoire (MERNY, 1970)
T. thornei Andrassy, 1954	USSR (GAGARIN, 1972)
Tylenchus sp.	USA (ATKINS *et al.*, 1955 *a*) Venezuela (LOOF, 1964), Ghana (ADDOH, 1971), Guyana (ANON., 1971), Cameroun (SAMSOEN & GERAERT, 1975)
Uliginotylenchus palustris (Merny & Germani, 1968) Siddiqi, 1971	Côte d'Ivoire (MERNY & GERMANI, 1968) Sénégal and Gambia (FORTUNER & MERNY, 1973)
U. rhopalocercus (Seinhorst, 1963) Siddiqi, 1971	Cameroun (SEINHORST, 1963) Côte d'Ivoire (MERNY, 1970), Nigeria (BRIDGE, 1972) Sénégal and Gambia (FORTUNER & MERNY, 1973)
Xiphinema attorodorum Luc, 1961	Senegal (FORTUNER, 1975)
X. bergeri Luc, 1973	Côte d'Ivoire (MERNY, 1970) Sénégal and Gambia (FORTUNER & MERNY, 1973)
X. cavenessi Luc, 1973	Côte d'Ivoire (LUC, 1973)
X. seredouense Luc, 1975	Guinée (LUC & DE GUIRAN, 1960)
X. insigne Loos, 1949	India (BIRAT, 1965), Bengla Desh (TIMM & AMEEN, 1960)
X. orbum Siddiqi, 1964	India (SIDDIQI, 1964)
X. rotundatum Schuurmans Stekhoven & Teunissen, 1938	Côte d'Ivoire (MERNY, 1970)
X. setariae Luc, 1958	Emp. Centrafricain (LUC, MERNY & NETSCHER, 1964)
Xiphinema sp.	Taiwan (LIN, 1970), Ghana (ADDOH, 1971)
Xiphinemella caudata Andrassy, 1970	Côte d'Ivoire (ANDRÁSSY, 1970)

Nematodes and rice plant

The relationship between parasites and rice plant have been investigated for endoparasites. Their penetration in the roots and subsequent development as well as their reproduction have been studied for species belonging to the genera *Hirschmanniella*, *Meloidogyne* and *Heterodera*. For some of the species our knowledge is restricted to fragmentary observations in the fields whereas for others laboratory experiments have been done and details are known about their relations with the plant.

NEMATODE POPULATIONS

Penetration of endoparasites

In *Hirschmanniella oryzae*, Van der Vecht and Bergman (1952) noted that males and females enter the young roots through the epidermis at some distance from the tip and move in both distal and proximal directions through the air channels. The thin lateral roots, having no air channels, are not infected. Mathur and Prasad (1972 *a*) observed nematodes near the central cylinder, producing hollows in the cortex.

Hirschmanniella mucronata enters the roots at

a distance of about 0,5 cm from the tip (Anon., 1972).

Hirschmanniella imamuri can enter the roots along their whole length but most frequently between 11 to 60% of the total length from the tip. After penetration, nematodes move into the cortex at the base of root. Adults can migrate as far as 6.3 to 10.3 mm (Goto, 1973).

Merny (1972 *a*, *b*) noted that all stages of *Hirschmanniella spinicaudata* can enter or leave rice roots and proposed a model derived from Nicholson's competition curve to express the number of individuals which penetrate in terms of the number of inoculated nematodes. The equation :

$$y = N\left[1 - \left(1 - \frac{a}{N}\right)^n\right]$$

in which n is the inoculum, N the maximum number of nematodes able to enter the root system of a plant and a the probability for a single nematode to enter the root system, fits the experimental results.

Ibrahim, Ibrahim and Rezk (1973) have observed that juveniles of *Meloidogyne incognita* enter the roots at the distal end and seldom in the zone of elongation. They are found in any part of the apical meristem or in vascular bundles without any particular orientation.

Meloidogyne graminicola penetration takes a minimum of 41 hours, when hypertrophy and hyperplasy begin in cortical cells, galls being formed in 72 hours (Patnaik, 1969).

All stages of *Hoplolaimus indicus* are able to penetrate but 4th stage juveniles and adults are most often observed in the roots. They produce inter- and intracellular galleries in the cortex which loses its rigidity : they also cause deformations in vascular bundles (Das & Rao, 1970).

Multiplication

Van der Vecht and Bergman (1952) observed that the multiplication rate of *Hirschmanniella oryzae* could reach thirteen per generation and Kuwahara and Iyatomi (1970) noted that, in Japan, two generations occured in one year, whereas Fortuner (1976) stated that three generations occur in Senegal during a rice crop. In Japan, the maximum population of parasites in the roots is observed at heading time whatever the date of planting.

Populations density in soil decreases after planting and increases after harvest when old roots begin to rot (Yokoo & Su, 1966). In Senegal, Fortuner (1976) observed that the maximum percentage of the total population present in the roots is reached between tillering and heading : he also noted in pot experiments that the maximum final populations was obtained with an inoculum of 300 individuals and more.

Kuwahara and Iyatomi (1970) observed that juveniles of *Hirschmanniella imamuri* hatched in the roots can escape after a certain time and become adult in the soil : only one generation occurs every year in Japan.

In pot experiments Merny (1970 *b*) studied the development of populations of *Hirschmanniella spinicaudata* in roots and soil in relation to inoculum. He observed that, when small inocula are involved, the increase of population did not fit perfectly the Verhulst-Pearl equation, formulated by Oostenbrink (1966) :

$$P_f = \frac{P_i}{b + c\,P_i}$$

Instead of the inoculum he considered as the initial population (P_i) the number of individuals having penetrated in the roots and the final population (P_f) should be expressed by the equation :

$$P_f = \frac{P_i + \frac{d}{c}}{\frac{a}{c}P_i + \frac{b}{c}}$$

in which $-\frac{d}{c}$ represents the smallest inoculum for which the subsequent development of a population can be expected because at smaller inocula there is a low probability of getting a gravid female or a female and a male having a chance to mate. Merny (1972 *a*) further observed that nematodes start to be observed in soil 90 days after inoculation and the soil-population increases during maturation of rice as if, lacking room and food, the nematodes escaped from the decaying roots.

In India, Das and Rao (1971) have noted that

Hirschmanniella mucronata was present in greater number in soil at heading time.

In *Meloidogyne graminicola*, Rao and Israel (1972 *c*) observed that low inocula led to higher multiplication rates, due to the fact that, at high initial densities, multiplication is hindered by competition for nutrients within the roots.

Merny (1972 *a*) noted that the reproduction rate in pots of *Heterodera oryzae* expressed as the ratio of the number of second stage juveniles hatching in the second generation and the number of second stage juveniles inoculated, was about six for initial densities between 50 and 200. The same low multiplication was observed as in *Hirschmanniella spinicaudata* at low initial densities.

Population development of *Heterodera elachista* (often mistaken for *H. oryzae*) on upland rice in Japan gave a series of peaks due to the hatching of eggs in successive generations : three peaks were observed on late maturing cultivars and two peaks on early or normal cultivars (Shimizu, 1973).

The population of *Pratylenchus zeae*, in Cuba, is maximum at heading and not at maturity (Gateva & Penton, 1971).

Populations of *Criconemoides onoensis* observed early in the crop in USA disappear at flooding and reappear after the drainage preceding harvest indicating that this species is not well adapted to flooded conditions (Hollis, 1969 *b*).

Reproduction and development

Most of the studies on reproduction concern sedentary endoparasites of the genus *Heterodera*.

In *Hirschmanniella oryzae*, Van der Vecht and Bergman (1952) noted that oviposition begins some days after penetration of adults and eggs laid in the roots hatch after four to five days. Nothing is known on the ovogenesis and sexuality of the different *Hirschmanniella* species.

Eggs of *Meloidogyne incognita* hatch between two and eight days in distilled water but second stage juveniles are obtained in one day in rice pots. Third stage juveniles were observed after eight days and fourth stage juveniles ten days after inoculation. The larval head is near the endodermis and its body in the cortex and young females appeared from the 15th day and egg masses after 20 days ; juveniles of the next generation appear at 35 days. The nematode induces an hypertrophy and hyperplasy of cells in the meristem, cortex endodermis and pericycle of the roots and giant cells form in the meristem, cortex and xylem after 10 days. As many as six giant cells per juvenile have been observed (Ibrahim, Ibrahim & Rezk, 1973).

Roy (1975) observed that root exudates of resistant or susceptible rice cultivars have no effect on the hatching of eggs of *Meloidogyne graminicola*.

Netscher (1969) studied ovogenesis and reproduction of the two *Heterodera* species known in West Africa and observed that *H. oryzae* is diploïd (2n = 18) and amphimictic while *H. sacchari* is triploïd (3n = 27) and parthenogenetic. Cadet, Merny and Reversat (1975) observed that, in *H. oryzae* sex was already determined in second stage juveniles, relative abundance of males in cases of overcrowding being due to preferential death of female juveniles, whereas Cadet and Merny (1978) have shown that in *H. sacchari* sex was determined later, each second-stage juvenile being able to develop into a male or a female adult according to external factors.

The life cycle of *H. oryzae* was studied by Berdon-Brizuela and Merny (1964) who established that the second moult occured after three to four days and the third moult nine to ten days after penetration, the first males appearing after thirteen days and the first females after sixteen days. Hatching of eggs in egg-masses and cysts has been studied by Merny (1972 *a*) in water and in soil. In water, hatching in cysts is stimulated by rice-root exudates. In soil, hatching in cysts lasts longer and reaches a higher level than in water while hatching in egg-masses is delayed so that egg-masses kept in soil for nine months are still able to liberate infective juveniles.

Influence of nematodes on the rice plant

Nematodes living in roots of rice or, at least, feeding on them inevitably induce troubles in the physiology of the plant. Symptoms induced to rice plant by root nematodes are never specific. The most frequent is a reduction in tillering.

Hirschmanniella oryzae

Van der Vecht and Bergman (1952) considered this species to be responsible for the disease known in Indonesia as "Omo Mentek". Later, Van der Vecht (1953) was less affirmative and only stated that the disease appeared when *H. oryzae* was present and rice growth conditions were very unfavourable. More recently, Ou (1965) stated that Omo Mentek was not caused by *H. oryzae* but by a virus. However, Van der Vecht and Bergman (1952) had established that *H. oryzae* could induce troubles in rice plant, namely growth retardation and reduction of tillering which could be beneficial for the cultivars grown in Java which suffer from an excess of tillering due to poor soil fertility.

Thorne (1961) estimated that, under favorable agronomic conditions there is little evidence of injury to rice by *H. oryzae* because rice roots develop at three stages of growth (seedling, tillering and end of tillering) and nematodes developing in the roots during one period remain there during the following one so that the amount of healthy roots is always sufficient to secure nourishment of the plant.

In Japan, decrease in tillering induced by *H. oryzae* is more important in soils with low rH, resulting in a disease called "Akiochi" and yield losses are more important in these soils. (Kawashima, 1964 *b*). Infested seedlings undergo growth retardation, height and weight of the plant are decreased and, at the same time, the browning of the roots is higher at high initial densities (Kawashima & Fujinuma, 1961). According to the same authors, nematodes interfere with the physiology of the roots, decreasing their oxidizing capacity and inducing their coloration by iron oxide.

H. oryzae decreased tillering and root weight in India (Mathur & Prasad, 1972 *b*). In the U.S.A. the parasite caused decay of the tip of primary roots in the layer of the soil with a high rH (Hollis, 1967).

In India *Hirschmanniella mucronata* reduces yield but not ear number and does not retard tillering but length and weight of roots increase with the size of inoculum, indicating that the plant compensates for the attack by the nematode (Panda & Rao, 1971).

Hirschmanniella spinicaudata, was recorded by Luc (1957) in Cameroon, associated with yellowing rice plants and the same symptoms have been observed in Upper-Volta (Germani, pers. comm.).

Hirschmanniella spp. stunted rice in Thailand (Buangsuwon *et al.*, 1971).

In India *Meloidogyne graminicola* causes a yellowing of the upper part of the leaves. Plants are stunted, roots proliferate, are thin and forked and bear characteristic galls (Roy, 1973). Similar symptoms were found in inoculated seedlings, tillers were smaller, heading occured earlier than normal and the grains were deformed, but rice will grow satisfactorily with up to 1 785 galls (Patnaik, 1969). In Laos the main attack is on seedlings in nurseries ; they become yellow, brown and dry out : galls are formed on upland rice but have not been observed on paddy although they will appear as soon as the irrigation water is removed.

In pot experiments in Thailand, *Meloidogyne* sp. caused a poor growth, reduction of tillering, delayed maturation and a yield decrease (Chantanao, 1962). Similar symptoms caused by *Meloidogyne incognita* and *M. javanica* were observed in Egypt (Ibrahim, Ibrahim & Rezk, 1972).

Joshi, Ibrahim and Hollis (1975) have noted that oxygen released by the roots was reduced in three-week-old infected rice seedlings : the number of galls increased with the size of inoculum although the growth was not affected.

In a pot experiment, in Costa-Rica, *Hypsoperine* (n. sp. ?) interfered with the growth of rice seedlings, roots showing apical thickenings with growth retardation : the aboveground symptoms, similar to nutritional deficiencies, consisted of leaf chlorosis and necrosis, poor tillering, stunting and lack of vigour, nutrient uptake being deficient in infested plants.

Heterodera elachista at initial densities of 0 to 10,000 cysts, decreased tillering from 7 to 2.7 tillers per plant (Oda *et al.*, 1963) : the height of plants and root weight were markedly reduced and grain yield decreased from 7.82 g to 3.15 g at the highest infestation level. In seedlings, there was leaf chlorosis and a reduction of tillering and rooting and it was noted that the capacity of roots to absorb iron and nitrogen was reduced and they turned brownish. The appearance of symptoms in a field was very

variable, being different in every year (Watanabe, 1963).

Heterodera sp. (different from *H. elachista* and *H. oryzae*) has been found on the roots of chlorotic rice plants in India (Rao & Jayaprakash, 1977).

Criconemoides onoensis. Roots attacked by parasites belonging to this species have a characteristic knotty appearance. They are shorter and less forked and the size and weight of roots and aerial parts of inoculated seedlings are reduced (Embabi, 1967). Deformation of the roots caused by this nematode mainly occurs in the layer of soil whith a high rH beneath the biochemically reduced zone (Hollis, 1967).

Interiano Muñoz (1970) could not ascertain the pathogenicity of *Criconemoides* sp.

Tylenchorhynchus martini. Seedlings inoculated in pots with 3,000 individuals per pint of soil (about 5,300 per liter) showed, after two weeks, significant reductions in length and dry weight of roots compared with non-inoculated controls. The effects were more severe when inoculated with "swarming" than with "non-swarming" nematodes : plants were stunded and chlorotic, nematode aggregates were observed *in vitro* around the roots and it was suggested that the nematodes inhibit the absorption of nutrients or excrete toxins (Joshi & Hollis, 1976).

Pratylenchus indicus. Rao and Prasad (1977) stated that this parasite can cause the death of rice 40 to 50 days after germination.

Yield losses

Determination of yield losses caused by nematodes is very difficult. Treatment of infested soils with nematicides often give good yield increases. But soil treatments are drastic, other pathogens can be killed and examples are known of yield increases in nematicide-treated soils which had not been caused by the destruction of nematodes but of other pathogens such a fungi or micro-arthropods. Although yield increases with nematicides are, in most cases, caused by nematode destruction, results of such trials must be interpreted with caution.

A better way to determine the part played by nematodes in yield decreases is to inoculate plants grown in pots on heat-sterilized soil and compare with non inoculated controls.

Field treatment

Treatments with D-D and DBCP in a field infested with *Hirschmanniella* sp., in Thailand gave increases in yield of 28 to 30%. Treatments of nurseries, infested with *Meloidogyne* sp., resulted in better seedling growth but to no increase in yield (Taylor *et al.*, 1966).

In Japan, D-D treatment of fields infested with *Heterodera elachista* increased yield by 30% (Nishizawa, Shimizu & Nagashima, 1972). Against the same parasite, D-D and EDB gave an increase of 20 to 70% (Yanaka *et al.*, 1962) but the authors thought the increase is too high to be explained by the destruction of nematodes and suggested that the chemicals had some side effect, favorable to plant growth. *H. elachista* caused heavy losses in rice over a period of four years ; yields were 2,870 kg/ha in the first year and 950 kg/ha in the fourth year (Watanabe *et al.*, 1963) and thus, these authors considered *H. elachista* responsible for the failure of continuous upland rice cropping in Japan.

The use of Dasanit (fensulfothion) against *Criconemoides onoensis* in the USA, resulted in an increase of 20% in paddy yield (Hollis, 1969 *a*) and, against *Tylenchorhynchus martini* and other nematodes, methyl bromide gave increases of 45% at harvest (Atkins, Fielding & Hollis, 1957).

Inoculation experiments

In Senegal, the vigour of paddy in fertilized microplots infested with *Hirschmanniella oryzae*, was much reduced as compared with plants in non-infested plots with yield increases of the order of 42%. However, the characteristics of grains (weight of 1,000 grains, germination, etc.) was the same in both conditions (Fortuner, 1974). Fortuner (1977) experimented on microplots, in soil free of nematodes. Half of the microplots were inoculated with *H. oryzae*. In each category, inoculated or control, half of the microplots received fertilizers. He ascertained that :

(*a*) in non-fertilized plots, the yield losses due to nematodes were higher (31%) than in fertilized plots (19%),

(*b*) the yield increase due to fertilization is higher in inoculated (36%) than in non-inoculated plots (17%).

Inoculation with 5,000 and 10,000 *Hirschmanniella mucronata* to one-day-old rice seedlings decreased the yield by 50% and 70% respectively. If parasites were inoculated to 40-day-old plants, the decrease was still important (45 and 65%). On 70-day-old plants there was no effect (Prasad & Rao, 1971).

Shimizu (1971) reported yield losses from 7.2 to 18.7% after inoculation with *Heterodera elachista:* the losses were higher when plants were inoculated between tillering and heading (Shimizu, 1972). In potted rice plants inoculated with 0, 400 and 4,000 juveniles of *Heterodera elachista* grain yield was 71.2 g, 67.2 g and 59.5 g respectively. Maximum losses occured when nematode penetration took place before heading. Under fields conditions losses were more severe when rice was sown early, the effect of the nematodes being more severe in the last stages of rice growth (Shimizu, 1976).

Inoculation of *Meloidogyne graminicola* 1,000 to 8,000 per plant decreased yield by 2.6 to 8% per 1,000 nematodes added (Rao & Biswas, 1973).

Associations with other pathogens

"Root browning" of rice, mainly caused by soil micro-organisms was slightly increased by the presence of *Hirschmanniella oryzae* (Lee & Park, 1975).

Nematodes and environment

For a parasitic nematode, the main factor in the environment is the presence of a host plant. However, other factors such as soil conditions can have an influence on their development, multiplication and also on their survival in the absence of a host.

Survival between rice crops

Hirschmanniella spp.

Two factors are especially important for the survival of *Hirschmanniella* spp. in the interval between two rice crops : soil moisture and presence or absence of host roots. As these nematodes are endoparasites, after rice has been harvested high populations are still inside the roots and a variable number are found in the soil.

In the laboratory Van der Vecht and Bergman (1952) observed that, in every conditions a high proportion of the initial population of *Hirschmanniella oryzae* was still alive after ten weeks. They noted that the death rate in a drying soil was about the same as in a wet soil or sand and that it is generally higher in soil or sand without roots than with roots. Thorne (1961) found numerous quiescent *H. oryzae* individuals in the dried up clay of rice fields in Thailand and Philippines during the dry season. In Japan, Kawashima (1962) states that nematodes survive in winter as juveniles or adults in dead rice roots ; in very wet fields they often hibernate in the egg stage but they seldom survive in well drained fields due to drying of soil in spring. In Korea, *H. oryzae* can survive for up to seven months in the water of flooded rice fields (Park, Han & Lee, 1970). In India, Mathur and Prasad (1973 *a*) have shown that, in aerated water, 50 to 60% of the nematodes were still alive after eight weeks but only 0 to 20% survived after sixteen weeks : in a soil sample allowed to dry for ten months and containing rice roots, 240 nematodes per liter of soil were still alive while a soil without roots contained no more living nematodes after the same period. Fortuner (1977) stated that in the Senegal River Delta *H. oryzae* can withstand very severe dry seasons between January and August. Nematodes leave the roots in August when the water comes. Gotô (1969) has reported similar effects and noted that most adults of *Hirschmanniella imamuri* after having hibernated in old rice roots are released in soil at planting time, in June. In a microplot trial with *H. oryzae* if soil remains wet after the harvest, roots decay and the nematodes in the roots are released into the soil ; populations decrease slowly and become eradicated after one year. In dry soil, both root and soil populations decrease slowly until, after flooding, populations are released from the roots into the soil (Fortuner, 1977). Merny (1972 *a*) observed that, in Ivory Coast, the survival of *Hirschmanniella spinicaudata* is better in roots than in soil

and is much longer if the soil containing roots becomes dry than if it remains flooded.

The results obtained by Merny (1972 *a*) and Fortuner (1977) are not in agreement with Van der Vecht and Bergman (1952) who observed that soil moisture had no effect on survival of nematodes. However, the latter authors have studied the survival of nematodes in soil, without roots and the experiments were made in Petri dishes, in thin layers of soil, with a good aeration while Merny and Fortuner worked in microplots and pots and hence the results are difficult to compare.

It can be concluded that :

1) Nematodes belonging to the genus *Hirschmanniella* survive longer in roots than in soil.

2) Survival of root populations is shorter in flooded soil due to quick decaying of the roots.

3) In soil, the survical of mobile individuals is better in wet conditions.

4) Due to anhydrobiosis, the persistance of populations out of the roots is better in dry conditions.

Little is known of the effect of temperature on nematode survival. In India, Mathur and Prasad (1973 *a*) reported that, in soil samples kept in sealed plastic bags for eight weeks, at different temperatures, 57.6% of *H. oryzae* individuals were still alive in bags kept at 15°, 90% at 35° and none at — 2°. In fallow fields, they have observed that the parasite could withstand high temperatures (35 to 45°) in May and June.

Heterodera oryzae

Juveniles of this species survive less than 30 days in soil in Ivory Coast and they die quicker in flooded than in wet soil ; eggs can survive in egg-masses for nine months and for more than two years in cysts (Merny, 1972 *a*). Reversat (1975 *a*) has shown that, although this species can live in flooded fields in heavy soils where oxygen is scarce, the juveniles have an aerobic metabolism. Under anaerobic conditions, they become inactive but, hence, they survive a longer time.

EFFECT OF IRRIGATION ON NEMATODE POPULATIONS

Rice nematodes are more or less adapted to flooded conditions. Fortuner (1977 *b*) observed an hydro-topographical gradient in the distribution of the nematode fauna of Senegalese rice fields. Comparing paddy fields and upland fields, as the water table goes down, there is a progressive decrease, ending in a disappearance, in upland rice fields, of species characteristic of flooded rice and other species, usually found associated with other crops, appear. Fortuner's experiments (1977) have shown that in Sénégal species belonging to the genus *Hirschmanniella* are the only ones which are perfectly adapted to constant flooding. *Tylenchorhynchus mashhoodi* is adapted to fields where the water table is close to the ground level ; during a flooded rice crop its populations decrease and increase again after the harvest, when the soil is well drained but wet enough to allow rice shoots to grow.

Yokoo and Su (1966) observed that populations of *Hirschmanniella oryzae* decrease rapidly after water has been removed and that this nematode was found in the 10 to 20 cm layer before drainage and 0-20 cm after. Fukazawa, Kobayashi and Nakata (1963) noted that more nematodes were found in fields badly or poorly drained. Another example of the specialization of *Hirschmanielle oryzae* is given by Kawashima (1962) who notes that this parasite does not attack upland rice except when grown in flooded conditions. *H. oryzae* commonly occurs in badly drained peaty and humiferous fields where "Akiochi" disease is common (Kegasawa & Kawashima, 1962).

Meloidogyne graminicola is poorly adapted to flooded conditions. Its penetration in roots is best when soil moisture is 32% and its development is favoured by a moisture of 20 to 30% and by soil dryness at rice tillering and earing (Rao & Israel, 1971 *a*, 1972 *b*).

Like *Tylenchorhynchus mashhoodi*, *T. martini* develops best at low soil moistures : 40 to 60% of field capacity (Johnston, T.M., 1958).

EFFECT OF SOIL CONDITIONS

Hirschmanniella oryzae appears to develop

better in clay soils of North Senegal than in the sandy soils of the South (Fortuner, 1977) and the highest populations in India, are found in heavy clay soils (Mathur & Prasad, 1971) On the other hand, Fortuner (1977) noted that *Hirschmanniella spinicaudata* developed equally well, in Senegal, on both types of soil.

Rao and Israel (1971 *a*) reported that soil pH had no effect on the development of *Meloidogyne graminicola* but both movement and penetration into roots were better in coarse textured soils (particles over 53 µm). Clay soils are less favourable and a linear relation has been observed between percentage of sand in soil and the activity of nematodes, the increase of their effect on root growth and the appearance of galls (Rao & Israel, 1972 *d*).

In *in vitro* experiments, penetration of *Heterodera oryzae* is best in artificial soil composed of particles between 100 and 160 µm and very poor if particles are bigger than 250 µm. On the other hand, with *Hirchmanniella spinicaudata*, penetration is best with particles between 160 and 250 µm and still occurs up to 630 µm : the optimum particle size for penetration is apparently related to the size of the nematode (Reversat & Merny, 1973).

Control

Although Van der Vecht and Bergman (1952) stated that cleaning the fields, keeping a good fertility and proper agronomic practices should allow rice to withstand attacks by *Hirschmanniella oryzae* without noticeable losses, control of rice nematodes is difficult and several kinds of control measures should be considered including agricultural pratices, varietal resistance, biological control and chemical control.

Cultural control

Planting conditions

Early planting decreases populations of *Hirschmanniella oryzae* and the number of juveniles of *H. imamuri* but did not seem to influence the number of adults of *H. imamuri* (Sato, Koyama & Koshihara, 1970). Higher populations of *Hirschmanniella oryzae* are reported in seedlings from flooded nurseries than from intermediate or dry nurseries or from directly sown fields (Miura & Shoji, 1964). Higher populations are found in planted up rice than in directly sown rice roots (Nakazato, Kawashima & Kurosawa, 1964).

Heterodera elachista normally attacks upland rice. However, Kawashima (1964 *a*) observed that flooded rice could be attacked if it was sown directly into dry land and flooded one month later : rice planted up traditionally in an adjoining field remained free of nematodes.

Crop rotations

In Japan, a crop of soybean reduced the populations of *Heterodera elachista;* three successive crops did not lead to complete eradication but the following upland rice crop yielded 2.8 to 3.7 times more than compared with rice which had been cultivated for more than four years (Nishizawa, Shimizu & Nagashima, 1972). After non-host plants had been cultivated for one year, *H. elachista* populations were reduced to 7-8% of the initial population and to 2-3% after two years, then a good upland rice yield was obtained but nematode populations built up again (Hoshino *et al.*, 1961)

In pot experiments, soybean, sweet potato and cotton have proved to be bad hosts of *Criconemoides onoensis* in USA (Alhassan & Hollis, 1969). One crop of soybean reduced the population of nematodes and a good rice yield was obtained : the beneficial effect was still obvious on the next rice crop. Hollis (1969 *b*) reported that maize is attacked by this nematode.

Effect of fertilization

In Japan, Tomonaga and Kurokawa (1964) have noted that calcium silicate and compost reduce *Hirschmanniella* sp. populations and increase yield. Ishikawa (1965) stated that nitrogenous fertilizers favour the development of nematode populations (without stating which species were involved) and increase the decay and browning of roots. The height and tillering of plants are improved. Inversely, potassic fertilizers and compost keep nematode populations at a low level.

Fertilizers containing respectively 64.3 and 30% of silicic acid and various micro-elements

reduced *Hirschmanniella* sp. by 15% and increased yield by 5% (Yokoo & Morimitzu, 1969).

In India, Mathur and Prasad (1972 *b*) noted that fertilizers improve plant growth as well as nematode populations. However, the same authors (1971) stated that populations of *Hirschmanniella oryzae* were lower in fields fertilized with urea.

Nitrogen at the rate of 40 kg/ha and/or phosphorus increase the reproduction of *Meloidogyne graminicola* (Rao & Israel, 1971 *a*).

Varietal resistance

Kawashima (1963) tested seventeen rice cultivars for their susceptibility to *Hirschmanniella oryzae* and found no difference between them. With the same parasite, Park, Han and Lee (1970) tested 270 cultivars and found that five of them were relatively resistant (less than one nematode per gram of roots).

There is a considerable literature on testing rice cultivars resistant to *Meloidogyne graminicola:*

Golden and Birchfield (1968) tested 30 cultivars and Manser (1968, 1971) tested 80 cultivars and no resistance was observed in both cases.

Sampath, Rao and Roy (1970) and Roy (1973) found two resistant cultivars and Rao *et al.*, (1969) reported that cultivars TKM 6 and Patna 6 were resistant while four others were moderately susceptible. In addition, the cultivar TKM 6 was also resistant to stem borer. Sampath, Rao and Roy (1970) stated that resistance to *Meloidogyne graminicola* has a chemical origin.

Penetration of juveniles of this parasite is the same in susceptible (IR 8, Pusa 2-21) as in resistant cultivars (IR 20, Basant Bahar) but subsequent development is reduced in resistant cultivars, a smaller number of galls being produced (Roy, 1975).

According to Jena and Rao (1974) the resistance to *M. graminicola* of cultivars Hamsa, IR 5, IR 47, IR 2, Manaharsali and Baharsia has no chemical origin but is due to the fact that they have a smaller number of roots, a denser rootlet system, a sclerified exodermis, a thin cortex and central cylinder, little phloem, much xylem and a high content of aspartic acid and alanine (Jena & Rao. 1974). Penetration is more rapid and life cycle shorter in susceptible than in resistant cultivars (Jena & Rao, 1976).

The cultivar International is resistant to *Meloidogyne incognita acrita* (Ibrahim, Ibrahim & Rezk, 1972) but Kumazawa (1965) found no cultivar resistant to *Heterodera elachista.* Twelve cultivars tested by Figueroa and Jimenez (1971) are all susceptible to *Hypsoperine* sp. (syn. of *Meloidogyne*).

Biological control

In Japan, a fertilizer containing 3% of spores of *Arthrobotrys* sp., a fungus predator of nematodes, applied at the rate of 60 kg-ha reduced the populations of *Hirschmanniella oryzae* and *Hirschmanniella imamuri*, and increased tillering by 7%, number of grains and straw weight by 10% and yield by 6% (Yokoo, 1971).

Gemma, Shibuya and Kikuchi (1964) observed that tadpoles could eat nematodes.

When rice fields are flooded the soil becomes anaerobic and populations of sulphate reducing bacteria increase : under these conditions populations of *Tylenchorhynchus marlini* decrease. Laboratory tests have confirmed that H_2S concentrations produced by bacteria were toxic to nematodes (Rodriguez-Kabana, Jordan & Hollis, 1965). The existence of the same phenomenon in Senegal has been shown in field observations and laboratory trials (Fortuner & Jacq, 1976). Microplot experiments have given good results and it might be possible to artificially increase bacteria activity after the harvest to further reduce the number of viable nematodes present in the soil. However, some or all eggs laid inside the roots are not killed (Jacq & Fortuner, 1979).

Chemical control

Fumigants

In Japan, numerous soil-treatment trials have been done with D-D. (dichloropropane-dichloropropene), EDB (ethylene dibromide), DBCP (dibromochloropropane), methyl bromide and metham-sodium. Results have been summarized

by Ichinoe (1968) who noted that yield increases caused by D-D cannot always be explained by the reduction in nematode population. Yield increases with DBCP are lower and EDB is phytotoxic, causing a dark green discoloration of leaves and excessive tillering. All chemicals tested reduce nematode populations during rice crop and the treatments have a beneficial effect on nitrifying bacteria and increase the quantity of nitrogen available in soil. Hence, the amount of nitrogenous fertilizers to be applied can be reduced. In addition various positive or negative effects have been observed on the severity of attacks by other pathogens, e.g. insects or fungi.

In Thailand, D-D, DBCP and methly bromide have been used to control *Meloidogyne* sp. in nurseries and *Hirschmanniella* sp. under field conditions. In nurseries vigour and weight of plants were increased and planting up could be made ten to forteen days earlier and in the field, yield was increased by 24 to 36% but the treatments were uneconomic (Taylor *et al.*, 1966 ; Taylor, 1968).

In India *Hirschmanniella oryzae* was controlled by D-D applications at the rate of 400 kg/ha injected at a depth of about 22 cm and by adding DBCP to irrigation water at the rate of 120 cm^3 per 100 m^2. Treatments were done three weeks before sowing in nurseries and five weeks before planting out (Mathur & Prasad, 1973 *b*).

In USA treatments against *Tylenchorhynchus martini*, *Hirschmanniella oryzae* and other nematodes with methyl-bromide applied under covers (100 g/m^2) is better than with EDB (113 l/ha at 83%), D-D (378 l/ha) or DBCP (47 l/ha). Methyl-bromide was equally active against *Helminthosporium oryzae* and *Echinochloa* but did not prevent a slight attack of "straighthead". Yield was increased by 45% (Atkins & Fielding, 1956 ; Atkins, Fielding & Hollis, 1957).

Non fumigants

In USA, treatments against *Criconemoides onoensis* with fensulfothion allows the highest yield increase when the chemical is applied early, on 25 cm high plants, before flooding of the field. Yield increase is then 20%, about 1,000 pounds of paddy. Ethoprophos destroys nematode populations but is phytotoxic. Disulfoton, Thomson Hayward 327-1 and carbofuran are less efficient than fensulfothion. Aldicarb treatment appears to increase nematode populations and weight of plants. (Hollis, 1969 *a*.)

Applications of phenamiphos, Dupont D-110 and fensulfothion incorporated by cover-cropping or flooding has caused the development of adventicious plants and unfortunately weeding with propanil was prohibited because it reacts with the nematicides and becomes phytotoxic (Hollis, 1972).

In India, Samantaray and Das (1971) have treated *Hirschmanniella* sp. and *Hoplolaimus* sp. with thionazin (12,5 l/ha) dichlofenthion (24 l/ha) and two fumigants : DBCP (11,5 l/ha) and metam-sodium (393 l/ha). After 45 days, both systemics had eliminated all nematodes, while DBCP had eliminated *Hoplolaimus* sp. and markedly reduced *Hirschmanniella* sp. populations ; metam-sodium was not effective after 60 days and no information was given about yield.

Fensulfothion, phorate and cytrolane are the most efficient chemicals against *Hirschmanniella mucronata* (Anon. 1973 *b*).

The following treatments are efficient against *Meloidogyne graminicola :*

- Soaking rice seeds for twelve hours in 500 p.p.m. of oxamyl or phorate or for 24 hours in 1,000 p.p.m. of fensulfothion or carbofuran (Prasad & Rao, 1976 *a*).
- Soaking seedling roots in 100 p.p.m. of oxamyl. (Prasad & Rao, 1976 *b*).
- In pots, after inoculation, application of 50 p.p.m. oxamyl or fensulfothion or 100 p.p.m. of carbofuran and DBCP (Prasad & Rao, 1976 *c*).

Prasad and Rao (1973) planted rice in pots containing *Tylenchorhynchus* sp. treated immediately with oxamyl, DBCP, dursban and phorate at rates from 100 to 2,000 p.p.m., either by foliar application or directly in the soil. Foliar applied oxamyl reduces the nematodes from 59.4-74.3% even at low concentrations while the other products are only efficient at 2,000 p.p.m. On the other hand, in the soil application, other products give control of 94 to 100% at all concentrations while oxamyl reduces the nematode population by 68-95% at concentrations from 100 to 2,000 p.p.m.

Chhabra, Sajjan and Singh (1974) found that carbofuran (1.5 kg/ha) fensulfothion (5 kg/ha) and aldicarb (3 kg/ha) applied one week after sowing were all efficient against *Tylenchorhynchus brassicae* in nurseries but phorate had no effect.

In Japan, Nishizawa, Shimizu and Nagashima (1972) applied methomyl granules (5%) at the rate of 40 kg/10 ares at sowing.

Miscellaneous

Yokoo, Ookuchi and Teramachi (1967), noted that applying an herbicide : 4-dichloro- 2-methylphenoxyacetic acid (MCPA) increased the populations of *Aphelenchoides* sp. while pentachlorophenol (PCP) and a diphenylether (MO) increased those of *Hirschmanniella oryzae.*

Mustard and "neem" oil-cakes reduce *Hirschmanniella oryzae* populations and improve plant growth (Mathur & Prasad, 1973 *b*).

In pots, maize-cakes increase n-butyric acid concentrations up to nematicidal proportions and propionic acid, which is also formed, is active against nematodes (Hollis & Rodriguez-Kabana, 1966). The effects of fatty acids on *Tylenchorhynchus martini* depends on their molecular weight ; the most efficient is butyric acid (Johnston, 1959).

Controlling *Criconemoides onoensis* in Louisiana stimulates weed growth more than rice growth. The control results in lower rice yields in fields infested with *Cyperus esculentus.* On the other hand, large and significant increases in yield of rice were obtained when weeds were removed and nematodes controlled (Hollis, 1977).

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