vary considerably depending on the time of infection and the cultivar. The disease is associated with the rice mealy bug, *Brevennia rehi* (*Ripersia oryzae* Green), and reported to be transmitted in a nonpersistent manner. Seedlings infested with mealy bugs that had fed on symptomatic rice plants for 8 hr developed chlorotic streak after 1 or 2 weeks. Plants infested with mealy bugs, but not chlorotic streak, showed stunting and leaf yellowing only. The chlorotic streak syndrome has not been associated with mealybug infestation outside India.

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(Prepared by H. Hibino)

Crinkle

Crinkle was first observed in patches in upland rice in Sierra Leone in 1976. Since then, it has been observed at a low incidence in the Ivory Coast, central Nigeria, and Liberia.

Leaves of emerging seedlings are crinkled or distorted and may develop pale yellow, lens-shaped lesions. Entire leaves may turn yellow, and roots are stubby and bushy. Seedlings may die or produce new tillers that grow normally. Panicles produced from seedlings with crinkle are poorly filled.

Attempts to transmit the crinkle condition have failed, but the condition was reproduced at a low frequency on healthy plants grown in soil from around diseased plants.

Selected Reference

Ou, S. H. 1985. Rice Diseases. 2nd ed. Commonwealth Mycological Institute, Kew, England.

(Prepared by H. Hibino)

Wrinkled Stunt and Witches'-Broom

Both wrinkled stunt and witches'-broom are associated with particular cultivars of rice, and the conditions are seed-transmitted. Wrinkled stunt occurs in the progeny of the cross IR454 and 71101/9. Symptoms include severe stunting with dark green, wrinkled, twisted leaves. Panicle exsertion is incomplete, and only a few of the spikelets set seed.

Witches'-broom occurs in the progeny of CICA 4. Plants show pronounced stunting and tiller profusely, producing up to 100 tillers. Panicles are produced but are small, with only 10–20 seeds.

Selected Reference

Ou, S. H. 1985. Rice Diseases. 2nd ed. Commonwealth Mycological Institute, Kew, England.

(Prepared by H. Hibino)

Diseases Caused by Nematodes

Nematodes are unsegmented roundworms that are aquatic. Plant-parasitic nematodes are typically microscopic, transparent, and vermiform; exceptions are the females of some genera, which become swollen and saclike. Plant-parasitic nematodes feed and reproduce on living plants and are capable of active migration in the rhizosphere, on aerial plant parts, and/or inside the plant. They are disseminated by wind, irrigation and flood water, tools, machinery, animals, and infected plant propagation materials.

The life cycle of a typical plant-parasitic nematode is simple and direct. An egg laid by the female develops into a first-stage juvenile, which usually undergoes a first molt within the egg shell and hatches as a second-stage juvenile. After hatching, the juvenile develops through two more stages, each completed by a molt, and becomes an adult after the fourth molt. The time required to complete the life cycle varies considerably, from a week to several months, depending on the genus and on temperature and moisture.

More than 150 species of plant-parasitic nematodes have been associated with rice or rice soils. A parasitic relationship with rice, however, has been demonstrated for only a few of these nematode species. Those of economic importance on paddy and deep-water rices are *Aphelenchoides besseyi* Christie, *Ditylenchus angustus* (Butler) Filipjev, *Hirschmanniella* spp., *Criconemella* spp., and *Meloidogyne* spp. Those of importance on upland rice are *Heterodera* spp., *Meloidogyne* spp., *Pratylenchus* spp., and *Hoplolaimus indicus* Das.

Estimates of annual yield losses due to plant-parasitic nematodes on rice worldwide range from 10 to 25%. The lower estimate corresponds to an annual monetary value of US$16 billion. Actual losses due to nematodes may be greater, because nematodes generally do not cause diagnostic symptoms on aboveground parts of plants, and damage is often attributed to other causes, such as nutrient deficiencies or other pathogens.

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(Prepared by J. C. Prot)

White Tip

White tip, caused by *Aphelenchoides besseyi* Christie, has been reported from most of the rice-growing countries of Africa, from North, Central, and South America, and from Asia, Eastern Europe, and the Pacific.

Symptoms

The common name *white tip* is based on the characteristic whitening of 3–5 cm of the leaf tip (Plates 111 and 112). The

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whitened tips eventually become necrotic and shred. The central part and the base of infected leaves are sometimes darker green than normal. The upper leaves are the most affected, and the flag leaf is often twisted, hindering the emergence of the panicle. Other symptoms include reduction in the length of the panicle, reduction in the number of grains, sterile flowers, misshapen grains, stunting of the plant, late ripening and maturation, and production of tillers from the upper nodes. Not all plants infected with *A. besseyi* show the characteristic leaf and panicle symptoms, although their yields are reduced. Symptoms similar to white tip may result from insect injuries or may be caused by other nematodes, such as *Ditylenchus angustus* (Butler) Filipjev.

Yield losses vary with cultivar, year, temperature, cultural practices, and other variable factors. In infested fields, the average losses range from 10 to 30%. In fields where all plants have been attacked, maximum losses of 70% for the most susceptible cultivars and 20% for the most resistant cultivars have been reported.

Disease Cycle and Epidemiology

A. besseyi parasitizes flooded rice as well as upland rice. The nematode survives from one season to the next in infected seeds and to a lesser extent on weeds and on ratoons and debris from the preceding rice crop. *A. besseyi* can survive in seeds in a dehydrated state for up to 3 years.

Reviviscent nematodes that emerge from seeds after planting are attracted by and feed on the primordia of emerging plants. Later, they move to the growing points of stems and leaves and feed ectoparasitically, causing obstruction of the xylem vessels and disintegration of the phloem cells. The nematode multiplies abundantly and is carried upward as the plant grows. *A. besseyi* eventually migrates to the developing panicle, punctures the inflorescence, and penetrates into the florets via the apicular opening, where it feeds on the ovaries, stamens, and embryos. The rate of reproduction is high in the florets before anthesis. After anthesis, reproduction declines and then ceases in maturing grains, and the nematode becomes dormant as the grains dehydrate.

A. besseyi is inactive if the atmospheric humidity is less than 70%, and the nematode only migrates on aerial plant parts when they are covered with a film of water. The optimum temperature for development of *A. besseyi* is 23–32°C, but the nematode is active from 13 to 43°C. *A. besseyi* is killed by temperatures exceeding 43°C. Ammonium sulfate, ammonium nitrate, calcium superphosphate, and potassium chloride increase the severity of the disease. The nematode is effectively spread by irrigation water.

A. besseyi is usually amphimictic, but parthenogenetic reproduction may occur. There are several generations in one season. The life cycle of the nematode takes 7–15 days, depending on temperature and humidity, and there are therefore several generations during a growing season.

A. besseyi has a wide host range, including Chinese cabbage, chrysanthemum, Italian millet, onion, soybean, strawberry, sugarcane, sweet corn, sweet potato, and yam. This nematode can also feed and complete its life cycle on many species of fungi.

Green weights of some cultivars inoculated simultaneously with *A. besseyi* and the fungus *Sclerotium oryzae* Cattaneo are significantly lower than those of plants inoculated with either organism alone.

Control

Since the nematode is seedborne, hot-water treatment of seed is the best control method for *A. besseyi*. For small quantities of seeds, a hot-water treatment of 10–15 min at 55–61°C, without presoaking, destroys the nematodes without affecting germination. For large quantities of seeds, presoaking for 24 hr in cool water followed by 15 min in water at 51–53°C is recommended. Chemical treatment of seeds with nematicides is also effective.

Burning straw, weeds, and new growth, and seeding directly into standing water are also recommended for control of *A. besseyi*.

Cultivars of rice differ in susceptibility to *A. besseyi*, and several have been reported as resistant: Arkrose; Asahi; Bluebonnet; Bluebonnet 50; Century 52; Century Patna 231; Chinoor; Fortuna; Gumartia; Improved Bluebonnet; Nira; Norin Nos. 6, 8, 37, 39 and 43; Nukata Ginbozu; Rescora; Texas Patna; Toxan 38; and TP49.

Nematicides applied as a root dip before transplanting or to the paddy water during transplanting can also be used to control *A. besseyi*.

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(Prepared by J. C. Prot)

Ufra

Ufra, caused by *Ditylenchus angustus* (Butler) Filipjev, has been reported from Bangladesh, Burma, Egypt, India (Uttar Pradesh and Ganges Delta), Madagascar, Malaya, the Philippines, southern Thailand, and Vietnam (Mekong Delta).

Symptoms

The symptoms vary considerably with the degree and time of infection. In the field, the earliest symptoms appear on plants that are more than 2 months old. Plants show malformations and chlorosis or mosaic discoloration of the upper leaves (Plates 113 and 114). Later, scattered dark stains appear on the leaves, and parts of the upper internodes of the stem turn dark brown (Plate 115). The disease is most typical and evident on the panicle, where two types of symptoms can be observed: the swollen ufra and the ripe ufra. Swollen ufra occurs when the nematode damages the panicle at an early stage; the panicle coils and remains enclosed within the leaf sheath, and there is a strong tendency for the stem to branch (Plate 116). The ripe ufra occurs when the nematode damages the panicle at a later stage; the panicle emerges but is distorted, bears sterile or empty, distorted spikelets at the base, and produces normal grains only near the tip (Plate 117).

Losses in infested fields range from 20 to 90%, with average losses estimated at 30% (Plate 118).

Disease Cycle and Epidemiology

D. angustus is mainly associated with deep-water rice. However, with the development of intensive rice cropping and irrigation, it has been reported in irrigated rice adjacent to deep-water rice fields.

D. angustus is an obligate ectoparasite. Reproduction is amphimictic, and at least three generations occur in one growing season. The nematode is able to survive from one crop to the next by remaining coiled in rice stubble and debris and in soil. Infested ratoons are also sources of inoculum. *D. angustus* can survive desiccation for at least 6 months, but the number of survivors declines over time, with an average half-life of about 2 weeks. The nematode becomes active when the fields are flooded.

Initially, the nematode parasitizes the terminal buds of newly sprouted seeds. It then migrates upwards as the rice plant grows, feeding on new tissue. During flowering and heading, *D. angustus* is found mainly on the stem just above the nodes, on the peduncles, and inside the glumes. The nematode becomes inactive when the plant matures.

The most favorable temperature for infection of rice is 28–30° C. The nematode is disseminated primarily by irrigation water.

With the exception of *Leersia hexandra* Sw., the known host range of *D. angustus* is confined to *Oryza* spp., namely, *O. alta* Swallen, *O. glaberrima* Steudel, *O. eichingeri* A. Peter, *O. latifolia* Desv., *O. meyerriana* Baill., *O. minuta* J. S. Presl. ex C. B. Presl., and *O. officinalis* Wall ex Watt, in addition to *O. sativa* L.

Control

Lengthening the time between crops by delaying sowing, transplanting after flooding, and using early-maturing cultivars all decrease the severity of ufra. Also, burning crop debris reduces the disease incidence by reducing the primary inoculum. Application of zinc also decreases the severity of the disease on zinc-deficient plants.

Cultivars B-69-1; R-16-06; Habiganj Boro II, IV, and VI; Lalchiken; Lohagor; and Monolata have been reported as resistant to *D. angustus*. In a recent trial conducted in Bangladesh, 116 of 432 entries tested, including Boishbish, Chamara, Kartiskail, Khama, and Shada Pankaish, appeared to be resistant.

Soil treatments with nematicides are effective against the nematode but costly. Nematicidal compounds applied as foliar sprays or at the preflowering stage have been reported to be effective in controlling ufra.

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(Prepared by J. C. Prot)

Rice-Root Nematodes

The common name *rice-root nematode* designates nematodes belonging to the genus *Hirschmanniella*. Several species of *Hirschmanniella* are associated with rice, and at least five may be of economic significance: *H. caudacrena* Sher, *H. imamuri* Sher, *H. mucronata* (Das) Luc & Goodey, *H. oryzae* (van Breda de Haan) Luc & Goodey, and *H. spinicaudata* (Schuurmans-Stekhoven) Luc & Goodey.

H. oryzae is present in most of the rice-growing countries in West Africa, and in Central and South America, Asia, Madagascar, the United States, and Portugal. *H. caudacrena* has been reported from the United States and Vietnam; *H. imamuri* from Japan, Korea, Nigeria, and Vietnam; *H. mucronata* from Bangladesh, India, the Philippines, and Thailand; and *H. spinicaudata* from Cameroon, Cuba, The Gambia, Ivory Coast, Nigeria, Senegal, Venezuela, and Vietnam.

Symptoms

Aboveground symptoms include retarded growth, reduction in the tiller number, stunting, chlorosis, and late maturation in severe cases. These symptoms are not diagnostic, however, because other factors may induce similar symptoms (Plate 119). Histopathological changes in infected roots include cell necrosis and formation of cavities resulting from the disruption of cell walls. It is estimated that 80 million hectares are infested with *Hirschmanniella* spp. Yield reduction estimations range from 10 to 35% in Asia and West Africa.

Disease Cycle and Epidemiology

Hirschmanniella spp. are well adapted to flooding and are more common in wet paddy soils than in well-drained ones. Between rice crops, the nematodes survive on weeds, in dead rice roots, and in soil (Plate 120). *H. oryzae* can survive under dry conditions for at least 5 months and under paddy water for up to 7 months.

Hirschmanniella spp. are migratory endoparasites of roots, but they are sometimes found in the coleoptile. At sowing or transplanting, they enter the seedling roots anywhere from the tip to the base, and all stages can penetrate the roots. The nematodes move within the roots, and a few days after infection, the females lay their eggs. Juveniles hatch and develop in the root cortex. Reproduction in *Hirschmanniella* spp. is bisexual. *H. imamuri* has one generation per crop, but *H. oryzae* may have two generations per crop. The nematodes generally leave the roots when the panicle appears, but many remain inside the roots until harvest.

Additional hosts for rice-root nematodes include many rice field weeds. Cabbage, cotton, maize, and sugarcane have also been reported to be hosts for *H. oryzae*.

Control

Incorporation of straw ash, neem, and mustard cakes into paddy soil is reportedly effective in reducing the population of rice-root nematodes. Intercropping with trap plants such as *Sesbania rostrata* Brem. or *Sphenoclea zeylanica* Gaertn., which are toxic to *Hirschmanniella* spp., also can be used to control rice-root nematodes. Biological agents such as nematode-trapping fungi and sulfate-reducing bacteria have also been reported to be effective against *Hirschmanniella* spp.

Some cultivars show a high level of resistance to rice-root nematodes, containing less than one nematode per gram of roots. In comparison, susceptible cultivars may have more than 100 nematodes per gram of roots. Only the cultivar TKMg has been reported to be immune to rice-root nematodes.

Nematicides applied as soil treatments or as root dips prior to transplanting have been reported to reduce rice-root nematode incidence in soil and seedling roots and significantly increase yields.

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(Prepared by J. C. Prot)

Root-Knot Nematodes

Several species of *Meloidogyne* are associated with rice: *M. arenaria* (Neal) Chitwood, *M. incognita* (Kofoid & White) Chitwood, *M. javanica* (Treub.) Chitwood, *M. graminicola* Golden & Birchfield, *M. oryzae* Mass, Sanders, & Dede, and *M. salasi* Lopez.

M. arenaria, *M. incognita*, and *M. javanica* are ubiquitous and of major economic significance in temperate, warm, and tropical regions. *M. graminicola* has been reported from Bangladesh, India, Laos, Thailand, the United States, and Vietnam; *M. oryzae* from Surinam; and *M. salasi* from Costa Rica and Panama.

Symptoms

Aboveground symptoms associated with the presence of *Meloidogyne* spp. include chlorosis, wilting, retarded maturation, and reduction in growth and tillering. *M. graminicola* reduces the elongation ability of deep-water varieties.

Root-knot nematodes induce hypertrophy and hyperplasia in the root meristem, cortex, endodermis, and xylem and the formation of giant cells in the meristem, cortex, and xylem. These transformations result in the formation of characteristic root galls and prevent root elongation (Plate 121).

On upland rice, root-knot nematodes can cause substantial yield loss. Average yield losses of 10–20% (up to 50%) have been observed in infested upland rice in West Africa and Asia. On irrigated or flooded rice, losses due to root-knot nematodes have not been estimated under field conditions. However, loss due to *M. graminicola* may be important in deep-water rice, because most plants infected with large numbers of the nematode are unable to grow above the water.

Disease Cycle and Epidemiology

Root-knot nematodes are poorly adapted to flooded conditions. *M. arenaria*, *M. incognita*, and *M. javanica* do not survive continuous flooding. *M. graminicola* does not invade rice roots growing in flooded soils, but it is able to survive inside roots for at least 5 weeks and in flooded soil for 5 months or more. Between rice crops, the nematodes survive as eggs in the soil or continue to reproduce on other crops or on weeds. The largest populations of *Meloidogyne* spp. are found in sandy or coarse-textured soils, and in these soils they may be found up to a depth of 30 cm. Clay soils are less favorable for *Meloidogyne* spp., and the nematodes are confined to the top 10 cm. Soil temperatures that are optimum for invasion of the roots and development and reproduction of the nematodes range from 25 to 30°C.

Root-knot nematodes are obligate endoparasites. The typical life cycle is exemplified by *M. graminicola*. Second-stage juveniles of *M. graminicola* infect the apical meristem of young seedling roots before flooding. Glandular secretions released during feeding cause the development of giant cells and root galls within 4 days. The nematode develops and reproduces by meiotic parthenogenesis within the host tissues. The females lay their eggs inside the galls, and juveniles hatch from the eggs and reinfect the same root. Inside the roots, *M. graminicola* can develop and reproduce normally for at least 36 days. In well-drained soil, at 22–29°C, the life cycle of *M. graminicola* is completed in 19 days. Nitrogen and phosphorus increase rate of development of *M. graminicola* progeny.

M. incognita and *M. javanica* can infect more than 700 plant species, and *M. arenaria* more than 300. Recorded hosts include numerous vegetables and food crops, cereals, cash crops, fruit trees, grasses, pasture legumes, and ornamentals. *M. graminicola* has a wide host range, including oats, bushbean, tomato, potato, plantain, sorghum, several species of the Cyperaceae and Poaceae, and *Sphenoclea zeylanica*.

Simultaneous infection by *M. javanica* and *Pyricularia grisea* (Cooke) Sacc. reduces the growth of rice plants more than either pathogen alone. Synergistic interactions between *M. javanica* and *Fusarium* spp. have also been reported.

Control

Continuous flooding is very effective for control of *M. arenaria*, *M. incognita*, and *M. javanica*, and it reduces infestation by *M. graminicola* to a minimum. Fallow or crop rotation with nonhost plants also reduces root-knot nematode populations. Rotations with groundnut, sweet potato, maize, and soybean are effective in reducing *M. graminicola* populations.

Cultivars resistant to *M. graminicola* include Baharsia, Bonnet 73, CH46, Dumai, Garem, Hamsa, IR2, IR5, IR47, LA110, Manoharsali, and Patni 6. Cultivars resistant to *M. incognita* and/or *M. javanica* include IR20, IS335, IS358, International, and Peta. Cultivars of *Oryza glaberrima* Steudel generally appear to be more resistant or tolerant of *M. incognita* and *M. javanica* than cultivars of *O. sativa* L.

Several nematicidal compounds applied as soil drenches, foliar sprays, seedling root dips, or seed soaks or in irrigation water give good control of root-knot nematodes and result in increased yields. Chemical treatments on a field scale are considered too costly, but they may be economical in nurseries.

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(Prepared by J. C. Prot)

Cyst Nematodes

Four species of cyst nematodes may cause economic damage to upland rice: *Heterodera elachista* Ohshima, *H. oryzae* Luc & Berdon, *H. oryzicola* Rao & Jayaprakash, and *H. sacchari* Luc & Merny.

H. sacchari has been reported from the Congo, Ivory Coast, Nigeria, Senegal, and Trinidad; *H. oryzae* from Bangladesh, India, Ivory Coast, Senegal, and Japan; *H. elachista* from Japan; and *H. oryzicola* from India.

Symptoms

No diagnostic symptoms are associated with rice cyst nematode infection. In severe cases, plants are stunted and have retarded growth, leaves are severely chlorotic, and the number of tillers is reduced. In Japan, *H. elachista* has been considered responsible for the failure of continuous upland rice cropping. In inoculation experiments, *H. elachista* suppressed yields 7.2–18% and *H. sacchari* suppressed yields 20–75%.

Disease Cycle and Epidemiology

Rice cyst nematodes are mainly associated with upland rice. However, *H. oryzae* and *H. sacchari* have been found on flooded rice, and *H. elachista* has been found on flooded rice sown in unflooded soil.

Between rice crops, *Heterodera* spp. survive as eggs in cysts and egg masses. When rice is present, second-stage juveniles hatch from the eggs and penetrate the rice roots. They affix their heads in the central root cylinder, and the cells there are transformed into syncytia. Juveniles can develop into males or females, and reproduction is amphimictic. Females lay eggs in a gelatinous matrix (the egg mass) or retain the eggs in their body, which turns into a cyst. The life cycle of *Heterodera* spp. takes approximately 1 month, and three generations can infect the same rice crop.

H. sacchari also infects sugarcane; *H. oryzae* is able to reproduce on banana; and *H. elachista* can reproduce on *Echinochloa crus-galli* (L.) P. Beauv.

Reproduction of *H. oryzicola* is inhibited in the presence of *Meloidogyne graminicola* Golden & Birchfield. *H. oryzicola* and the seedling blight fungus *Sclerotium rolfsii* Sacc. cause higher seedling mortality when they infect simultaneously than when either pathogen infects alone.

Control

Continuous flooding, fallow periods, or crop rotation with soybeans or sweet potatoes reduce populations of *H. elachista.*

The cultivars Lalnakanda 41, CR143-2-2, and TKM6 have been reported resistant to *H. oryzicola.*

Soil fumigation significantly reduced populations of *H. elachista* and significantly increased yield.

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(Prepared by J. C. Prot)

Other Nematodes

Stunt Nematodes

Tylenchorhynchus brassicae Siddiqi, *T. gladiolatus* Fortuner & Amougou, *T. martini* Fielding, and *T. mashhoodi* Siddiqi & Basir are not adapted to continuous flooding but may cause economic damage in rainfed rice. These nematodes suppress the length and dry weight of roots in inoculation experiments.

Ring Nematodes

Criconemella onoensis Luc, which causes characteristic knotting on roots, significantly reduces rice yield in Louisiana and Texas.

Other *Criconemella* spp. have been associated with rice in many rice-growing countries.

Lesion Nematodes

Pratylenchus spp. commonly parasitize roots of upland rice. Severe damage has been reported for *P. zeae* Graham in Zimbabwe and *P. indicus* Das in India.

Lance Nematodes

Hoplolaimus indicus Das parasitizes upland rice in India. Associated with the fungus *Sclerotium rolfsii* Sacc., it increases the severity of seedling blight.

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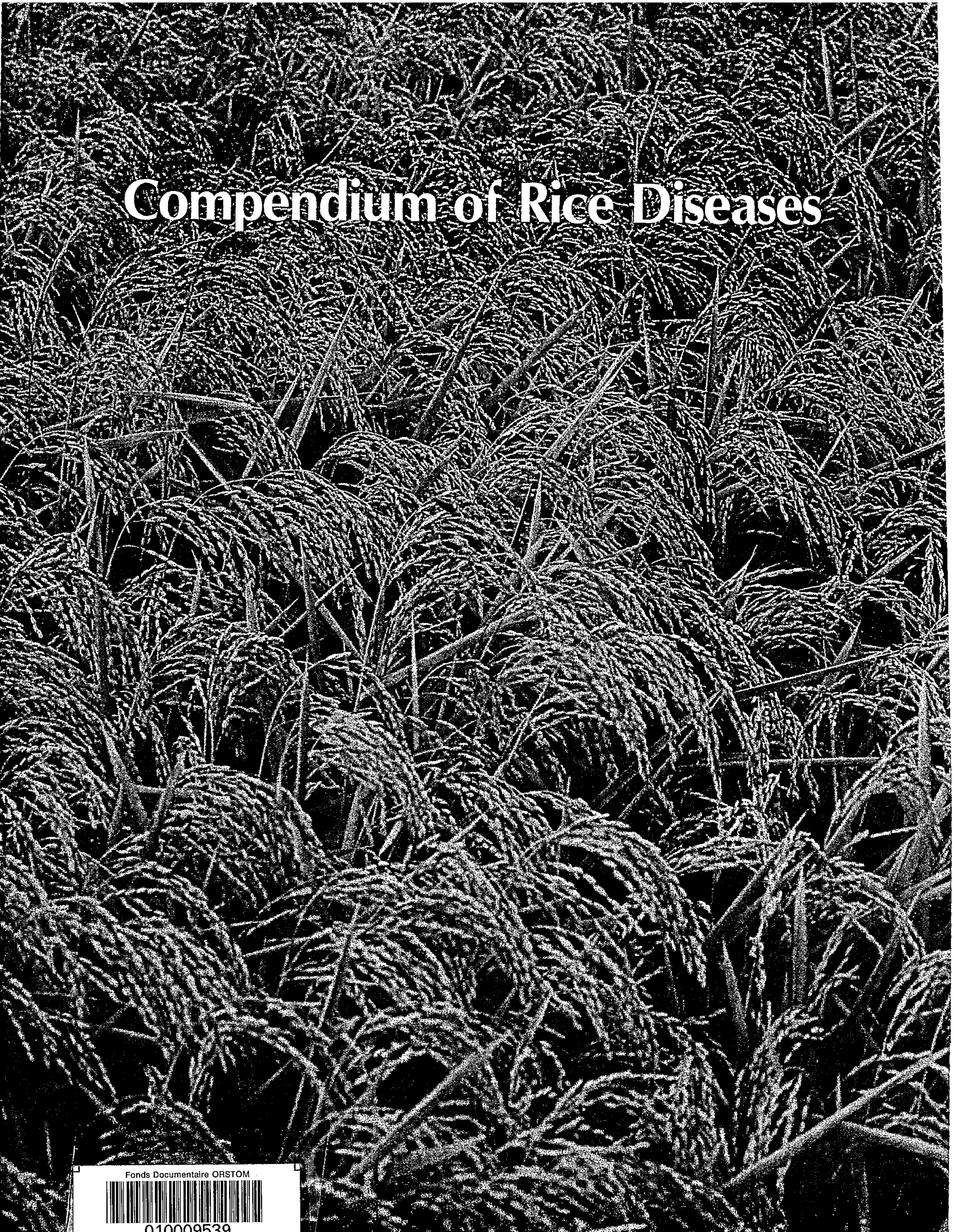

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