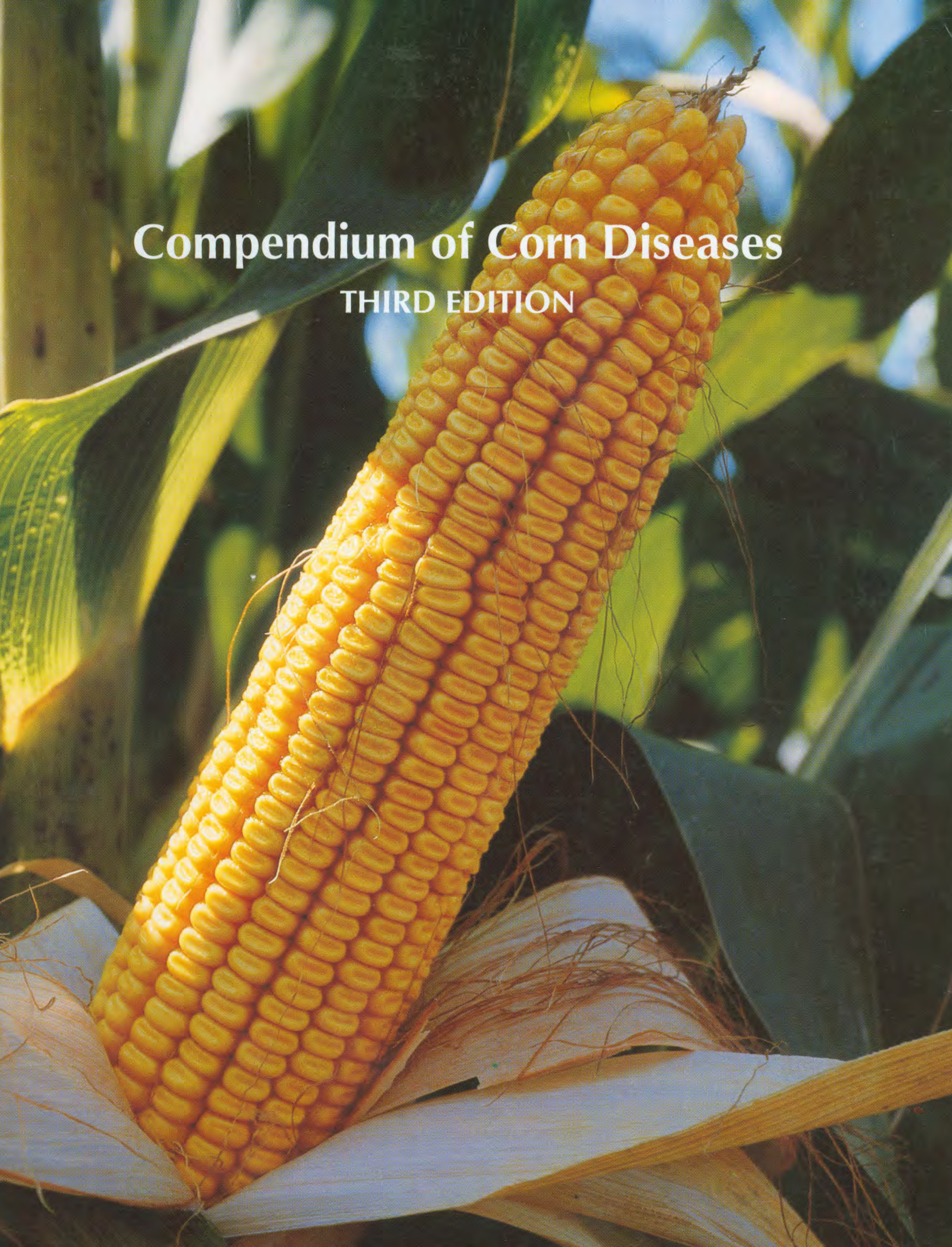
Compendium of Corn Diseases

THIRD EDITION



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(Prepared by M. L. Carson)

Downy Mildews

Ten species of three genera of downy mildew fungi are reported as pathogens of corn. Six species occur fairly often and four infrequently. Individually, they fill specific regional or global niches. At one time and in certain regions, some downy

TABLE 1. (*continued*)

Disease Causal Organism	Fruiting Structures	Symptoms	Geographic Distribution
Tar spot complex *Phyllachora maydis* Maubl., *Monographella maydis* Müller & Samuels and *Coniothyrium phyllachorae* Maubl.	Perithecia of the primary pathogen, *P. maydis*, an obligate parasite, are immersed and nearly spherical and bear cylindrical asci (8–10 × 80–100 µm) with short pedicels. Ascospores (5.5–7 × 9–12 µm) are one-celled, fuliginous, and broadly ellipsoidal.	Black, sunken, oval to circular glossy spots (0.5–2.0 mm in diameter) may merge to form stripes up to 10 mm long (Plate 52).	Cool, humid areas at high elevations in Latin America
Banded sheath blight *Rhizoctonia solani* Kühn	Sclerotia (1–5 mm in diameter) are spherical to oval and brown to black. Mycelium on ear husks appears pale brown and cottony; upon microscopic examination, it is hyaline, septate, and branched at right angles.	Large, gray, tan, or brown discolored areas alternate with dark bands on infected leaves and leaf sheaths (Plate 53).	Hot, humid environments in the tropics and subtropics
Hyalothyridium leaf spot *Hyalothyridium maydis* Latterell & Rossi	Pycnidia (150–180 µm in diameter) are immersed, globose, thin walled, and subhyaline to pale brown with dark ostioles arising from stomata. Conidia (16–28 × 23–40 µm) are hyaline, muriform, and broadly oblong with 10–15 cells that often separate at maturity.	Small, tan, elliptical spots with brown borders to large, almost circular, light brown blotches up to 1.5 cm diameter sometimes cover most of the leaf surface (Plate 54). Other fungi, e.g., *Leptosphaerulina australis* and *Astromella* spp., may be involved and responsible for variable symptoms.	Humid areas of Mexico, Costa Rica, and Colombia
Fusarium leaf scorch *Fusarium moniliforme* J. Sheld.	See Fusarium Stalk Rot and Fusarium Kernel or Ear Rot in the text.	Water-soaked spots occur mainly on whorl leaves and turn white and papery with brown borders. The whorl does not open, and leaf tips turn downward. Occasionally, necrotic spots develop on higher portions of the stalks.	Warm, dry regions of the Caribbean
Didymella leaf spot *Didymella exitialis* (Mor.) Müller	Pseudothecia (90–130 µm in diameter) are dark brown to black and submersed. Asci (8–12 × 40–60 µm) are eight spored, cylindrical, and bitunicate. Ascospores (4–5.5 × 12–14 µm) are uniseptate, hyaline, and ellipsoidal.	Small, elongate or elliptical leaf spots with brownish margins occur. Lesions enlarge and coalesce, forming white to cream-colored streaks or patches in which perithecia are sometimes formed.	India
Selenophoma leaf spot *Selenophoma* spp.	Pycnidia are hyaline with membranous walls. Alpha conidia (2.8–4.7 × 24–50 µm) are one celled and lunate. Beta conidia are also formed.	Eyespot lesions with concentric circles are surrounded by chlorotic halos.	Colombia, above 2,700 m
Leptosphaeria leaf spot *Leptosphaeria zeae* G. L. Stout and *L. variiseptata* G. L. Stout	Perithecia (50–200 µm in diameter) are globose. Ascospores (3.5–6 × 14–23 µm) are cylindrical, light brown, and two septate. A pycnidial stage (*Phoma* sp.) is also produced.	Small, tan or cream-colored lesions become large and concentric or streaked and cover large areas.	Himalayas and Illinois
Alternaria leaf spot *Alternaria alternata* (Fr.:Fr.) Keissl.	Conidia (9–18 × 20–63 µm) are obclavate, obpyriform, ovoid, or ellipsoidal; pale to midgolden brown; and smooth or verruculose and often have a short beak. They have up to eight transverse septa and commonly have several longitudinal or oblique septa. *A. alternata* is cosmopolitan.	Chlorotic streaks become necrotic on leaves of all ages. Tissue damage, e.g., from insect feeding or embedded sand grains, followed by a prolonged dew period are apparently essential for infection.	Central corn belt of the United States
Diplodia leaf spot *Stenocarpella maydis* (Berk.) Sutton (syns. *Diplodia maydis* (Berk.) Sacc., *D. zeae* (Schwein.) Lév.	See Diplodia Stalk Rot in the text.	Oval leaf spots occur with pycnidia scattered in the necrotic areas (Plate 55).	Caribbean islands[a]

[a] Most corn grown in the United States is immune to leaf spot caused by *S. maydis*, even though it is susceptible to ear rot and stalk rot caused by the same fungus.

mildews were the major factors limiting corn production. However, since the late 1970s, the development of resistant cultivars, the use of chemical protectants, and improvements in cropping and cultural practices have greatly diminished the losses.

Most of the downy mildew pathogens of corn did not originate on this New World crop, but they possessed the ability to either attack corn when it was introduced into the Old World or to adapt and infect it. When this occurred or when a pathogen was introduced into warm, humid climates, one or more downy mildew diseases often became major problems.

Downy mildew fungi are obligate parasites. The leaf is penetrated directly by an infection peg from an appressorium formed over or near a stoma, and this is followed by vesicle formation in the substomatal chamber. The coenocytic mycelia of the fungi grow intercellularly, and host cell membranes are invaginated by haustoria.

Delineation of species is sometimes uncertain. The principal characteristics used to distinguish species are the shape and dimensions of conidia or sporangia; the size of conidiophores or sporangiophores and the degree and kind of branching; the length of sterigmata; and the shape, color, and morphology of the oospores and the oogonial envelope. Host range and symptoms are also often used in species identification (Table 2).

The use of isozyme analysis and other chemical-based techniques may provide better means of differentiating species in the future. However, since definitive direction for combining or separating species within this genus is lacking, the diseases are discussed here as they have been previously described.

TABLE 2. Downy Mildews of Corn

Pathogen (Disease Name)	Sporangiophores or Conidiophores[a]	Sporangia or Conidia	Oospores	Geographical Distribution	Hosts Other Than Corn	Seedborne Seed-Transmitted
Peronosclerospora sorghi (sorghum downy mildew)	Hyaline, 180–300 µm long, bloated, usually dichotomously branched two to three times, septate near base, ephemeral	Conidia hyaline, oval to almost spherical, 14.4–27.3 × 15–28.9 µm; germinate by germ tube	Usually brown to subhyaline, spherical, 25–42.9 µm in diameter; germinate by germ tube	North America, Central America, Asia, Africa, South America, Australia, Europe	*Euchlaena* spp., *Panicum* spp., *Pennisetum* spp., *Sorghum* spp., *Andropogon* spp.	Yes, in pericarp and scutellum Yes, only on freshly harvested seeds
P. maydis (Java downy mildew)	Hyaline, long (150–550 µm), bloated, dichotomously branched two to four times, ephemeral	Conidia hyaline, spherical to subspherical, 17–23 × 27–39 µm; germinate by germ tube	Unknown	Australia, Indonesia	*Zea mays mexicana* × *Z. mays* hybrids, *Euchlaena* spp., *Pennisetum* spp., *Tripsacum* spp.	Yes Only before seeds are dried
P. philippinensis (Philippine downy mildew)	Hyaline, long (150–400 µm), bloated (widening abruptly) dichotomously branched two to four times, ephemeral	Conidia hyaline, elongate ovoid to round cylindrical, 17–21 × 27–39 µm, and slightly rounded at apex; germinate by germ tube	Rare or nonexistent; spherical, smooth walled, 22.6 µm in diameter; germinate by side germ tube	Philippines, Indonesia, India, Nepal, China, Thailand, Pakistan	*Avena sativa*, *Euchlaena* spp., *Zea mays mexicana* × *Z. mays* hybrids, *Saccharum* spp., *Sorghum* spp.	Yes, in embryo and endosperm Yes, at 36% moisture, not at 14%
P. sacchari (sugarcane downy mildew)	Hyaline, 160–170 µm, bloated, widening gradually, dichotomously branched two to three times, ephemeral	Conidia hyaline, elliptical, oblong to conical, 15–23 × 25–41 µm with round apex; germinate by germ tube	Yellow to yellow brown, globular to slightly angular; 40–50 µm in diameter; germinate by germ tube	Australia, Fiji Islands, Japan, Nepal, New Guinea, India, Philippines, Taiwan, Thailand	*Euchlaena* spp., *Saccharum* spp., *Sorghum* spp., *Andropogon* spp., *Tripsacum* spp.	Yes, in embryo Yes, only at moisture levels above 20%
Sclerospora graminicola (Graminicola downy mildew, green ear of pearl millet)	Hyaline, long (av. 268 µm), bloated, nonseptate, irregularly dichotomously branched, ephemeral	Sporangia hyaline, broadly elliptical, 12–21 × 14–31 µm, with a papillate operculum; germinate by zoospores	Pale brown, spherical, usually smooth walled, 22.5–35 µm in diameter; said to germinate by germ tube or by sporangia	Worldwide, but rare on maize and found only in Israel and the United States	*Euchlaena* spp., *Panicum* spp., *Pennisetum* spp., *Saccharum* spp., *Setaria* spp., *Sorghum* spp., *Agrostis* spp., *Chaltochloa* spp., *Echinochloa* spp., *Holcus* spp.	No No
Sclerophthora macrospora (crazy top)	Hyaline, short (av. 13.8 µm), simple, hyphoid, determinate	Sporangia hyaline, lemon shaped, operculate, 30–65 × 60–100 µm; germinate by numerous zoospores	Hyaline to pale yellow, develop mainly in vascular bundles, 45–75 µm in diameter; germinate by sporangia	North America, Mexico, South America, Europe, Africa, Asia	*Avena sativa*, *Digitaria* spp., *Panicum* spp., *Setaria* spp., *Sorghum* spp., *Triticum* spp., and numerous others	No No
S. rayssiae var. *zeae* (brown stripe downy mildew)	Hyaline, short, hyphoid, determinate	Sporangia hyaline, ovate to almost cylindrical, operculate, 18.5–26 × 29–66.5 µm; germinate by zoospores	Brown, spherical, 29.5–37 µm in diameter; germinate by sporangia	India, Nepal, Pakistan, Thailand	*Digitaria* spp.	Yes, in embryo Yes

[a] Length and branching of conidiophores and sporangiophores in species of *Sclerospora* and *Peronosclerospora* vary, depending somewhat on ambient air conditions during their formation.

Symptoms of downy mildews are similar. Both systemic and local lesions develop. Symptoms are affected by the age of the plant at infection, the species of the pathogen, and the environment. Systemically infected plants exhibit mottling, chlorotic streaking, malformation of reproductive organs, and/or excessive tillering. Plant hormone levels often change after infection, resulting in these bizarre symptoms. When systemic infection occurs, plants are often barren.

Peronosclerospora and *Sclerospora* spp.

Mildews caused by *Peronosclerospora* and *Sclerospora* spp. are often referred to the "true" downy mildews of corn. *Peronosclerospora* spp. produce conidia that germinate by germ tubes. *Sclerospora* spp. produce sporangia that germinate by producing zoospores, although direct germination occasionally occurs. Sporangia are operculate, and conidia have no apical modification. Oospores are not sufficiently distinctive to distinguish species. The oogonial wall is 1–2 µm thick and is typically fused with the thicker (3–6 µm) oospore wall. Oospores have been reported to survive in nature for 6–10 years. The asexual spores are thin walled, fragile, and short lived. Apparently, oospores need to undergo about 1 month of exposure in soil and are stimulated by root leachates to germinate. Most oospores germinate by a germ tube and can penetrate the plant directly. They can remain viable after passing through the digestive tract of animals and can be carried on seed surfaces and in host debris. When oospores cause infection, the first seedling leaf does not become chlorotic, as occurs when the infection results from internal seedborne mycelia.

Conidia and sporangia are produced at night. Between approximately 2300 and 2400 hours, one to four conidiophores or sporangiophores emerge from stomata; and between 2400 and 0100, spores begin to form. The majority of conidia and sporangia mature between 0200 and 0300 and are shed between 0200 and 0700, most between 0200 and 0300. They are disseminated primarily by wind. Because of the fragile nature of these spores, they apparently cannot be carried more than a few hundred meters and remain viable.

Germination of conidia and sporangia usually occurs in less than an hour, and free water is required. Leaf penetration occurs approximately 1–2 hr after germination and always through stomata. Invasion of mesophyll cells follows. The first symptoms usually appear in about 3 days as chlorotic, circular spots, flecks, and/or streaks, which elongate in both directions parallel to the veins. The outward development ceases or slows after a few days. The downward movement of mycelia continues to the shoot apex, and systemic infection results from its colonization. In resistant plants, the infection remains localized. Systemic symptoms occur after 5–14 days and do not occur in plants after 3.5–4 weeks of growth. Conidia are produced in large numbers (up to 100,000/cm^2) in chlorotic tissue for a period of time until senescence. When profuse oospore production occurs, leaves shred and asexual reproduction is sparse or absent.

Sorghum Downy Mildew

Sorghum downy mildew occurs in Africa, Asia, Australia, Central America, Europe, North America, and South America.

Symptoms

Systemically infected plants are chlorotic and sometimes stunted and occasionally have white-striped leaves and abnormal seed set (Plates 56 and 57). The chlorotic area of a leaf always includes the base of the blade, and the transverse margin is usually sharply defined between the diseased and healthy tissue, appearing further up the blade in each successively formed leaf ("half-leaf symptom") until the whole blade is chlorotic. Leaves of infected plants tend to be narrower and more erect than those of healthy plants, and shredding may occur. A white, downy growth may appear on both surfaces of infected leaves. In some regions, the tassels of diseased plants may exhibit phyllody. Tolerant plants may show symptoms of systemic infection but have normal seed production. Other plants may be barren. Long, narrow, chlorotic, local lesions develop on some corn lines. Ear shanks may be elongated. Oospores, if present, tend to appear in the ear bracts and leaves within the striped areas.

Causal Organism

Sorghum downy mildew is caused by *Peronosclerospora sorghi* (W. Weston & Uppal) C. G. Shaw (syns. *Sclerospora sorghi* W. Weston & Uppal and *S. graminicola* var. *andropogonis-sorghi* Kulkarni). The conidiophores (180–300 µm long) are erect, spreading, fragile, hyaline, and usually dichotomously branched and emerge singly or in groups from stomata on the lower and sometimes the upper sides of leaves. The conidia (14.4–27.3 × 15–28.9 µm) are hyaline, oval to subspherical, and borne on elongated, tapered sterigmata about 13 µm long. They germinate by germ tubes in free water and penetrate corn leaves through stomata. The oogonia (40–55 µm in diameter) are spherical and embedded among mesophyll cells between fibrovascular bundles. The oospores (25–42.9 µm in diameter; average 36 µm) are hyaline and spherical with light yellow outer walls.

Disease Cycle and Epidemiology

The oospores of *P. sorghi* can survive several seasons in the soil. They germinate by germ tubes and attack underground parts of susceptible seedlings, which become systemically infected. No infection by oospores occurs if seedlings emerge in cool soil. Conidia on the leaves are disseminated by the wind and provide secondary inoculum, which can induce systemic infection in plants up to 4 weeks old. Oospores of *P. sorghi* are produced less frequently and abundantly on corn than on sorghum and appear in both hosts only in systemically infected plants. The fungus has been detected within the pericarp and scutellum of seed. Oospores are also commonly found in glume tissue of systemically infected sorghum and are a major source of primary inoculum for infection of sorghum. Corn has glumes that are much less developed and are not usually present in commercial seed. Thus, there is little if any seed transmission. Transmission to corn seedlings has occurred from seed grown in sterile soil but only from freshly harvested or immature seed.

Conidia are produced at temperatures of 17–29°C (the optimum is often 24–26°C, depending on the geographic origin of the isolate). Germination of conidia requires a saturated atmosphere or free water, and moderate temperatures of 21–25°C are optimal for most isolates. High levels of systemic infection can occur at 11–32°C with a wet period of 4 hr or longer. The conidia are delicate and lose their viability after 3–4 hr.

P. sorghi also infects cultivated and wild sorghum, Johnson grass, and teosinte. In the midwestern United States, shattercane is an important wild host. Oospores are disseminated over long distances on seed surfaces (especially on sorghum seed) and in debris mixed with seed.

Control

Resistant hybrids offer the best and most economical means of control. Resistance varies in the germ plasm studied in various corn-growing areas. In the United States, three major genes have been identified. Two exhibit dominance, and one is recessive. In Thailand, polygenic resistance has been found and is attributable mostly to dominance and additive genetic variance. Results from Venezuela closely resemble those from Thailand. In both Indian and Venezuelan studies, significant maternal effects have also been shown to condition resistance. Genotypes that emerge rapidly often escape penetration by oospores in the soil.

Planting corn in cool soils (below 20°C) is highly recommended if oospores may be present in soil. This may allow the seeds to germinate and escape infection by oospores, which usually will not grow at temperatures below 20°C. Rotation of corn with sorghum should be avoided where the disease occurs, and corn should not be planted adjacent to sorghum because it can serve as a source of inoculum. Shatter-cane should be destroyed in areas where the disease occurs. Systemic fungicides applied as seed treatments and/or foliar sprays may be valuable in some situations.

Java Downy Mildew

Java downy mildew is of great importance in Indonesia, where yield may be reduced by 40%. It also occurs in Australia. The most severe damage occurs when corn is planted late or the rainy season begins early, especially if the crop has been overfertilized with nitrogen or planted after corn or sugarcane.

Symptoms

White to yellow streaks (Plate 58), which become necrotic and brown, are characteristic leaf symptoms. The fungus may become systemic, causing severe chlorosis in the upper leaves. Infected plants may be stunted and sterile and often lodge. Downy growth on the chlorotic streaks is common. Plants more than 4 weeks old are highly resistant to infection.

Causal Organism

Java downy mildew is caused by *Peronosclerospora maydis* (Racib.) C. G. Shaw (syn. *Sclerospora maydis* (Racib.) Butl.). The pathogen produces two kinds of hyphae: straight and sparsely branched and lobed and irregularly branched. Clustered conidiophores arise from stomata and are dichotomously branched two to four times. The branches are robust and 150–550 µm long with basal cells 60–180 µm long. Conidia (17–23 × 27–39 µm) are hyaline and spherical to subspherical. Oospores have not been reported.

Disease Cycle and Epidemiology

Infected corn plants grown during the dry season are the primary source of inoculum in Indonesia. The fungus may survive as mycelium in kernels, but this is a minor source of inoculum. Infection by conidia occurs through stomata of young plants, and lesions elongate toward the meristem, inducing systemic infection. Conidia and conidiophores are produced superficially on wet leaves in the dark. If infection arises from seed, the cotyledonary leaf is always infected. Seed transmission occurs when freshly harvested seeds from diseased plants are used. No seed transmission has been detected from seeds dried prior to planting.

Formation of conidia requires free moisture, darkness, and temperatures below 24°C. Conidia germinate under these conditions to produce germ tubes. Other hosts include teosinte and *Tripsacum*, *Euchlaena*, and *Pennisetum* spp.

Control

Resistant hybrids and varieties are recommended in areas where the disease occurs. Resistance in corn has been shown to be polygenic with additive gene action.

Philippine Downy Mildew

Philippine downy mildew is the most serious downy mildew disease in the Philippines, where yield losses are 15–40% or more. It also occurs in China, India, Indonesia, Nepal, Pakistan, and Thailand.

Symptoms

Systemic symptoms may appear in the first true leaf as complete chlorosis or chlorotic stripes 9 days after planting. Local symptoms may appear when plants are in the two-leaf to three-leaf stage until tassels and silks are formed. In general, infected leaves have long, chlorotic streaks with a downy growth of conidia and conidiophores (Plate 59). Tassels may be malformed and produce less pollen. Ears may be aborted, resulting in partial or complete sterility. If infection occurs early, plants are stunted and may die.

Causal Organism

Philippine downy mildew is caused by *Peronosclerospora philippinensis* (Weston) C. G. Shaw (syn. *Sclerospora philippinensis* Weston). The mycelium is branched, slender (8 µm in diameter), irregularly constricted, and inflated. The small haustoria (2 × 8 µm) are simple and vesiculiform to subdigitate. Erect conidiophores (15–26 × 150–400 µm) grow out of stomata and are dichotomously branched two to four times. Branches are robust. Sterigmata are ovoid to subulate, slightly curved, and 10 µm long. The conidia (17–21 × 27–39 µm) are elongate ovoid to round cylindrical, hyaline, and slightly rounded at the apex. *P. philippinensis* is indistinguishable from *P. sacchari* by isozyme analysis.

Disease Cycle and Epidemiology

Conidia of *P. philippinensis* germinate and form germ tubes, which penetrate leaves through stomata. Penetration is followed by intercellular invasion of the mesophyll cells. The fungus then grows through the leaf sheath into the stem and becomes established in the shoot apex, where it persists. Invasion of the shoot apex produces chlorotic streaks on the lower leaves and later on the younger leaves. The pathogen does not invade the roots. The fungus is seedborne and may be transmitted by planting seed that has not been fully dried. Conidia and conidiophores are produced on chlorotic areas on the leaf blades and sheaths. Wind and splashing water are the main means of conidial dispersal. Four-week-old plants are highly resistant. Oospores are not produced in corn tissue.

Night temperatures of 21–26°C and free moisture are essential for conidial production, germination, and infection. The optimal temperature for spore germination is 19–20°C. Physiologic races of the fungus exist. The host range of *P. philippinensis* includes oats (by inoculation), teosinte, cultivated and wild sugarcane, and cultivated and wild species of sorghum. Some of these hosts may be reservoirs for inoculum.

Control

The use of resistant hybrids and cultivars is the best method of control. Initial studies on the inheritance of resistance showed that a few genes exhibiting partial dominance in combination with seedling vigor were involved in resistance. Subsequent studies identified polygenically inherited levels of resistance whose expression was dependent upon inoculum load. At light disease pressure, resistance was completely dominant; at moderate disease pressure, resistance was partially dominant but mostly additive; and at high disease pressure, resistance appeared recessive. Systemic fungicide seed treatments and fungicidal sprays on leaves can be used if the disease is severe.

Sugarcane Downy Mildew

Severe outbreaks of sugarcane downy mildew on corn have limited corn production in Australia, Fiji Islands, and Taiwan. Yield losses of 30–60% have been reported. The disease appears to be confined to tropical and subtropical regions and has also been reported from Japan, Nepal, New Guinea, India, the Philippines, and Thailand. It is a potential threat to corn production, particularly in Asia.

Symptoms

Sugarcane downy mildew is characterized by local lesions that lead to systemic infection. Initial lesions are small, round, chlorotic spots on the leaves that appear 2–4 days after infection. Symptoms of systemic infection are pale yellow to white stripes or streaks at the bases of the third to sixth oldest leaves. Several streaks may form in each leaf and may extend the length of the leaf. On the leaves of some cultivars or on older leaves, the streaks may be narrow and discontinuous. On late-infected or mildly infected plants, streaks may disappear as plants approach maturity. White, downy, or powdery masses of conidia and conidiophores appear on both leaf surfaces and on the leaf sheaths and husks. This downy growth is usually produced at night when temperatures are moderate (25°C), especially when dew is present. Plants may be distorted and have small, numerous, poorly filled ears and improperly formed tassels. Ear shanks may be elongated.

Causal Organism

Sugarcane downy mildew is caused by *Peronosclerospora sacchari* (T. Miyake) C. G. Shaw. (syn. *Sclerospora sacchari* T. Miyake). Conidia and conidiophores are superficial. The conidiophores are erect, hyaline, and 160–170 μm long, arising singly or in pairs from stomata. The conidia (15–23 × 25–41 μm) are hyaline, elliptical, and oblong or conical with a round apex and thin, smooth walls. The oospores (40–50 μm in diameter) are globular or slightly angular and yellow with walls 3.8–5 μm thick. The conidia and oospores germinate by hyaline, slender, nonseptate germ tubes, which are 3.8 μm wide. *P. sacchari* is indistinguishable from *P. philippinensis* by isozyme analysis.

Disease Cycle and Epidemiology

The fungus overseasons as mycelium in sugarcane. Conidia produced on diseased sugarcane are disseminated by wind or in splashing water to corn leaves. Under favorable conditions, germ tubes from conidia penetrate corn leaves through stomata, and tiny, round lesions covered with ectophytic mycelia form at infection sites. The mycelium spreads intercellularly by inserting knoblike haustoria into host cells. After the endophytic mycelium invades tissues at the growing point, the first streaks appear on young leaves. Once established in corn seedlings, the fungus produces large numbers of conidia that serve as secondary inocula for corn or sugarcane seedlings. The role of oospores in infection under natural conditions has not been established. The fungus has been detected in embryos, and while freshly harvested seeds from infected plants have been shown to transmit the disease, no transmission occurred when the seeds were dried to less than 20% moisture.

Moisture, temperature, and the age of the plants are the important factors in disease development. The optimum temperature for conidial formation, germination, and infection is 20–25°C in the presence of free water. Sporulation is nocturnal and decreases with increasing light intensity. Plants less than 1 month old are very susceptible but become resistant with age. Conidia are wind-borne but are viable for only a few hours, even under optimal conditions. Other hosts of *P. sacchari* include sugarcane, teosinte, gama grass, broom corn, and grain sorghum. Long-range dissemination is by mycelia in sugarcane sets.

Control

Use of resistant hybrids and cultivars is the most practical method of control. A single dominant allele designated *Dmr* from one of four sources in combination with a recessive gene from another source and polygenic resistance from other sources have been demonstrated to condition high levels of resistance to sugarcane downy mildew. Because of the development of resistant corn hybrids and resistant sugarcane, this disease is no longer of consequence in Australia and Thailand. Cultural practices such as the use of pathogen-free sugarcane sets and the isolation of corn in disease-free areas where sugarcane is not grown can provide some control. If practical, roguing and destruction of diseased plants and use of fungicides (systemic seed treatments and sprays) are recommended in some areas.

Rajasthan Downy Mildew

Rajasthan downy mildew has been reported as a significant problem in the Rajasthan region of India.

Causal Organism

Rajasthan downy mildew is caused by *Peronosclerospora heteropogoni* Siradhana, Dange, Rathore, & Singh. The conidiophores measure 14.3–25.0 × 81.6–142.8 μm. Conidia (14.3–20.4 × 14.3-22.4 μm) are globose and hyaline. Oospores are tuberculate and 24.5–36.7 μm in diameter. This fungus was previously identified as *P. sorghi*. However, *P. heteropogoni* infects *Heteropogon contortus* and *P. sorghi* does not. Conidia produced on *H. contortus* appear to be the primary inoculum source to infect corn, since oospores are produced abundantly on *H. contortus* but are not produced on corn. Planting corn early allows it to escape infection by developing resistance before large numbers of conidia are produced on *H. contortus*. Corn planted late can be severely damaged.

Spontaneum Downy Mildew

In about 1920, Spontaneum downy mildew was reported to be serious on corn in the Visayan Islands of the Philippines. During recent years, it has been rare on corn in the Philippines and has not been reported elsewhere on corn except in Thailand. Other hosts include wild and cultivated sugarcane, teosinte, eulalia, *Euchlaena luxurians*, and *Sorghum* spp.

Causal Organism

Spontaneum downy mildew is caused by *Peronosclerospora spontanea* (Weston) C. G. Shaw (syn. *Sclerospora spontanea* Weston). Conidiophores are erect, hyaline, and 350–550 μm long and emerge singly or in groups from stomata on the lower leaf surfaces. Each is comprised of a basal cell, a main axis, and a more or less complex dichotomously branched system. The main axis is usually expanded above the septum to 22.7–28.6 μm and constricted below the branches to about 21 μm. The conidia are hyaline, elongate, and ellipsoidal or cylindrical with rounded apices, lack a papilla, and are borne on slender, straight sterigmata about 13 μm long. Most conidia are 11–21 × 25–65 μm, compared with those of *P. sorghi*, which are 14.4–27.3 × 15–28.9 μm. The oogonia (55.1–82.1 μm) are amber brown and usually irregularly developed with several folds in the wall; the wall thickness is variable. The spherical oospores are mostly 39.2–53.3 μm (mean 45.4–48.8 μm) in diameter. The spore wall is hyaline to pale amber and 1.8–6.1 μm thick. Oospores have not been reported in corn tissue.

Leaf Splitting Downy Mildew

Corn is susceptible to *Peronosclerospora miscanthi* (T. Miyake) C. G. Shaw (syn. *Sclerospora miscanthi* T. Miyake) when inoculated, but infection has not been found to occur naturally. The fungus attacks eulalia, sorghum, and sugarcane in Taiwan and the Philippines.

Graminicola Downy Mildew

Graminicola downy mildew, also called "green ear," occurs on various grasses throughout the world. It has been found in corn only in Israel and the United States and is rare in both countries. In the United States, it passes from *Setaria* spp. and in Israel, from pearl millet. It occurs very infrequently and has been of no economic importance for the past 65–70 years.

Symptoms

Common symptoms include grayish blotching and mottling of leaves with a white, arachnoid to downy growth that develops on discolored areas, chlorotic streaking or striping, and stunting. Leaves may be thick, corrugated, and fragile. Symptoms usually appear 10 days after the plumule emerges. Affected plants will occasionally outgrow the disease.

Causal Organism

Graminicola downy mildew is caused by *Sclerospora graminicola* (Sacc.) J. Schröt. Sporangiophores are long (average 268 μm), nonseptate, and stalklike with a slightly bulbous foot. Sporangia (12–21 × 14–31 μm) are borne on short sterigmata, two to six on a branch, and have a prominent papillate operculum at the apex. They are broadly elliptical. Each sporangium germinates by releasing four to eight or more irregularly kidney-shaped, biciliate zoospores 9–12 μm in diameter. Sporangia are reported to germinate occasionally by germ tubes, but these reports probably result from germ tube formation from encysted zoospores trapped within sporangia. The oospores are pale brown and 22.5–35 μm in diameter and germinate by germ tubes. The oogonia are 30–60 μm in diameter with reddish brown or amber brown, heavy, uneven outer walls 4–12 μm thick.

Disease Cycle and Epidemiology

Primary infection occurs from oospores that overwinter in the soil, where they can survive for at least 3 years. Some remain viable after passage through the alimentary canals of cattle. The mode of germination is still uncertain. Corn seedlings are systemically infected. Disease development and spread are favored by light rains or heavy dews and moderate night temperatures, conditions optimal for production of sporangia. Secondary spread to other hosts is by wind-borne sporangia produced superficially, but only where free moisture on plants is sustained. The fungus is not reported to be seedborne.

Temperatures of 24–32°C for 2 days after planting are conducive to heavy infection. The optimal temperature for sporangial formation and germination is 17°C; the maximum is 34°C. Species of *Agrostis, Chaltochloa, Echinochloa, Euchlaena, Holcus, Panicum, Pennisetum, Saccharum, Setaria,* and *Sorghum* are susceptible to natural or artificial inoculation. Severe losses are encountered in pearl and foxtail millets. Strong physiologic specialization exists; most isolates from pearl millet do not attack *Setaria* spp. and vice versa.

Control

No control is needed for corn.

Crazy Top

Crazy top occurs in most areas with temperate or warm climates. It appears rarely in tropical areas but is widespread in the United States and has been reported in Canada, Mexico, South America, eastern and southern Europe, Africa, and Asia. Crazy top causes substantial losses only in very localized areas.

Symptoms

Symptoms vary greatly with time of infection and degree of host colonization by the fungus. Generally, excessive tillering (six to 10 tillers per plant), rolling, and twisting of the upper leaves appear first (Plate 60). The most characteristic symptom is the partial or complete proliferation of the tassel, which continues until the tassel resembles a mass of leafy structures (Plate 61). These modified, leaflike inflorescences are described as "crazy top." Phyllody of ears also may occur. Leaves of severely infected plants are often narrow, straplike, and leathery. Stunting and chlorotic striping of leaves may also occur.

Causal Organism

Crazy top is caused by *Sclerophthora macrospora* (Sacc.) Thirumalachar, C. G. Shaw, & Narasimhan (syns. *Sclerospora macrospora* Sacc. and *Phytophthora macrospora* (Sacc.) Ito & I. Tanaka).

Sporangia occur rarely on corn grown in the field but can be obtained by incubating excised young, diseased leaves. Their production decreases markedly with increased plant age and does not occur on intact leaves. When the sporangia are induced in complete darkness at an optimal temperature of 24–28°C, they are hyaline, lemon shaped, operculate, 30–65 × 60–100 μm, and attached to short, simple, sporangiophores emerging from stomata. The sporangia germinate by the release of numerous biciliate, subspherical to reniform, hyaline zoospores or occasionally by germ tubes. After a period of motility, the zoospores encyst and produce germ tubes. The oospores are hyaline to yellowish, multinucleate, somewhat globose, and 45–75 μm in diameter with granular contents. They germinate by a thin-walled tube bearing a sporangium, which in turn produces zoospores. The mycelium is coenocytic, thin walled, intercellular, and abundant in meristematic tissues.

Histopathology

The mycelium of *S. macrospora* can be detected in brace roots, stalk tissue, leaves, and floral structures of affected plants by staining with zinc chloriodide. The mycelium stains a deep purplish blue while the host tissue remains nearly colorless. The oogonia and oospores are situated in "nests" of several spores in vascular bundles or in their parenchymatous sheath cells within straplike leaves and leaf sheaths of stunted plants (Fig. 12).

Disease Cycle and Epidemiology

The oospores germinate in saturated soil to produce sporangia from which zoospores escape and penetrate host tissues. After a short period of motility, they encyst, and each produces a germ tube. The mycelium develops systemically and is most abundant in meristematic tissues. The sporangia are produced at night on sporangiophores projecting from stomata in the leaves, but these are produced sparingly on corn. Oogonia are produced abundantly in infected tissues.

Crazy top develops when soils have been flooded shortly after planting or before plants are in the four- to five-leaf stage. Pooling of soil and water in the whorl of small plants can also lead to infection. Saturation for 24–48 hr is sufficient for infection to occur, probably by initiating germination of soilborne oospores and providing water for movement of zoospores to

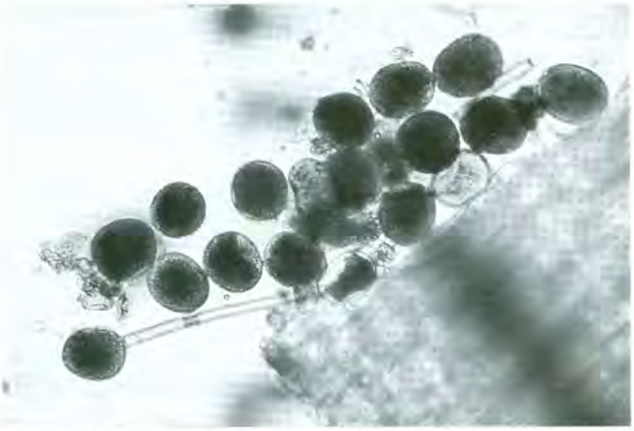

Fig. 12. Oogonia and oospores of *Sclerophthora macrospora* in infected leaf tissue. (Courtesy D. G. White)

infection sites on corn. Diseased grasses may provide sporangial inoculum. Infection occurs at a wide range of soil temperatures. The optimal temperature for sporulation on excised leaves is 24–28°C; for sporangial germination it is 12–16°C (22–25°C for finger millet in India). Seed transmission of the pathogen has been demonstrated from freshly harvested seeds but is generally considered unimportant in dissemination of the fungus.

S. macrospora has been reported on more than 140 species of Gramineae. Hosts include oats, wheat, sorghum, rice, crabgrass, witch grass, green foxtail, St. Augustine's grass, and barnyard grass. It causes considerable losses on finger millet in India.

Control

Adequate soil drainage should be provided, or planting in low, wet spots should be avoided.

Brown Stripe Downy Mildew

Brown stripe downy mildew, a disease that causes local lesions, can be very destructive in India and has been reported from most corn-growing areas of that country. A 63% loss in grain yield has been recorded in the Tarai region of India. It has also been reported in Nepal, Pakistan, and Thailand. The disease is most severe in areas that receive 100–200 cm of rain annually.

Symptoms

Initially, lesions develop on the leaves as narrow, chlorotic or yellowish stripes, 3–7 mm wide; they have well-defined margins and are delimited by the veins (Plate 62). The stripes later become reddish to purple. Lateral development of lesions causes severe striping and blotching. Seed development may be suppressed, and the plant may die prematurely if blotching occurs prior to flowering. Sporangia on the leaves appear as a downy or woolly growth on both surfaces of the lesions. Floral or vegetative parts are not malformed, and the leaves do not shred.

Causal Organism

Brown stripe downy mildew is caused by *Sclerophthora rayssiae* var. *zeae* Payak & Renfro. The oogonia (33–44.5 µm in diameter) are subglobose, thin walled, and hyaline to light straw-colored. Oospores (29.5–37 µm in diameter) are spherical to subspherical with smooth, glistening walls that are 4 µm thick and confluent with the oogonia. They have hyaline contents, including a prominent oil globule. Oospores and oogonia are numerous and scattered in the leaf mesophyll or under stomata. Sporangiophores are short and determinate and arise from hyphae in the substomatal spaces. Sporangia (18.5–26.0 × 29.0–66.5 µm) are produced sympodially in groups of two to six and are hyaline, ovate to cylindrical with a prominent peduncle, and smooth walled and individually produce four to eight zoospores on germination. The encysted zoospores are hyaline, spherical, and 7.5–11 µm in diameter.

Disease Cycle and Epidemiology

S. rayssiae var. *zeae* survives as oospores in infected debris in the soil. Upon germination, the oospore produces a sporangiophore bearing a sporangium that liberates four to eight zoospores. In the presence of enough moisture or at high temperatures, the sporangium may produce a germ tube that can also infect corn leaves. The pathogen can also overseason in crabgrass as oospores or as mycelium from which sporangia are produced. Secondary spread is by sporangia. While the fungus can be detected within the embryo of corn seeds and has been shown to be seed transmitted when seeds from infected plants are planted in sterile soil immediately after harvest, seeds dried to 14% moisture or less and stored for 4 weeks or more do not transmit this or other downy mildew diseases.

Sporangia are produced and germinate at optimal temperatures of 22–25 and 20–22°C, respectively, while oospores are formed at higher temperatures. Soil temperatures of 28–32°C favor disease development. Sporangial production, germination, and infection require a film of moisture for 12 hr or longer. Zoospores germinate at 15–30°C (optimum 22–25°C). Zinc deficiency predisposes plants to infection.

Control

Use of resistant hybrids and cultivars is the most practical method of control. In studies conducted in India, it was determined that resistance is polygenically inherited with additive gene action predominating. Partial dominance occurs in the nonadditive component, and epistasis has been detected in some crosses. Additionally, cultural practices such as planting before the rainy season begins may be of value. Fungicide seed treatments followed by systemic foliar sprays provide excellent control.

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(Prepared by D. R. Smith and B. L. Renfro)

Ergot

Ergot, also known as horse's tooth (*diente de caballo*), occurs in certain humid valleys of central Mexico.

Symptoms

Sclerotia replace the kernels, and each ear may contain one to several. Honeydew from the sclerotia is filled with small, hyaline, ovoid spores.

Causal Organism

Ergot is caused by *Claviceps gigantea* Fuentes, de la Isla, Ullstrup, & Rodriguez (anamorph *Sphacelia* sp.). Sclerotia (2–5 × 5–8 cm) are first white to cream colored, soft, sticky, and hollow. Mature sclerotia are comma shaped (resembling a horse's tooth) and white to grayish brown and have pink to lavender centers (Plate 63). Those beneath the husks are lighter in color. Perithecia are flask shaped and arranged peripherally in stromatic heads. The asci in the perithecia are cylindrical and hyaline. Ascospores (1.5 × 176–186 µm) are filiform, hyaline, and nonseptate. Macroconidia (4.2–5.8 × 8.3–27 µm) are elliptical, and microconidia (2.5–3.3 × 4.2–6.7 µm) are ovoid. Both spore types are hyaline and nonseptate. *C. gigantea* can be isolated by surface sterilizing mature sclerotia and plating fragments of the horny interior on glucose-yeast extract agar at 24°C. Colonies attain their maximum diameter (about 1.5 cm) in about 4 weeks.

Disease Cycle

The fungus overwinters as sclerotia on the ground or mixed with seed. The sclerotia germinate in the spring to produce stalked stromata with heads containing many embedded perithecia with asci (Plate 64). The ascospores serve as primary inoculum. These spores are forcibly ejected and carried by the wind to floral parts of susceptible corn plants. The developing hyphae produce macroconidia and microconidia in a sticky matrix (honeydew), which can cause secondary infections. Insects may be important in conidial transmission.

Epidemiology

Ergot is endemic in certain high, cool, humid valleys of central Mexico. Disease development is favored by mean temperatures of 13–15°C and high levels of rainfall (1,000 mm, or 40 in., per year).

Control

No control is reported.

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(Prepared by D. G. White)