
Smuts

Smuts, of the fungus order Ustilaginales, are named for their sooty black spore masses. Like the rusts, they belong to the Basidiomycetes and are all plant parasites, of most economic importance on cereals and grasses, but they differ from rusts in having a less complicated life history and in being able to live part of their lives saprophytically in rich organic matter or in culture media. There are two spore forms. The teliospore, usually called a chlamyospore, is formed by the rounding up of a hyphal cell. In addition to a thin inner endospore wall, it has a thick outer exospore wall, usually dark, smooth or ornamental. Teliospores are formed singly or united into balls. They can be distributed long distances by wind, and spores of some species remain viable for years. Some have to ripen several months before they can germinate.

Occasionally the teliospore puts out a germ tube that penetrates host tissue directly. More often it produces a promycelium that gives rise to sporidia, which can bud to more sporidia. Classically true smuts have been divided into two families on the type of sporidial formation: Ustilaginaceae, with sporidia produced on the sides of a four-celled promycelium, and Tilletiaceae, with sporidia produced at the end of a one- or two-celled promycelium. Fischer, however, points out that there are so many variations that it is preferable to include all species in a single family, Ustilaginaceae, and to differentiate the species on the basis of morphological characters and the host family. This is logical, but we include here the families as they are

given in most textbooks and also the false smuts, Graphiolaceae (Ustilaginales), which have an uncertain taxonomic position.

There are three types of infection with smuts, with control measures modified according to type. The mycelium always penetrates the young host tissue directly; it does not enter through stomata.

1. Infection of seedlings as the seed germinates, from spores adhering to the outside of the seed or present in soil; controlled by dusting seed and planting in noninfested soil.
2. Seedling infection by mycelium within the seed as a result of ovary infection from spores germinating on the stigma; controlled by treating seed with hot water.
3. Infection of any actively growing meristematic tissue (roots, shoot, tassels, or young ears) by spores transported by wind from decaying plant material; controlled, partially, by spraying or dusting susceptible plants.

Burrillia

Tilletiaceae. Sori in various host parts, often in leaves, rather permanently embedded. Spore balls with a central sterile mass surrounded by fertile teliospores but no sterile cortex (surface layer). Teliospore hyaline to yellowish, rather firmly united. On water plants.

Burrillia decipiens Leaf Smut of floating heart (*Nymphoides*).

Cintractia

Ustilaginaceae. Sori usually in ovaries, black, more or less agglutinated spore masses with a peridium. Teliospores single, olive to reddish brown, formed from a fertile stroma surrounding a central columella of host tissues. On Cyperaceae and Juncaceae.

Doassansia

Tilletiaceae. Sori usually in leaves; spore balls large and conspicuous, with a sterile layer around fertile cells. Teliospores pale yellowish brown to hyaline, thin walled. Germination often *in situ*. On water plants.

Doassansia epilobii Leaf Smut on epilobium.

Entyloma

Tilletiaceae. Sori generally in leaves forming light spots, giving the name white smut, or slightly raised darker blisters. Teliospores produced singly but often adhering in irregular groups – hyaline to pale green, yellow, or brown. Sporidia formed on the surface give the white powdery appearance.

Entyloma calendulae Calendula White Smut. Spots are pale yellow, turning brown to black, 1/4 inch in diameter. The smut is common but not very serious in commercial calendula plantings around San Francisco. Plant debris should be cleaned up, perhaps the location changed.

Entyloma compositarum, White Smut of composites, boltonia, calendula, erigeron, eupatorium, gnaphalium, golden-glow, helenium, and prairie coneflower.

Entyloma dactylidis (*E. crastophilum* and *E. irregulare*). Bluegrass Blister Smut, on *Poa* spp., Oregon, Washington, Minnesota, North Dakota. Gray-black, blister areas in leaves from subepidermal masses of chlamydo-spores. A series of fine dotlike masses of sporidia (conidia), appear scattered in rows along surface of the blisters.

Entyloma dahliae Dahlia Leaf Smut, a European disease occasionally reported here. It showed up in one location in California where overhead watering was used, but disappeared when the practice was discontinued. Leaves are marked by more or less circular spots, first yellow-green, then brownish and dry. Primary spores germinate in leaves and send projections to the outside, where secondary spores are formed to spread the disease. Late planting seems to increase disease incidence.

Entyloma ellisii Spinach Smut. An occasional disease with infected leaves pale and worthless. Spores are produced in irregular, marginal necrotic lesions.

Entyloma lineatum Smut of wild rice.

Entyloma polysporum Leaf Smut of gaillardia, golden-glow, senecio, sylphium, and sunflower.

Graphiola

Ustilaginales. This family and genus are sometimes included in the smuts, sometimes not. The sori are erumpent, enclosed in a compact black peridium on leaves of palms. The spores are formed in parallel chains, and bud laterally to form two or more sporidia, which become somewhat colored with thickened walls.

Graphiola phoenicis False Smut of palms, Leaf Spot on queen, canary date, royal and Washington palms and on palmetto. Leaves are yellow-spotted with small black scabs or warts having a dark, horny outer surface and long, flexuous sterile hyphae protruding from an inner membrane containing powdery yellow or light brown spore masses. Seriously infected leaves may die.

The disease occurs on date palm where humidity is continuously high, but is checked in desert areas best suited to date culture. Kustawy variety is less susceptible than some others. The disease also appears on small ornamental palms in greenhouses and conservatories. Cut out and burn infected leaves or parts.

Mycosyrinx

Ustilaginaceae. Spores united in pairs; sori with a double peridium in swollen pedicels and peduncles. Mostly tropical.

Mycosyrinx osmundae Inflorescence Smut on osmunda fern.

Neovossia

Tilletiaceae. Sori in ovaries, semi-agglutinated to powdery. Teliospores borne singly, each with a long pedicel appendage, and producing many sporidia.

Neovossia iowensis On grains, affecting kernels in the dough stage.

Schizonella

Ustilaginaceae. Sori in leaves; short to long striae; black, agglutinated teliospores in pairs, germinating with three-to four-celled promycellium with lateral sporidia. Two species on Cyperaceae.

Sorosporium

Ustilaginaceae. Spores loosely united into balls, readily separable by pressure, in various hosts, more often in reproductive parts. Germination by promycelium and sporidia or germ tube. Mostly on grains.

Sorosporium saponariae Flower Smut of silene.

Sporisorium

Ustilaginaceae. Sori in various host parts but mostly in inflorescence; granular to powdery, covered at first by a peridium. Teliospores single, formed around a central columella. Germination usually with sporidia. Most species on grains and grasses, sometimes causing severe stunting.

Sphacelotheca cruenta (see *Sporisorium cruentum*). Loose Kernel Smut on sorghum, causing smutting and excessive branching.

Sphacelotheca reiliana (see *Sporisorium holci-sorghii*). Head Smut of corn, in Pacific states and scattered locations in South.

Sphacelotheca sorghi (see *Sporisorium sorghi*). Covered Kernel Smut.

Kernels replaced by smut galls

Sporisorium cruentum (formerly *Sphacelotheca cruenta*). Loose Kernel Smut on sorghum, causing smutting and excessive branching. Controlled by seed treatment and resistant varieties.

Sporisorium holci-sorghii (formerly *Sphacelotheca reiliana*). Head Smut of corn, in Pacific states and scattered locations in South. Galls on tassels and ears breaking into loose dark brown spore masses. Do not plant in a smutted field for 2 years; use certified seed, resistant hybrids.

Sporisorium sorghi (formerly *Sphacelotheca sorghi*). Covered Kernel Smut. Kernels replaced by smut galls.

Thecaphora

Ustilaginaceae. Sori in various host parts, mostly inflorescence; powdery or granular. Spores firmly united into balls, with no sterile cells. Chiefly on Leguminosae and Convolvulaceae.

Tilletia

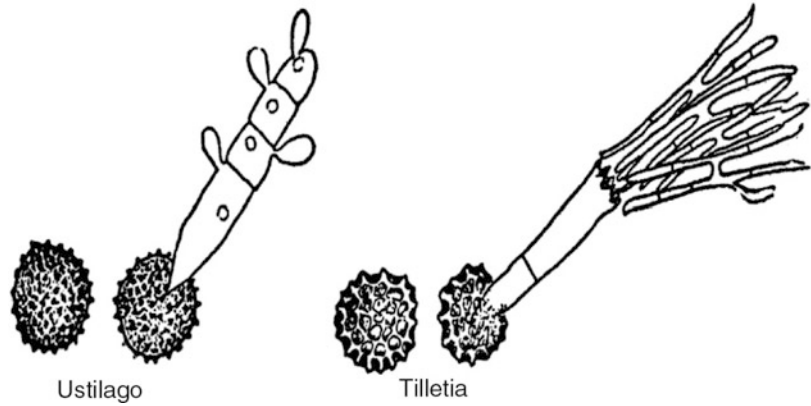
Tilletiaceae. Sori mostly in ovaries, occasionally in vegetative parts of host forming a powdery or semi-agglutinated spore mass, often foetid. On grains and grasses, called bunt; interior of seed a solid mass of spore balls (see Fig. 1).

Tilletia buchloëana Bunt of buffalograss.

Tilletia caries Dwarf Bunt of wheat. Plants a fourth or half size of healthy plants.

Tilletia foetida Stinking Smut, Common Bunt of Wheat, on wheat and wheat grasses wherever grown, occasionally on rye. A major agricultural disease, especially in Pacific Northwest, this is of historical importance as the first disease controlled by seed disinfection. In 1670 a ship was

Fig. 1 Smut Spores. *Ustilago* (left), spiny chlamydospore germinating with promycelium and sporidia formed at sides; *Tilletia* (right), reticulate chlamydospore with long H-shaped sporidia formed at end of promycelium and sometimes forming small secondary sporidia



wrecked off the Coast of England, but the cargo of wheat was salvaged, free from bunt because of its salt-water bath. Dark smut balls replace kernels, and there is a fishy odor. Plants are stunted, but not as much as with dwarf bunt. Spore balls are broken in threshing and seed contaminated. Many materials are offered for seed treatment. Seed dealers treat seed for farmers in special machinery at low cost.

Tilletia pallida Bunt on velvet and creeping bent grass, Oregon, Rhode Island. Seeds are filled with black spores, plants stunted. The disease is serious where grass is grown for seed, with up to 80 % nonviable seed.

Urocystis

Tilletiaceae. Sori mostly in leaves and stems, blackish; embedded in host tissues. Spore balls permanent, without sterile cortex but sometimes with a layer of hyaline, hyphal fragments. On Liliaceae, Primulaceae.

Tuburcinia trienthalus (see *Urocystis trienthalus*). Leaf and Stem Smut of starflower.

Urocystis trientalis (formerly *Tuburcinia trientalis*). Leaf and Stem Smut of starflower.

Urocystis

Tilletiaceae. Sori usually in leaves, stem sheaths, occasionally in flowers; dark brown to black, powdery to granular. Spore balls with distinct

sterile spores on the surface, only a few fertile spores. Sori without peridium.

Urocystis agropyri Flag Smut of wheat, also on wheat grass, red top, and bluegrasses. Symptoms are similar to those of stripe smut.

Urocystis anemones (including *U. hepaticae-trilobae*). Leaf and Stem Smut of anemone, hepatica, and trautveteria.

Urocystis carcinodes Smut of aconite, baneberry, clematis, and cimicifuga.

Urocystis colchici (Fischer includes *U. cepulae* in this species). Leaf Smut of autumn crocus, camassia, Solomons-seal and false Solomons-seal.

Urocystis gladiolicola Gladiolus Smut. This disease had been intercepted several times at quarantine and appeared once in California fields, in 1950, but apparently is eradicated there. Growers should be on the lookout for corms with low blister swellings, with ridges paralleling veins, bluish black, breaking open to expose dense black spore balls. Seedlings exhibit blistering, shredding, and necrosis of stem and leaf tissues; they die if the disease is severe.

Urocystis kmetiana Floral Smut of field pansy (*Viola bicolor*).

Urocystis magica (*U. colchici*). Onion Smut, general on onion, also on leek, shallot, garlic, and chives. This is the most destructive onion disease, found in the Connecticut Valley as early as 1861 and thence spread to all northern onion-growing sections, but more important where onions are grown from seed rather than sets as in most home gardens. Black elongated

blisters or pustules of spores break out on scales or leaves of young plants. Many plants die; others survive and have black or brown smut pustules on the cured bulbs. Plants are stunted but not rotten, although smut may be followed by secondary rot organisms.

The spores can live in soil for years, but infection is possible only in young plants from the second day after seed germination until the seedling is in first leaf, a period of 10 to 15 days. The spore is able to penetrate the onion through root and cotyledon but cannot enter a true leaf. After entrance it spreads through the seedling until it reaches the leaves to form fruiting pustules just below the epidermis. When this ruptures, spores are dropped, to be disseminated by running water and tools, on feet of persons and animals, and on roots of transplanted vegetables. Onion smut is confined to states with cool summers, optimum soil temperature for infection being 72 °F.

Urocystis tritici Flag Smut of wheat. Plants are dwarfed with twisted leaf blades; sheaths are marked with grayish-black stripes; diseased tissues dry up and are shredded. Infected plants rarely produce heads.

Ustilago

Ustilaginaceae. Sori in various host parts; spore masses powdery to agglutinated; usually dark brown to black, in some species yellow to purple without a peridium. Spores single, not united in balls (see Fig. 1).

Ustilago avenae Nigra Loose Smut, general on barley.

Ustilago avenae (including *U. perennans*). Black Loose Smut on oats and some grasses. Individual flowers in panicle are largely replaced by a spore mass. The young seedling is diseased from the seed, and the fungus grows systemically in the plant.

Ustilago buchloes Stripe Smut on grass.

Ustilago bullata Head Smut on many grasses.

Ustilago esculenta Smut on wild rice.

Ustilago heufleri Erythronium Smut. Large dusty pustules lead to cracking and dying of leaves of dogtooth violet.

Ustilago hordei Covered Smut of barley. Heads are converted into hard, black, smutted masses, enclosed within thin membranes.

Ustilago kollerii Covered Smut of oats. Spore balls remain intact within glumes until threshing, when spores are distributed over surface of seed, ready to infect young seedlings.

Ustilago maydis (*U. segetum*). Corn Smut, Boil Smut, general on corn but most destructive to sweet corn. The average annual loss is 3 to 5 % but it can be 100 % in any one field. The fungus was described in Europe in 1754 and not reported here before 1822, but it may be native along with its host. There are many physiological races, and smut resistance is likely to be correlated with lack of vigor, so that it has been hard to breed desirable resistant varieties.

Any plant parts aboveground may be attacked – stalks, prop roots, leaves, tassels, husks, and ears (see Fig. 2). Large boils are formed, at first covered with a greenish white membrane, said to be good eating when boiled or fried. Later the membrane breaks and releases myriads of dark chlamydo-spores. The plant is often distorted. Infections are local; each boil is formed where a spore lands, and there is no systemic growth through the plant. The fungus is not seed-borne, and germinating seedlings are not affected. Chlamydo-spores winter in soil, corn debris, and manure. They produce sporidia, which may bud to form secondary sporidia, and these are carried by wind and other agencies to corn plants, which are 1 to 3 feet high. Mycelium from spores of two sexes is needed for active development. Spores formed in the first boils provide inoculum for secondary infection of ears.

Corn smut thrives in warm weather, optimum temperature for spore germination being 80° to 92 °F. Heaviest infection occurs when scant rainfall in early stages of growth is followed by moderate rainfall as corn approaches maturity. Vigorous plants are most susceptible, but may escape the most serious effects because of their rapid growth. Spores retain viability 5 to 7 years. They remain viable in passage through an animal into manure, but are killed by the acids in silage.

Fig. 2 Corn smut



Control Seed treatment is not effective. Some hybrid varieties are rather resistant. Most reliance in home gardens should be placed on cleanliness, cutting off and burning all smutted parts before the boils break open to release spores.

Ustilago mulfordiana Fescue Smut on fescue grasses.

Ustilago tritici Nuda Loose Smut. Normal heads replaced by black powdery masses.

Ustilago striiformis Stripe Smut, general on grasses – wheatgrasses, redtop, bentgrasses, fescues, ryegrass, and bluegrass; does not occur on cereals. Long dark narrow striations develop in leaves; as the sori mature, spores are freed, and the blade splits into ribbons. Plants are

systemically infected, make poor growth, and inflorescences are stunted or absent. Perennial mycelium may overwinter in the plant.

Ustilago violacea Anther Smut of carnation, dianthus, lychnis, and silene. Infected plants grow slowly, produce many weak axillary shoots; stem internodes are shortened; flower buds are short and squatty; calyxes tend to split; flowers are sprinkled with black sooty dust from the anthers, whose pollen grains are replaced by smut spores. The fungus enters through flowers or injured surfaces and grows systemically. Spores are spread on cuttings. Control by roguing diseased plants before flowering. Do not take cuttings from plants with grassy or bushy habit.