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Head Smut of Sorghum, Sudangrass, and Corn, Caused by *Sphacelotheca reiliana* (Kühn) Clint.

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Head smut, caused by the fungus *Sphacelotheca reiliana* (Kühn) Clint., is a disease of sorghum, sudangrass, and corn. The symptoms of the disease on these plants are described and compared. Findings of California field surveys since 1957 are reported. Varietal susceptibilities of host plants are indicated where known, with results of recent field tests, notably on the immunity of Lahoma sudangrass. Attempts to infect johnsongrass were negative.

The disease is transmitted in nature by soil-borne spores, which initiate infection during pre- and postemergence growth. The incidence of infection is proportional to the amount of inoculum built up in the soil—as by continuous cropping to susceptible sorghum or by carry-over of the fungus in volunteer plants. The significance of smut mycelium in various plant tissues is considered. High and low soil temperatures are unfavorable for the infection of corn.

Two distinct race groups occur in *S. reiliana*—one pathogenic on sorghum and one on corn. From cross-inoculation results, it is postulated that the corn race may have evolved from one of the sorghum races.

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Head Smut of Sorghum, Sudangrass, and Corn, Caused by *Sphacelotheca reiliana* (Kühn) Clint.[1]

HEAD SMUT, caused by the fungus *Sphacelotheca reiliana* (Kühn) Clint., is a disease of sorghum, sudangrass, and corn. Kühn described the fungus in 1875 and named it *Ustilago reiliana* in honor of its discoverer, Dr. Reil, who sent him the original specimen from Egypt in 1868 (Potter, 1914). The classification of this smut "has been juggled from *Ustilago* to *Cintractia,* to *Sphacelotheca,* to *Sorosporium,* and back to *Sphacelotheca*" (Fischer and Hirschhorn, 1945).

The first reports of head smut on sorghum and corn in the United States originated in Kansas (Failyer and Willard, 1891; Norton, 1895). Mackie (1920) made the first report from California, where he found the disease on both orange sorgo and field corn. Halisky, Smeltzer, and Houston (1959) reported the disease on sudangrass in California. In general, the occurrence of head smut on these crops has been sporadic during the past six decades, and losses have been considered negligible. Since 1955, however, the disease has burgeoned in the sorghum areas of California, Texas, and the Midwest, coinciding with the introduction and wide acceptance by growers of smut-susceptible hybrid sorghums. With the cooperation of Dr. Dale G. Smeltzer, the author recorded varying amounts of head smut in California on 38 grain-sorghum hybrids, 11 old-line grain sorghums, 8 forage-sorghum hybrids, 2 forage sorgos, and 7 sudangrass varieties.

In surveys since 1957 (fig. 1), the author has found head smut on grain sorghum in 16 counties of California, on sudangrass in six counties, and on field corn in five counties. No head smut was found on the ubiquitous johnsongrass, *Sorghum halepense* (L.) Pers., in California. Attempts to infect this perennial species by planting in soil inoculated with teliospores or by injecting suspensions of sporidia gave only negative results.

The purpose of the present work is to study head smut on sorghum, sudangrass, and corn as to distribution and symptoms (table 1) and to ascertain the pathogenicity of *S. reiliana* to each of these hosts. The work includes consideration of varietal reactions, pathogenic specialization, ecologic factors, and cultural practices, all of which influence disease incidence markedly.

THE PATHOGEN

Sphacelotheca reiliana is primarily a soil-borne pathogen. Teliospores from smutted heads, scattered by wind and rain, overwinter in the soil and become the main source of infection. The fungus attacks susceptible hosts in the

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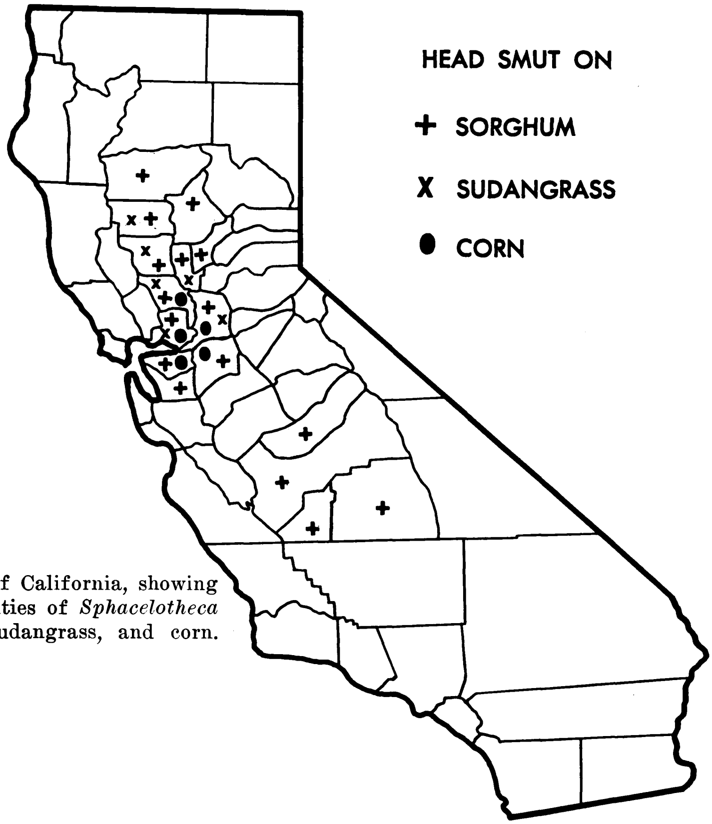

Fig. 1. Outline map of California, showing the distribution by counties of *Sphacelotheca reiliana* on sorghum, sudangrass, and corn. (Surveys 1957 to 1961.)

TABLE 1

COMPARISON OF HEAD SMUT CHARACTERISTICS ON SORGHUM, SUDANGRASS, AND CORN

Symptom or reaction	Sorghum	Sudangrass	Corn
Sporulation site......	Inflorescence	Inflorescence, leaves, culms	Tassels, ears, leaves
Sorus................	Black, powdery sorus covered by a thick white peridium	Slender, compact, black sorus covered by a white peridium	Coarse, dry, granular, black sorus, covered by white peridium
Sori in leaves.........	Occasional in Leoti sorgo	Frequent in Greenleaf sudan, occasional in Sweet 372	Frequent in King Philip and Oregon Evergreen
Dwarfing............	Pronounced in infected lateral tillers	Common in infected culms	Often pronounced when tassel is smutted
Floral sterility.......	Partial or complete; very common	Sterile panicles common on infected plants	Ears often aborted, stalks barren
Phyllody.............	Common on infected lateral tillers or axillary branches	Common in sterile panicles	Bizarre, proliferated tassels; rudimentary leaf buds in place of ears
Susceptible varieties.	Leoti and Sumac sorgos, Combine 7078, RS-610, NK-210, AMAK R-10, PAG-515S, and others	Greenleaf, Sweet 372, and others	King Philip, Oregon Evergreen, and others
Resistant varieties...	Feterita, hegari, RS-630	See table 3. Lahoma immune	None known

seedling stage, and the resulting infection is systemic (Potter, 1914; Mankin, 1953; Leukel, 1956; Halisky and Petersen, 1962). In sorghum and sudangrass, the lateral buds also carry infection in their meristematic tissues and frequently develop into smutted tillers. In the course of systemic infection the mycelium invades the undifferentiated floral tissues, and part or all of these tissues develop into a smut sorus as a result of host-parasite interaction. Fine, threadlike strands—vestiges of the vascular system of the host inflorescence—run through the sori and are diagnostic of infection by *S. reiliana.* The outer layers of smut mycelium adhere together to form a shiny, white membrane, the peridium. Usually the disease is not detected until an infected inflorescence emerges and the sorus becomes visible. Secondary effects of infection by head smut are dwarfing, sterility, and phyllody—the development of bizarre, leafy proliferations in sterile panicles (fig. 2*C*, 2*D*).

Soon after the sorus emerges from the sheath, the peridium ruptures and releases dark-brown to black, powdery spore masses. Microscopically, the individual teliospores appear reddish-brown. They are globose, 9μ to 12μ in diameter (Fischer, 1953), and finely echinulate.

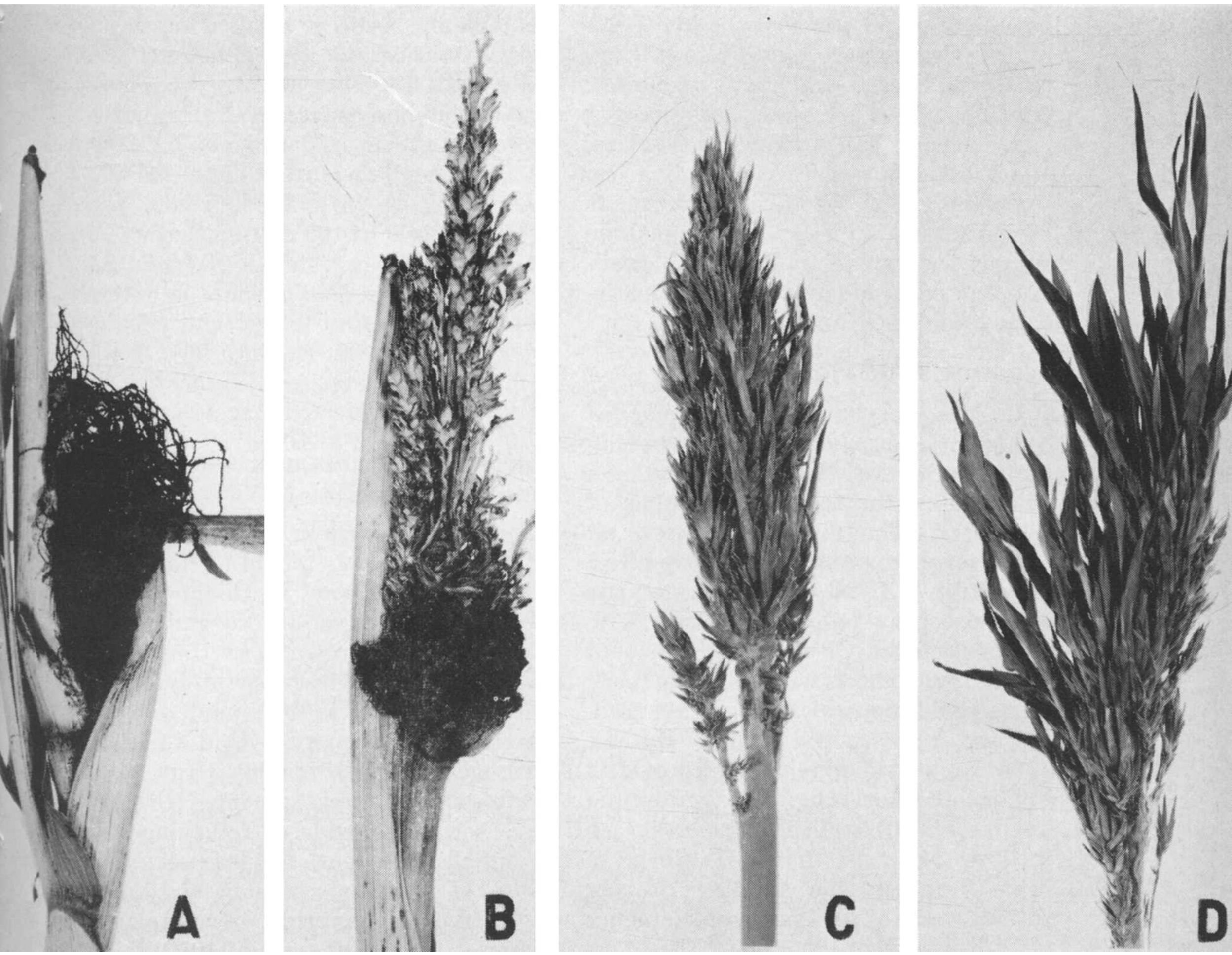

Fig. 2. Symptoms of head smut in grain sorghum: *A, B,* head smut sori in place of panicles; *C, D,* foliar proliferation in panicles, induced by *Sphacelotheca reiliana* infection.

When a teliospore of *S. reiliana* germinates, it produces a septate promycelium (basidium) with lateral sporidia (basidiospores). Mankin (1953), working with corn smut, demonstrated the existence of plus and minus mating types among the sporidia, indicating heterothallic sexuality in this smut. Both mating types occur in approximately equal numbers among the sporidia borne on each basidium. A monosporidial line is of either the plus or the minus mating type, but not both. Such a culture is not pathogenic to susceptible seedlings, whereas a sporidial mixture of plus and minus mating types produces infection readily when injected into the growing point of a seedling.

HEAD SMUT OF GRAIN SORGHUM

Head smut of grain sorghum, *Sorghum vulgare* Pers., is well established in California. Between 1957 and 1960 it was found in Butte, Colusa, Glenn, Sacramento, San Joaquin, Solano, Sutter, and Yolo counties, with the highest incidence (10 to 50 per cent) in the delta region. Traces were found also in Contra Costa, Fresno, and Madera counties. During 1961 the disease was reported in Alameda, Kings, Tehama, Tulare, and Yuba counties. Thus, in only a few years since 1955, when head smut made its appearance in hybrid sorghums, the fungus has spread to 16 of the state's 22 sorghum-producing counties and become established in their soils.

Symptoms and Host Response

In the sorghums, sporulation of *Sphacelotheca reiliana* usually occurs in the inflorescence. However, it has been observed on the foliage and culms of Leoti sorgo. The smut causes part or all of the sorghum panicle to develop into a sorus (figs. 2*A*, 2*B*, 3*A*)—a large mass of dark, spiny teliospores, each 9μ to 12μ in diameter. The sorus, first evident at heading time, is covered by a thick, white peridium, which fragments readily and releases the spores. Halisky (1961) reported an albinic mutant with buff-colored sori (fig. 3*B*) containing hyaline, smooth-walled teliospores, each 9.1μ to 12.7μ in diameter. Since *S. reiliana* infects the seedlings during several weeks of pre- and postemergence growth (Leukel, 1956), sori often develop on late tillers that are dwarfed and obscured by the foliage, while the main stalks remain free of smut sori.

When a sorus does not develop in the panicle, the infection may cause withering or blasting of individual florets (fig. 4) and partial or complete sterility of the inflorescence. Frequently, sterile panicles are borne on stunted tillers on a plant that bears a typical sorus on the main stalk. Phylloid inflorescences may appear on late tillers or on branches originating from axillary buds (fig. 2*C*).

In one field, the author measured 200 stalks of Ryer 15 grain sorghum. The average height of 100 nonsmutted stalks was 31.4 inches and that of 100 smutted stalks was only 14.0 inches—a reduction in height of 55.4 per cent. On the other hand, Reed, Swabey, and Kolk (1927) found "no special indication of stunting of an infected sorghum plant."

Varietal Reactions and Smut Incidence

Uniformly ripening old-line varieties of grain sorghum—including the well-known Double Dwarf 38, Double Dwarf Yellow Sooner, Ryer 15, Norghum, and Reliance—were grown in California for many years. The discovery of cytoplasmic male sterility in sorghum led to the development of many hybrid varieties with increased grain yields. Growers in grain-sorghum areas accepted the hybrid sorghums widely, following the profitable precedent of hybrid corn. Because of their spectacular ability to yield, the new hybrids have replaced many of the old-line varieties. One hybrid, RS-610, outproduced the established California varieties by 33 per cent in 1957 and by 28 per cent in 1958. However, many hybrids carry an unwelcome susceptibility to head smut. When the smut is once established in a soil, it attacks old-line sorghum varieties and new hybrids with almost equal virulence. Some of the most susceptible hybrid sorghums are those with Combine 7078 in their pedigrees.

Although several commercial hybrids possess tolerance or, in some instances, resistance to head smut, their yield is often lower than that of certain susceptible hybrids. For example (table 2), in 1960 the high-yielding, smut-susceptible RS-610, with 9.25 per cent head smut, yielded 8,756 pounds per acre on Grand Island, Sacramento County—699 pounds more than the smut-resistant variety DeKalb C-44A, which had only 0.25 per cent infection. The 1961 survey showed that the susceptible hybrid PAG-515S yielded 6,200 pounds of grain per acre in a commercial field in Solano County, in spite of 16.2 per cent smut infection. The ability of these and other susceptible hybrids—AMAK R-10, NK-210, and Frontier 400B—to give high yields in the presence of considerable smut infection makes probable the perpetuation of head smut in commercial sorghum fields.

Fig. 3. Two color types of head smut sori on NK-210 hybrid sorghum: *A*, common black sorus; *B*, buff-colored sorus produced by an albinic mutant of the head smut fungus.

The best potential control for head smut in sorghums lies in the selection and development of high-yielding resistant hybrids. According to the literature (Reed and Melchers, 1925; Stewart and Reyes, 1958), RS-630, feterita, and hegari appear resistant to head smut, whereas the sweet sorgos are highly susceptible. The milo types have been considered resistant to head smut but have now been found susceptible. In recent trials on smut-inoculated soil, four milo varieties developed head smut as follows: 47 per cent in Ryer 15, 35 per cent in Double Dwarf 38, 12 per cent in Double Dwarf Yellow Sooner, and 7 per cent in Dwarf Yellow Milo.

HEAD SMUT OF SUDANGRASS

Head smut occurred sporadically in California on sudangrass, *Sorghum sudanense* (Piper) Stapf, variety California 23, for a number of years before 1955, when the new variety Greenleaf was introduced from Kansas to be grown as a certified seed crop. As the acreage of Greenleaf sudan increased in central California, smut became widespread—probably as the result of introducing a susceptible variety into an environment favorable for the natural propagation of the disease. Between 1957 and 1959 head smut occurred commonly on Greenleaf sudan in Colusa, Glenn, Sacramento, Solano, Sutter, and

TABLE 2

RELATION OF GRAIN YIELD TO SMUT INCIDENCE IN SEVEN VARIETIES OF SORGHUM INFECTED BY *SPHACELOTHECA REILIANA**

Variety	Yield†	Smut infection‡
	lbs/acre	*per cent*
RS-610	8,756	9.25
AMAK R-10	8,637	8.75
Frontier 400B	8,625	6.75
NK-135	8,208	2.00
DeKalb C-44A	8,057	0.25
Asgrow Ranger	7,195	4.75
Ryer 15	6,319	0.50

* Test conducted in 1960 by the University of California Agricultural Extension Service, in naturally infested fields on Grand Island, Sacramento County. Data cited by courtesy of Dr. Vern Marble, Extension Agronomist.
† Average of two replications. Moisture 14 per cent.
‡ Based on number of infected panicles.

Yolo counties (Halisky and Smeltzer, 1961). Sudan crops were disqualified from seed certification when traces of head smut were found, although head smut had not previously been recognized as an economic disease of sudangrass. California seed growers suffered such losses that the acreage of Greenleaf sudan grown for seed dropped from 2,579 acres in 1957 to 138 acres in 1960

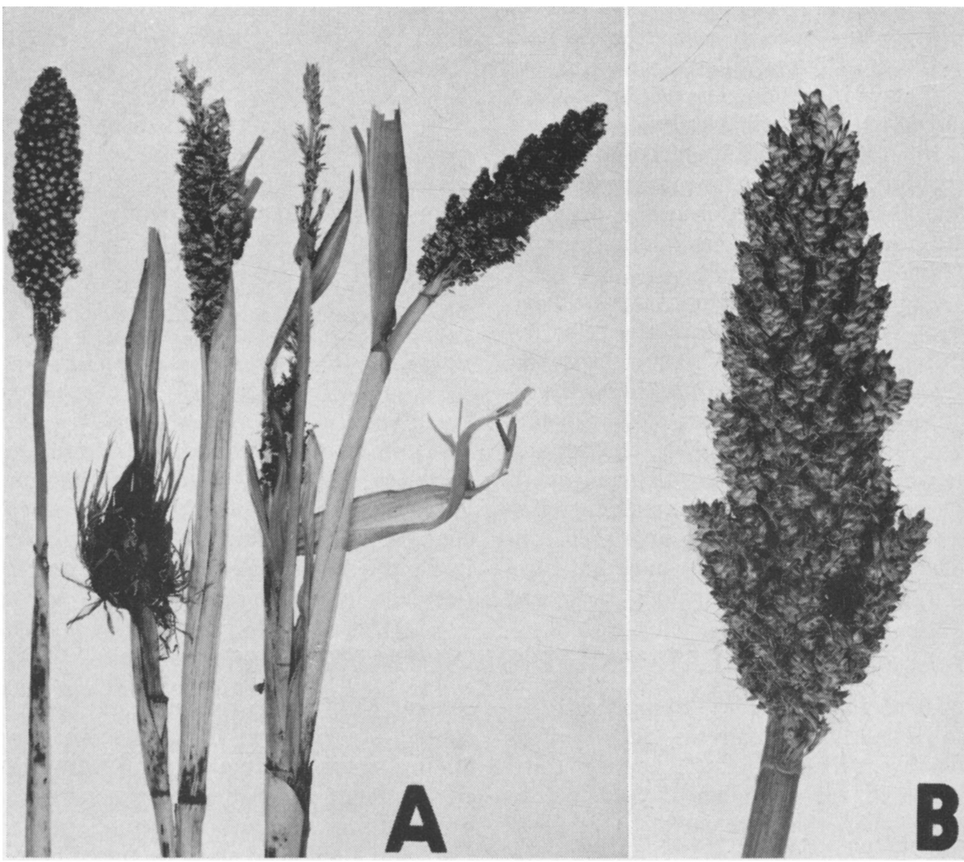

Fig. 4. Common symptoms of head smut in Ryer 15 grain sorghum: *A*, healthy panicle and two diseased stalks; *B*, enlargement of the sterile panicle shown in *A*, right.

(Halisky and Smeltzer, 1961). When the head smut tolerance for certification of sudangrass seed was raised from zero to trace, in 1961, only 10 per cent of fields failed to qualify for certification.

Symptoms and Systemic Infection

The presence of *Sphacelotheca reiliana* in sudangrass is seldom evident before the panicle emerges. Smutted panicles emerge as compact sori several centimeters long, each covered by a white peridium (fig. 5*B*). The peridium ruptures soon after emergence, exposing spore masses and shredded vestiges of the vascular system of the inflorescence (fig. 5*C*).

Sporulation by *S. reiliana* is not limited to the panicles. It has been observed on the foliage and culms of Sweet 372 sudan and Greenleaf sudan, where it indicates pronounced susceptibility. Heavily infected sudan plants often have shredded and dwarfed culms and tattered foliage where sori have developed.

S. reiliana does not always sporulate in infected sudangrass. Infected plants may bear sterile panicles, or infected panicles may be only partially replaced by sori. In such instances, sterility and phyllody (fig. 5*D*) are usually part of the disease syndrome. Panicle sterility is attributed to the presence of systemic mycelium in the vascular tissues of impaired inflorescences. Histologic studies (Halisky and Petersen, 1962) on sterile panicles from infected sudangrass plants showed the presence of smut hyphae in sieve-tube elements, xylem vessels, and adjacent parenchymatous tissues.

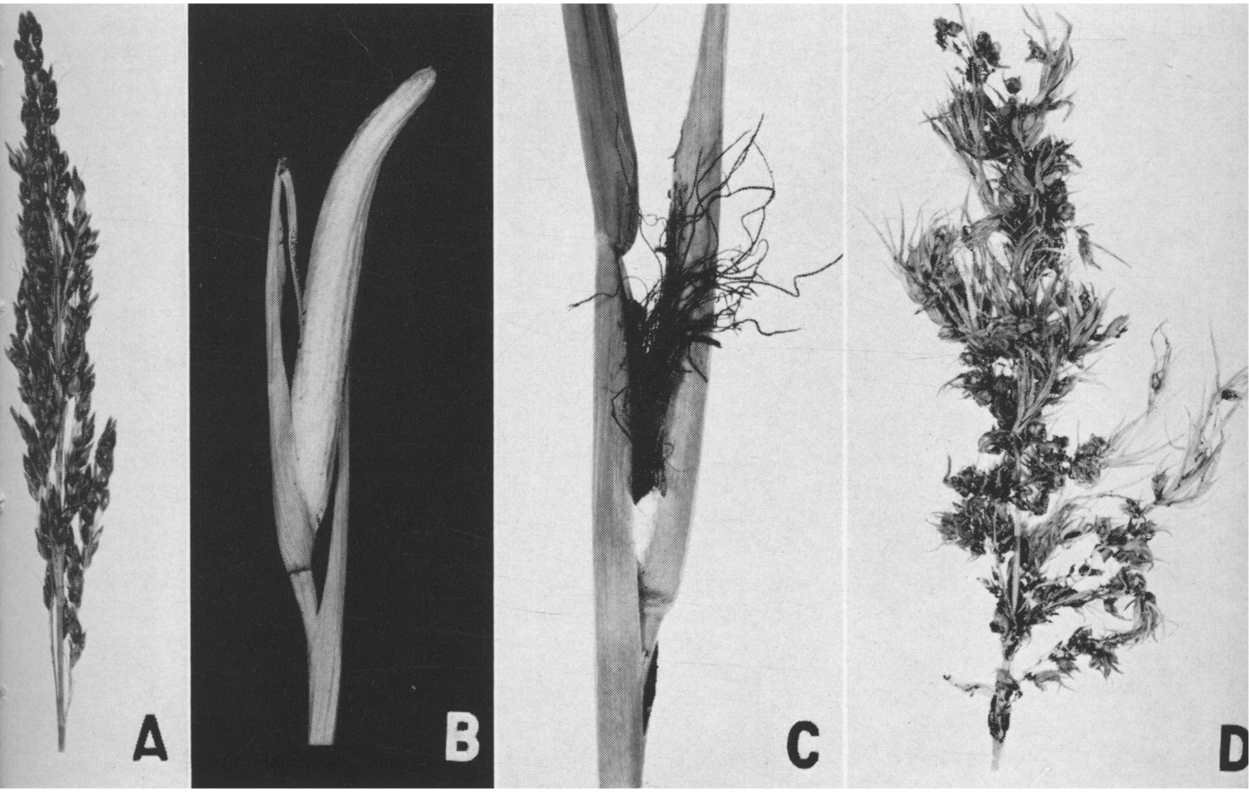

Fig. 5. Head smut in Greenleaf sudangrass: *A,* healthy panicle; *B,* closed sorus of *Sphacelotheca reiliana,* covered by a thick, white peridium; *C,* open sorus, showing shredded vestiges of the vascular system of the panicle; *D,* distorted panicle, showing foliar proliferation.

Further evidence that *S. reiliana* is a systemic parasite is the production of smutted panicles in second-growth tillers from latent crown buds. In six varieties of sudangrass and two of sorgo (Halisky and Petersen, 1962), the infection level of head smut in regrowth tillers was comparable to that in the original stands, showing the persistence of smut mycelium in the crown buds.

Varietal Reactions

In table 3, the author presents infection data for eight varieties of sudangrass grown in smut-inoculated soil at Davis in 1959. Two varieties were rated susceptible to head smut, one intermediate, four resistant, and one immune. The immune variety, Lahoma, tested for three more years, showed a total absence

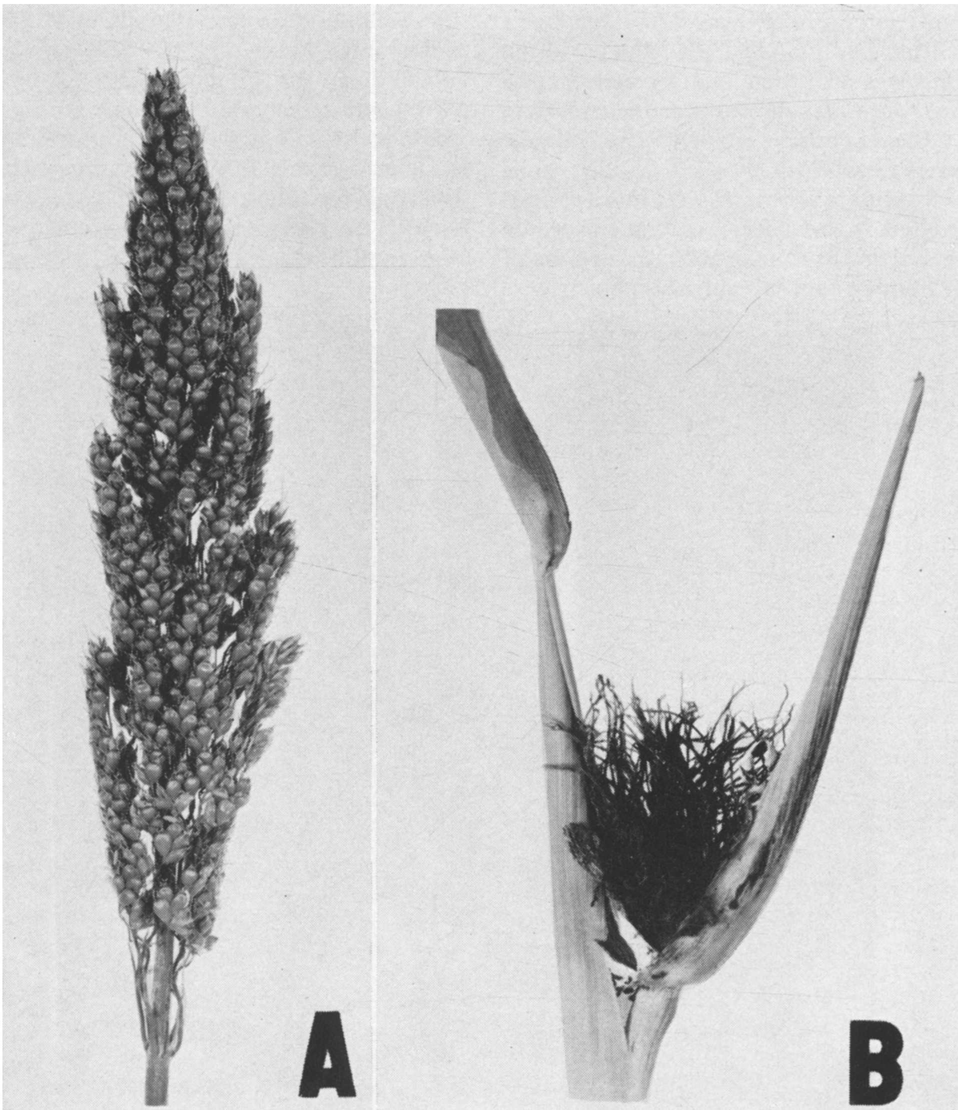

Fig. 6. Leoti sorgo, a common parent in sudangrass pedigrees: *A,* healthy panicle; *B,* sorus of *Sphacelotheca reiliana,* showing shredded vestiges of the vascular system of the host panicle.

TABLE 3
REACTION OF SUDANGRASS VARIETIES TO INFECTION BY *SPHACELOTHECA REILIANA**

Variety	Panicles	
	No. examined†	Smutted
		per cent
Greenleaf	321	54.65
Sweet 372	312	44.90
California 23	382	7.40‡
DeKalb Sudax	228	4.82
Tift	337	2.25
Wheeler	376	2.13
Piper	332	1.15
Lahoma	211	0.00

* Soil in test plots at Davis was inoculated in December, 1958, with teliospores from smutted Greenleaf sudangrass and seeded in April, 1959.
† Average of two replications, examined in August, 1959.
‡ In another test, 18.1 per cent infection was found in 227 panicles of var. California 23.

of head smut. Varieties Wheeler and DeKalb Sudax, tested again in 1961, showed resistance. The susceptibility of many sudangrass varieties is probably due to the wide use of the smut-susceptible Leoti sorgo, *Sorghum vulgare* var. *saccharatum* (L.) Boerl. (fig. 6), in their parentage (Halisky, Smeltzer, and Houston, 1959). Leoti sorgo is used because of other important characteristics, such as sweet stalks, waxy-type seed, yellow plant color, and resistance to certain bacterial and fungus leaf diseases.

CROSS-INFECTION STUDIES

Volunteer plants of sudangrass commonly grow along roadsides and irrigation ditches, in pastures, and in irrigated fields planted to other crops. When these volunteers are infected by *Sphacelotheca reiliana,* they provide a reservoir of inoculum from which winds disseminate smut spores. By cross-infection tests in field plots, Halisky, Smeltzer, and Houston (1959) established that the race of smut from Greenleaf sudangrass and that from Ryer 15 sorghum were equally infective to susceptible varieties of sudangrass and of sorghum.

In a commercial field in Yolo County, head smut was found in the Greenleaf sudangrass crop in the 1957 survey, and the disease has been observed on volunteer sudangrass in that field every year since. In 1958 it was present in the crop of Ryer 15 grain sorghum as well as in the sudangrass volunteers, providing circumstantial evidence of cross infection. The field was cropped to canning tomatoes in 1959 and to pink field beans in 1960. In 1961, when the field was summer-fallowed, sudangrass volunteers were still present along the edges of the field, and eight infected plants were found.

Field tests by the author in 1960, in plots inoculated with smut spores from sudangrass, resulted in an average infection of 21.6 per cent (range from 7 to 47 per cent) in eight old-line sorghum varieties: Ryer 15, Double Dwarf 38, Dwarf White Durra, Norghum, Chiltex, Double Dwarf Yellow Sooner, Reliance, and Dwarf Yellow Milo, and 23.1 per cent (range from 13 to 40 per cent) in seven sorghum hybrids: RS-610, T-601, E-56A, E-62A, RS-590, T-660, and RS-650. These results indicate the potential threat of sudangrass smut to commercial sorghum production.

HEAD SMUT OF FIELD CORN

Head smut of corn, *Zea mays* L., recurs periodically in the river deltas and the intermountain valleys of the Pacific Coast states and Mexico (fig. 7). Although *Sphacelotheca reiliana* on corn was first found in Kansas, reports indicate that it is now localized in the western regions of the United States but is practically unknown in the Corn Belt or on the Great Plains. It has been studied in Washington (Dana and Zundel, 1920; Mankin, 1953), in Oregon (Bressman and Barss, 1933), in California (Mackie, 1920; Halisky, 1962), and in Mexico (Lopez *et al.,* 1959; Rockefeller Foundation, 1960 and 1961).

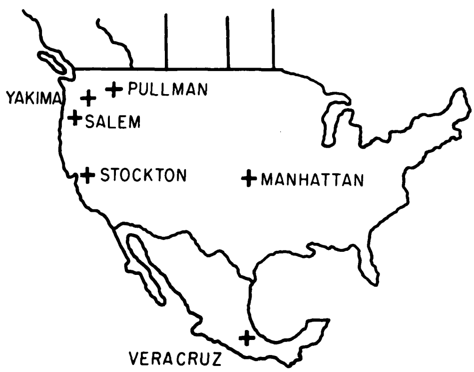

Fig. 7. Outline map of North America, showing the distribution of head smut in field corn.

Mackie (1920) found head smut on King Philip maize in the peat soils of the Sacramento–San Joaquin delta region. Surveys conducted by the present author from 1958 through 1962 showed the disease common in the deltas of Sacramento, San Joaquin, and Solano counties and sporadic in adjacent Contra Costa and Yolo counties. In 33 cornfields harboring the disease, infections ranged from trace to 39 per cent.

Head Smut Syndrome in Corn

As in sorghum and sudangrass, the mode of infection of corn by head smut is of the seedling-infecting type (Mankin, 1953) and results in a systemic distribution of mycelium in the apical primordial tissues. Sporulation by *S. reiliana* may occur in tassels (fig. 8*A*),

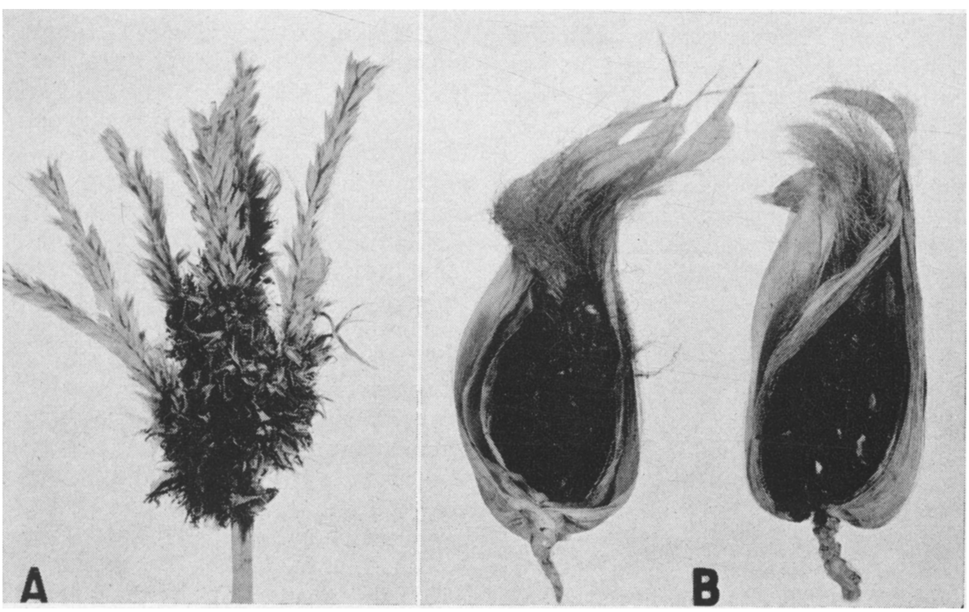

Fig. 8. Head smut sori in Kingscrost KY7A field corn: *A,* tassel partially replaced by a smut sorus; *B,* two ears completely replaced by sori, showing sporulation of *Sphacelotheca reiliana.*

in ears (fig. 8*B*), and occasionally in leaves of infected corn plants. The sori appear coarser and more granular than those on sorghum. Tassel infection may be confined to individual spikelets and result in anomalous shootlike growth, or the entire tassel may proliferate and form bizarre leafy structures. Ears of infected corn plants may be smutted or they may be aborted, with rudimentary leaf buds in place of normal ears. In some plants the tassels remain healthy while sori form in the ears, but most frequently sori develop only in tassels and the ears are aborted. Often sori form at both sites on the same plant. In a study of King Philip maize in commercial fields where head smut occurred commonly (Halisky, 1962), sporulation in the ears was independent of tassel sori, whereas terminally smutted plants usually bore either smutted or aborted ears (table 4). Plants with smutted tassels were severely dwarfed, often to less than one half of the normal plant height. The average height of 50 terminally smutted plants was 3.75 feet, in contrast to 7.63 feet for the 12 nonsmutted plants measured in the same field.

Varietal Reactions

In the 33 smut-infested cornfields surveyed from 1958 through 1962, head smut was most prevalent on King Philip hybrid maize, a grower-developed variety of Indian corn intermediate in type between a flint and a dent corn, dating back to 1900 (Smith, 1936). Other field-corn hybrids found infected with *S. reiliana,* in order of decreasing disease severity in these commercial fields, were PAG-323, PAG-347, Kingscrost KY7A, Pioneer 352, Pioneer 302, and Asgrow 300. The susceptible Oregon Evergreen sweet corn was not grown in the commercial fields surveyed in the California delta.

GALL SMUT OF CORN

A different smut disease, caused by *Ustilago maydis* (DC.) Cda. and known as common smut, gall smut, or boil smut, is found also in California wherever corn is grown. This disease often causes barren plants, with corresponding reductions in yield (Smith, 1936). Galls are produced on any aboveground part of the plant and appear as tumorlike growths from 1 to 6 inches in diameter. Both kinds of smut are present in the delta region, often in the same field and occasionally on the same plant. Differentiating characters of the two smut diseases found on corn in North America are presented in table 5.

FACTORS AFFECTING INCIDENCE OF HEAD SMUT

The amount of head smut in a given field appears to be cumulative, increasing with each successive susceptible crop. After three to five years of continuous sorghum culture, smut counts in representative fields revealed infection in 40 to 50 per cent of the panicles.

Infection level is related to the concentration of soil-borne teliospores. The author tested four susceptible sorghums and two susceptible sudangrass varieties in soil inoculated with smut spores, using a 10-foot row for each variety in each test. With 20 cc of teliospore inoculum per foot of plot row, 33.2 per cent of all panicles in the six varieties were infected. With 120 cc of the same inoculum per foot of plot row, the infection level of each variety was approximately doubled, bringing the amount of infection in the six varieties to 61.7 per cent.

Experiments by the author with seed-borne inoculum produced negligible amounts of infection. When 400 seeds of Ryer 15 grain sorghum were dusted heavily with teliospores of *Sphacelotheca reiliana* and planted in smut-free soil, only 1.55 per cent of the panicles

TABLE 4
SPORULATION SITE OF *SPHACELOTHECA REILIANA* ON
KING PHILIP MAIZE*

Symptoms	Smutted plants	
	number	*per cent*
Ears smutted, tassels healthy	159	10.52
Tassels smutted, ears aborted	843	55.75
Ears and tassels both smutted	510	33.73
Totals	1,512	100.00

* Data compiled from individual examination of smutted corn plants in commercial fields of King Philip maize in the California delta, 1959–1961 (Halisky, 1962).

became infected, in four replications averaging 97 plants each. At the same time, 400 smut-free seeds from the same lot were planted in smut-inoculated soil, with the result that 34.7 per cent of the panicles became infected.

In the author's experience, spores of *S. reiliana* that are exposed under natural conditions to the vagaries of winter weather initiate a greater amount of infection than do spores stored artificially at constant low temperature under dry laboratory conditions. The exact reason for this difference in spore behavior is not known, but it is probably related to spore dormancy and maturation phenomena. For all field experiments reported here, the soil was inoculated in the fall so that spores would receive the normal winter conditioning.

Soil Temperature and Moisture

Conditions in the soil are of paramount importance, because the soil is where head smut infection takes place. The author conducted soil-temperature studies in four tanks of soil inoculated with spores of *S. reiliana* from smutted field corn. The tanks were maintained at constant temperatures in the greenhouse, with 70 to 81 plants of King Philip maize in each tank. The graph (fig. 9) shows that soil temperatures between 21° and 28°C were favorable for smut infection, whereas relatively low (14°C) or relatively high (35°C) soil temperatures substantially reduced the

TABLE 5
DIFFERENTIATING CHARACTERS OF TWO CORN SMUTS

Character	Head smut	Gall smut
Causal organism	*Sphacelotheca reiliana* (Kühn) Clint.	*Ustilago maydis* (DC.) Cda.
Propagation	Soil-borne teliospores	Wind-borne sporidia
Infection	Seedling infection; mycelium systemic	Local infection through wounds or meristematic tissue; mycelium localized
Sporulation site	Tassels and ears, occasionally leaves	Axillary buds, ears, tassels, stalks, prop roots
Sorus	Coarse, dry spore masses with broken strands of vascular tissue	Soft, powdery spore masses without strands
Teliospores	Globose, spiny, 9 μ–12 μ diameter, reddish-brown	Globose, spiny, 7 μ–10 μ diameter, olive-brown
Gall formation	None, but vegetative proliferation common	Tumorlike growths, 1″–6″ diameter, on any aboveground part
Other symptoms	Plants dwarfed, ears often aborted	Stalks distorted, often broken

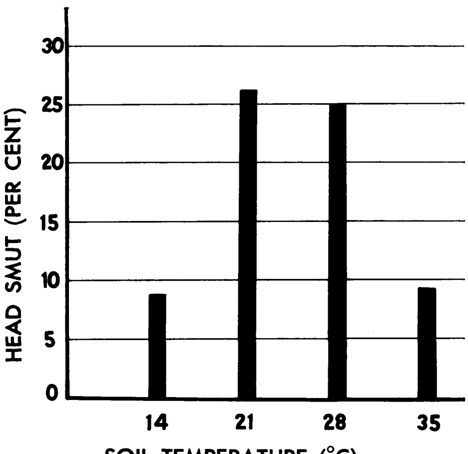

Fig. 9. Effect of soil temperature on infection of King Philip maize by soil-borne spore inoculum of *Sphacelotheca reiliana.*

amount of infection. Results suggest the possibility of reducing the incidence of head smut in field corn by early planting in cool soil.

Incidence of head smut in sorghum plantings is greatest in areas of low soil moisture (Christensen, 1926). The effect of this factor was evident in many sorghum fields in the California survey. Areas of moisture stress, usually found along edges of fields and on small knolls, were recognizable by sparse stands and heavily smutted plants.

Chemical Treatment of Seed

Chemical treatment of seed with hexachlorobenzene did not prevent infection in Leoti sorgo by soil-borne spores of *S. reiliana.* The explanation for this failure may be that the infective period extends over several weeks (Leukel, 1956), during which the chemical probably deteriorates in the soil. Table 6 shows the negative results of seed treatment with three formulations of hexachlorobenzene, each applied at two dosage levels. In contrast to these results with *S. reiliana,* hexachlorobenzene seed treatment is used widely in the Pacific Northwest against infection of wheat by soil-borne spores of the common bunt smuts (*Tilletia* spp.). Treatments there have been highly effective (Fischer and Holton, 1957).

PATHOGENIC SPECIALIZATION IN *SPHACELOTHECA REILIANA*

The author conducted cross-inoculation tests on a selection of susceptible sorghum and corn varieties growing in sterilized soil in the greenhouse, with sporidia rather than teliospores for inoculum. Teliospores of *Sphacelotheca*

TABLE 6

TRIAL OF HEXACHLOROBENZENE AS A SEED TREATMENT AGAINST SOIL-BORNE* HEAD SMUT (*SPHACELOTHECA REILIANA*) OF LEOTI SORGO

Formulation†	Dosage	Amount of infection‡			
		Replicate 1	Replicate 2	Replicate 3	Average
	oz/bu	*per cent*	*per cent*	*per cent*	*per cent*
No Bunt 40 (dust)§	1	43	62	59	54.7
No Bunt 40 (dust)	2	45	44	55	48.0
Colloidal HCB (liquid)§	1	46	53	42	47.0
Colloidal HCB (liquid)	2	47	37	40	41.3
Sanocide (dust)‖	1	47	53	43	47.6
Sanocide (dust)	2	61	24	39	41.3
Control	0	46	51	56	51.0

* Soil was inoculated the preceding fall with teliospores from infected sorghum.
† All formulations contained 40 per cent active hexachlorobenzene.
‡ Each replicate consisted of a 10-foot plot row with a stand of 40 to 86 plants (average 55). Plot arrangements were randomized. The percentage of infection was based on plant counts. L. S. D. at 0.05 = 17.6%; at 0.01 = 24.6%.
§ Chipman Chemical Company., Inc.
‖ California Chemical Company—Ortho Division.

TABLE 7

REACTION OF SORGHUM AND CORN VARIETIES TO INOCULATION WITH SPORIDIA OF TWO DISTINCT RACES OF *SPHACELOTHECA REILIANA**

Plant and variety	Sorghum race (albinic)		Corn race (black)	
	Number of plants		Number of plants	
	Inoculated	Smutted	Inoculated	Infected
Sorghum:				
AMAK R-10 hybrid	95	84	9	0†
NK-210 hybrid	103	81	16	0†
Ryer 15	104	90	10	0†
Corn:				
Golden Cross Bantam	12	0‡	11	11
Inbred Line B-164	8	0‡	9	9
Indian maize	10	0‡	9	9
King Philip maize	10	0‡	7	7
Kingscrost KY7A	8	0‡	10	10
Oregon Evergreen§	139	26‖	16	15
Pfister 347	8	0‡	11	11

* Cultures of sporidia were injected into seedlings growing in sterilized soil in the greenhouse.
† Neither malformation nor smutting was found in any of the sorghum plants inoculated with sporidia of the corn race.
‡ No plants were smutted, but a few showed some foliar distortion caused by systemic smut infection.
§ Open-pollinated sweet corn variety, from seed supplied by Ferry-Morse Seed Company, Mountain View, California.
‖ Infection and malformation in 64 plants, sporulation in 26 of these.

reiliana germinated on 1.5 per cent potato dextrose agar and produced promycelia with lateral sporidia. The sporidial colonies, containing mixtures of plus and minus mating types, multiplied on the agar by rapid budding. Cultures were then transferred to potato dextrose broth[2] in 250-ml flasks and shaken for 7 to 10 days on a rotary shaker at room temperature (25°C) to promote further multiplication of sporidia. Turbid broth cultures containing masses of sporidia were injected with a sterilized hypodermic syringe into the tissues of the experimental seedlings. Any confusion of results by possible inoculum contamination was eliminated by using the typical dark, spiny-spored corn smut from King Philip maize and the visibly distinct smooth-spored albinic mutant of the sorghum race group from NK-210 hybrid sorghum.

The sorghum varieties tested were apparently immune to the corn isolate of *S. reiliana* used (table 7), but several plants in each of the corn varieties inoculated with the albinic sorghum smut showed some malformation. Oregon Evergreen sweet corn was the only one of the corn varieties tested that showed definite susceptibility to the albinic race from sorghum. Infection developed in 64 of the 139 inoculated seedlings, and infected seedlings of this variety were severely stunted. Many of them produced peculiarly deformed foliage and proliferated tassels (fig. 10*A*). Sporulation occurred in 26 of the 64 infected plants of Oregon Evergreen (fig. 10*B*) but not in any of the other corn varieties tested. Al-Sohaily and Mankin (1960) reported comparable cross-inoculation experiments in South Dakota. They used sudangrass smut from California and the susceptible sweet corn variety North Star.

DISCUSSION

It is generally recognized that two pathogenically distinct race groups exist in *Sphacelotheca reiliana*, one on the sorghums and one on corn (Reed, Swabey, and Kolk, 1927; Bressman and Barss, 1933; Mankin, 1953; Halisky and

[2] Broth from 200 gm of boiled potatoes plus 10 gm of dextrose and distilled water to make 1 liter.

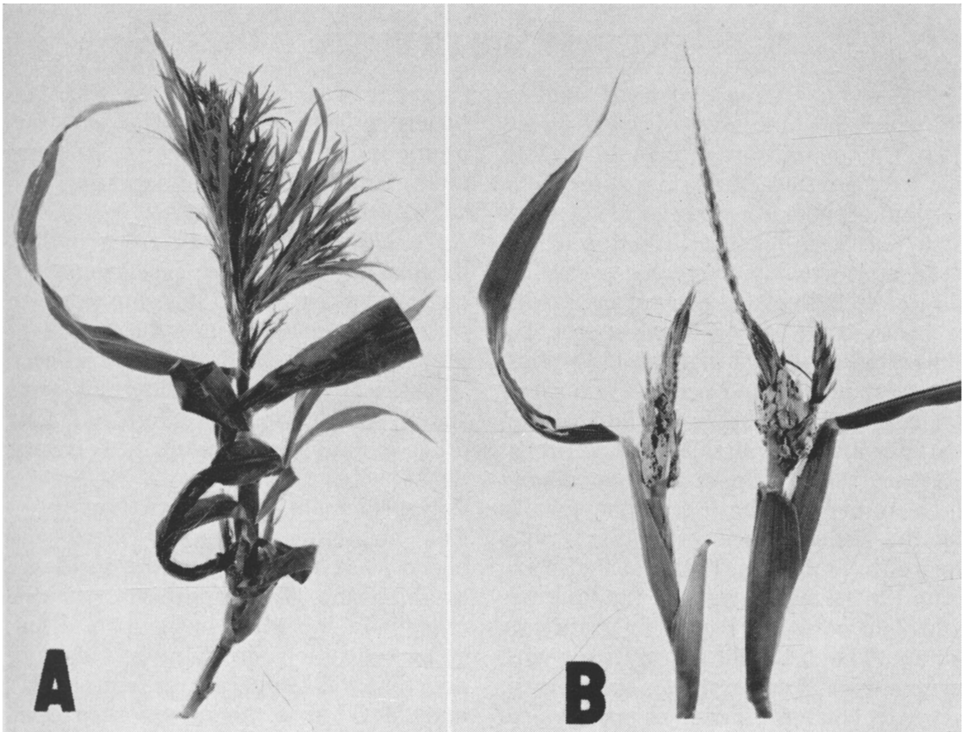

Fig. 10. Oregon Evergreen sweet corn infected by the albinic race of *Sphacelotheca reiliana* from sorghum: *A*, infected plant, showing proliferated tassel and distorted foliage; *B*, smut sori formed in infected tassels.

Smeltzer, 1961). Each group is a subspecific entity, consisting of one or more pathogenic races (Al-Sohaily, 1960). These race groups may be classified as *formae speciales*. However, more research is needed to clarify the taxonomy and nomenclature pertaining to pathogenic specialization and race designations within this species.

The possibility that the sorghum race group of *S. reiliana* may have given rise to the corn race merits consideration, because the sorghum races are more widely distributed and they do infect corn occasionally (Reed, Swabey, and Kolk, 1927; Al-Sohaily and Mankin, 1960). Head smut appeared on corn in Kansas within four years of its original appearance on sorghum in that state. The sorghum races not only have a wider host range and a wider geographic distribution than the corn race but also show more genetic variability, as evidenced by the appearance of the albinic mutant.

The disease on corn has not become established in the Corn Belt or on the Great Plains. In California, where corn head smut has persisted in the delta region for more than 40 years, it has not spread to other corn-growing regions of the state. The reason for this localized distribution may lie in the acid reaction of the peat soils of the California delta, usually between pH 5.5 and 6.0. Krüger (1962) demonstrated the importance of pH for spore germination in corn head smut by showing that a higher percentage of spores germinated in acid than in alkaline soils.

SUMMARY

The recent increase of head smut in the grain-sorghum areas of the Midwest, Texas, and California coincided with the introduction of highly susceptible sorghum hybrids, whose wide acceptance may result in continuation of the head smut problem for many years. The disease is difficult to control because it is transmitted by soil-borne spores, because the infection persists in volunteer host plants, and because several of the susceptible hybrids outyield any resistant variety available at present.

Sporulation of *Sphacelotheca reiliana* in a susceptible host occurs typically in the inflorescence, which is transformed into a sorus. Foliar sori also are found in certain varieties of sudangrass and field corn but rarely in grain sorghum. The infection is systemic and may induce floret sterility and certain growth aberrations, such as bizarre proliferations of the inflorescence. Dwarfing of hosts is common; the amount of dwarfing was determined by measurements in fields of mature Ryer 15 sorghum and King Philip maize. Moisture stress favors infection of sorghum.

Pathogenic specialization occurs in *S. reiliana,* with one race group limited to corn and the other pathogenic not only to grain sorghums but also to sorgos, forage-sorghum hybrids, sudangrass varieties, and some sweet-corn varieties. Lahoma sudangrass was found immune to head smut, and four other sudangrass varieties were resistant.

Experiments have shown that infection originates primarily from soil-borne smut spores; that the incidence of infection is proportional to the amount of inoculum built up in a soil, as by continuous cropping to sorghum; and that soil temperatures between 21° and 28°C favor the infection in corn. Experimental infection of johnsongrass was not successful.

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