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A Study of *Sphacelotheca occidentalis,* Cause of Kernel Smut of Big Bluestem

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Sphacelotheca occidentalis causes kernel smut disease of *Andropogon gerardii,* a prairie grass. The smut fungus is systemic, perennial, causes severe stunting, and sporulates in florets. Spores develop in gall-like sori composed of grass and fungal cells. Spores initiate in a meristematic area near the base of the sorus, and progressively more mature spores are found toward the sorus tip. The cylindrical sori have a central columella of host vascular tissue permeated by hyphae, sporogenous hyphae and developing teliospores that surround the columella, and a peridium of host and fungal cells. Sporogenous hyphae ramify in a gelatinous matrix that disappears as the teliospores enlarge. Teliospores become ornamented as they enlarge; mature teliospores bear two sizes of spines. Sorus and teliospore characters suggest that *S. occidentalis* belongs in *Sporisorium.*

Kernel smut has been collected on native and planted bluestem prairies in Iowa since 1978 when it was first reported in the state. Colonies of diseased bluestem are especially prevalent in several native prairies of northwest Iowa.

INDEX DESCRIPTORS: Smut, *Sphacelotheca, Sporisorium,* big bluestem

Big bluestem (*Andropogon gerardii* Vit.) is a common perennial grass of native Iowa prairie remnants and roadsides. It has also been planted in restored prairies. *Sphacelotheca occidentalis* (Seym.) Clint., which causes "kernel smut" of big bluestem, was first collected in Iowa in 1978 (Knaphus and Tiffany, 1986). Since then it has been reported from a number of planted bluestem stands and native prairies, suggesting its distribution in the state may be increasing. Possible long-term effects of the disease on big bluestem populations are unknown. One of the goals of this study was to assess current statewide distribution trends of the disease.

We also were interested in the distribution of kernel smut in the prairies where it occurs. Patches of heavily infected populations often are found annually among healthy populations on a given prairie. Casual observations indicate the fungus perennates in the host and spreads slowly from plant to plant, but the route of infection is not known. We attempted to document the rate of disease spread by establishing permanent plots in areas with diseased and healthy plants.

The third objective of this study was to follow disease progress in the host. Information about soral ontogeny and sporogenesis in *S. occidentalis* is relevant to current taxonomic studies in *Sphacelotheca* and related genera.

The genus *Sphacelotheca* was established for *Ustilago hydropiper,* a smut of *Polygonum* (DeBary 1887), and characterized by the spore-producing sori that form in ovaries. DeBary noted that mature sori featured an axile columella, an outer peridium of sterile fungal cells, and spores that developed between these structures. Subsequent observations of superficially similar sori in grasses led to the transfer of many graminicolous smuts to *Sphacelotheca.*

Langdon and Fullerton (1978) made a strong case for restricting *Sphacelotheca* to *Polygonum* smuts. Although mature sori of the graminicolous smuts resemble those of the type species, they develop in a very different way. The grass-infecting smuts do not entirely replace existing host structures with sori; instead, sori result from concurrent growth of host and fungus. The persistant columella making up the axis of the cylindrical sorus is composed of grass vascular tissue, and the peridium often includes grass epidermal cells as well as fungal cells. Langdon and Fullerton (1978) suggested that *Sporisorium* Ehrenberg probably could accommodate many of the approximately 100 grass-infecting species currently in *Sphacelotheca* (Fischer and Holton 1957). A few have been transferred to *Sporisorium* (Langdon and Fullerton 1978; Vánky 1987; Durán 1987), but Durán (1987) has suggested that studies of sorus ontogeny should precede extensive transfer of species (Durán 1987). The relevance of our observations of sorus development in *S. occidentalis* to such transfers will be discussed.

MATERIALS AND METHODS

Field methods

All diseased plants examined were naturally infected and collected from native prairie remnants in northwest Iowa and planted bluestem sites in central Iowa (Fig. 1). A few diseased plants from the North 40 prairie at Iowa Lakeside Laboratory in Dickinson County were dug, potted, and maintained in the greenhouse where they continued to manifest disease symptoms.

Diseased populations were located in July 1987. A section of ¾ inch diameter steel pipe approximately ½ m long was driven halfway into the ground to mark the center of each plot. Individual diseased plants were located by recording a distance and compass bearing from the center points. A small numbered metal tag on a wire was pushed into the ground next to each diseased plant to provide an unobtrusive and reliable method for relocating plants in subsequent years. In 1988 the plots were revisited in late June and observed periodically until mid-August; in 1989 they were again visited several times in late June and July.

A second type of plot was established at Cayler Prairie to follow the long-term progression of disease. The center of the plot was marked as previously described in the midst of a severely smutted population of bluestem. Four smaller stakes were placed 50 feet from the center 90° to each other. The plot was read by stretching a metal tape from the center to the end of each arm of the cross and then counting the numbers of diseased and healthy culms in ¾ m quadrats. A count of diseased and healthy plants was made on July 17, 1987.

Histological methods

Infected culms were cut at ground level, placed in plastic bags, and returned to the laboratory. Sori of various ages were dissected from the

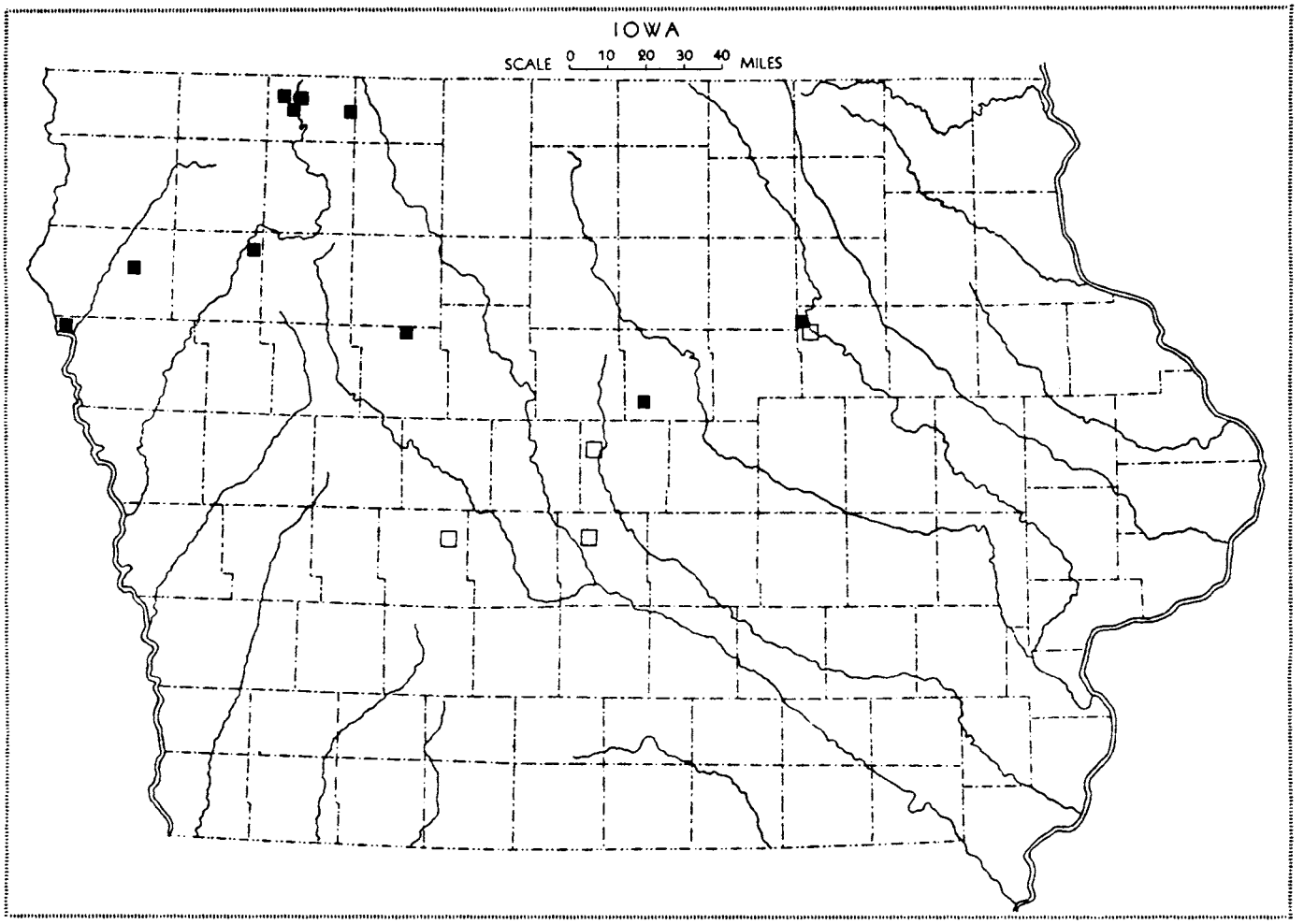


Fig. 1. Collection sites of *S. occidentalis* in Iowa. Solid symbols represent collections from native stands; open symbols indicate collections from planted bluestem stands.

spikelets, cut in small pieces, and placed immediately into fixative. Small pieces of stem, root and rhizome tissue were also fixed for sectioning, as were uninfected inflorescence pieces of various ages for comparison.

Material for light microscopy was processed in one of two ways. Some was fixed in FAA (formalin: acetic acid: 50% alcohol in proportions of 2:1:17), dehydrated in an ethanol gradient, transferred to xylene and gradually infiltrated and embedded in paraffin. Sections 8-10 μm thick were cut on a rotary microtome and attached to glass slides. They were stained in aqueous hemalum and safranin for routine examination. Other specimens were fixed and embedded in resin as for Transmission Electron Microscopy (TEM) described below. Sections 0.5-1.5 μm thick were cut with glass knives on a Reichart Ultracut E microtome, affixed to glass slides, and stained with methylene blue-azure II-basic fuchsin (Berlyn and Miksche 1976) or toluidine blue O.

Specimens for TEM were fixed for 8-24 hr at 4°C in 4% glutaraldehyde/3% paraformaldehyde in 0.1 M phosphate buffer at pH 7.0. After a buffer rinse, they were post-fixed for two hr in similarly buffered 1% osmium tetroxide, again rinsed in buffer, dehydrated in ethanol, transferred to acetone, and finally infiltrated with Spurr's resin. Specimens infiltrated slowly, so infiltration times were increased to about 3 days. Resin was polymerized at 60°C for 24 hr. Thin sections were cut with glass knives on a Reichart Ultracut E ultramicrotome, picked up on copper grids, stained with ethanolic uranyl acetate and aqueous lead citrate, and viewed and photographed on an Hitachi HU-11C transmission electron microscope.

Material for scanning electron microscopy (SEM) was fixed and dehydrated to absolute ethanol as for TEM. Specimens were then frozen in liquid nitrogen, fractured with a razor blade and returned to ethanol. These pieces were critical point dried, mounted on copper stubs with silver paint, sputter-coated with gold-palladium, and viewed and photographed with a JEOL JSM-35 scanning electron microscope.

RESULTS AND OBSERVATIONS

Field observations

No systematic attempt to determine the total range of *S. occidentalis* was made, but available collection data document the distribution of disease in northwest Iowa native prairies and in central Iowa planted bluestem stands (Fig. 1). Smutted plants tagged in 1987 were diseased in following years, which suggested that the mycelium was perennial in the host. Diseased sods maintained in the greenhouse continued to periodically produce smutted culms for over a year. In the field, smutted culms often appeared before nearby

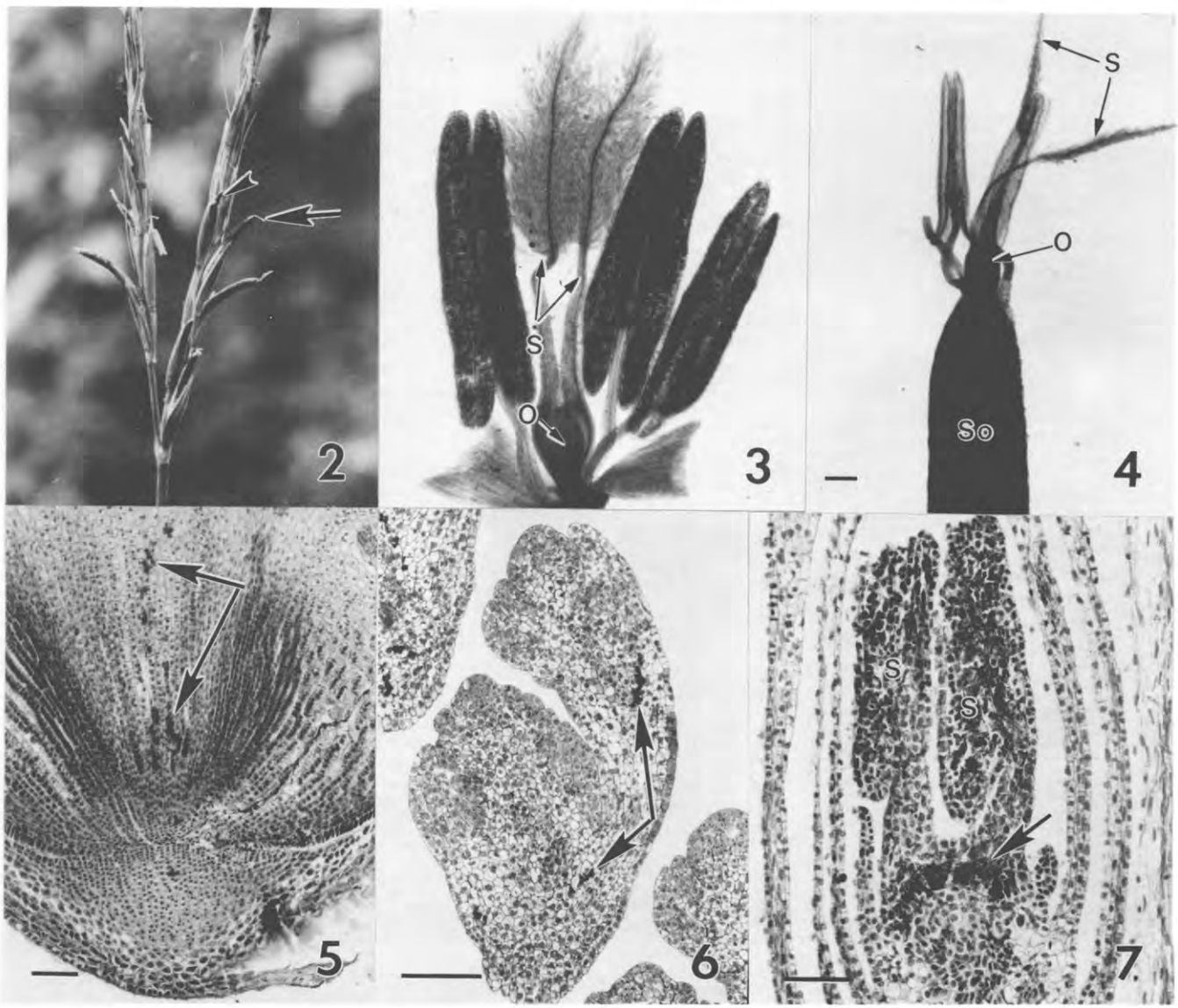
healthy plants flowered. Sometimes, however, plants produced healthy inflorescences early in the season and smutted ones later. Flowering was suppressed in both diseased and healthy plants during extremely dry summers. Spring burning of the prairies did not seem to affect disease expression in the host.

Diseased plants were sometimes dramatically stunted, producing sori on culms less than 10 cm tall. Infected plants in the greenhouse weakened gradually, and their root systems were poorly developed compared to those of healthy plants.

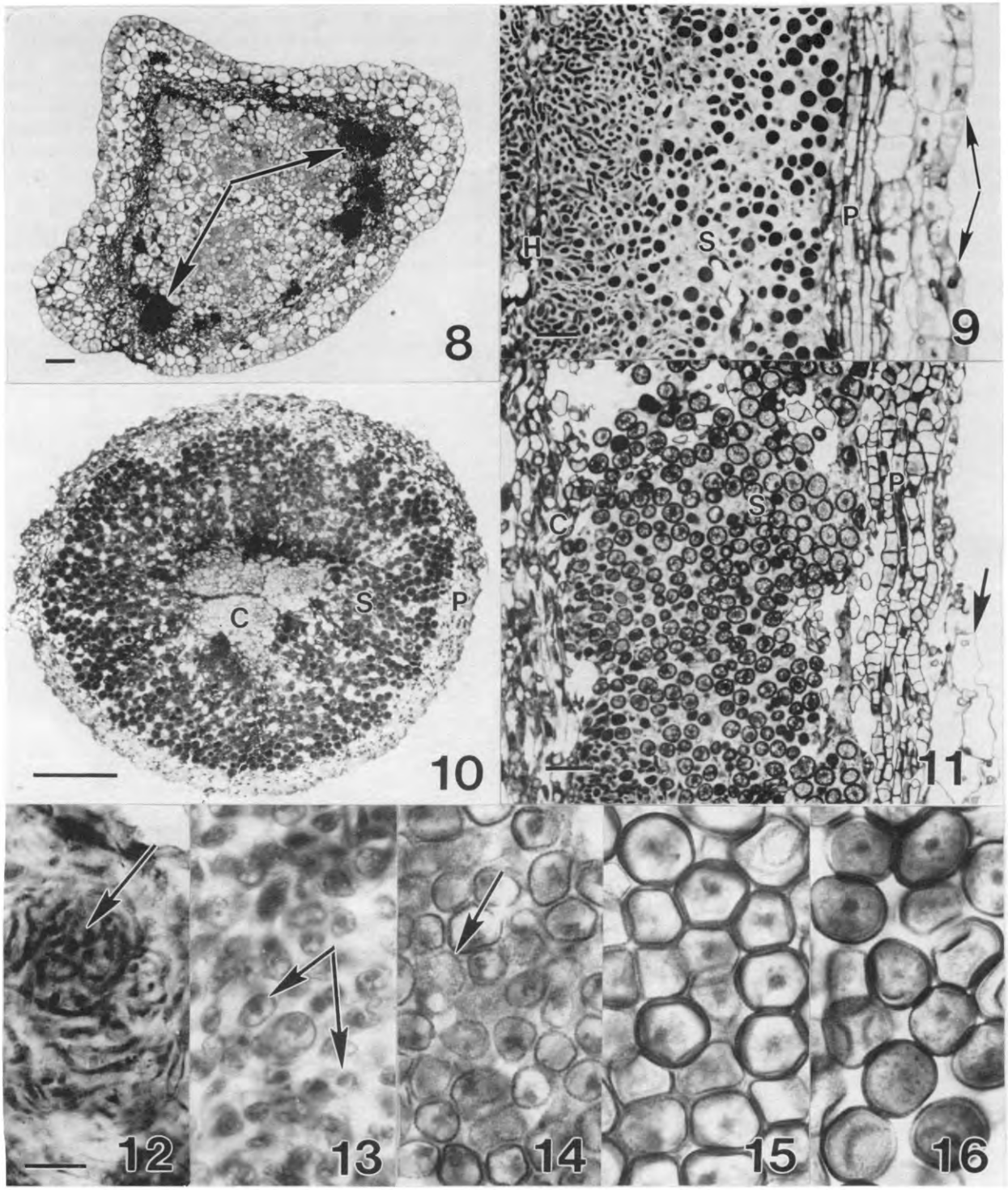
The inflorescence of big bluestem consists of a peduncle terminated by several spikelet-bearing branches — the "turkey foot." Each node of a spikelet-bearing branch normally bears a pair of spikelets, one sessile and the other stalked. The sessile spikelet is perfect and the pedicellate one is male. Sori were usually 2-8 mm long at maturity and formed in both sessile and pedicellate spikelets of diseased plants (Fig. 2). Usually most spikelets in a diseased inflorescence were smutted, but on some culms only a few spikelet pairs were smutted. On such culms the sori were sometimes more than 1 cm long, and the plants were not severely stunted. Normal caryopses were often produced in the upper spikelets of partially smutted inflorescences. Atypical sori were found most often in populations of planted bluestem.

Light microscopy

Each healthy floret contained three large stamens and an ovary with two feathery stigmas (Fig. 3). Atrophied stamens and ovaries were seen at the tips of young sori (Fig. 4), indicating that the main part of



Figs. 2-7. *Spacelotheca occidentalis* on big bluestem. Fig. 2. Diseased bluestem inflorescence, with sori in both sessile (arrow) and pedicellate (arrowhead) spikelets. Approx. 2X. Fig. 3. Whole mount of healthy floret, with three stamens, ovary (O), and stigmas (S). Fig. 4. Whole mount of diseased floret, with poorly developed stamens, ovary (O), and stigmas (S) found at the apex of the sorus (So). Bar = 100 μm for Figs. 3 and 4. Fig. 5. Longitudinal section of paraffin-embedded root with scattered hyphae (arrows) behind root apex. Bar = 100μm. Fig. 6. Longitudinal section of resin-embedded spikelet pair primordium. Note scattered hyphae in sessile and pedicellate spikelets (arrows). Bar = 100 μm. Fig. 7. Longitudinal section of paraffin-embedded older infected spikelet. Stamens (S) are infected; hyphae are aggregated below the point of stamen insertion (arrow). Ovary is out of the plane of section. Bar = 30 μm.



Figs. 8-16. *Sphacelotheca occidentalis* on big bluestem. Figs. 8-11 from resin embedded material; Figs. 12-16 from paraffin embedded material. Fig. 8. Cross section of young sorus. Cylinder of hyphae (arrows) surrounds central vascular bundles and is enclosed by outer layers of host cells. Bar = 20 μm. Fig. 9. Longitudinal section of young sorus. Sporogenous hyphae (H) are in the center, maturing spores (S) surround them, and the fungal peridium (P) and host cells (arrow) enclose the whole. Note gelatinous matrix around developing spores. Bar = 20 μm. Fig. 10. Cross section of older sorus, with central columella of vascular bundles (C), mature spores (S), and outer peridium (P). Bar = 100 μm. Fig. 11. Longitudinal section of older sorus. Part of columella (C) is left of the spore mass (S). Fungal peridium (P) is intact, but only remnants of host cells (arrow) remain. Bar = 20 μm. Figs. 12-16 show spore development sequence. Bar = 10 μm for Figs. 12-16. Fig. 12. Sporogenous hyphae (arrow) are coiled and dense. Fig. 13. Young uninucleate spores (arrows). Fig. 14. Wall ornamentations (arrow) are visible when spores are still small. Fig. 15. Spores are sometimes polyhedral due to compression. Fig. 16. Single mature spores, somewhat agglutinated.

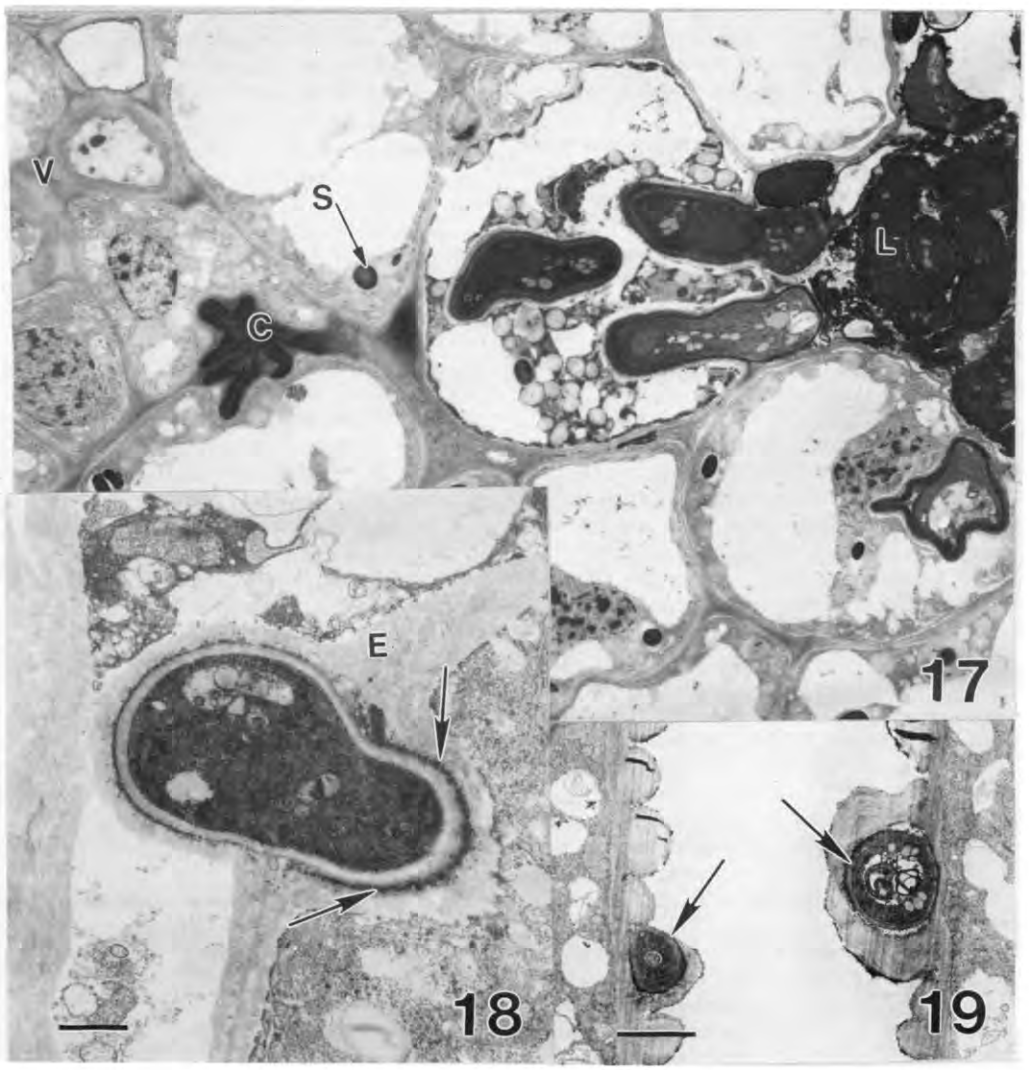
the sorus developed below the point of insertion of the flower parts in diseased florets.

Mycelia were found in vegetative host tissues, typically near nodes and in root tips (Fig. 5). Sparse mycelia were found in both sessile and pedicellate spikelet primordia of partially differentiated inflorescences (Fig. 6). Development of stamens and ovaries was arrested as mycelia colonized the rachillae between and below the floral whorls in infected florets (Fig. 7). Rachillae thickened and elongated as a result of concurrent host and fungal growth. Occasionally infected remnants of the lodicules remained near the base of the sorus. The bracts subtending the floret sometimes contained hyphae but their development apparently was unimparied.

Sori were composed of host and fungal cells. Hyphae aggregated in intercellular spaces in a cylinder around the central vascular bundles in young sori (Fig. 8). Luttrell (1987) referred to these hyphal aggregates as lacunal mycelium to distinguish them from the more usual type of intercellular mycelium where individual hyphae occupy small spaces between host cells. Lacunal hyphae at the bases of sori were not differentiated, but near apices sporogenous hyphae with gelatinizing cell walls were distinguished from thick-walled peridial hyphae (Figs. 9-11).

Sori were enclosed by several layers of host cells that eroded away as they matured to expose a peridium consisting of thick-walled fungal cells (Fig. 9). Regular files of peridial cells enclosed the sporogenous hyphae, developing spores, and central columella (Fig. 10). The peridium ruptured irregularly at maturity and released the powdery teliospores (Fig. 11).

It was difficult to interpret sporogenesis and early stages of spore development in paraffin and resin sections. Sporogenous hyphae initially were twisted and coiled around each other (Fig. 12) but presumably disarticulated to form very small, dense cells embedded in a matrix (Figs. 9, 13). Sporogenesis and spore maturation occurred rapidly, and few intermediate stages were seen. Single nuclei were clearly visible in young and mature teliospores (Figs. 13-16). Mature teliospores were agglutinated to free and polyhedral (Fig. 16), yellowish-brown by transmitted light, and ranged in size from 8-16 μm.



Figs. 17-19. *Sphacelotheca occidentalis*. Tranmission electron microscopy. Fig. 17. Parasitic mycelium near lacunal area (L) in a young sorus. Collapsed hyphae (C) are near developing tracheary elements (V). Note starch grains (S) in host cells. Bar = 3 μm Fig. 18. Intracellular hypha encased by host cell wall material (E). Note dark layer between encasement and fungal wall (arrows). Bar = .5 μm. Fig. 19. Mature tracheary element wth hyphae enclosed in secondary wall thickening (arrows). Bar = .5 μm.

Electron microscopy

Both intracellular and intercellular hyphae were seen in transmission electron micrographs of parasitized host tissue. Host cells near lacunal areas often contained several hyphae, some of them with collapsed walls (Fig. 17). An interfacial material consisting of two recognizable layers was found between the host plasmalemma and the cell wall of intracellular fungal hyphae (Fig. 18). The material next to the fungal cell wall stained heavily. A second layer of material was found between the dark layer and the host plasmalemma. This encasement was similar to and usually continuous with the host cell wall. Haustoria were not observed. Intracellular and intercellular hyphae were seldom associated with extensive visible alterations in the cytoplasm of host cells, especially at a distance from the lacunal areas. Hyphae were present in and between phloem and parenchyma cells, and sometimes in tracheary elements (Fig. 19).

Attempts to follow the process of sporogenesis ultrastructurally were frustrated by fixation and sectioning difficulties presented by the sporogenous hyphae and the gelatinous matrix in which the spores developed. The matrix appeared to form from hyphae that distintegrated and left behind remnants of the septa, and from gelatinizing walls of spore initials (Fig. 20). Ultrastructural detail in sporogenous hyphae was poorly preserved. Paired nuclei were observed in some lacunal hyphae, but it was not possible to determine whether nuclear fusion occurred in sporogenous hyphae or young teliospores.

Ornamentation of teliospore walls began when spores were small. The first indication of spine development was the formation of electron dense deposits above plasma membrane depressions within the moderately electron dense primary wall (Fig. 21). A second series of spines developed, followed by a uniform layer of dense material (Fig. 22). Finally, an inner zonate layer was seen in the mature spore (Fig. 23). The primary wall persisted as sheath remnants around the two series of spines (Fig. 24).

DISCUSSION

Our conclusion that *S. occidentalis* is perennial in big bluestem agrees with Dunleavy's (1956) observations. We also noted variation in expression of the disease. Big bluestem plants may not flower every year, and during the extremely dry summers of 1988 and 1989 few flowering culms, smutted or otherwise, were observed at many of the driest collecting sites. Whether the disease affects the ability of bluestem plants to withstand unfavorable growing conditions is not known, but poorly developed root systems and apparent progressive decline in vigor evidenced by stunted tillers of various heights suggest that disease may affect plant survival. Lack of flowering during dry summers prevented counts of diseased and healthy individuals in the populations marked in 1987, so we were unable to draw conclusions about the rate of disease spread through the bluestem populations.

The presence of partially smutted inflorescences and production of healthy inflorescences by infected plants suggest a dynamic host-parasite relationship. It is possible that environmental conditions affect relative growth rates of host and parasite, with inflorescences or parts of inflorescences sometimes "outgrowing" the fungus. This possibility is supported by observations from studies of *S. reiliana*, which causes sorghum head smut. Wilson and Frederiksen (1970) observed sorus variation that apparently depended upon the relative maturity of the spikelet invaded by parasitic hyphae. They also found that individual plants produced both healthy and diseased spikelets. Perhaps plants vary in their susceptibility, more resistant plants developing fewer sori.

"Kernel smut" does not accurately describe the disease caused by *S. occidentalis*. The attachment of stamens at or near the apex of the sorus and the occasional presence of lodicules near the base indicates that the axis of the floret constitutes the major part of the sorus. The columella, composed of several vascular traces, also suggests derivation from the floral axis rather than from individual organs. It is possible that many graminicolous smuts considered to be ovary-infecting actually form sori from the axis below the floral structures. This is difficult or impossible to demonstrate in mature specimens. Determining whether sorus initiation is of taxonomic use requires ontogenetic studies in a variety of smut fungi.

The occasional presence of atrophied ovaries atop sori in normally staminate bluestem spikelets indicates that the fungus stimulates abnormal development of rudimentary floral structures. A similar situation occurs in male spikelets of *Buchlöe dactyloides* (Nutt.) Englm. infected by *Tilletia buchloeana* Kellerm. and Sw. (Norton 1896). Production of both ovarian and staminal galls in pedicellate spikelets has also been reported in big bluestem infected with *Sorosporium everhartii* (Hansing and LeFebvre 1941).

Dunleavy's (1956) inability to observe mycelium of *S. occidentalis* in very young spikelets with the sectioning and staining techniques he used is understandable. Scattered hyphae in young spikelet primordia are difficult to distinguish because they create no visible disturbances in the grass cells, and most stains used to differentiate hyphae from plant cells also readily stain meristematic host cells. The spherical inclusions Dunleavy thought might be hyphal fragments within host cells were probably starch grains.

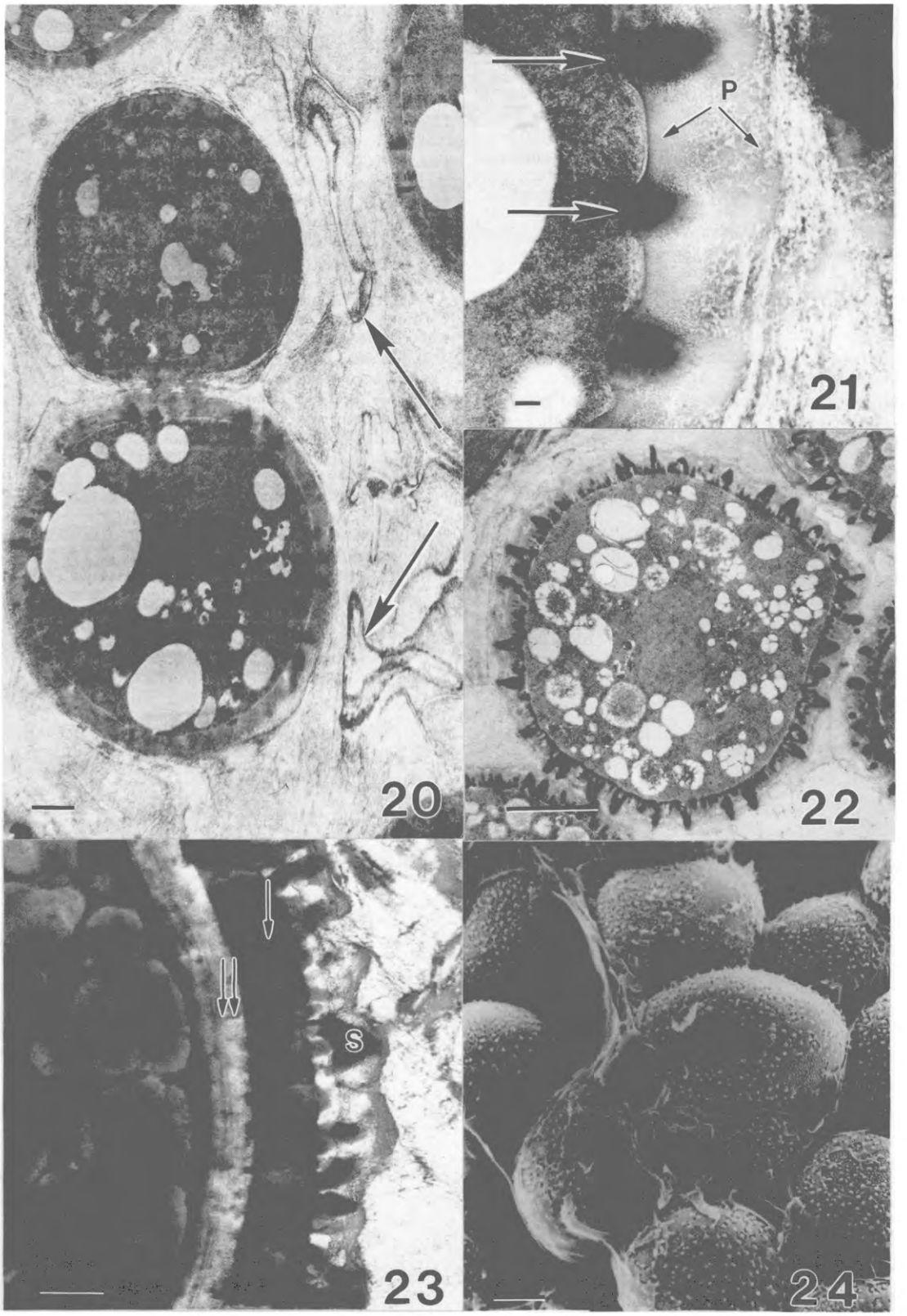
Dunleavy (1956) described only intracellular mycelium, but we observed intercellular mycelium as well. There was little difference in appearance between host-parasite interfaces in intracellular and intercellular hyphae, but the interfacial layer between the encasement and the fungal cell wall was found more often in intracellular hyphae.

Separation of the fungal cell wall from the host plasmalemma by a cell wall-like sheath has previously been described from smut fungal infections (DeBary, 1887; Luttrell, 1987). Fullerton (1970) looked at a number of graminicolous smuts and described hyphae at the bases of sori. He observed that penetrated host cells formed an extensive "encapsulation" around the hyphae that resembled host cell wall material. If these cell walls subsequently underwent secondary thickening, the encapsulations also became thickened. The presence of fungal hyphae within the wall thickenings of tracheary elements in our study of *S. occidentalis* corroborated Fullerton's observations.

It has been suggested that the timing of nuclear fusion may differ in the two families of smut fungi (Lutman 1910), with fusion taking place in the developing spore in the Tilletiaceae, but earlier in members of the Ustilaginaceae. Although we were unable to pinpoint exactly when nuclei fused in *S. occidentalis*, we observed only single, presumably diploid nuclei in immature spores, indicating that nuclear fusions occur during sporogenesis.

The ultrastructure of smut teliospore walls is known mostly from a few species of *Tilletia*. Development of the wall and spines in *S. occidentalis* was very similar to that described for *Tilletia caries* (DC.) Tul. and *T. controversa* Kuhn (Hess and Weber 1976) and *T. indica*

Figs. 20-24. *Sphacelotheca occidentalis*. Transmission electron microscopy (Figs. 20-23) and scanning electron microscopy (Fig. 24). Fig. 20. Young spores in matrix material. Immature upper spore lacks spines. Remnants of hyphal walls (arrows) are found in the matrix. Bar = 1 μm. Fig. 21. Early stage of spine formation. Plasma membrane is depressed beneath developing spines (arrows) as they protrude into primary wall (P). Bar = 0.1 μm. Fig. 22. Two sizes of spines are visible on older spores. Bar = 5 μm. Fig. 23. Two continuous wall layers are found beneath the spines (S) in the mature spore; one appears similar to the spines in density (arrow) and the other is less dense (double arrows). Bar = 0.5 μm. Fig. 24. Remnants of the matrix are between spores. Large and small spines protrude through the primary spore walls. Bar = 5 μm.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(Roberson and Luttrell 1987). One notable difference was the origin of the primary wall within which the spines developed. In *T. indica* teliospores formed from the tips of sporogenous hyphae, and the primary wall of the spore was continuous with the wall of the parent hypha. In *S. occidentalis* teliospores formed from individual disarticulated hyphal cells. The primary wall thus was a product of the spore initial.

Sphacelotheca occidentalis can clearly be accommodated in *Sporisorium* as it is currently delimited (Vánky 1987). The sorus contains host elements that develop simultaneously with the sterile fungal elements and sporogenous hyphae.

ACKNOWLEDGEMENTS

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Distribution information reported here was compiled from herbarium records and from recent collections. We are especially grateful to Carl and Linda Kurtz, Mark Loeschke, Kay Niyo, and Judy Shearer for collections of smutted specimens. Thanks to Dr. G. Knaphus for field assistance.

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