

# Septoria Disease of Gramineae in Western United States

By  
RODERICK SPRAGUE



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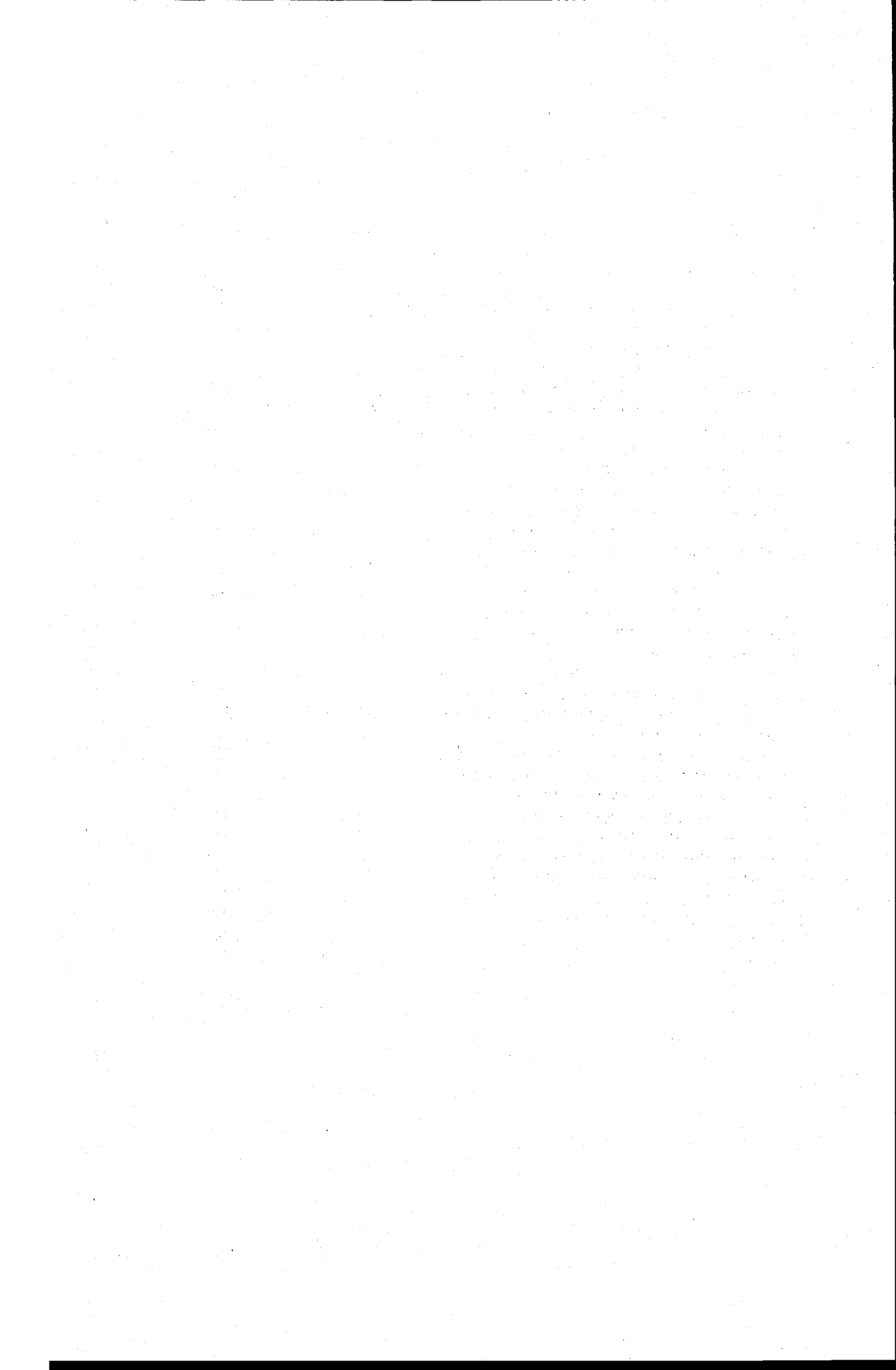
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# Septoria Disease of Gramineae in Western United States<sup>1</sup>

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## INTRODUCTION

It is the purpose of this paper to present the results of studies of the life history and taxonomy of the species of *Septoria* as they occur on Gramineae in Oregon and Washington, together with comparable data from certain other Western and Northern Great Plains States. While this study has been largely confined to the States of Oregon and Washington, some data are included for many of the species for most of the area west of the Mississippi River. Recent field observations (1940-43) have been made in certain of the Northern Great Plains States, particularly North Dakota, South Dakota, and Nebraska.

Species of *Septoria* attack 94 species of grains and grasses in the western United States. New information on these fungi is of special importance because of increasing interest in leaf- and glume-spot diseases of cereals and renewed need for information on related diseases of grasses.

## METHODS OF PROCEDURE

The following practices were employed for all species unless otherwise stated:

1. Several hundred collections of *Septoria* from the far West were assembled and studied in comparison with considerable foreign and domestic

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<sup>2</sup>The writer expresses his deepest appreciation for the aid and suggestions of his colleagues, particularly A. G. Johnson, in the preparation of this manuscript. He is indebted also to many others and especially to John A. Stevenson, Edith Cash, E. M. Wakefield, W. B. Cooke, George W. Fischer, H. Sydow, David H. Linder, Juan C. Lindquist, F. D. Bailey, and to the late J. J. Davis, for collections and data of invaluable help in furthering this study during the past 14 years.

material. In the Herbarium at Oregon State College, Corvallis, Oregon, there are at present a total of 591 collections from 26 states and 16 foreign countries and provinces.

2. Pure cultures (numbered with the prefix S) were obtained from 231 collections from Oregon, Washington, and California. These were grown on Difco potato dextrose agar and maintained at approximately 5° C.

3. Cross inoculation studies were made in the greenhouse and in the field by spraying plants, grown from seed, with pycnosporous suspensions obtained from pure cultures or from fresh host material. The inoculated plants were incubated in various ways, some in spray chambers, others in glass containers, and still others in glassine bags. Bell jars were satisfactory but large-size lamp chimneys (4-inch base) also were used. The results with glassine bags were erratic and, therefore, these bags were used only in the field during protracted rainy weather. The results from inoculations have not always been consistently satisfactory. The heaviest infection was obtained in December 1939 to March 1940 by incubating inoculated plants under moist cheesecloth out-of-doors for several days in rainy weather.

4. Camera lucida drawings from all available collections were made, to a scale of X2000, of pycnosporous mounted in water.

5. Photomicrographs (X170, X336, or X600) were made of many collections for comparison. Photographs of prepared slides of pycnosporous were not reliable as the shrinkage, particularly in the filiform spored species, produced noncomparable results.

6. Paraffin sections from material embedded either by the short dioxan method (69)<sup>1</sup> or by the butyl alcohol technique (122) were made of pycnidia from more than 450 collections.<sup>2</sup> Dried herbarium specimens were soaked in  $\frac{1}{2}$  per cent Aresket solution (detergent) for 30 minutes, then successively in 50 per cent dioxan, 100 per cent dioxan, changed once, then in dioxan 4 parts and xylol 1 part, vacuumed in soft paraffin and finally in hard paraffin (52° F.). Ehrlich's commercial haematoxylin was the most satisfactory stain, although Phloxine B in 80 per cent ethyl alcohol gave an excellent differential stain for the spores, the inner hymenial layer of the pycnidia, and the hyphae in the host tissue.

7. Camera lucida drawings of portions of cross sections of the pycnidial wall were made from the prepared slides, also X2000. Often the sections were made from old herbarium specimens and, therefore, were slightly shrunken, in most instances, in comparison with fresh material.

<sup>1</sup>Numbers in parentheses refer to Literature Cited, p. 135. gratefully acknowledged. Duplicate slides from this study are filed in the Mycological Collections, Bureau of Plant Industry, Soils, and Agricultural Engineering, U. S. Department of Agriculture, Beltsville, Md.

## THE GENUS SEPTORIA

Fries (44, p. 78) first used the name *Septaria* as follows: "A fusidio differt sporidiis cylindricis et septatis. Typus: *Sept. ulmi* (Stilbosp. Uredo. Decand.)". But since this was in 1819 and antedates the accepted date (1828) for Fungi Imperfecti of the International Rules of Botanical Nomenclature, this early description is not valid. Fries described *Septoria* in 1828 (45, pp. 117-118) as a genus with unilocular pycnidia and cylindrical, septate, hyaline spores, exuding in the form of irregular cirrhi. He listed *S. ulmi*, *S. oxyacanthae*, and *S. fraxini*. In 1829, Fries (46, p. 480) stated that *Septoria* had septate, fusiform, hyaline spores exuding in cirrhi from simple pycnidia. At this time he added *S. rosae* Desm. and *S. heraclei* Desm. The present concept of *Septoria* is largely based on the description as emended by Saccardo in 1884 (86, v. 3, p. 474). He considered *Septoria* to have erumpent pycnidia with septate or pluriguttulate, rarely eguttulate, bacillar or filiform hyaline pycnospores. Grove (54) detailed the popular conception of the genus as outlined by Saccardo.

Following Fries, Wallroth (115, p. 176) described *Phleospora*, which is generally considered to differ from *Septoria* Fries as emended by Saccardo, in having imperfectly formed pycnidia, which are thin-walled and lack a well-rounded top. The spores are fusiform-bacillar and two to many septate. Three of Fries' citations in *Septoria* have been transferred to *Phleospora*. They are *S. heraclei*, *S. ulmi*, and *S. oxyacanthae*. Diedicke (31) rejected *Phleospora*, which he considered only an intermediate genus between *Septoria* and *Cylindrosporium*. Maire (71, p. 125) proposed conserving *Phleospora* and rejecting *Septoria*. This sweeping destruction of a well recognized, if emended genus, would substitute a less recognized genus, which certainly would need a great deal of emending to make it replace *Septoria*. The most recent comprehensive discussion of the genus *Septoria* is by Wakefield (114). She recommends that *Septoria* Sacc. be conserved as distinct from *Septoria* Fr. (45), which was described as a nonpycnidial genus synonymous with *Phleospora* Wal. (115). She and the writer are, therefore, in agreement that the modern concept of the genus *Septoria* should be retained. The writer, therefore, follows this course and retains the genus *Septoria* as described by Saccardo.

*Phlyctaena* Desm. (as *Phlyctema*) (30) has subcutaneous erumpent pycnidia, which are subhysteroid and poorly constructed. Saccardo (86, v. 3, p. 593) states that the spores are elongate-fusoid to filiform. Bender (7) classifies the spores as falcate and the pycnidia as growing mostly on stems. Grove (54) states that the spores are filiform to elongate-fusoid and very

Plate 1. Photomicrographs of cross sections of pycnidia from prepared slides stained in Ehrlich's haematoxylin. (X170) A, *Septoria ammophilae*, type; B, *S. elymi-europaei* on *Elymus europaeus* collected by Jaap in Bavaria; C, *Diplodina lolii* Zimm., type. The pycnidia have thin walls as in most species of *Ascochyta*; D, *S. stipina* Died., type; E, *S. infuscans* on *Elymus triticoides*, Davis, California, 1939; F, *S. macropoda* var. *septulata* on *Poa compressa*, Rainier, Oregon, March 12, 1937 (O.S.C. 10,946); G, *S. poliomela* Sydow, type; H, *S. calamagrostidis* on *Trisetum canescens* Mehl Creek Road, Douglas County, Oregon, March 7, 1939; I, *Stagonospora* sp. on *Elymus virginicus*, Lansing, Michigan, 1900; J, *Septoria macropoda* var. *septulata*, same collection as in Plate 1, F, larger pycnidium; K, *S. tritici* var. *lolicola* on *Lolium perenne*, 6 miles north of Eugene, Oregon, March 7, 1939 (O.S.C. 449); L, *S. elymi* on *Agropyron repens*, Madison, Wisconsin; M, *S. jaculella* on *Bromus carinatus* near Eugene, Oregon, March 7, 1939; N, *S. elymi* on *Agropyron repens*, 6 miles north of Eugene, Oregon; O, *S. microspora* Ellis. Cross section of pycnidium (partly broken away at base); P, *Stagonospora arenaria* Sacc. on *Agropyron repens*, Delmoor Bog, Oregon, August 17, 1939 (O.S.C. 724).



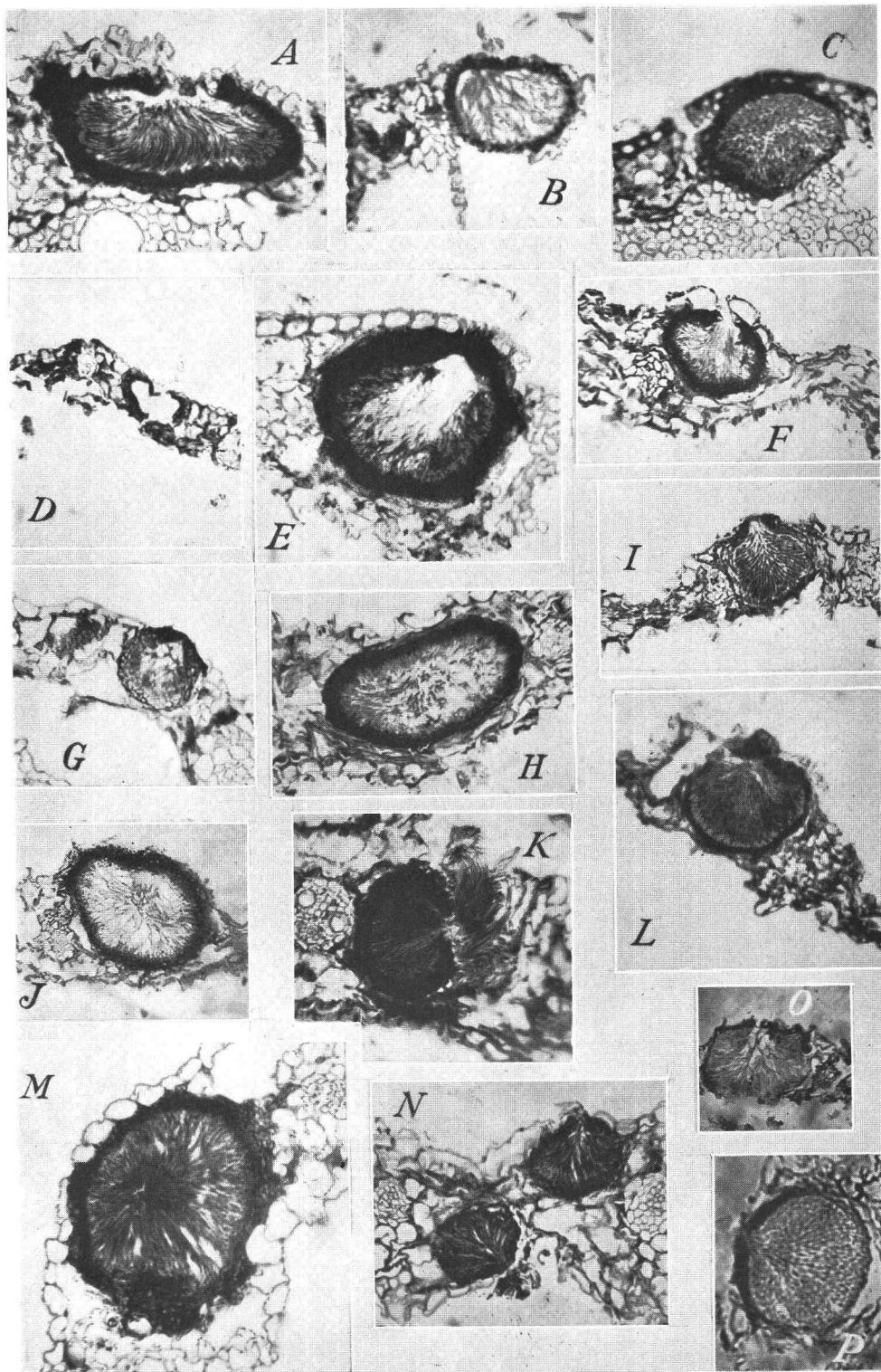
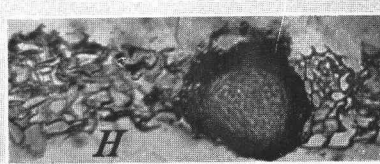
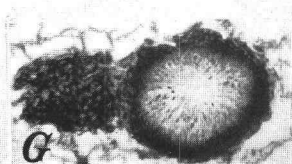
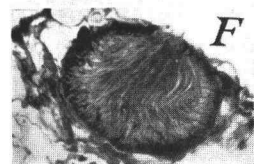
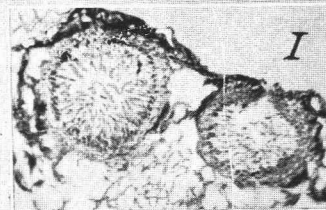
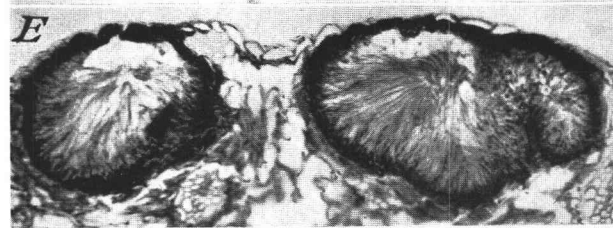
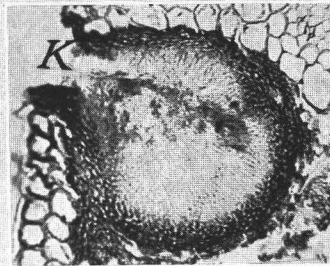
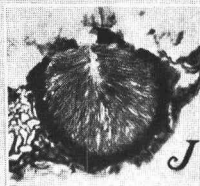
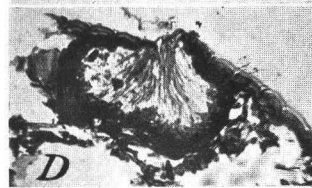
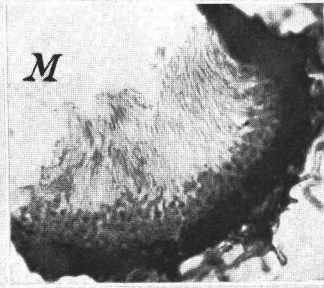
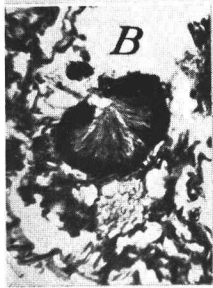
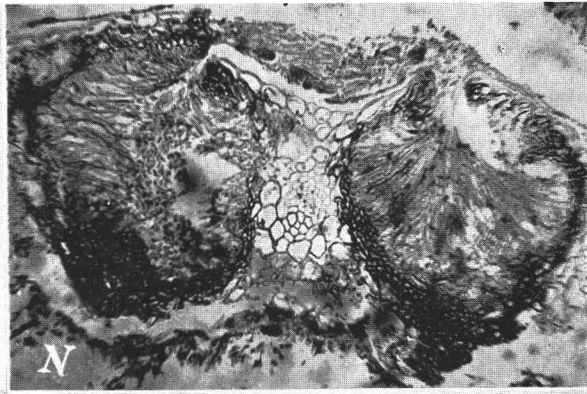
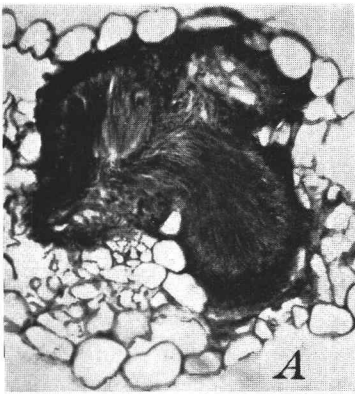


Plate 2. Photomicrographs of cross sections of pycnidia from prepared slides stained in Ehrlich's haematoxylon. (X170, except M, which is X600) A, *Septoria jaculella* on *Bromus rigidus* near Coburg, Oregon, March 7, 1939, showing chambered and ill-formed pycnidial walls in this collection; B, *S. passerinii* on *Sitanion hystrix*, Mt. Hood National Forest, Oregon; C, *S. calamagrostidis* f. *koeleriae* on *Koeleria cristata*, Corvallis, Oregon; D, *S. passerinii* on *Hordeum vulgare*, Corvallis, Oregon; E, *S. macropoda* var. *grandis* on *Poa nervosa*, Missoula, Montana; F, *S. tritici* f. *avenae* on *Avena sativa*, Eugene, Oregon; G, *S. jaculella* on *Bromus laevipes*, Heller. Microspore stage followed by prosenchymatous tissue; H, *S. elymi-europaei* Jaap, Obersdorf, Bavaria. Cross section of pycnidium with prosenchymatous material forming; I, *S. oude-mansii* on *Poa compressa*, Corvallis, Oregon, January 9, 1939; J, *S. bromi* Sacc. on *Bromus commutatus*, Lane County, Oregon (O.S.C. 251); K, *S. pacifica* on *Elymus mollis*, Newport, Oregon, December 15, 1937 (O.S.C. 36); L, *S. triseti* Speg. on *Agrostis tenuis*, Comstock, Oregon, March 7, 1939. Cross section of typical small pycnidium; M, *S. passerinii* on *Hordeum distichon*, Kiev area, Russia (X600), showing basal portion of microsporous pycnidium; N, *S. arctica* on *Calamagrostis nutkaensis*, Delmoor Bog, Oregon, August 7, 1939; O, *S. tritici* f. *holci* on *Holcus lanatus*, Corvallis, Oregon (O.S.C. 10,360); P, *S. infuscans* on *Elymus glaucus* (O.S.C. 8444); Q, *S. tritici* on wheat, Linn County, Oregon (O.S.C. 225), small pycnidium containing microspores.



narrow or hooked at the end. He transferred most of the British collections to *Phomopsis*. *Phlyctaena* does not appear to be of any importance in the present study.

In 1846, Durieu and Montagne (34, pp. 588-589) recognized three sections in the genus *Septoria*, namely: *Euseptoria* Dur. and Mont., *Ascospora* Fries, and *Rhabdospora* Dur. and Mont. The first had septate, subclavate spores, the second had cylindrical spores, and the third had filiform spores. Later, Castagne (18) recognized *Septoria*, *Ascospora*, and *Rhabdospora* as separate genera, which, with the exception of *Rhabdospora*, are universally recognized today. It appears that Durieu and Montagne's classification, which includes an ascomycetous genus, is too inaccurate to recognize even in part.

*Rhabdospora* Dur. and Mont. (34) includes species of *Septoria* growing on woody instead of herbaceous material. Grove retained the genus *Rhabdospora* (54) on the basis of a pseudoparenchymatous thick pycnidial peridium. Because of the herbaceous nature of the grasses under study, this genus has little, if any, place in the present investigations.

The scolecosporous or filiform-spored species of *Septoria* are generally recognized as typical for the genus. Most texts (19) segregate *Septoria*, in the *Scolecosporae*, from *Ascochyta* and *Stagonospora*, in the *Didymosporae* and *Phragmosporae*, by stating that the *Septoria* spores are narrow, not broad as in *Ascochyta* and *Stagonospora*. This is obviously unsatisfactory as everyone's idea of narrow versus broad is not alike. In addition, the species of *Stagonospora* described on Gramineae have particularly narrow spores. The writer studied the spore measurements given in literature of a large number of species of *Stagonospora*, *Ascochyta*, *Phyllosticta*, and *Septoria*. On nongramineous hosts, the typical, recognizable *Stagonospora* has more or less cylindrical spores that average from 3 to 8 times as long as broad, while those of *Septoria* generally average at least ten times as long as broad. The fungi on grasses, however, have been described so that it is necessary to seek the same fungus in *Septoria*, *Stagonospora*, or even *Ascochyta*. A number of *Stagonospora* species have been described with spores 8 to 10 or even 15 times as long as broad, while the same or a similar fungus under another name occurs in *Septoria*. It is suggested that all fungi in this group that have spores predominantly less than 10 times as long as broad should be placed in the genus *Stagonospora*, everything else being equal, while those with spores predominantly over 10 times as long as broad should be placed in the genus *Septoria*, if other characters fit. Those that range from 8 to 14 times as long as broad must be placed according to the judgment of the worker. The following characters tend to segregate the two genera:

1. *Stagonospora* usually has short, cylindrical or poorly developed pycnophores while those of *Septoria* are often well developed, ampulliform, subulate, or filiform.

2. The pycnidia of *Stagonospora* appear subtranslucent, golden, and thin-walled, under an oil immersion lens with critical illumination, while in *Septoria* they are more opaque, golden brown or darker, and wall thickness variable. (Plate 1, I.)

3. Pycnidia of *Stagonospora* tend to be more definitely erumpent and mammiform than those of *Septoria*.

4. In pure culture on potato dextrose agar, *Stagonospora* is typically cottony, while *Septoria* is usually yeasty (mucose) or variously carbonaceous, less often cottony, with scanty mycelia the rule.

5. To the naked eye, *Septoria* pycnidia usually appear as flattened, black, elliptical to circular specks while *Stagonospora* are often pale-brown and less prominently distinguished from the host tissue.

Recently Kirschstein (63, p. 138) describing *Septoria siegensis* Kirsch. on *Arrhenatherum elatius* (L.) Beauv. stated, "man sollte alle Arten auf Flecken lebender Blätter zu *Septoria* und alle andere hier in Frage kommenden zu *Stagonospora* stellen." This would place emphasis on pathogenicity and would, to some extent, segregate the large, cylindrical-spored species of *Stagonospora* found on dead leaves of certain grasses from the smaller, confusing species that are morphologically close to the genus *Septoria*. The difficulties of this means of segregation are obvious; there are still all stages of intermediates in size as well as in pathogenicity. The writer, therefore, prefers to follow the general suggestions above outlined.

The filiform-spored species of *Septoria* are fundamentally different from the cylindrical-spored species of *Stagonospora* or *Ascochyta*, but the two intergrade, and unfortunately, the intergrading is particularly acute in the complex on Gramineae. The writer continues to differentiate the convenient genera *Septoria*, *Ascochyta*, *Stagonospora*, and *Phyllosticta* although the last three are closely related with the general pycnidial morphology that Diedicke discussed for the *Hyalodidymae* (32).

Those species of sphaeropsidaceous fungi with falcate, nonseptate spores in small globose pycnidia such as *Septoria donacis* Pass., *S. culmifida* Lind (64, p. 276), and one-septate *S. curva* Karst. (62) are more properly placed in *Selenophoma* Maire (100) and, therefore, are not discussed in this paper.

## SEPTORIA Sacc.

Pycnidia subepidermal, slightly erumpent, in spots on leaves, sheaths and

stems; globose to lens-shaped, golden-brown to black, ostiolate, parenchymatous; outer layers of wall of one to several layers of polygonal brown cells, inner layers subhyaline to hyaline producing differentiated pycnophores from either creeping hyphae or more or less bulbous initials on the inner surface; pycnospores hyaline or chlorinous, elongate, 0- to multiseptate, predominantly at least ten times as long as broad, straight, sinuous, fusiform, scolecosporous or filiform. Typical isolation from pycnospores on potato dextrose agar is either a slimy (conidial) or scurfy (pycnidial) or subcottony colony.

### FACTORS USED IN THE DETERMINATION OF SPECIES AND THEIR SUBDIVISIONS

In differentiating species and their subdivisions, the following points were noted:

1. Pycnospores of most species of *Septoria* are larger with more septations in winter collections, in most cases, than in comparable collections made in the summer. Septations usually are 1, 3, and 7, depending on whether there were one, two, or three nuclear divisions in the spores. Some species, however, are characterized by 2-septate spores while 5-septate ones are common in others. In some species, the number of nuclear divisions evidently is dependent on the available cell nutrients; that is, large spores produced in humid winter weather may have two or even three nuclear divisions, while later in the season, when the weather is warmer and drier, the same species may produce aseptate or 1-septate spores.
2. Pycnidia collected in summer were usually more deeply imbedded in the host, darker, smaller, and more nearly spherical than the larger, flatter, and paler pycnidia grown in winter. The lesions formed in summer were more often delimited and less extensive than those formed in winter.
3. Consistent, slight, morphological variations, even with distinct host ranges, usually were considered as representing only taxonomic forms or, where limited to few obscure morphological factors, merely races.
4. The length/width ratio of the pycnospores was considered to be of taxonomic significance, and also the average length and width of pycnospores, if the collections were made under diverse ecological conditions and verified by pure culture studies.
5. Because of the specific pathogenicity requirements of many of the fungi, host range is given less importance than in works on more actively parasitic groups. A fungus that is limited to a single species of grass can be listed as a race of a morphologically identical fungus on another species of

grass, all things, including growth in pure culture, considered. There is a strong tendency today to reduce the number of species of fungi in an effort to simplify the taxonomy of the groups. This tendency is exemplified by Fischer's work on grass smuts (42).

6. Indications are that the host range of *Septoria* species tends to be limited somewhat to individual grass tribes. It is apparent, as suggested in the previous paragraph, that the species of *Septoria* must have evolved through their association with certain hosts, but more extensively physiologically than morphologically. The sharply delimited host range of certain races has tended to force workers into describing more species of *Septoria* than are morphologically or practically warranted. Garman and Stevens (47), among others, have pointed this out. Students of this group, however, must consider the fact that the family Gramineae is a vast and complicated one and the opportunity for variation in leaf spot fungi on these favorably situated hosts has been greater than in many other comparable groups of host plants. The close proximity of grasses to the moist soil and their tendency to grow in dense stands favoring high humidity are probably accountable for the complexity of species on these hosts.

7. Minor racial differences, including variations in pathogenicity, were noted but were not given critical considerations, as the difficulty of obtaining consistent infections with these parasites made comparable pathogenicity studies extremely unreliable under the conditions at Corvallis, Oregon. With improved technique, it is expected that further racial differences will become evident, particularly in those species attacking cultivated cereals and grasses.

8. Unless pure cultures were about the same age and freshness, comparable studies meant little. Such fungi as *Septoria tritici* Rob. produced yeasty colonies in a number of consecutive transfers after isolation, but eventually developed carbonaceous mycelia and finally "staled" to a pale pink or white cottony growth with little or no production of conidia. Some cultures retained their vigor after as long as 6 years on potato dextrose agar, while others had to be discarded much sooner. "Staling" is possibly associated with the dual phenomenon in imperfect fungi discussed by Hansen (55).

### SEPTORIA TRITICI Rob.

In the Pacific northwest, *Septoria tritici* Rob. causes a common speckled leaf spot or blotch on wheat emmer, spelt, and pollard wheat in Oregon and on wheat in Washington, California, Idaho, and Montana. *S. tritici* f. *avenae* (Desm.) comb. nov. occurs on species of oats, *S. tritici* Rob. var. *lolicola* Sprague and A. G. Johnson var. nov. on English rye grass (*Lolium perenne*

L.) and western rye grass (*L. multiflorum* Lam.) in Oregon, and *S. tritici* f. *holci* form. nov. on velvet grass (*Holcus lanatus* L.). These species are discussed separately as follows.

### SEPTORIA TRITICI Rob. on TRITICUM Spp.

Despite the work of Beach (6) and of Weber (117), who showed that *Septoria tritici* was the cause of *Septoria* leaf blotch of wheat in the United States, there persists the belief, which has been developed by such texts as Cooke (23), that there are several species of *Septoria* with filiiform spores on wheat, particularly *S. graminum* Desm. (29) and *S. tritici* Rob. (28), the former having narrower spores than the latter.

#### GEOGRAPHICAL DISTRIBUTION AND ECONOMIC IMPORTANCE IN THE WESTERN UNITED STATES

*Septoria tritici* is particularly common on wheat in western and intra-mountain Oregon and Washington. After the winter snows leave the fields in portions of the Columbia Gorge, the wheat leaf rosettes show almost 100 per cent infection. Later, when warm, dry weather prevails, the new growth is free from the leaf spot. The fungus unquestionably retards the plants and is more detrimental than most observers suspect.

In western Oregon proper, *Septoria tritici* on wheat is very destructive during open winters. It was particularly so during the frost-free winter of 1933-34. In February 1939, fields were examined in which 100 per cent of plants and 98 per cent of the leaves were infected, while 60 per cent of the leaf surface was killed. Suneson<sup>1</sup> reported *S. tritici* as common and destructive following the exceptionally moist winter at Davis, California, in 1938. The writer collected *S. tritici* on wheat in a number of counties in California in May 1939. It was common in Yolo, Yuba, Sutter, and Solano counties, but injury was confined to the early season. The warm, dry weather after February completely checked the disease except in irrigated fields. The injury in the western part of Oregon and Washington is not confined to late winter attacks. The first attack sometimes is followed by late season injury during rains in May and June. This late season injury results in lesions not only on the leaves but on the sheaths and even on the heads of the plants. The late season and midseason spread is correlated with abundant precipitation. During dry periods, injury by *S. tritici* diminishes and affected leaves wither and die.

<sup>1</sup>Suneson, C. A. U. S. Department of Agriculture, Bureau of Plant Industries, Plant Dis. Rptr. 22: 181. 1938. (Mimeographed.)



In eastern Oregon, wheat is moderately injured by *Septoria tritici* in Umatilla County, and the disease has been found west of Pendleton in a region having possibly only 12 inches average annual precipitation. Moderate amounts occur in the Grande Ronde Valley, Union County. Central Oregon and Washington are almost free from *S. tritici* during average years, while it is apparently not abundant in the Palouse region. Schade<sup>1</sup> reported one collection from Moscow, Idaho, made by Willis in 1919. Collections from the vicinity of Bozeman, Montana, indicate that winter wheat is moderately attacked early in the season. The disease was extremely rare on spring wheat in the Northern Great Plains in 1940-42.

Infection of spelt (*Triticum spelta* L.) was noted in plots in Lincoln County, Oregon, in 1934 and 1935. Vernal and Khapli emmer (*T. dicoccum* var. *farrum* Bayle) were parasitized in field plots in Benton County, Oregon, in 1937, and Alaska wheat (*T. turgidum* L.) showed some leaf spotting in June 1936, at Granger, Oregon.

The disease appears to be most serious on the earlier maturing varieties. Johnston<sup>2</sup> found that Kawvale was particularly susceptible in southeastern Kansas. He states that "most of the soft red winter varieties were also heavily infected while the leaves of hard red winters showed fewer brown lesions."

#### PURE CULTURE AND ARTIFICIAL INOCULATIONS

Thirty isolations were made from wheat collected in western, eastern, and southern Oregon, adjacent southern Washington, northern California, Denmark, and Morocco.

In their early stages of growth (5° C.), the colonies produced pale, flesh-colored mucose or "yeasty" masses of conidia and germinating conidia. None of the cultures varied to any extent from the others. After several months or sometimes years, the colonies showed wide variations owing to differences in amount of "staling." The colonies on transfers from fresh conidia go through several stages of development in culture:

1. Minute, pin point white colonies of stellately radiating mycelia (10 to 20 days).
2. Pale, flesh-colored, glistening, disciform colonies resembling colonies of yeast on potato dextrose agar (15 to 30 days).
3. Carbonization with olive gray or black stroma covering colony (25 to 40 days).

<sup>1</sup>Schade, Arthur L. A preliminary list of the parasitic fungi of Idaho. U. S. Department of Agriculture, Bureau of Plant Industries, Plant Dis. Rptr. Suppl. 95: 77-113, 1936. (Mimeographed.)

<sup>2</sup>Report of June 10, 1939, of C. O. Johnston, Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

4. Felty olive, gray, or black mycelia (25 to 30 days).
5. Tufts of gray, mottled, or even white or pink aerial-hyphae (30 to 60 days) "staling" to slow growing subcottony, nonsporulating colonies after several years in cultures transferred quarterly.

There is usually considerable so-called saltation in the older "staling" cultures and one might conclude by study of cultures that have been repeatedly transferred for a period of years that the worker was dealing with a complex of races or strains. Given cultures of virtually the same history, there is no racial difference that is outstanding in any of the thirty cultures seen. Luthra, Sattar, and Ghani (68) found that a collection of *Septoria tritici* from India grew more slowly than one obtained from the Centralbureau v. Schimmelkultures (Baarn, Netherlands). The culture from the Netherlands was possibly somewhat older as indicated from its white color.

Inoculation trials were conducted from 1930 to 1939 in the greenhouse or in the field at Corvallis, Oregon, with both conidia from pure culture or pycnosporos from viable field material. The summarized results, shown in Table 1, are included with those obtained with *Septoria tritici* isolated from hosts other than wheat and with *S. macropoda* and varieties from *Poa* spp.

Tests were run mostly during the months of December to April in a cool, unheated greenhouse or outside in a partly shaded, cool location.

*Septoria tritici* attacked Golden, Hybrid 128, and Kharkov wheat about equally, and Holland somewhat less. In one case, it caused speckling on *Poa pratensis* L. and on *P. annua* L. It is of special interest that slight infection was obtained on *P. secunda* Presl. Infections were obtained also on spelt, which agrees with the results obtained by Weber (117). The results obtained with the other fungi will be discussed later. *Septoria tritici* failed to infect a large number of grass hosts.

#### MORPHOLOGY

**PYCNIDIA.** The pycnidia are golden brown, substomatal, ostiolate, usually distinctly flattened, ellipsoid, and have thin walls. They are from 60 to 200  $\mu$  in diameter, averaging usually 100-150  $\mu$ . The walls are composed of several (2-5) outer layers of golden brown, oblong, box-shaped, thin-walled cells, then 1 to 4 intermediate layers of polyhedral compacted cells, and inside this is a thinner area of hyaline tissue that gives rise to narrowly ampulliform pycnophores. Grove (54, p. 422; 53, p. 210) lists *Septoria graminum* Desm. var. *crassipes* Grove on leaves of wheat and states that this variety has short ampulliform cuspidate sporophores measuring 10-13 x 2.5-3  $\mu$ . The illustrations of Grove (53) indicate that he had the same fungus as the one

on wheat in the western United States. The specimens of *S. tritici* have flask-shaped to almost cylindrical pycnophores measuring 5-13 x 1.3-3  $\mu$  (Figure 1, B, C, D, F, G, L, N).

**PYCNOSPORES.** *Septoria tritici* has two kinds of pycnospores: macrospores and microspores, sometimes found in the same pycnidium.

The macrospores are those most commonly observed. A large number of collections have been examined for the morphology of the macrospores (Figure 1, A, B, H, I, J, M). Those studied include all of *S. tritici* in the general collections in the Mycological Collections, Bureau of Plant Industry, U. S. Department of Agriculture, those sent by the late J. J. Davis from the University of Wisconsin, as well as about 60 collections made in the Pacific Northwest, and scattering ones from Europe, one from Chile, and one from Morocco (Malençon).

The spores were found to vary considerably in size, depending on the humidity and temperature at the time of their development. The winter spores are longer than the summer spores, which agrees, in general, with the findings of Beach (6) and Weber (117). Spores collected in rainy weather in July in the Willamette Valley are only moderately dwarfed (Figure 1, H, J), but collections made by P. A. Young in Montana and at Mt. Vernon, Washington, in late spring have appreciably smaller spores. The specimen that was kindly sent by air mail from Rabat Maroc (Morocco) by G. Malençon had relatively short, blunt spores (Figure 1, M) for *S. tritici*, 33-60 x 1.6-2.3  $\mu$  (mean size 47 x 2.0  $\mu$ ). The small size was probably due to low relative humidity. Spore measurements from representative collections in the western states are given in Table 2.

The microspores are hyaline, curved or hooked, aseptate, 5-9 x 0.3-1  $\mu$  (Figure 1, A, K, N). The minute microspores can be mistaken for bacteria and are probably more widespread than literature indicates. In certain small pycnidia (Plate 2, Q), which measure 45-50  $\mu$  in diameter, the microspores are produced almost or completely to the exclusion of macrospores. In slightly larger pycnidia (55-70 x 60-80  $\mu$ ) macrospores are intermingled with the microspores. In stained sections of pycnidia, the microspores are commonly arranged in rows as if they had been produced in chains from the ampulliform pycnophores. They may be produced also on the tips of abortive macrospores (Figure 1, N). Microspores have been collected in Oregon both on wheat, *Triticum aestivum* L., and on Vernal and Khapli emmer, *Triticum dicoccum* var. *farrum*.

#### TAXONOMY

The writer (95) has recently pointed out that *Septoria graminum* Desm. is a species apparently confined to *Brachypodium* spp. and is quite distinct

Table 1. SUMMARIZED RESULTS FROM INOCULATING *Septoria tritici* AND *S. macropoda* ON VARIOUS GRASSES

Plants inoculated	Number of leaves infected (+) or not infected (—) by —									
	<i>S. macropoda</i>		<i>S. macropoda</i> var. <i>septulata</i>		<i>S. macropoda</i> var. <i>grandis</i>		<i>S. tritici</i>	<i>S. tritici</i> f. <i>avenae</i>	<i>S. tritici</i> f. <i>holci</i>	<i>S. tritici</i> var. <i>lolicola</i>
	Isolated from <i>Poa annua</i> <sup>1</sup>		Isolated from <i>Poa pratensis</i> <sup>2</sup>		Isolated from <i>Poa ampla</i> <sup>1</sup>	Isolated from <i>Poa secunda</i> <sup>2</sup>	Isolated from <i>Triticum aestivum</i> <sup>4</sup>	Isolated from <i>Avena sativa</i> <sup>1</sup>	Isolated from <i>Holcus lanatus</i> <sup>5</sup>	Isolated from <i>Lolium</i> spp. <sup>5</sup>
	(+) (—)		(+) (—)		(+) (—)	(+) (—)	(+) (—)	(+) (—)	(+) (—)	(+) (—)
<i>Agropyron cristatum</i> .....	—	—	—	—	—	—	—	—	0 97	0 72
<i>Agrostis alba</i> .....	0 62	0 150	0 120	—	0 100	0 160	—	—	0 216	0 140
<i>A. palustris</i> .....	0 139	0 635	—	0 100	0 450	0 400	0 100	—	0 1,150	—
<i>A. tenuis</i> .....	0 95	0 715	0 45	—	0 452	0 480	—	—	0 860	0 200
<i>Arrhenatherum elatius</i> .....	—	0 95	—	—	0 88	0 228	—	—	0 175	—
<i>Avena byzantina</i> .....	0 95	0 40	—	0 38	0 40	0 162	—	—	0 250	0 100
<i>A. sativa</i> .....	0 82	0 98	0 70	0 22	0 30	0 589	85 410	—	0 345	0 140
<i>Brachypodium mucronatum</i> .....	—	0 35	0 50	—	0 32	0 207	—	—	0 78	0 90
<i>B. pinnatum</i> .....	0 67	0 172	—	0 60	0 40	0 140	0 60	—	0 65	0 86
<i>B. ramosum</i> .....	—	0 55	0 168	—	0 86	0 119	—	—	0 105	0 72
<i>Bromus carinatus</i> .....	0 42	0 510	—	—	0 95	—	0 85	—	0 293	0 78
<i>B. inermis</i> .....	—	0 60	—	—	—	0 60	—	—	0 139	—
<i>B. mollis</i> .....	—	—	—	—	—	—	—	—	0 65	—
<i>B. rigidus</i> .....	0 31	0 70	0 68	0 45	—	—	0 35	—	0 50	—
<i>Calamagrostis nutkaensis</i> .....	—	—	—	—	—	—	—	—	0 241	0 31
<i>Cynodon dactylon</i> .....	—	0 40	0 40	—	—	0 157	—	—	0 60	—
<i>Dactylis glomerata</i> .....	—	0 100	—	—	0 50	0 48	0 50	—	0 205	0 39
<i>Danthonia californica</i> .....	0 29	0 37	0 16	0 50	—	0 45	0 130	—	0 50	0 20
<i>Deschampsia caespitosa</i> .....	—	0 80	—	—	—	—	—	—	0 30	—
<i>Elymus glaucus</i> .....	—	—	—	—	—	0 61	0 35	—	0 50	0 46
<i>Festuca idahoensis</i> .....	—	0 475	—	—	—	0 63	0 70	—	0 100	—
<i>F. myuros</i> .....	0 70	0 280	0 35	0 40	0 30	0 19	—	—	0 50	0 30
<i>F. ovina</i> .....	—	0 95	0 70	—	0 58	0 200	—	—	0 70	0 60
<i>F. rubra</i> .....	—	0 160	—	—	0 130	0 419	—	—	0 395	0 130
<i>F. rubra</i> var. <i>commutata</i> .....	—	0 580	0 80	0 250	0 65	0 305	0 45	—	0 1,205	0 110

Table 1. SUMMARIZED RESULTS FROM INOCULATING *Septoria tritici* AND *S. macropoda* ON VARIOUS GRASSES—Continued

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Plants inoculated	Number of leaves infected (+) or not infected (—) by —																	
	<i>S. macro-poda</i>		<i>S. macropoda</i> var. <i>grandis</i>		<i>S. macropoda</i> var. <i>septulata</i>		<i>S. tritici</i>	<i>S. tritici</i> f. <i>avenae</i>	<i>S. tritici</i> f. <i>holci</i>	<i>S. tritici</i> var. <i>lolicola</i>								
	Isolated from <i>Poa annua</i> <sup>1</sup>		Isolated from <i>Poa pratensis</i> <sup>2</sup>	Isolated from <i>Poa compressa</i> <sup>1</sup>	Isolated from <i>Poa ampla</i> <sup>1</sup>	Isolated from <i>Poa secunda</i> <sup>3</sup>	Isolated from <i>Triticum aestivum</i> <sup>4</sup>	Isolated from <i>Avena sativa</i> <sup>1</sup>	Isolated from <i>Holcus lanatus</i> <sup>5</sup>	Isolated from <i>Lolium</i> spp. <sup>5</sup>								
	(+)	(—)	(+)	(—)	(+)	(—)	(+)	(—)	(+)	(—)	(+)	(—)						
<i>F. rubra</i> var. <i>heterophylla</i> .....	0	65	0	190	.....	.....	0	65	0	257	0	190	0	65				
<i>F. tenuifolia</i> .....	.....	.....	0	185	0	110	0	65	0	129	0	71	0	40	0	22		
<i>Holcus lanatus</i> .....	0	45	0	190	0	35	0	58	0	265	0	601	0	290	765	1,815	0	416
<i>Hordeum vulgare</i> .....	0	60	0	65	0	150	.....	.....	0	59	0	131	.....	.....	0	275	0	120
<i>Koeleria cristata</i> .....	.....	.....	0	603	.....	.....	0	25	0	50	0	302	.....	.....	0	140	.....	.....
<i>Lolium multiflorum</i> .....	.....	.....	0	70	0	60	0	38	0	225	.....	0	95	0	166	49	314	.....
<i>L. perenne</i> .....	0	58	0	295	0	75	.....	.....	0	160	0	533	0	120	0	70	57	291
<i>Phalaris arundinacea</i> .....	.....	.....	0	38	.....	.....	.....	.....	0	69	.....	0	120	.....	0	65	0	35
<i>P. bulbosa</i> .....	.....	.....	.....	.....	.....	.....	.....	.....	0	87	0	169	.....	.....	0	145	0	65
<i>Phleum pratense</i> .....	.....	.....	0	90	.....	.....	0	50	0	263	0	145	.....	.....	0	35	.....	.....
<i>Poa ampla</i> .....	.....	.....	0	374	0	60	7	40	0	140	0	298	.....	.....	0	90	.....	.....
<i>P. annua</i> .....	40	128	148	745	.....	.....	0	40	0	357	0	441	0	185	0	340	.....	.....
<i>P. compressa</i> .....	0	63	7	580	19	235	0	90	0	260	0	281	.....	.....	0	15	.....	.....
<i>P. juncifolia</i> .....	0	19	0	65	.....	.....	0	45	16	214	0	59	.....	.....	0	510	0	70
<i>P. nemoralis</i> .....	.....	.....	0	740	0	200	0	80	0	426	0	57	.....	.....	0	120	.....	.....
<i>P. nevadensis</i> .....	.....	.....	0	570	0	95	0	45	0	15	0	413	.....	.....	0	959	0	349
<i>P. pratensis</i> .....	0	260	405	1,256	.....	.....	0	100	0	293	0	654	0	315	0	30	.....	.....
<i>P. scabrella</i> .....	.....	.....	0	30	.....	.....	0	35	.....	.....	6	263	.....	.....	.....	.....	.....	.....
<i>P. secunda</i> .....	.....	.....	0	385	.....	.....	0	50	158	485	5	42	.....	.....	0	20	.....	.....
<i>P. trivialis</i> .....	0	225	0	1,048	.....	.....	0	120	0	350	0	600	0	150	0	875	0	65
<i>P. vaseyochloa</i> .....	.....	.....	0	38	.....	.....	0	30	0	140	0	30	.....	.....	.....	.....	.....	.....
<i>Polypogon monspeliensis</i> .....	.....	.....	.....	.....	0	22	.....	.....	0	79	0	70	.....	.....	0	60	.....	.....
<i>Secale cereale</i> .....	.....	.....	0	38	0	80	.....	.....	0	70	0	135	.....	.....	0	75	.....	.....
<i>Triticum aestivum</i> .....	0	88	0	275	0	95	.....	.....	0	285	180	561	0	340	0	685	0	365
<i>T. spelta</i> .....	.....	.....	.....	.....	0	32	.....	.....	0	218	36	325	0	65	0	180	0	48

<sup>1</sup>=one isolation; <sup>2</sup>=five isolations; <sup>3</sup>=three isolations; <sup>4</sup>=six isolations; <sup>5</sup>=two isolations; <sup>6</sup> flecking only, no sporulation, on a small percentage of the leaves.

Figure 1. *Septoria tritici* (except E and G): A, Microspore and macrospore stage on wheat collected by C. A. Suneson, 40 miles south of Davis, California, April 21, 1938; B, cross section of pycnidial wall and pycnosporos, on wheat near Warwick, Washington, March 9, 1938 (O.S.C. 134); C, cross section of pycnidial wall on wheat from Denmark collected by Ernst Gram; D, cross section of pycnidial wall, on wheat, Pendleton, Oregon (O.S.C. 10,362); E, cross section of pycnidial wall of *Septoria tritici* f. *avenae* on *Avena sativa*, Astoria, Oregon, (O.S.C. 133); F, cross section of pycnidial wall, on spring-sown wheat, Benton County, Oregon, July 10, 1937 (O.S.C. 8344); G, cross section of pycnidium from type of *S. neglecta* Sacc.; H, pycnosporos from spring-sown wheat, Benton County, Oregon, July 10, 1937 (O.S.C. 8344); I, pycnosporos from wheat, Granger, Oregon, December 8, 1937; J, pycnosporos, and K, microspores from Khapli emmer (*Triticum dicoccum* var. *farrum*), Benton County, Oregon, June 1936 (O.S.C. 8397); L, cross section of pycnidial wall on wheat, Friend, Oregon (O.S.C. 985); M, pycnosporos from wheat from Rabat, Morocco, collected by G. Malençon, April 26, 1939; N, microspores, young macrospores, and pycnophores from cross section of pycnidium on wheat, East Farm, Linn County, Oregon, March 25, 1938 (O.S.C. 225). (All X1000)

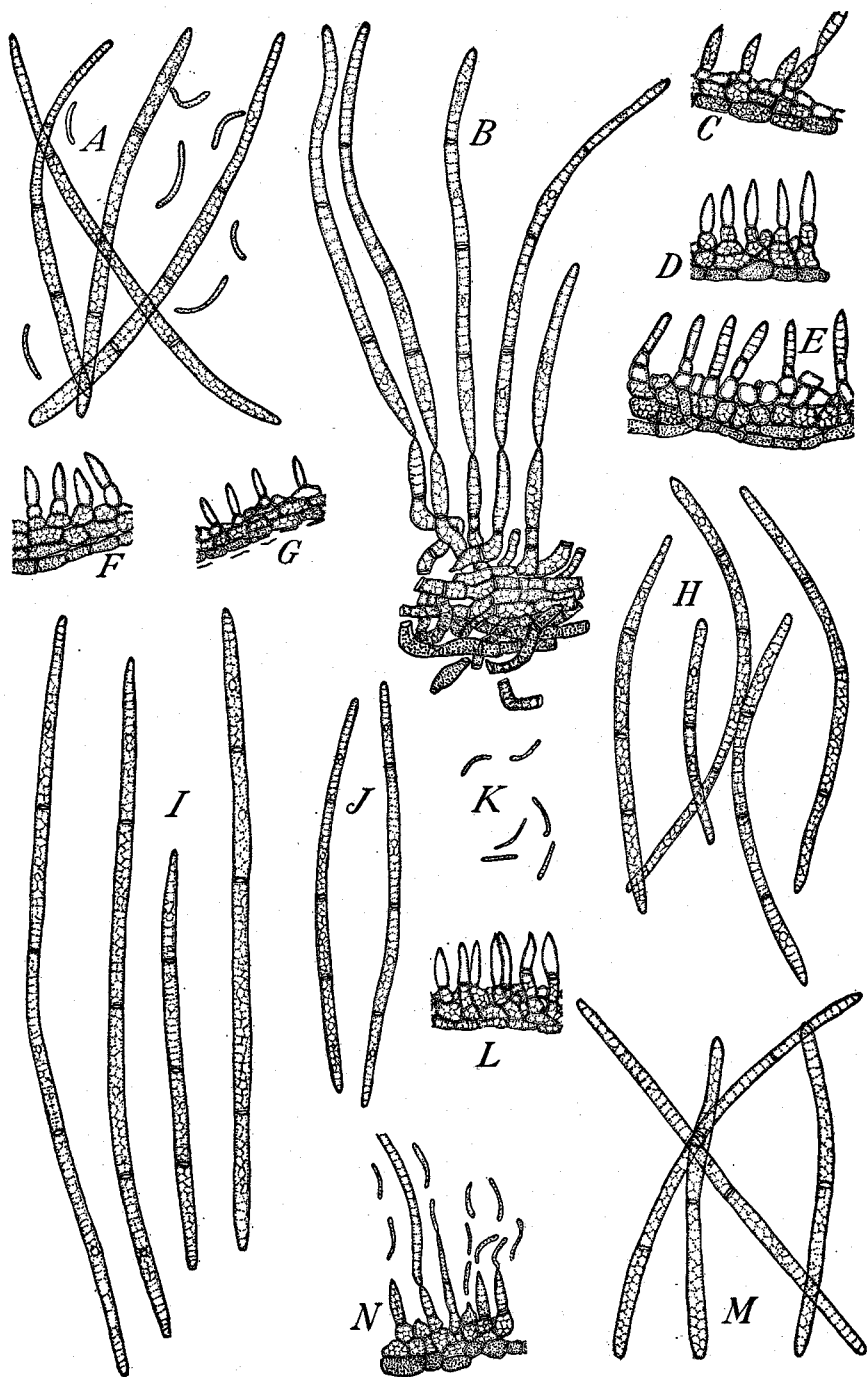


Table 2. DIMENSIONS OF MACROSPORES FROM DIFFERENT COLLECTIONS OF SEPTORIA TRITICI ON TRITICUM SPP. IN THE WESTERN UNITED STATES

Host	Location	Collector and number	Date collected	Spore dimensions $\mu$
Wheat: ( <i>Triticum aestivum</i> )....	Granger, Oreg.	Sprague, O.S.C. 8499	Dec. 8, 1937	50-98 x 1.8-2.2
<i>Triticum aestivum</i> .....	10 mi. west of Pendleton, Oreg.	Sprague, O.S.C. 125	Mar. 10, 1938	60-89 x 1.9-2.5
<i>Triticum aestivum</i> .....	High Prairie, Wash.	Sprague, O.S.C. 444	Mar. 14, 1939	45-80 x 1.7-2.4
<i>Triticum aestivum</i> .....	Warwick, Wash.	Sprague, O.S.C. 438	Mar. 14, 1939	55-98 x 2.1-2.6
<i>Triticum aestivum</i> .....	Pendleton, Oreg.	Sprague, O.S.C. 10,362	Mar. 14, 1935	53-60 x 1.6-2.0
<i>Triticum aestivum</i> .....	Forest Grove, Oreg.	Sprague, O.S.C. 439	Mar. 15, 1939	44-82 x 1.8-2.4
<i>Triticum aestivum</i> .....	High Prairie, Wash.	Sprague, O.S.C. 46	Mar. 24, 1931	33-60 x 1.4-2.0
<i>Triticum aestivum</i> .....	East Farm, Linn Co., Oreg.	Sprague, O.S.C. 160	Mar. 26, 1938	42-80 x 2.0-2.3
<i>Triticum aestivum</i> .....	Medford, Oreg.	R. W. Fowler, O.S.C. 166	Apr. 18, 1938	50-91 x 1.7-2.1
<i>Triticum aestivum</i> .....	Davis, Calif.	C. A. Suneson, O.S.C. 183	Apr. 21, 1938	51-67 x 1.8-2.1
<i>Triticum aestivum</i> .....	Bozeman, Mont.	P. A. Young, Mont., 111,486	Apr. 28, 1933	60-73 x 1.7-2.0
<i>Triticum aestivum</i> .....	S. Fork, Alsea River, Oreg.	Sprague, O.S.C. 191	May 7, 1938	58-89 x 1.8-2.1
<i>Triticum aestivum</i> .....	6 mi. south of Monroe, Oreg.	Sprague, O.S.C. 195	May 10, 1938	51-69 x 1.6-2.0
<i>Triticum aestivum</i> .....	7 mi. west of Dallas, Oreg.	Sprague, O.S.C. 727	May 12, 1939	47-88 x 1.8-2.3
<i>Triticum aestivum</i> .....	Spring Hill, Mont.	P. A. Young, Mont., 113,245	June 15, 1938	22-56 x 1.4-1.8
<i>Triticum aestivum</i> .....	Mt. Vernon, Wash.	P. A. Young, Mont., 111,485	June 26, 1938	24-58 x 1.5-2.0
<i>Triticum aestivum</i> .....	South Benton Co., Oreg.	Sprague, O.S.C. 8344	July 10, 1937	48-65 x 1.8-2.3
Spelt: ( <i>Triticum spelta</i> ) .....	Alsea Valley, Oreg.	Sprague, O.S.C. 10,365	Feb. 20, 1935	42-67 x 1.7-2.8
Khapli emmer: ( <i>Triticum dicoccum</i> var. <i>farrum</i> ) .....	Benton Co., Oreg.	Sprague, O.S.C. 8379	July 13, 1937	48-64 x 1.4-1.7
Alaska wheat: ( <i>Triticum turgidum</i> ) .....	Granger, Oreg.	Sprague, O.S.C. 10,680	June 10, 1936	36-84 x 1.8-2.8



from *S. tritici*. Weber strongly contended that *S. tritici* was the common scolecosporous species on wheat in Wisconsin (117). While the spores from collections in the Pacific Northwest average somewhat narrower than the measurements given by Weber, the writer has concluded that all material of *Septoria* on *Triticum aestivum* that has filiform or scolecosporous pycnospores belongs in *S. tritici* with the possible exception of *S. triticina* Lobik and *S. triticicola* Lobik (67), which are not available for comparison. Differences in spore width apparently are due to environmental conditions. *S. triticicola* Lobik has spores  $26.3-48.3 \times 3.3-3.9 \mu$  and *S. triticina* Lobik  $36.2-55.9 \times 3.3-3.6 \mu$ . They appear to be different from *S. tritici*. *Septoria neglecta* Sacc. (87, p. 18) on wheat has continuous, straight to slightly curved spores, borne on small pycnophores (Figure 1, G), which approach those of *S. tenella* Cke and Ell., on *Festuca*, but from the small delimited lesions, the season that they were collected (July 20), and the small size of the pycnidia, the writer believes that *S. neglecta* is only a stunted summer condition of *S. tritici*. *Septoria nymantina* Sacc. (88, p. 563) on wheat represents a similar collection.

In 1916, Grove (53, p. 210) described and illustrated "*Cytospora*" spores on ampulliform pycnophores of *Septoria graminum* Desm. var. *crassipes* Grove on wheat from Australia. The microspores were  $8-10 \times 0.75 \mu$ . These spores undoubtedly are the microspores of *S. tritici*. They agree perfectly with the microspores from collections on wheat and emmer made in Oregon. Whether the presence of microspores indicates any morphological, sexual, or racial differences is not known.

Grove (53, p. 210) stated that *Septoria graminum* var. *crassipes*, which also has macrospores  $50-65 \times 1.5-2 \mu$ , is similar to *S. macropoda* Pass. and *S. littoralis* Speg., on certain grasses, and that the spores but not the sporophores are the same as those of *S. briosiana* Mor. described on wheat. The presence of bulbous or ampulliform pycnophores is not unusual in species of *Septoria* on Gramineae; in fact, this kind appears to be the most common one encountered.

*Septoria briosiana* Mor. (73, p. 39) has the microspores ( $9-11 \times 0.5-0.75 \mu$ ) borne on very elongate "basidia"  $32-40 \times 1.5-2 \mu$ . It is believed that the microspores in these cases are borne on abortive macrospores, which have assumed a pycnophorous nature due to abnormalities of humidity, temperature, or food relations.

*Septoria diedickeana* Baudys et Picb. (4) on wheat leaves has spores  $35-50 \times 1.5 \mu$  and they are 1- to 3-, rarely 5-septate. As illustrated, they resemble *S. elymi*. They are referable to *S. tritici* until it is shown that *S. elymi* actually occurs on *Triticum* in which case *S. diedickeana* could be assigned to *S. elymi*.

The synonymy of *Septoria tritici* Rob. is as follows: *Septoria tritici* Rob. 1842 (28).

- Syn.: *S. graminum* var. *b. tritici* Desm., 1847 (30).  
*S. tritici* Rob. f. *tritici-vulgaris* Thuem., 1876<sup>1</sup>.  
*S. cerealis* Pass. f. *tritici-vulgaris* Thuem., 1878<sup>2</sup>.  
*S. tritici* Thuem., 1879 (fide Pass. 77, p. 46).  
*S. graminum* Desm. f. *tritici-vulgaris* Thuem., 1880<sup>3</sup>.  
*S. briosiana* Mor., 1886 (73).  
*S. neglecta* Sacc., 1913 (non *S. neglecta* Earle, 1897 (87)).  
*S. nymanina* Sacc., 1913 (88).  
*S. graminum* Desm. var. *crassipes* Grove, 1916 (53).  
*S. diedickeana* Baudys et Pich. 1924 (4).  
*S. triticina* Unamuno, 1930 (110).

The writer credits *S. tritici* Rob., not to Desmazieres, who published the description (28), but to Roberge to whom Desmazieres credits the description. Literature almost unanimously credits the latter, but reference to the original description shows that Roberge is the authority.

## SEPTORIA TRITICI Rob. on AEGILOPS CYLINDRICA

Shrunk herbarium material of *Septoria tritici* was found on a mounted sheet of *Aegilops cylindrica* Host. collected for George S. Hammond at Budapest, Hungary, in June 1881. While this fungus has not been reported on this host from the west, it is mentioned here because *A. cylindrica* is an escape in certain western areas and is used in cross breeding with wheat.

The material from Hungary showed bluish-hyaline, shrunk spores 34-45 x 0.9-1.3  $\mu$ , but they were so badly collapsed that it is believed that they were wider than this originally. The pycnidia were 60-120  $\mu$  in diameter and 50-96  $\mu$  deep, strongly flattened, wall 5-12  $\mu$  thick with the outer brown layer distinctly crushed. The inner layers consist of hyaline cubical to globose cells giving rise to narrowly subulate or cylindrical pycnophores that measured 1-1.5  $\mu$  wide and 4  $\mu$  high.

The fungus is apparently stunted material of *Septoria tritici* Rob.

## SEPTORIA TRITICI Rob. f. AVENAE (Desm.) Comb. Nov.

In earlier studies, the writer (94) concluded that this was a physiologic race of *Septoria tritici* strictly confined to oats. Additional material has per-

<sup>1</sup>Thueman, F. de, Herb. Mycol. Oecon. (Exsiccati), No. 403. 1876.

<sup>2</sup>Thueman, F. de, Herb. Mycol. Oecon. (Exsiccati), No. 602. 1878.

<sup>3</sup>Thueman, F. de, Myc. Univ. (Exsiccati), No. 1791. 1880.

mitted further study and it is now believed that this form, which is restricted to oats, is morphologically as well as physiologically distinguishable from *S. tritici* Rob. on wheat.

#### RECENT ECONOMIC IMPORTANCE

The disease was common and locally destructive in 1934 on both common oats (*Avena sativa* L.) and red oats (*A. byzantina* K. Koch). During most years, it occurs also on the wild oat (*A. fatua* L.), which is particularly susceptible and serves as a carrier in late winter. Since 1934, the disease has been seen in Benton, Washington, Multnomah, Linn, Douglas, Lincoln, Jackson, and Clatsop counties in Oregon. It also has been collected on common winter oats in Klickitat County, Washington, and on red oats and wild oats in southwestern Washington. It is more severe on red oats (*A. byzantina*) than on common oats (*A. sativa*).

#### PURE CULTURE AND HOST RANGE STUDIES

Pure culture and host range studies have been detailed previously (94), but additional inoculations have been made, the results of which are given in Table 1. The fungus was confined to oats.

#### MORPHOLOGY

The pycnidia of *Septoria tritici* f. *avenae* are very similar to those of *S. tritici* (Plate 2, F), differing only in the slightly looser structure of the peridium, and in the stouter pycnophores, which are ampulliform to subcylindric,  $4-7 \times 1.3-1.6 \mu$ . The pycnophores develop from hyaline, somewhat bulbous initials (Figure 1, E). While *S. tritici* f. *avenae* has slightly narrower spores than *S. tritici* on wheat, the former may be readily distinguished from the latter by its more sinuous spores.

#### TAXONOMY

The differences between *Septoria tritici* on wheat and oats are not only that of a physiologic race but of a morphologic form. The writer, therefore, replaces *S. tritici* "physiologic form on oats" with the slightly less cumbersome *S. tritici* Rob. f. *avenae* (Desm.) comb. nov.

SEPTORIA TRITICI Rob. Var. LOLICOLA Sprague and  
A. G. Johnson Var. Nov. and S. LOLIGENA Nom. Nov.

Both perennial ryegrass (*Lolium perenne* L.) and Italian ryegrass (*L. multiflorum* Lam.) are attacked by a long-spored fungus that will be

designated *Septoria tritici* var. *lolicola* Sprague and A. G. Johnson var. nov. This fungus occurs in Benton, Yamhill, Tillamook, Columbia, Douglas, Linn, Lane, and Washington counties, Oregon. Particularly on tall volunteer Italian ryegrass, the fungus is common from January to March. In addition, a short-spored fungus on *L. multiflorum*, collected near San Francisco, California, March 1, 1942, by W. B. Cooke, will be referred to *S. loligena* nom. nov.

#### SYMPTOMATOLOGY

The blotch or mottle caused by *Septoria tritici* var. *lolicola* is at first green or yellowish, but later turns fuscous to deep brown. The pycnidia are obscure because of the dark color of the older lesions. The lesions caused by *S. loligena* are fuscous to deep chocolate brown, somewhat paler in the center, with borders surrounded by lighter areas.

#### PURE CULTURE AND INOCULATION STUDIES

In pure culture, *Septoria tritici* var. *lolicola* resembles *Septoria tritici* from wheat. It stales after about 2 years.

Inoculations, made from 1932 to 1940 and summarized in Table 1, produced mild infections on *Lolium perenne* and *L. multiflorum* but none on the other grasses inoculated, except on wheat where there was questionable flecking in a few instances.

The cultures of *Septoria loligena* are entirely distinct from those of *S. tritici* var. *lolicola*, but resemble those of *Stagonospora arenaria*. They are slow growing, cottony, rose-buff color, with an irregular or fluted margin. On potato dextrose agar, under refrigerator conditions (5° C.), the fungus formed pycnidial initials but did not form mature pycnidia. In culture the fungus is slightly deeper buff or rosy buff in color and grows somewhat slower than *St. arenaria*. In culture, the development of *S. loligena* is about intermediate between *St. arenaria* on *Elymus glaucus* Buckl. from near Corvallis, Oregon, and a variant of *St. arenaria* on *Agropyron repens* (L.) Beauv. from Seaside, Oregon, collected by F. D. Bailey.

#### MORPHOLOGY

**PYCNIDIA.** The pycnidia of *Septoria tritici* var. *lolicola* are subglobose to globose, sometimes ellipsoid (Plate 1, K), 80-150 x 90-180  $\mu$ , mostly 120-150 x 120-150  $\mu$  in diameter. The walls are relatively thin, deep amber, brown, with one or two outer layers of oblong cells, two or three inner layers of intertwined lighter, polyhedral cells, which give rise to hyaline cells pro-

ducing slightly pyriform to subcylindric pycnophores measuring 4 to 8  $\mu$  long and 1.5-2.3  $\mu$  wide (Figure 2, B, C, G). The total pycnidial wall is usually not over five to six cells thick, totaling as much as 15  $\mu$  thick. Summer material, collected June 30, 1919, at Corvallis, Oregon, by G. R. Hoerner, has minute pycnidia in non-delimited lesions.

The pycnidia of *Septoria loligena* are light golden brown to brown, thin walled and, therefore, somewhat *Stagonospora*-like, subglobose, not prominent, 80-120  $\mu$  in diameter.

**PYCNOSPORES.** The pycnospores of *Septoria tritici* var. *lolicola* are hyaline, sometimes with coarse protoplasm, sometimes containing small oil drops, which, in slightly immature specimens, are as large as 1  $\mu$  in diameter. The spores usually are slightly enlarged at the base, curved or sinuous, sometimes whip-like, 0- to 5-septate, commonly 1- to 3-septate, 21-85 x 1.3-2.8  $\mu$  (Figure 2, A, D, E, F). On *Lolium perenne* L. and less often on *L. multiflorum* Lam., the spores are often more variable with short, 1-septate spores occurring with the larger ones (Figure 2, D, F). They differ from *Septoria tritici* on wheat in having a slightly more whiplike appearance, which is due to the slightly enlarged bases and somewhat more tapering distal portions. The material collected in early summer by G. R. Hoerner has 1-septate spores, 22-29 x 1.1-1.7  $\mu$ .

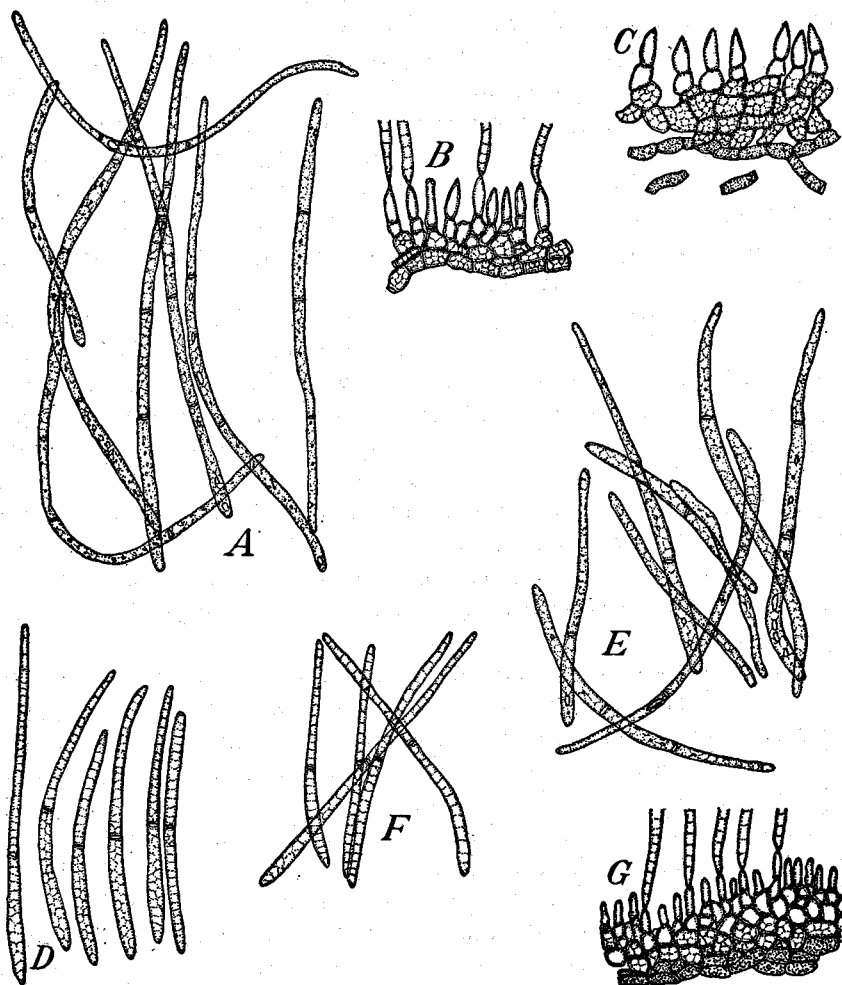
The pycnospores of *Septoria loligena* are bacillar, clear hyaline, 3-septate, 28-45 x 2.7-4.2  $\mu$ . They are, therefore, clearly distinct from those of *S. tritici* var. *lolicola*. They average 37.6 x 3.7  $\mu$  or approximately ten times as long as broad.

#### TAXONOMY

*Septoria graminum* Desm. var. *lolii* Montagne was described and specimens of it on *Lolium perenne* were issued by Desmazieres<sup>1</sup> in 1851 as No. 2169 in his *Fungi Cryptogames de France*. Desmazieres stated that Montagne described this variety in a letter to the distinguished Castagne ("in litt. ad Cl. Cast."). Castagne (18) described *Rhabdospora lolii* in 1851. Comparison of the descriptions of Castagne and Montagne strongly indicated that Montagne had sent the same material to Castagne as to Desmazieres and that *S. graminum* var. *lolii* and *R. lolii* were described from the same collection. Some of the same wording appears in both descriptions copied probably from Montagne's letter to Castagne. This is further substantiated by examination of Desmazieres No. 2169. A fungus on the rachis of this collection is a true *Ascochyta* with 0- to 1-septate spores, 15-20 (mostly 17) x 2.8-3.5  $\mu$ , very

<sup>1</sup>Desmazieres, J. B. H. J. *Plantes Cryptogames de France (Exsiccati)* (Ed. 1) Fasc. 44, No. 2169. 1851.

Figure 2. *Septoria tritici* var. *lolicola*: A, Pycnospores from *Lolium multiflorum*, East Corvallis, Oregon, December 16, 1935 (O.S.C. 10,366); B, cross section of pycnidial wall on *L. multiflorum*, Scappoose, Oregon, March 8, 1938 (O.S.C. 120); C, cross section of pycnidial wall on *L. multiflorum*, East Corvallis, Oregon (O.S.C. 160); D, pycnospores on *L. multiflorum* near Scappoose, Oregon, March 8, 1938 (O.S.C. 120) (small, otherwise typical); E, pycnospores from *L. perenne*, Granger, Oregon, December 16, 1935 (O.S.C. 10,383); F, pycnospores from *L. perenne*, collected by D. A. Boyd at Stevenson, Ayrshire, Scotland, June 1918; G, cross section of pycnidial wall, on *L. perenne*, Burnett Siding, Benton County, Oregon, April 18, 1938 (O.S.C. 165). The pycnospores are smaller and more nearly cylindrical than in most collections. (All X1000)



similar to the description briefly given in Desmazieres' No. 2169. On the glumes, however, are 0- to 2-septate hyaline, subflexuous spores,  $23-52 \times 1.2-2.6 \mu$ , which more nearly approach those of *R. lolii* Cast. The latter, however, was described as having hyaline acicular, nonseptate spores  $30 \times 4 \mu$ . It seems clear, therefore, that there are two or possibly three fungi on the same material: (1) one described by Montagne and distributed by Desmazieres<sup>1</sup> in 1851 as *S. graminum* var. *lolii* Mont. (spores 0- to 1-septate,  $15-20 \times 2.8-3.5 \mu$ ); (2) another described by Castagne (18, pp. 75-76), also in 1851, as *R. lolii* Cast. (spores  $30 \times 4 \mu$ ), which, in 1892, became *S. lolii* (Cast.) Sacc. (86, vol. 10, p. 386), and which we call *S. loligena*; and (3) a third which has spores  $25-52 \times 1.2-2.6 \mu$  and which we call *S. tritici* var. *lolicola* Sprague and A. G. Johnson var. nov.

Saccardo ignores *Septoria graminum* var. *lolii* Mont. (86), but Oudemans (76) credits it to Desmazieres. Oudemans also lists *S. lolii* West. (not *S. lolii* (Cast.) Sacc.). *Septoria lolii* West. was collected by Bellyneck near Namur, Belgium, and issued as Westendorp and Wallay's Herbarier Cryptogamique No. 1148. Material in the Mycological Collections, Bureau of Plant Industry, U. S. Department of Agriculture, has spores  $13-17 \times 3.3-3.5 \mu$ . The packet gives as synonym "*S. herbarum* var. *lolii* Mont.," but this synonym is corrected to *S. graminum* var. *lolii* Mont. in an article by Westendorp (119). It is clear that Westendorp considered this fungus the same as Montagne's and raised the varietal name to specific rank as suggested originally by Desmazieres on the label of his<sup>1</sup> No. 2169.

*Septoria graminum* var. *lolii* Mont. is evidently the same as *Diplodina lolii* Zimm., which has oblong-fusiform spores  $14-20 \times 2-3 \mu$ . The type of this agrees with *S. graminum* var. *lolii* Mont. and with an *Ascochyta* that causes a common leaf and head blotch on *Lolium perenne* in Oregon, which will be referred to later.

The long-spored *Septoria* occurs in Oregon on *Lolium perenne* L. and *L. multiflorum* Lam. It agrees with the long-spored *Septoria* found in Desmazieres' No. 2169. It has septate spores, which are definitely narrower and longer than those described for *Rhabdospora lolii*, which latter is believed to be the same as *S. loligena*, collected by W. B. Cooke in California on *L. multiflorum*. The Oregon fungus is referred to the following new variety of *S. tritici* from which species it differs sufficiently to warrant being given varietal rank.

*Septoria tritici* Rob. var. *lolicola* Sprague and A. G. Johnson var. nov. Lesions indefinite on leaves, sheaths and glumes, at first green, later yellow, grayish-brown, brown or Saccardo umber to isabelline, sometimes reddish, in

<sup>1</sup>See footnote on page 29.



old lesions, white in the center; pycnidia moderately prominent, scattered or in rows parallel to the leaf veins, usually subglobose to globose, sometimes ellipsoid, 80-150 x 90-180  $\mu$ , mostly 120-150 x 120-150  $\mu$ , ostiole 10-25 x 10-30  $\mu$  in diameter, peridia as much as 15  $\mu$  thick, pale to deeper amber brown, smooth, outer cells subcubical to oblong, inner cells interwoven, polyhedral, giving rise to pycnophores, 3-6 x 1.5-2.3  $\mu$ , slightly pyriform to subcylindric, ends acute with blunt terminal; pycnosporous numerous, hyaline, with small oil drops, 0- to 5-septate (mostly 1- to 3-), slightly enlarged at base, and tapering to rounded base, distal cells tapering to subwhiplike, slightly to strongly curved, 31-85 x 1.3-2.8  $\mu$ , in Oregon collections on leaves in winter, or 22-30 x 1.1-1.7  $\mu$  in summer material in Oregon, or 23-52 x 1.2-2.6  $\mu$  on the glumes in Desmazieres' Plant Cryptogames de France, No. 2169, in part.

On *Lolium perenne* L. and *L. multiflorum* Lam. in Europe and North America.

Description based on Desmazieres' Plantes Cryptogames de France, No. 2169, in part.

Maculis diffusis, centro pallidis; pycnidiis prominulis, globosis v. subglobosis, 80-150 x 90-180  $\mu$ , ostiolatis; pycnosporulis numerosis, hyalinis, 0-5-septatis, obclavato-filiformibus, (heime) 31-85 x 1.3-2.8  $\mu$  et (aestate) 22-30 x 1.1-1.7  $\mu$ .

Verified material from Corvallis, Oregon, which was used in the emended description, is deposited in the Mycological Collections, Bureau of Plant Industry, Soils, and Agricultural Engineering, U. S. Department of Agriculture, Beltsville, Maryland, and in the Mycological Herbarium at Oregon State College, Corvallis, Oregon.

As stated above, the fungus on Desmazieres' No. 2169, with short, 1-septate spores, described as *Septoria graminum* var. *lolii* Mont., also occurs on *Lolium perenne* in Oregon. In reality this fungus belongs in the genus *Ascochyta*. Recently an article by Cavara was found (Zeitschr. f. Pflanzenzucht. 3, Jan. 1893) indicating that he referred this fungus to his *Ascochyta desmazieri*. According to Article 58 of the International Rules of Botanical Nomenclature (13), neither Montagne's var. *lolii* of *S. graminum* var. *lolii* nor *S. lolii* West, which was raised to specific rank from Montagne's var. *lolii*, can be accepted as valid for a species name. Cavara's *A. desmazieri*, therefore, is the only available legitimate specific name. Thus synonyms are as follows:

ASCOCHYTA DESMAZIERE Cav.

Syn: *Septoria graminum* var. *lolii* Mont. (1851)

*Septoria lolii* West. (1857)

*Diplodina lolii* Zimm. (1914) (121, pp. 101-102)

Hab. on *Lolium perenne*, France, Belgium, Moravia, and Oregon, U.S.A.

It is regretted that further study has not been made to determine if *Ascochyta desmazieri* is not a phase of *Septoria lolii* (Cast.) Sacc., which is being referred to *S. loligena*. The symptoms are very similar and they are often associated in a way to indicate that they may be phases of one species. Pure cultures of *A. desmazieri* are not yet available.

The short-spored fungus on *Lolium multiflorum*, collected by W. B. Cooke in California, which is the same as *Septoria lolii* (Cast.) Sacc., while close to *Stagonospora arenaria*, is probably better considered in *Septoria*. The specific epithet of *S. lolii* (Cast.) Sacc. is not available for the genus *Septoria* as it is a later homonym of *S. lolii* West., and, therefore, a new name is necessary. We propose *Septoria loligena* nom nov. *S. loligena* has 0- to 3-septate spores, 28-45 x 2.7-4.1  $\mu$ , borne in thin-walled golden brown pycnidia. Castagne listed spores 30 x 4  $\mu$ , which measurements are within the range of those of *S. loligena*. In the event that *S. loligena* later is proved the same as *Ascochyta desmazieri*, both are not referable back to *Septoria lolii* West. as the latter was derived from *S. graminum* var. *lolii* Mont. and, therefore, would not be valid because of *S. loligena*. To summarize, we have on species of *Lolium* the following:

1. *Septoria tritici* var. *lolicola* Sprague and A. G. Johnson (Pycnosporos filiform 0- to 5-septate, 31-85 x 1.3-2.8  $\mu$ )
2. *Septoria loligena* Sprague (Pycnosporos bacillar, 0- to 3-septate, 28-45 x 2.7-4  $\mu$ )

Syn: *Rhabdospora lolii* Cast. (1851)

*Septoria lolii* (Cast.) Sacc. (1892)

3. *Ascochyta desmazieri* Cav. (Pycnosporos bacillar, 0- to 1-septate, 15-20 x 2.8-3.5  $\mu$ )

Syn: *Septoria graminum* var. *lolii* Mont. (1851)

*Septoria lolii* West. (1857)

*Diplodina lolii* Zimm. (1914)

It should be added that Passerini (77) described *Septoria murinum* on leaves of *Hordeum murinum* L. and spikes of *Lolium perenne*. Thuemen (105), however, described *S. murinum* Thuem. the same year, and Saccardo, believing that the last mentioned name took priority over Passerini's, proposed *S. passerinii* for the species on *Hordeum* and *Lolium*. Since *Hordeum* was given first in Passerini's description, it is considered the type of *S. passerinii* Sacc. The fungus on *Lolium* is believed to be distinct from *S. passerinii* and is probably *S. tritici* var. *lolicola*.

Grove (54) listed *Septoria bromi* var. *brachypodii* Sacc. on *Lolium perenne* collected by D. A. Boyd from Stevenson, Ayrshire, Scotland, June 1918, spores 30-40 x 1-1.5  $\mu$ . This material represents early summer mate-

rial of *S. tritici* var. *lolicola*. The spores are 1- to 2-septate, short, stiffly curved or straight and measure  $26-35 \times 1.3-2.0 \mu$ , although many are collapsed to  $0.9$  to  $1.3 \mu$  wide (Figure 2, F). It may be added that the type of *S. bromi* var. *brachypodii* on *Brachypodium sylvaticum* (Huds.) Beauv. has been shown (95) to be a synonym of *S. graminum* Desm.

### SEPTORIA TRITICI Rob. F. HOLCI Form. Nov.

A very common leaf spot on velvet grass (*Holcus lanatus* L.) occurs in winter and spring in western Oregon and adjacent Washington.

#### SYMPTOMATOLOGY

The indefinitely bordered, irregular lesions frequently cover large portions of the leaf. At first, they are yellow-green, then vinaceous buff to vinaceous fawn or true fawn, later becoming Saccardo umber in the center of the lesions. The pycnidia are very prominent on dew-covered leaves in the field, but in dried material they are obscured by the leaf hairs. In well-developed specimens, the pycnidia are numerous, one typical specimen averaging 335 pycnidia to the square centimeter. The pycnidia frequently occur in parts of the leaf where traces of green still persist and thus produce a mottling of green, yellow, and buff, which increases the indefiniteness of the lesion.

#### PURE CULTURE STUDIES

The fungus grows very slowly on potato dextrose agar, producing a pale, flesh-colored, yeast-like growth consisting at first only of conidia. Eventually, the colonies become gray to black stromatic. In general, the fungus resembles *Septoria tritici* from wheat except that it sporulates less abundantly, grows somewhat slower, and the spore masses tend to be slightly paler than those of *S. tritici*.

#### ARTIFICIAL INOCULATIONS

A total of ten series of inoculations were conducted at Arlington Farm, Arlington, Virginia, Corvallis, Oregon, and along a mountain creek (water about  $5^{\circ}$  C.) near Corvallis from 1932 to 1940. Six of these series gave positive infection on *Holcus lanatus* L. and these are summarized in Table 1. Infection as high as 65 per cent of the leaves on *H. lanatus* was obtained in December 1939 by spraying plants with spore suspensions, covering with moist cheesecloth, and incubating out-of-doors in rainy weather at Corvallis.

All other series in spray chambers were distinctly less successful. The fungus apparently is strictly confined to species of *Holcus*.

#### MORPHOLOGY

**PYCNIDIA.** The ostiolate, slightly erumpent pycnidia have relatively thin walls ( $10-12\ \mu$  thick), are large ( $65-210\ \mu$ ) (Plate 2, O) and differ from those of *Septoria tritici* var. *lolicola* in being less flattened and particularly in being more rounded on the ostiolar half and in having darker pigmentation in the outer cells of the pycnidia, which gives them smoky or sepia tints under the microscope. Specimens examined had an outer layer of dark, flattened, elongated cells and an inner layer of intertwined lighter ones on which hyaline pycnophore initials and pycnophores were produced. In large specimens, the pycnophores were similar to those of *S. tritici* var. *lolicola* in size ( $3.5-5.7 \times 1.4-2.1\ \mu$ ), but appeared to be proportionately slightly broader at the base or more strongly cuspidate (Figure 3, D, G).

**PYCNOSPORES.** The spores are filiform-scolescosporous, sometimes slightly swollen at the base, with clear, hyaline contents, 1- to 4-septate,  $35-105 \times 1.3-2.0$  ( $1.0-2.1$ )  $\mu$  (Figure 3, A, B, C, H, J). They are slightly narrower than those of *Septoria tritici* on wheat but are otherwise similar.

#### TAXONOMY

The type of *Septoria holci* Pass. (77) was said to have spores  $20-25 \times 3\ \mu$ . Type material sent from Italy and examined minutely by the writer had neither pycnidia nor spores surviving attacks of herbarium insects. It was indicated by correspondence that the rest of the type was in a similar condition. *Septoria holci* appears to be close to *S. affinis* Sacc. (84, p. 194) on *Brachypodium pinnatum* (L.) Beauv., which has spores  $25-30 \times 2-2.5\ \mu$ , and also is similar to *S. nodorum* Berk. on wheat. Unamuno (109) reported *S. holci* with spores  $25-35 \times 3\ \mu$ , which is even nearer to *S. affinis* than to the type of *S. holci*. None of the Oregon and Washington material is at all like *S. holci* except O.S.C. 8485, which has spores averaging  $23 \times 1.7\ \mu$ , and which is excluded from immediate consideration (Figure 3, F).

Material sent from Kew, England, on *Holcus mollis* L. was collected by C. A. Boyd near West Kilbride, Ayrshire, Scotland, on November 18, 1924. The spores were straight or curved, filiform, with bases sometimes slightly enlarged, but not obclavate, 2- to 3-septate, and  $38-66 \times 1.2-1.7\ \mu$ , averaging  $56 \times 1.4\ \mu$  (Figure 3, B). They are similar to those of *Septoria graminum* Desm. They were borne, however, in relatively prominent, erumpent, golden-brown pycnidia,  $140-215 \times 100-130\ \mu$ . It is believed that this fungus

is the same species as the somewhat larger-spored but otherwise similar Oregon material of *S. tritici* f. *holci*.

Grove (54) gives *Holcus* as one of the hosts of *Septoria bromi*. The Oregon material of *S. tritici* f. *holci* is not *S. bromi* because *S. bromi* has narrowly obclavate spores and *S. tritici* f. *holci* has typical filiform spores with basal cells only moderately enlarged, nor does *S. tritici* attack *Bromus* spp.

Unamuno (109, pp. 15, 16), in discussing *Septoria holci*, states that it differs from *S. holcina* Unamuno principally by the spores of the former having more numerous cross walls. The latter, which is reported as possibly a parasite on *Entyloma crastophyllum* Sacc., has 1- to 2-, rarely 3-, septate spores,  $15-28.5 \times 3-4 \mu$ , in pycnidia  $118-129 \mu$ . A description of *S. holcina* was very kindly furnished by Padre Unamuno.

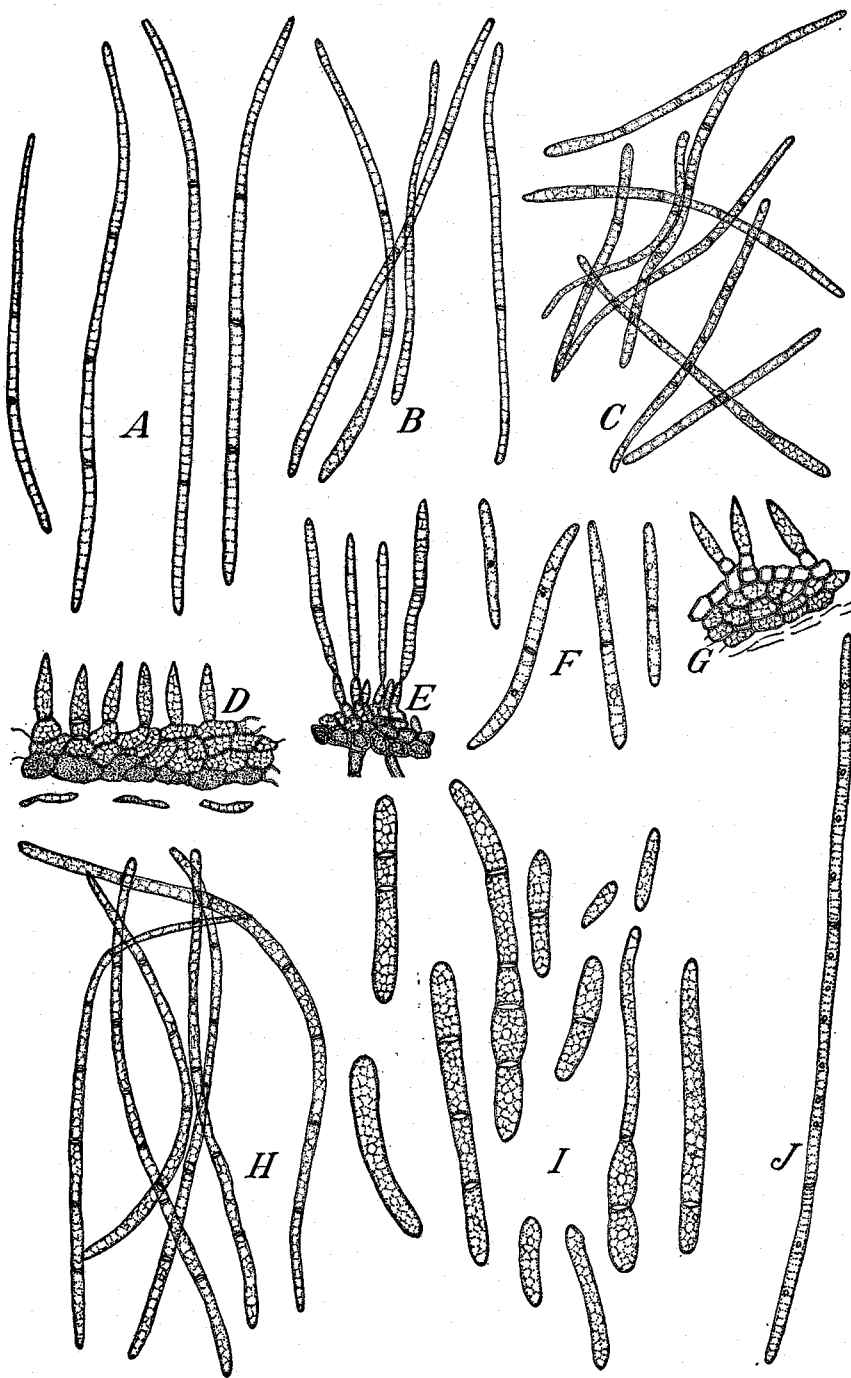
*Septoria tritici* f. *holci* has spores averaging nearly the same width as those of *S. tritici* var. *lolicola* on *Lolium* spp. They are approximately the same shape and are variable in size as in the *Lolium* material. The spores are different only in the extreme lengths they attain on *Holcus*, in excess of  $100 \mu$  in some specimens. The spores on *Holcus* average  $66 \times 1.6 \mu$  and those on *Lolium*,  $56 \times 1.6 \mu$ . Because of determinable differences in pycnidia and spores, as well as a distinct host range, the fungus on *Holcus* is considered an undescribed morphological form of *S. tritici*.

*Septoria tritici* Rob. forma *holci* form. nov. Lesions occur on the lower leaves of the plant, mostly indefinitely bordered, irregular, coalescing to cover all or large portions of the leaf. Lesions at first are yellow green to vinaceous buff to vinaceous fawn or fawn, later becoming Saccardo umber in the center of the lesions. Pycnidia moderately prominent, scattered or grouped in rows parallel to the veins, erumpent but deep seated, visible from both surfaces, hypophyllous, sometimes distinctly flattened, often subglobose to globose, ostiolate, dark brown to black brown; pycnidial wall  $10-12 \mu$  thick, outer portion of dark crushed oblong polyhedral cells surrounding intertwined lighter polyhedral cells (about  $2 \mu$  diameter) producing hyaline pycnophore initials; pycnophores are hyaline, ampulliform to nearly cuspidate,  $3.5-5.7 \times 1.4-2.1 \mu$ ; pycnosporules, exuded in very short, pale, flesh-colored cirrhi or guttulae, straight or somewhat curved, less often strongly curved, except at distal cells, scolecosporous slightly broadened at base, crystal-hyaline contents, cross walls obscure in many collections, 1-4 (0-5) septate,  $30-80 \times 1.4-1.8 \mu$  (spring collections),  $35-105 \times 1.4-2.5 \mu$  (winter collections), rarely narrower.

On *Holcus lanatus* L. in Oregon (type, O.S.C. 10,367) and Washington and *H. mollis* in Scotland.

Pycnidiiis brunneo-nigris,  $65-210 \mu$ , globosis, v. subglobosis; pycnosporulis filiformibus, 1-4-septatis, (hieme)  $35-105 \times 1.4-2.5 \mu$  et vere  $30-80 \times 1.4-1.8 \mu$ .

Figure 3. *Septoria tritici* f. *holci*: A, Pycnospores from *Holcus lanatus* near Troutdale, Oregon (O.S.C. 10,227); B, pycnospores from *H. mollis*, West Kilbride, Ayrshire, Scotland, D. A. Boyd, November 18, 1924; C, pycnospores from *H. lanatus*, Corvallis, Oregon (smaller than usual) (O.S.C. 10,360-A); D, cross section of pycnidial wall on *H. lanatus* from 3 miles east of Blodgett, Oregon (O.S.C. 85), typical for the species; E, cross section of pycnidial wall on *H. lanatus* from near Tangent, Oregon, (O.S.C. 8485) showing black, thin walls, small pycnophores and pycnospores; F, pycnospores from O.S.C. 8485 (see Figure 3, E); G, cross section of pycnidial wall on *H. lanatus* from 3 miles south of Newport, Oregon, December 18, 1937, (O.S.C. 37); H, same collection as in Figure 3, C, but with larger, more typical spores (O.S.C. 10,360-B); I, conidia from pure culture (S119), isolated from *H. lanatus* grown on potato dextrose agar at 5° C. (O.S.C. 8485); J, pycnospore from *H. lanatus* near Corvallis, Oregon, February 8, 1938 (O.S.C. 45), showing extreme length frequently found in late winter collections. (All X1000)



One specimen tentatively assigned to *Septoria tritici* f. *holci*, O.S.C. 8485, warrants separate citation because further study with more and better material may indicate that it is not this fungus. It produces minute, shrunken, globose, black pycnidia in indefinite gray or stramineous lesions. The pycnidia are 35-38  $\mu$  high by 35-40  $\mu$  in lateral diameter. The wall, which is about 9  $\mu$  thick, is composed of one very heavily pigmented stromatic outer layer of cells surrounding a slightly lighter colored inner layer of globular tightly packed cells, which give rise to subhyaline pycnophore initials and produce obscure cylindrical pycnophores, 3-4 x 1-1.5  $\mu$  (Figure 3, E).

The pycnospores are straight to slightly flexuous, bacillar to fusiform-cylindric, 0- to 1-septate, 14-28 x 1.5-2.4  $\mu$  (Figure 3, F). In pure culture (S119) the conidia were 0- to 3-septate, 15-40 x 2.5-3  $\mu$  (Figure 3, I). The cultures were at first yeasty, pale flesh-colored, then crustose with gray, later brown-gray, mycelia. Small pycnidia were formed in later stages.

While this specimen, O.S.C. 8485, is considered fall material (October 15, 1937) of *Septoria tritici* f. *holci*, the pycnidia are so exceedingly small, and the spores in culture and on the host so different from those of the other collections of *S. tritici* f. *holci*, the writer is skeptical of his diagnosis. It is possible, also, for instance, that this may represent summer material of *S. holci* Pass.

The pycnidia are typical for *Septoria holci* Pass. (77), but the vermiform 3-septate spores of *S. holci* Pass., which measure 20-25 x 3  $\mu$  as collected in summer (August) in Great Britain (54), are certainly distinct from those of O.S.C. 8485. In pure culture (S119) the spores are sometimes 3-septate and mostly 3  $\mu$  wide, but they are not vermiform. *S. affinis* Sacc. has rod-shaped spores measuring 25-30 x 2-2.5  $\mu$ , but its spores are 4-5 septate, hyaline, later yellowish green. The collection O.S.C. 8485 is, therefore, assigned to *S. tritici* f. *holci*, but further study of similar material is needed. Lindquist recently (1941) sent material of a leaf spot on *Holcus lanatus* from La Plata, Argentina, which showed scattered, minute, globose, black pycnidia, 45-55  $\mu$  diameter. The spores were rod-shaped, nonseptate, 9-11 x 0.9-1.2  $\mu$ . This material appears to be a species of *Phyllosticta*, but may represent a microsporous phase of the same fungus as O.S.C. 8485, *S. tritici* f. *holci*.

### SEPTORIA MACROPODA Pass. on POA Spp.

*Septoria macropoda* Pass. and its varieties are known to attack fourteen species of *Poa* in the far west. The fungus is believed to be polymorphic with two varieties and a number of physiologic races as recognized in this study.



## GEOGRAPHIC DISTRIBUTION AND HOST RANGE

In Oregon, the species is common on *Poa annua* during the winter months in the Willamette Valley and occurs during all months of the year in the fog-frequented areas along the coast. It has been collected also in China (R. H. Porter) and in Europe (11, p. 327). Recently Maire and Werner (72) reported *Septoria graminum* on *Poa annua* from Morocco, which no doubt is *S. macropoda*.

*Septoria macropoda* var. *septulata* (Gonz. Frag.) Sprague (97) is widespread on *Poa pratensis* in western Oregon and Washington and occurs at least as far east in Oregon as Pendleton, and Weber (118) reported it from Wisconsin in 1923. St. John P. Chilton has sent the writer a number of collections from State College, Pennsylvania. There are collections also from Indiana, Idaho, Minnesota, Virginia (Lefebvre), and Iowa. The writer recently collected it in several places in Minnesota, Montana, Nebraska, North Dakota, South Dakota, and Wyoming. It is abundant throughout the northern United States and adjacent Canada. This variety was originally described from Spain on *P. pratensis* (51, p. 22).

The native prairie and transition zone blue grasses (*Poa secunda*, *P. vaseyochloa* Scribn., *P. canbyi* (Scribn.) Piper, *P. scabrella* (Thurb.) Benth., *P. nevadensis* Vasey, *P. arida* Vasey, *P. ampla* Merr.) are very commonly attacked by a large-spored variety, *S. macropoda* var. *grandis* var. nov., in early spring in eastern Oregon, Washington, Wyoming, Montana, North Dakota, South Dakota, and northern California. This fungus, which occurs in native blue grasses over wide areas of the west, has not been recognized until recently.

## PURE CULTURE STUDIES

Cultures of *Septoria macropoda* resembled the slow-growing mucose, later carbonaceous, cultures of *S. tritici* f. *avenae* and *S. tritici* var. *lolicola*, but cultures of *S. macropoda* var. *septulata* were darker and the spore exudate scarcely pink, more often sordid cream-colored or tawny. The cultures of *S. macropoda* var. *septulata* became covered with black carbonaceous stroma faster than those of *S. tritici*. In culture, *S. macropoda* var. *grandis* from *Poa secunda* were indistinguishable from *S. macropoda* var. *septulata*, but the spore exudate was, if anything, more often cream to pale cream rather than sordid cream to tawny. One culture from *P. vaseyochloa* had a distinctly brown appearance and the spore exudate was tawny. The cultures from *P. ampla* were isabelline to pale flesh conidial exudate, with gray tones overlying the later developing black stroma. The gray coloring consisted of a short, velvety mycelium that grew over the black carbonaceous stroma. This

gray coloring was also found in cultures of *S. macropoda* var. *grandis* isolated from *P. secunda*.

#### SYMPTOMATOLOGY

On *Septoria macropoda* on *Poa annua*, the lesions are elliptical, at first greenish-mottled, later brown or straw-colored, finally bleached, off-white. They occur most often where the leaf is in contact with the ground, or where water collects at the base or in the cupped center of the leaf.

On *S. macropoda* on *Poa kelloggii* Vasey, the lesions occur usually at the tips of the leaves and are obscure and brown-mottled. The collection studied represents drought-inhibited summer material.

On *Septoria macropoda* var. *septulata* on *Poa pratensis*, the lesions occur at the leaf tips or scattered along the blade and are dark gray to brown, sometimes 3 mm. long. They may be bordered by red, maroon, or yellow bands of dying tissue. The large pycnidia are often obscured by the dark color of the lesions. In old lesions, the pycnidia become prominent because the color of the lesion often fades to straw or faint buff. The symptoms of the collection on *Poa compressa* L. are similar to those on *P. pratensis*.

On *Septoria macropoda* var. *grandis* on *Poa secunda*, the lesions occur on basal leaves in winter (they have been collected as early as December in Washington) and on the sheaths, leaves, and leaf bases in spring, as late as May 25 in North Dakota. They vary from deep brown to gray and are sometimes delimited by the veins of the leaf in late spring. Material collected following the open winter of 1933-34 showed a very prolific spotting but usually the injury is slight to moderate on this small semidesert and prairie grass. Symptoms on *P. vaseyochloa* are similar to those on *P. secunda* except that the lesions on the very small leaves are, as a rule, smaller on the former.

Collections of *Septoria macropoda* var. *grandis* on *Poa ampla* made under pines (*Pinus ponderosa*) showed gray-mottled lesions with extensive rows of prominent pycnidia arranged somewhat parallel to the leaf veins. In old lesions, the diseased tissue was nearly white. Collections on *P. scabrella* and on *P. nevadensis* were similar but less extensive lesions were present, except on the heavily infected material from the North Fork of the Feather River, California (O.S.C. 619).

*Septoria macropoda* var. *grandis* on *Poa nervosa* (Hook.) Vasey from Missoula, Montana, represents scanty material of dried basal leaves with prominent black pycnidia.

A specimen of *Septoria macropoda* var. *grandis* on *Poa cusickii* Vasey from Drummond, Montana, found on a herbarium sheet collected by C. Leo

Hitchcock, consists of a few dried filiform leaves without determinable symptoms except the black conspicuous pycnidia.

#### ARTIFICIAL INOCULATIONS

Inoculations were made with spore suspensions obtained in some cases from field grown leaf spots or with conidia from pure cultures grown in the refrigerator (4-5° C.).

Erratic results were obtained with every type of inoculation equipment used. With inoculated plants, however, kept in an unheated greenhouse or out-of-doors in the shade of evergreen shrubs, relatively satisfactory results were obtained during February and March from 1932 to 1940. The results are summarized in Table 1. Since this work covers 9 years, the results were obtained under a great variety of conditions and, therefore, it is believed that the consistently negative results are significant. The relative amounts of infection cannot be relied on, as one or two successful infections were often followed by a series of completely negative infections. While the large number of trials tended toward more reliable averages, the end results are felt still to be short of differences necessary to distinguish clearly small racial differences in the fungi.

*Septoria macropoda* from *Poa annua* did not attack any species of *Poa* tested except *P. annua*. *S. macropoda* var. *septulata* from *P. pratensis*, which readily attacked *P. pratensis*, was twice successful on *P. annua* and also appeared to cause spotting but no sporulation on *P. nemoralis* L., *P. nevadensis*, and *P. secunda*. *Poa trivialis* L., the type host of *S. poae-trivialis* Cocc., was not infected by any of the species or varieties of *Septoria* tested. *Septoria macropoda* var. *grandis* from *P. secunda* failed to attack the host from which it was isolated in two trials but was strongly parasitic on it in two other tests and weakly so on *P. juncifolia* Scribn. It caused spotting on *P. pratensis* and doubtful flecking on *P. annua* in the first trial and none in several subsequent ones. In still later trials, it caused heavy spotting on *P. secunda* but none on the other species of *Poa*.

*Septoria tritici* from wheat (Table 1) (S60, S47, S122) and *S. tritici* f. *avenae* from oats (S80) were confined to their original hosts, although culture S47 of *S. tritici* once caused spotting on *Poa pratensis*.

The culture isolated from *Poa compressa* did not attack any grasses except mildly on the leaves of *P. compressa*.

#### MORPHOLOGY

PYCNIDIA. On *Poa annua*, the pycnidia of *Septoria macropoda* are sub-epidermal, slightly erumpent, mostly flattened and appressed to the upper leaf

Figure 4. *Septoria macropoda*: A, Pycnospores from type of *S. annua*; B, cross section of pycnidial wall on *Poa annua*, Black Earth, Wisconsin, J. J. Davis; C, cross section through very thin pycnidial wall, on *P. annua*, from Corvallis, Oregon (O.S.C. 10,354); D, pycnospores from *P. kelloggii* Vasey, Union Creek, Jackson County, Oregon, F. P. Sipe, February 18, 1934 (O.S.C. 10,758); E, cross section of pycnidial wall and pycnospores, on *P. annua*, Corvallis, Oregon, (O.S.C. 10,354); F, cross section of thin pycnidial wall, on *P. annua*, Corvallis, Oregon, (O.S.C. 10,361). (All X1000)

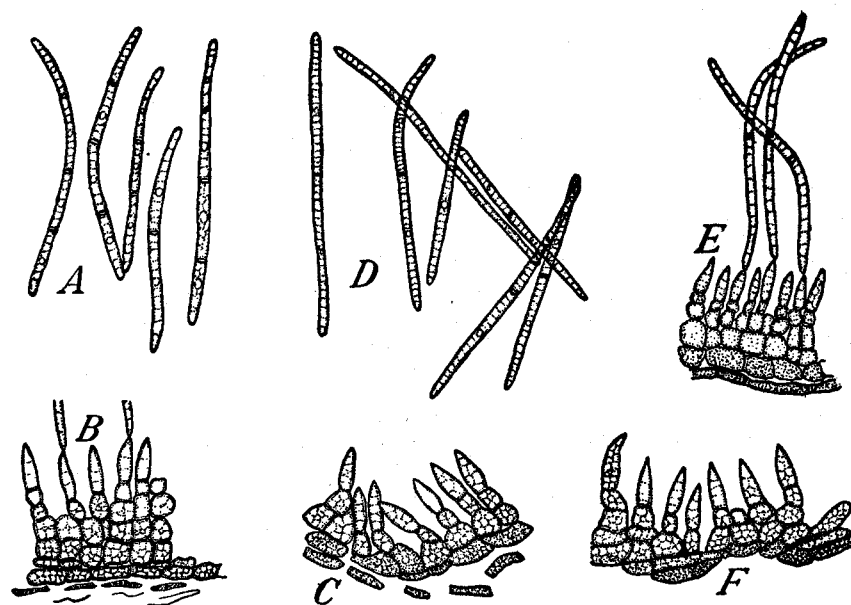


Figure 5. *Septoria macropoda* var. *septulata*: A, Pycnospores from *Poa pratensis* near Dundee, Oregon (O.S.C. 10,349); B, pycnospores from *P. pratensis*, Alsea Valley, Oregon, April 3, 1933 (O.S.C. 10,345); C, cross section of pycnidial wall, on *P. pratensis*, Five Rivers, Lincoln County, Oregon, May 25, 1937 (O.S.C. 8301); D, cross section of pycnidial wall on, and E, pycnospores from *P. compressa*, from Rainier, Oregon (O.S.C. 10,946); F, pycnospores from *P. pratensis* near Havana Station, Umatilla County, Oregon, March 15, 1935 (O.S.C. 10,352); G, pycnospores from *P. nervosa*, Lyle, Washington, May 13, 1935 (O.S.C. 8143); H, pycnospore from *P. pratensis*, Corvallis, Oregon, December 15, 1937 (O.S.C. 26); I, pycnospores from *P. pratensis*, State College, Pennsylvania, November 3, 1938, St. J. P. Chilton. (All X1000)

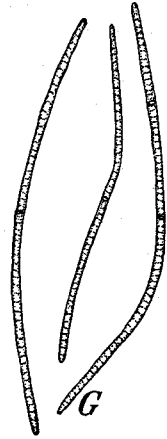
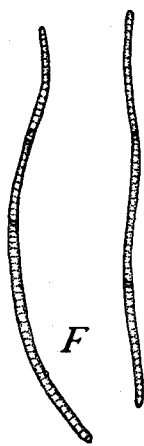
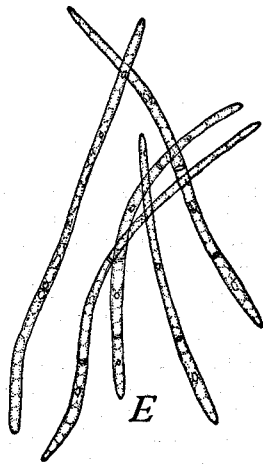
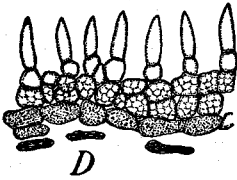
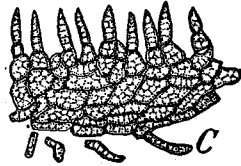
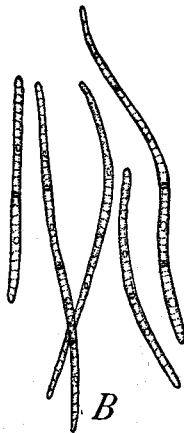
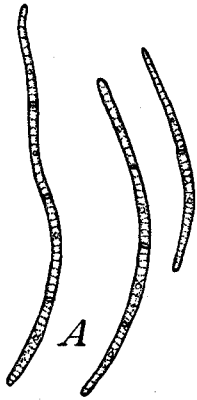
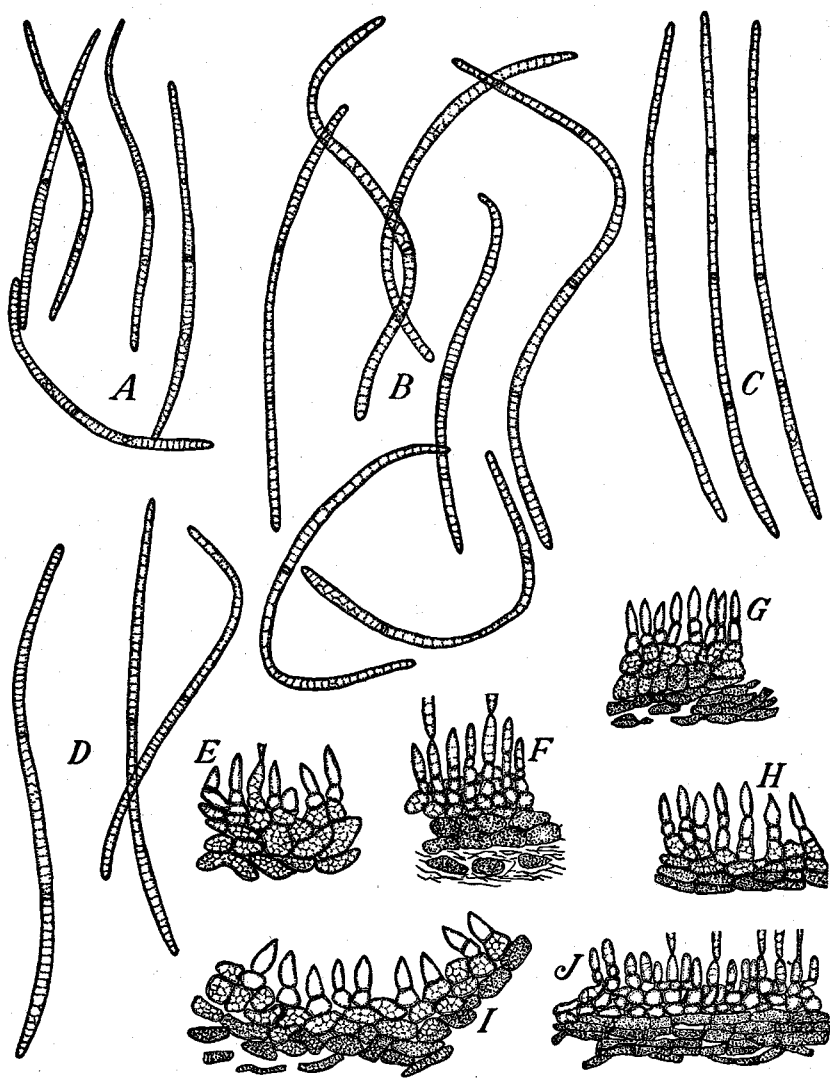


Figure 6. *Septoria macropoda* var. *grandis*: A, Pycnospores from *Poa secunda*, High Prairie, Washington, May 13, 1935 (O.S.C. 8146); B, pycnospores from *P. secunda* near Warwick, Washington (O.S.C. 103); C, pycnospores from *P. cusickii*, Drummond, Montana, C. L. Hitchcock; D, pycnospores from *P. scabrella*, under pines 12 miles northeast of Lyle, Washington, March 9, 1938 (O.S.C. 144); E, cross section of pycnidial wall on *P. secunda*, near Warwick, Washington, March 9, 1938 (O.S.C. 103); F, cross section of pycnidial wall, on *P. nevadensis*, Blue Mountains, Oregon (O.S.C. 10,355); G, cross section of pycnidial wall, same collection as in Figure 6, E, showing somewhat different development in outer cells of the peridium; H, cross section of pycnidial wall, on *P. ampla*, Old Highway, Klickitat Canyon, above Lyle, Washington (O.S.C. 8165); I, cross section of pycnidial wall on *P. secunda*, High Prairie, Washington, March 31, 1937 (O.S.C. 4); J, cross section of pycnidial wall, on *P. secunda*, near Warwick, Washington (O.S.C. 103). (All X1000)





epidermis. A few are subglobose. The walls are thin ( $5-11\ \mu$ ), light brown, and consist of three to four layers of oblong to irregularly polyhedral cells merging into two to four inner layers of hyaline cells, which produce subulate or subcylindric pycnophores,  $4-7 \times 1.5-2.5\ \mu$  (Figure 4, B, C, E, F).

The pycnidia are  $60-135 \times 66-160\ \mu$  and are most commonly  $50-80\ \mu$  high.

On an old specimen of *Poa howellii* Vasey and Scribn., the dark brown pycnidial walls of *Septoria macropoda* are somewhat shrunken in prepared slides. The pycnidia are ellipsoid in cross section. The peridium, which is about  $9$  to  $12\ \mu$  thick, is composed of several layers of corky-appearing, polyhedral cells with an inner layer of intertwined cells producing small ampulliform pycnophores, which in the old plasmolyzed material are very small in comparison with those of *S. macropoda* on *P. annua*. They measure  $2-3 \times 0.8-1.0\ \mu$ .

On *Poa kelloggii*, the pycnidia of *Septoria macropoda* are subglobose,  $80-110 \times 70-85\ \mu$  dark, with somewhat thin ( $4.5-6\ \mu$ ) but closely knit walls consisting of two or three layers of brown polygonal to rectangular cells surrounding polygonal to subglobose pycnophore initials that produce small, subulate pycnophores. They measure  $3-4 \times 1.2-1.5\ \mu$  but the material appears somewhat shrunken and they are, no doubt, somewhat larger than this in fresh material.

On *Poa pratensis* and *P. compressa*, the pycnidia of *Septoria macropoda* var. *septulata* are subepidermal, slightly erumpent, and vary from somewhat flattened globose to true globose (Plate 1, F, J). The pycnidia are less flattened than those on *P. annua*, the walls are more compact, thicker ( $5-9\ \mu$  thick) and the pycnidia are darker. The pycnophores are elongate flask-shaped to nearly filiform,  $3-6 \times 1.5-2\ \mu$  (Figure 5, C, D).

The pycnidia are  $60-180 \times 70-240\ \mu$  although  $160\ \mu$  is the more common length. They are  $50-95\ \mu$  deep.

On *Poa secunda*, *P. ampla*, *P. nevadensis*, *P. vaseyochloa*, and *P. scabrella*, the pycnidia do not reach the occasional extremes found in *Septoria macropoda* var. *septulata* on *P. pratensis* but measure  $65-190\ \mu$  and are  $40-90\ \mu$  high. The pycnidia are typically subepidermal with a flattened, less often rounded base, and a rounded or flattened top. In cross section, their outline varied from almost rectangular to elliptical to circular (Plate 2, E). In some instances, the large pycnidia were incompletely multichambered. The pycnidial walls of *S. macropoda* var. *grandis* consist of 3 to 5 interwoven layers of polyhedral, brown cells surrounding an equally thick layer of less compactly formed hyaline tissue. The entire wall is from  $7$  to  $14\ \mu$  thick, mostly  $9$  to  $11\ \mu$ . The pycnophores are ampulliform, subulate, or subcylindric. They measure  $3-6$  ( $3.5-4.5$ )  $\times 1.3-2.3\ \mu$  (Figure 6, E, F, G, H, I, J).

A collection of *Septoria macropoda* var. *grandis* on *Poa nevadensis* from Oregon has normally ampulliform pycnophores measuring  $4.5 \times 1.3\text{--}1.6 \mu$ , and the walls, which are about  $14 \mu$  thick, consist of an outer area of heavily pigmented cells, totaling  $9 \mu$  thick, and an inner layer of hyaline cells (Figure 6, F). The abundant material on *P. nevadensis* from the North Fork of the Feather River in California is similar in all respects to the collections on *P. secunda* as shown by a study of prepared slides.

The collection on *Poa vaseyochloa* from the upper Klickitat Creek, Washington (O.S.C. 8114) has stoutly formed pycnophores.

**PYCNOSPORES.** The pycnospores of the various collections are filiform to very narrowly filiform-clavate and 1- to 3-septate. The spores of *Septoria macropoda* on *Poa annua* are small, about  $35\text{--}40 \times 1.3 \mu$  (Figure 4, A, E), those of *S. macropoda* var. *septulata* on *P. pratensis* and *P. compressa* are more typically  $40\text{--}50 \times 1.5 \mu$  (Figure 5, A, B, E, F, G, H, I), while spores of *S. macropoda* var. *grandis* on *P. secunda*, *P. cusickii*, *P. ampla*, and *P. scabrella* represent a third deviation, the spores of which average as large as  $60 \times 2 \mu$  (Figure 6, A, B, C, D). A collection of *P. howellii* is distinct in having very long, slender pycnospores.

The spores of *Septoria macropoda* var. *septulata* on *Poa pratensis* are typically needle-like with obscure cross walls, pointed ends and scarcely swollen near one end. Some collections of *S. macropoda* var. *grandis* on *P. secunda* are similar but most of the collections on this grass have coarser spores with slightly more prominent cross walls, blunter ends, and often strongly curved or even flexuous (Figure 6, B). In winter material collected on High Prairie and vicinity, the spores of *S. macropoda* var. *grandis* on *P. ampla* were close to those of *S. tritici*, in size, those on robust plants of *P. secunda* were somewhat narrower, while collections of this variety on *P. vaseyochloa* were still narrower.

It is apparent from examination of many specimens that the spores of *Septoria macropoda* are somewhat variable, but not only on different hosts and in different seasons, but on the same hosts at the same season of the year.

In summer material of *Septoria macropoda* var. *septulata* on *Poa pratensis*, the spores are often thread-like, while late spring or summer material of *S. macropoda* var. *grandis* on *P. secunda* becomes very similar to winter material of *S. macropoda* var. *septulata*, from *P. pratensis*. Summer material on *P. annua* from the coast of Oregon is variable with a tendency for the spores to be short and nonseptate or 1-septate.

The pycnospores of *Septoria macropoda* from *Poa kelloggii* (Figure 4, D) are similar to those on *P. annua*. The collections on *P. nervosa* from Lyle, Washington (Figure 5, G) resemble *S. macropoda* var. *septulata*.

The spores of *Septoria macropoda* var. *grandis* on *Poa nervosa* and *P. cusickii* from Montana are long, narrow, and needle-like (Figure 6, C). They range from  $45\text{--}75 \times 1.2\text{--}1.8 \mu$  and are mostly 3-septate. They are larger than those of *S. macropoda* var. *septulata* on *P. pratensis* from western Oregon but are narrower than the robust spored material of *S. macropoda* var. *grandis* on *P. secunda* and other bluegrasses.

#### TAXONOMY

Passerini (77) described *Septoria macropoda* in 1879. The same collection had been issued as Thuemen's Myc. Univ. No. 593 and as Rabenhorst's Fungi Eur. No. 2255 under the name *S. graminum* Desm. f. *sclerochloae durae* Thuem. The material in Thuemen's Myc. Univ. No. 593 has prominent, flattened, black pycnidia, on bleached leaves, containing filiform-bacillar, 0- to 2-septate, hyaline spores,  $27\text{--}36 \times 1.4\text{--}1.8 \mu$ . *Sclerochloa dura* (L.) Beauv. was at one time recognized as a species of *Poa* (*P. dura* (L.) Scop.). On comparing Thuemen's Myc. Univ. No. 593 with the material on *Poa* spp., the writer is convinced that the spores and pycnidia of Thuemen's Myc. Univ. No. 593 are morphologically identical with those of *S. annua* Ell. and Ev.

*Septoria poae-annuae* Bres. (11) is indistinguishable from *S. annua* Ell. and Ev. (40) but *S. poae-trivialis* Cocc. (20, p. 153) is illustrated with somewhat broader but no longer spores than *S. macropoda*. *Poa trivialis*, however, was not attacked by any of the Oregon collections. The fungus called *S. poae-trivialis*, therefore, may represent a distinct variety of *S. macropoda*, but, at least for the present, it is assigned to this species. The synonymy of *Septoria macropoda* Pass. is as follows:

*Septoria macropoda* Pass., 1879 (77)

Syn. *Septoria graminum* Desm. f. *sclerochloae durae*, Thuem. 1876<sup>1</sup>

*S. poae-trivialis* Cocc., 1896-97 (20)

*S. annua* Ell. and Ev. Nov., 1900 (40)

*S. poae-annuae* Bres. Dec., 1900 (11)

The original spelling of *Septoria macrapoda* Pass. (77) was corrected by Saccardo in 1884 (86, v. 3, p. 561) to *S. macropoda* Pass., as it should be known.

The original description of *Septoria macropoda* is somewhat confusing in that bulbiform "basidia" are listed as  $30\text{--}40 \times 0.7 \mu$ . The material issued by Thuemen appears, from crushed pycnidia, to have cuspidate pycnophores similar to those in Oregon material on *Poa* spp. and also similar to those of *S. tritici*. It is clearly apparent that no morphological difference of any sig-

<sup>1</sup>Thuemen. Myc. Univ. (Exsiccati) No. 593. 1876.

nificance occurs between *S. macropoda* and the fungi on *Poa* spp., long known as *S. annua*. In addition, *S. macropoda* has been recognized on *P. compressa*. This host without authority citation was listed by Saccardo in 1889 (86, v. 13, p. 889). It is reported on *P. pratensis* from Iowa.

*Septoria macropoda* appears to be a polymorphic species ranging from the small spored fungus on *Poa annua* through an intermediate condition on *P. pratensis* to a variety on native-prairie species of *Poa* that has spores approaching those of *S. tritici* in size. The size of the spores of the fungus on *P. ampla* (O.S.C. 8144, 8165) is particularly close to the size of those of *S. tritici*. They differ only in the fact that the spores, which may average as large as  $60 \times 2 \mu$ , do not reach the extreme length sometimes found in *S. tritici*, the pycnidia are more irregular than in *S. tritici* and less often flattened against the epidermis of the upper side of the leaf, and have darker pigmentation in the pycnidial walls with a sharper line of demarcation between the dark outer cells and the hyaline inner layer.

The collections of *Septoria macropoda* var. *septulata* on *Poa pratensis* have intermediate size spores, which are more needle-like than those of *S. macropoda* on *P. annua*, but otherwise are similar to the species proper.

It is therefore possible to find on bluegrasses transitions from *Septoria macropoda* to *S. tritici*. Weber (117) found, furthermore, that *S. tritici* sometimes was able to attack *Poa pratensis*, although the writer has not been able to infect wheat with any of the collections of *S. macropoda* or its subdivisions. All of the collections on species of *Poa* that approach the spore size of *S. tritici* are, therefore, assigned for convenience to *S. macropoda*. Those of the collections on *P. annua* and *P. kelloggii*, which have small spores, are evidently the species proper (Figure 4). The needle-like spores of the similar material on *P. pratensis*, *P. compressa*, and *P. nervosa* (in part) (Figure 5) appear to be the same as those of *S. poae-annuae* var. *septulata* Gonz. Frag. (51), which Gonzalez Fragoso (52, p. 67) described later as *S. poae-pratensis*. The writer has made the following disposition of this form:

*Septoria macropoda* Pass. var. *septulata* (Gonz. Frag.) Sprague (97)

Syn. *S. poae-annuae* var. *septulata* Gonz. Frag., 1920 (51)

*S. poae-pratensis* Gonz. Frag., 1926 (52)

This differs from *Septoria macropoda* on *Poa annua* in having larger, needle-like spores,  $40-60 \times 1.3-1.7 \mu$ , borne in more variable pycnidia with stouter, often browner peridia. Gonzalez Fragoso (52, p. 67) illustrated needle-like spores of his *S. poae-pratensis*, which were  $30-45 \times 1.2-1.5 \mu$ .

*Septoria macropoda* var. *septulata* in Oregon consists of one weakly pathogenic race on *Poa compressa* and one somewhat variable race on *P. pratensis*. The collection on *P. nervosa* from near Lyle, Washington, appears

to be summer material of the same race that occurs on *P. pratensis*.

*Septoria macropoda* var. *septulata* is the same as the fungus Weber (118, p. 11) left unclassified in his study of the fungus on *Poa pratensis*.

The native bluegrasses, which form a considerable portion of the sod-grass range land of portions of the semiarid Columbia Basin and which have for endless periods been isolated from other species of bluegrasses, harbor a distinct variant from *Septoria macropoda* as it occurs on *Poa annua*. While it is just as reasonable to assume that this may be a variant from a larger species such as *S. tritici*, it is considered simpler to class it with *S. macropoda* as *S. macropoda* var. *grandis* var. nov. The technical description is as follows:

*Septoria macropoda* var. *grandis* var. nov.

Spores larger than in the intermediate variety, *Septoria macropoda* var. *septulata*, 50-70 x 1.5-2.4  $\mu$  (winter) to 40-60 x 1.4-1.9  $\mu$  (late spring), slightly enlarged at one end. Merges with *S. tritici* in some collections but differs in having the pycnidia typically flattened at the base more often than at the top. Pycnophores subulate to ampulliform. On *Poa ampla*, *P. nevadensis*, *P. scabrella*, *P. secunda*, and *P. vaseyochloa* in the prairies and range lands of eastern Oregon and Washington extending south on *P. nevadensis* at least to Plumas County, California, and eastward on *P. nervosa* and *P. cusickii* in Montana, and on *P. arida*, *P. canbyi*, and *P. secunda* in the Northern Great Plains to North Dakota and South Dakota. Type: On *P. secunda* Presl, High Prairie, Washington (O.S.C. 8146).

Pycnosporulis (heime) 50-70 x 1.5-2.4  $\mu$  et vere 40-60 x 1.4-1.9  $\mu$ .

*Septoria macropoda* var. *grandis* is mainly of one race (Race 1) on *Poa secunda*, but material from northern Klickitat County, Washington, on *P. vaseyochloa* differed materially in having darker colored spore masses in culture and in slight morphological characters and is called Race 2. Culture S129, obtained from *P. ampla*, differed slightly from cultures of Race 1 obtained from *P. secunda*, and in addition inoculations have been negative on *P. ampla* with material from Race 1 from *P. secunda*, while culture S129 from *P. ampla* infected that host but not *P. secunda*. The fungus from *P. ampla*, therefore, is assigned to Race 3. Since Race 1 thus far has not attacked *P. nevadensis* in inoculation trials, the fungus on this host is believed to be either Race 3 or a distinct one. The fact that Race 1 will mildly attack *P. juncifolia*, a grass closely related to *P. nevadensis*, is further suggestive.

Material on early spring foliage of *Poa secunda* from western North Dakota, particularly from the Killdeer Mountains, shows strongly curved spores 40-66 x 1.3-1.9  $\mu$ . This Northern Great Plains material is similar to Montana material of *Septoria macropoda* var. *grandis*. While the spores are

slightly more slender than is typical for the variety *grandis* from the Columbia Basin, it is closer to this variety than to the needle-like spores of the variety *septulata*. The closely related nature of all components of *S. macropoda* is disclosed by a study of the many collections available to the writer who is convinced, however, of the desirability of recognizing two varieties of this species.

Material collected during abnormally wet weather in August 1941, at Jackson, Wyoming, disclosed aberrant material on *Poa pratensis* with spores ranging from normal ones of *S. macropoda* var. *septulata* to ones similar to *S. bromi* Sacc. and swollen ones as large as *Stagonospora arenaria* Sacc. This apparently represents *in situ* arrested germination of an unusual type.

It should be added that the spores of a collection on *Poa howellii* closely resemble those of *Septoria calamagrostidis* (Lib.) Sacc. Examination of the material on an old herbarium specimen, at Oregon State College, collected at Shell Rock (Columbia River) by Thomas Howell, shows that the fungus is on this species of grass and not on a possible fragment of *Agrostis* sp. collected inadvertently with *P. howellii*. Pycnidial characters indicate relationship to *S. macropoda* and this, together with the fact that the fungus was collected in summer, leads the writer to believe that the slenderness of the spores is due partly to drought as well as to age of the herbarium specimen. Although the spores from this specimen are slightly longer and apparently somewhat narrower than those of *S. macropoda* var. *grandis*, it is tentatively referred to this variety.

The above-mentioned fungus is not like *Septoria macrosperma* Speg. (92) on *Poa forsteri* R. A. Phil. from Argentina, which has been seen by the writer. This latter is a distinct species with very long, multiseptate spores,  $75-90 \times 1-2 \mu$ .

It should be added that the falcate-spored species on *Poa* such as *Rhabdospora groenlandica* Lind (*Septoria nebulosa* Rostr. non Desm.) on *P. cenisia* All. from Greenland (65) or *S. semilunaris* Joh. on *P. glauca* Vahl from the same region (83) belong in *Selenophoma* and are distinct from *S. macropoda*. In addition, *S. oudemansii* Sacc. (86, v. 3, p. 563) (1) described originally as *S. poae* Oud. (74, p. 150) on *P. nemoralis* (75) will be further discussed in this paper.

### SEPTORIA OUDEMANSII Sacc. on POA Spp.

*Septoria oudemansii* Sacc. is an obscure but widespread parasite on *Poa* spp. The writer has collected it on *P. pratensis* in Oregon, Washington, North Dakota, Wyoming, Nebraska, and Minnesota. In addition, it was

found in material sent to him for determination by John Hardison from Ann Arbor, Michigan, by George Fischer from Culdesac, Idaho, and by W. B. Cooke from Mt. Shasta, California. While Seymour lists it on *Poa flexuosa* var. *elongata* Blytt, and on *Hierochloe alpina* (Sw.) Roem. and Schult. (91), it had not apparently been recognized in this country until the writer found it on *Poa pratensis* in Klickitat County, Washington, in February 1935.

#### SYMPTOMATOLOGY

In winter in humid western Oregon and Washington the fungus caused light purple, finally straw colored lesions on the leaves of *Poa pratensis* and *P. compressa*. Some of the spots were small and scattered, but most of them were confined to the distal parts of the leaves. In some cases extensive lesions caused death of the leaves. The light colored pycnidia were very pale and while visible to the naked eye, they were obscure, particularly when the leaves were wet.

The lesions on *Poa pratensis*, *P. compressa*, *P. canbyi*, *P. secunda*, *P. juncifolia*, and *P. nevadensis* from the Rocky Mountains and the Northern Great Plains are obscure, confined to leaf tips or are faded to neutral straw color. At Mandan, North Dakota, the fungus is not rare on *P. pratensis* and *P. canbyi*, but is usually of little economic importance. It was, however, comparatively severe in plots in late August, 1943. It is usually more common in the Red River Valley on *P. pratensis*, *P. compressa*, and in grass experimental plots occurs there on *P. nevadensis*, and on *P. arachnifera* Torr. in the Mandan plots.

#### PURE CULTURE STUDIES

The spores isolated from *P. compressa* and *P. pratensis* from Corvallis germinated slowly on potato dextrose agar, forming branching mycelium, which for some time after the colonies became visible to the naked eye was pure white. Later the margin of the white compact cottony colony turned olive gray, and the substratum became olivaceous. Older cultures were mottled gray, cream, white, and dull buff intermingled. Pycnidia were sometimes formed in pure culture.

#### MORPHOLOGY

**PYCNIDIA.** The pycnidia are yellow-brown, subglobose, somewhat erumpent and average 85-180  $\mu$  in diameter. They have well formed walls consisting of a yellow-brown outer layer, which is 6-7  $\mu$  thick surrounding a hyaline layer 4-4.5  $\mu$  thick (Plate 2, I). The outer layer is composed of



tightly packed coarse polygonal cells, which have solidly filled cell contents. The hyaline inner cells, which are smaller than the yellow-brown outer ones, give rise to bulbous pycnophores,  $4-5 \times 1.8-2.2 \mu$ . The spores often remain attached by their narrower end after the material has been sectioned and stained. The pycnidia are distinct from many of the *Septoria* spp. on grasses in their light color and large, closely packed cells. Their structure is nearer *Selenophoma* than *Ascochyta*, except that the pycnophores are atypical.

PYCNOSPORES. Material from Corvallis, Oregon, on *Poa compressa* has both microspores and macrospores present, but in most collections macrospores are more common. They are typically cylindrical, but are slightly thicker at the central septum. Some spores are tapered nearly to lanceolate form. The contents are bright hyaline with small uniform oil drops adjacent to the septum. The macrospores range from  $12-24 \times 1.7-2.8 \mu$ , averaging 7.3-9 times as long as wide. The microspores range from  $4 \times 2 \mu$  to sizes approaching those of macrospores.

Material on *Poa juncifolia* growing in plots at Mandan, North Dakota, was severely injured by *S. oudemansii* in August and September, 1943. Spores were seen in this material that ranged from true *Ascochyta* types to 3-septate ones up to  $55 \times 3-4 \mu$ . They were bacillar, hyaline, and the larger spores were slightly constricted at the septa. One mount showed spores mostly  $35-55 \times 3-4 \mu$ , and from this pure cultures were obtained that were macroscopically identical with ones obtained from the *Ascochyta* spore phase ( $11-18 \times 2.5 \mu$ ) on *Poa nevadensis* from the same plot on the same date. The colonies were at first white, but later became gray with a deep green to olive substrate on potato dextrose agar.

In pure cultures the spores from Oregon material were narrow,  $13-19 \times 1.4-1.8 \mu$ , 1-septate and straight, averaging just ten times as long as broad.

#### TAXONOMY

*Septoria oudemansii* Sacc. was originally described as *S. poae* Oud. (74), but on account of the prior name *S. poae* Catt., a quite different fungus on rice, Saccardo renamed the fungus as it is now generally known (86). Allescher proposed *Rhabdospora oudemansii* Allesch. (1), and he also suggested that the fungus possibly belonged in *Diplodina*. The description stated that the type had few minute pycnidia producing hyaline 1-septate lanceolate spores  $12 \times 2.3 \mu$ . The spores from the type represent the minimum length of western material. Since the type is not available at this time, it is not possible to determine if the scant data that is given on spore dimensions is an average for the type or simply that of a few spores seen.

The fungus that the writer discusses appears to be *S. oudemansii*. While

the most common phase of this fungus is its *Ascochyta* 1-septate condition the 1943 Mandan material justifies leaving the fungus in *Septoria*, because under certain conditions, not well understood, it reaches a *Septoria* type of development.

### SEPTORIA ELYMI Ell. and Ev. on ELYMUS and AGROPYRON

*Septoria elymi* Ell. and Ev. occurs on species of both *Elymus* and *Agropyron* in the Pacific Northwest.

#### GEOGRAPHIC DISTRIBUTION

The collections shown in Table 3 were made in Oregon and Washington.

The disease is very common on *Elymus glaucus* in late winter and early spring in pastures and second growth woods in western Oregon. The disease is also very common along creeks and in scattered oak thickets in the Columbia Gorge of Oregon and Washington as far east as central Klickitat County, Washington. The fungus occurs on *Agropyron spicatum* (Pursh) Scribn. and Smith in this latter section and is prevalent along the shores of the Columbia River on *A. inerme* (Scribn. and Smith) Rydb. and *A. repens* in certain localized areas.

*Septoria elymi* is also relatively prevalent from Minnesota and Iowa west into Montana on *Agropyron repens*, *A. smithii* Rydb., *A. trachycaulum* (Link) Malte, *A. subsecundum* (Link) Hitchc. and *Elymus canadensis* L. It occurs on *Elymus triticoides* Buckl. in coastal California and on *A. spicatum* in Wyoming.

#### SYMPTOMATOLOGY

The disease produces a leaf blotch, which varies from pale gray to tan or fuscous. The pycnidia are numerous, giving the lesions a characteristic salt and pepper aspect. The lower leaves are often all dead in severe attacks; and most of the leaves in such cases have long lesions covered with pycnidia.

#### PURE CULTURE STUDIES

Isolations developed as small pale cream, later flesh pink colonies of yeasty conidial masses. These colonies later became covered with mouse gray, short, felty growth. Isolations from species of *Agropyron* tended to produce darker carbonaceous growth than the strains isolated from western Oregon material of *Elymus glaucus*. An isolation from *E. glaucus* from

Table 3. LIST OF COLLECTIONS OF SEPTORIA ELYMI ELL. AND EV. MADE IN OREGON AND WASHINGTON

O.S.C. number and host	Location	Collection date	Dimensions of		Iso- lated
			Pycnidia	Pycnospores	
			$\mu$	$\mu$	
10,378 <i>Agropyron inerme</i> .....	Rowena, Oreg.	Feb. 18, 1934	75-137	30-43 x 1.4-2.1	+
10,925 <i>Agropyron spicatum</i> .....	Klickitat Hills, Wash.	Feb. 18, 1934	72-132	30-45 x 1.3-2.0	+
172 <i>Agropyron spicatum</i> .....	Near Wishram, Wash.	Apr. 8, 1938	80-135	29-48 x 1.4-2.0	-
28 <i>Elymus glaucus</i> .....	Corvallis, Oreg.	Dec. 15, 1937	60-80 x 55-70	30-50 x 1.3-1.7	+
44 <i>Elymus glaucus</i> .....	Oak Creek, Benton Co., Oreg.	Feb. 8, 1938		20-50 x 1.3-1.7	
78 <i>Elymus glaucus</i> .....	Near Wren, Oreg.	Feb. 21, 1938	80-125 x 60-88	35-50 x 1.2-1.6	-
89 <i>Elymus glaucus</i> .....	Wren, Oreg.	Feb. 21, 1938	85-125 x 60-75	42-75 x 1.5-2.0	+
175 <i>Elymus glaucus</i> .....	East Farm, Linn Co., Oreg.	Mar. 26, 1938	81-123 x 72-109	36-55 x 1.2-1.9	
176 <i>Elymus glaucus</i> .....	High Prairie, Wash.	Apr. 7, 1938	75-150	23-40 x 1.0-1.3	+
392 <i>Elymus glaucus</i> .....	Near Kellogg, Lane Co., Oreg.	Feb. 18, 1939	85-140 x 68-104	33-56 x 1.3-1.8	-
393 <i>Elymus glaucus</i> .....	Elk Creek, Lane Co., Oreg.	Mar. 7, 1939	90-158	36-49 x 1.3-1.9	+
394 <i>Elymus glaucus</i> .....	6½ mi. north of Eugene, Oreg.	Mar. 7, 1939	80-125 x 60-100	30-63 x 1.3-1.9	-
395 <i>Elymus glaucus</i> .....	Hardscrabble Creek, Lane Co., Oreg.	Mar. 7, 1939	80-130 x 70-100	25-50 x 1.4-1.8	-
8,065 <i>Elymus glaucus</i> .....	4 mi. east of Bingen, Wash.	Feb. 26, 1935	60-115 x 95-180	26-46 x 1.1-1.8	+
8,128 <i>Elymus glaucus</i> .....	Goldendale Valley, Wash.	Mar. 16, 1934	140-235	39-48 x 1.1-1.4	+
8,131 <i>Elymus glaucus</i> .....	6 mi. east of Bingen, Wash.	Feb. 26, 1935	110-130	33-42 x 1.4-1.6	-
8,129 <i>Elymus glaucus</i> .....	Lyle, Wash.	Feb. 26, 1935	100-135	32-44 x 1.4-1.7	-
10,393 <i>Elymus glaucus</i> .....	East Corvallis, Linn Co., Oreg.	May 9, 1935	80-120	27-49 x 1.3-1.7	+
10,411 <i>Elymus glaucus</i> .....	Peavy Arboretum, Benton Co., Oreg.	Jan. 21, 1936	105-140	35-55 x 1.4-2.1	+
10,368 <i>E. glaucus</i> var. <i>jepsoni</i> .....	Alsea Mts., Benton Co., Oreg.	Mar. 16, 1934	45-80 x 70-120	30-46 x 1.0-1.8	+

\*Plus sign indicates isolations made; minus sign indicates isolations not made.

Linn County, Oregon, and one from High Prairie, Klickitat County, Washington, produced an abundance of dark orange conidial exudate from convoluted subcarbonaceous colonies for several weeks at 5° C. Isolations from *Agropyron smithii*, Marshall, North Dakota, produced pale pink mucose masses, which eventually became covered with mouse gray, short, felty mycelium as in the Oregon isolates.

#### CROSS INOCULATION STUDIES

Most of the inoculations were made with conidia from pure cultures. Inoculated plants were incubated out-of-doors (November to March) with the leaves covered with large size (4-inch) lamp chimneys plugged with excelsior and cloth. The results of inoculations are given in Table 4.

Culture S123, isolated from *Elymus glaucus* from High Prairie, caused typical lesions on *E. glaucus*, *Agropyron dasystachyum* (Hook.) Scribn., *A. repens*, and *A. spicatum*. While it caused etching on *E. canadensis* and *E. condensatus* Presl., mature pycnidia did not develop. The plants of *E. canadensis* were grown from seed gathered on the Umatilla River near Umatilla, Oregon. On the basis of results to date the race of *S. elymi* from High Prairie attacks *E. glaucus* readily, *A. spicatum* moderately, while *E. canadensis* among others may be somewhat resistant to it. *Agropyron cristatum* (L.) Gaertn. was not attacked by it in trials made in November-December 1939. In fact, observations indicate that *A. cristatum* is resistant to most leaf-spotting fungi.

#### MORPHOLOGY

**PYCNIDIA.** On *Elymus glaucus*, the pycnidia are typically flattened, 95-200 x 60-160  $\mu$ , ostiolate, brown, subepidermal and have thin walls. The wall is composed of several intertwined layers of brown polyhedral to elongate cells. These give rise to narrowly ampulliform to subulate pycnophores, averaging 3.5  $\mu$  long and 1- to 1.5  $\mu$  wide (Figure 7, Q, M).

On *Agropyron spicatum*, the pycnidia are flattened, 65-130 x 60-115  $\mu$  and subepidermal as in *Elymus glaucus*. The structure of the wall, which is 7 to 12  $\mu$  thick, is similar to that on *E. glaucus* (Figure 7, O) and the pycnophores are subulate, 3 x 2-2.3  $\mu$ , sometimes 1-septate and up to 5 to 6  $\mu$  long.

On *Agropyron repens*, material from Wisconsin, including the type of *Septoria agropyri* Ell. and Ev. (39, p. 163), was furnished through the courtesy of the late Dr. J. J. Davis. Local material from Oregon and a collection from China also were sectioned.

The pycnidia are subspherical to flattened 80-125 x 75-120  $\mu$  (Plate 1, L)

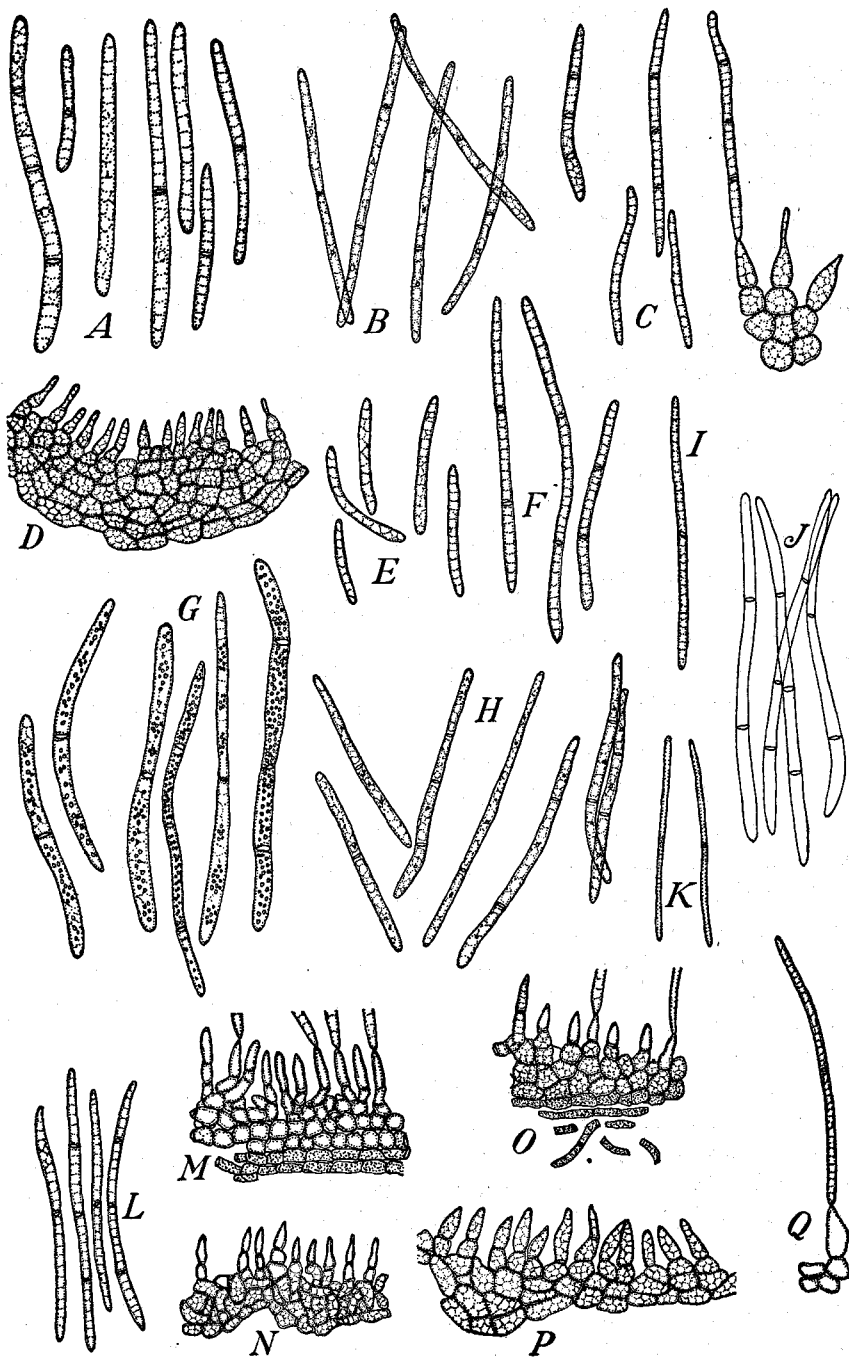
Table 4. RESULTS OF INOCULATING CEREALS AND GRASSES WITH SEPTORIA ELYMI

Plants inoculated	Number of leaves infected (+) or not infected (—) by inoculating <sup>1</sup> with cultures isolated from—							
	<i>Elymus glaucus</i> (Culture S123)						<i>Agropyron inermis</i> (Culture S79)	
	Series 1		Series 2		Series 3			
	(+)	(—)	(+)	(—)	(+)	(—)	(+)	(—)
<i>Agropyron subsecundum</i> .....	0	30	.....	.....	.....	.....	.....	.....
<i>A. cristatum</i> .....	.....	.....	.....	.....	0	130	0	38
<i>A. dasystachyum</i> .....	.....	.....	.....	.....	10	88	.....	.....
<i>A. repens</i> .....	.....	.....	.....	.....	6	90	.....	.....
<i>A. smithii</i> .....	.....	.....	.....	.....	.....	.....	8	72
<i>A. spicatum</i> .....	5	17	9	38	.....	.....	0	45
<i>Agrostis palustris</i> .....	0	115	0	132	0	105	.....	.....
<i>A. tenuis</i> .....	0	130	0	155	0	115	.....	.....
<i>Avena sativa</i> .....	0	40	0	68	0	75	.....	.....
<i>Brachypodium pinnatum</i> .....	0	37	0	100	0	100	.....	.....
<i>Bromus mollis</i> .....	0	65	0	20	.....	.....	.....	.....
<i>Dactylis glomerata</i> .....	.....	.....	0	40	0	39	.....	.....
<i>Elymus canadensis</i> .....	0	25	S <sup>2</sup>	40	.....	.....	.....	.....
<i>E. condensatus</i> .....	0	30	0	26	4	49	.....	.....
<i>E. glaucus</i> .....	3	28	19	40	17	58	.....	.....
<i>Festuca rubra</i> var. <i>commutata</i> .....	0	210	0	240	.....	.....	.....	.....
<i>Holcus lanatus</i> .....	0	112	0	105	0	100	.....	.....
<i>Hordeum vulgare</i> .....	0	55	0	45	0	33	.....	.....
<i>Koeleria cristata</i> .....	.....	.....	0	30	.....	.....	.....	.....
<i>Poa annua</i> .....	0	35	0	50	0	105	.....	.....
<i>P. nemoralis</i> .....	0	90	0	45	.....	.....	.....	.....
<i>P. pratensis</i> .....	0	70	0	175	0	210	.....	.....
<i>P. secunda</i> .....	.....	.....	0	45	.....	.....	.....	.....
<i>P. trivialis</i> .....	0	85	0	50	0	50	.....	.....
<i>Triticum aestivum</i> .....	0	48	0	55	0	60	.....	.....

<sup>1</sup>Series 1, inoculated March 18, 1938; Series 2, December 8, 1938; Series 3, November 19, 1939.

<sup>2</sup>Spotting but no pycnidia found.

Figure 7. *Septoria elymi*: A, Pycnosporos from pure culture S123 isolated from *Elymus glaucus*, Corvallis, Oregon; B, pycnosporos from *E. glaucus* var. *jepsonii*, Alsea Mts., Oregon, March 16, 1934 (O.S.C. 10,368); C, pycnosporos with fragments of hyphae including pycnophores (water mount) from *Agropyron repens* from Madison, Wisconsin, G. F. Weber, May 15, 1921; D, *Septoria* (?) *elymi* on *A. repens*, cross section of pycnidium, Silver Creek Falls, Oregon, May 25, 1935 (O.S.C. 19,282); E, *S. (?) elymi* (*Ascochyta* form) on *Agropyron repens*, near Eugene, Oregon, March 7, 1939 (O.S.C. 465); F, pycnosporos from *Agropyron ciliare* (Trin.) Franch., West Lake, Chekiang, China, R. H. Porter, April 29, 1925; G, pycnosporos from pure culture from *A. inerme*, Rowena, Oregon, February 1934; H, pycnosporos from *E. canadensis*, London, Ontario, type of *S. elymi* Ell. and Ev.; I, pycnosporos from *E. glaucus*, High Prairie, Washington, April 7, 1938 (O.S.C. 176); J, pycnosporos from type of *S. bromi* var. *elymina* Davis ad. int.; K, pycnosporos of *S. (?) elymi* from *A. repens*, Silver Creek Falls, Oregon, May 27, 1935; L, pycnosporos from type of *S. agropyri*; M, cross section of pycnidial wall on *E. glaucus*, same collection as Figure 7, I; N, cross section of pycnidial wall, on same collection as Figure 7, D; O, cross section of pycnidial wall, on *A. spicatum*, hills near High Prairie, Washington, February 18, 1934 (O.S.C. 10,925); P, cross section of pycnidial wall, on *A. ciliare* from West Lake, Chekiang, China, R. H. Porter, April 29, 1925; Q, pycnosporos with attached pycnophores from *E. glaucus*, 2 miles west of Corvallis, Oregon, February 15, 1937. (All X1000)



with most of them strongly flattened. The outer part of the cell wall is composed of somewhat elongated interwoven cells that merge with polyhedral cells of the interior. The walls are variable in thickness, some are  $5\ \mu$  thick, others thicker and up to  $13\ \mu$  (Figure 7, P). The pycnophores are prominent, subulate,  $4.8-7.5 \times 1.5-2.9\ \mu$  (Figure 7, C). They arise from globular to polyhedral cells. One collection on *Agropyron repens* from Silver Creek Falls, Marion County, Oregon, has pycnidial walls composed of small closely packed cells (Figure 7, D, N) producing numerous narrowly subulate to cylindrical pycnophores,  $3-4.5 \times 0.9-1.6\ \mu$ .

**PYCNOSPORES.** On *Elymus* spp., the spores are 0- to 3-septate, commonly 3-septate, filiform-bacillar, clear hyaline,  $25-50 \times 1.2-2.1\ \mu$  (Figure 7, A, B, H, I, J). A collection on *E. canadensis* var. *robustus* (Scribn. and Smith) Mackenz. and Bush from Rockwell City, Iowa, had 2-septate slightly stouter spores,  $40-56 \times 1.8-2.4\ \mu$ , and recently Hardison sent similar material on *E. glaucus* from Ann Arbor, Michigan.

On *Agropyron* spp., the spores are 0- to 3-septate, filiform-cylindric, blunt at the base, narrowed at the apex,  $30-45 \times 1.3-2.1\ \mu$  (rarely  $3\ \mu$ ). The only difference between the spores on *Elymus* spp. and those on *Agropyron* spp., is the tendency for those of the latter to be more nearly cylindrical than those on *Elymus* spp. (Figure 7, C, F, G, L). The difference is slight.

#### TAXONOMY

*Septoria elymi* Ell. and Ev. (37, p. 132) was described on *Elymus canadensis*, as having spores  $15-25 \times 1.5-2\ \mu$ . The writer examined type material from London, Canada, and found spores  $23-42 \times 1.6-2.3\ \mu$  (Figure 7, H). The fungus on *E. glaucus* from Oregon and Washington is the same as *S. elymi* Ell. and Ev. (non Rostr. 82).

While there are no other species of *Septoria* described on *Elymus* that are close to *S. elymi*, there are a number of species on *Agropyron* spp. that must be considered.

*Septoria phyllachoroides* Pass. (78, p. 102; 86, v. 10, p. 403) has pycnidia in a phyllachoroid matrix and spores cylindrical, straight or curved, obscurely 3-septate, hyaline,  $25-35 \times 2.5-3.0\ \mu$ . Another fungus of this kind, *Stagonospora inquilina* Bub. et Picb. is associated with *Phyllachora graminis* with spores  $15-22 \times 3-3.5\ \mu$ . Still another fungus, *S. fusispora* Died., is similar to *S. phyllachoroides* but it is near to *S. nodorum* according to Rosen (81). All of this group and also a fungus collected by F. D. Bailey on *Agropyron repens* near Seaside, Oregon, are referable to *Stagonospora*, the latter to *St. arenaria* Sacc., and have no connection with *S. elymi*. *Septoria agropyrina* Unamuno (110) also is very different from *S. elymi* from Oregon, as *S. agropyrina* has



continuous, very large fusiform spores,  $46.5-71.5 \times 3-3.5 \mu$ . Bisby, Buller, Dearness et al. (10), report a large spored *Septoria* on *A. tenerum* [*A. trachycaulum* (Link) Malte] and *A. richardsoni* Schrad. [*A. subsecundum*] from Manitoba. These collections, which they referred to *S. agropyri* Ell. and Ev., have spores  $37-52 \times 2-3 \mu$ . *Septoria agropyri-ramosi* Muraschkinski (59) has large, yellowish-green 8- to 15-septate spores,  $74-126 \times 8.5-11 \mu$ . It is distinctly different from any species of *Septoria* on *Agropyron* spp. from Oregon that have been seen to date.

*Septoria agrestis* Sacc. (*S. agropyri* Brun.) (14) is a synonym of *S. elymi* Ell. and Ev. *Septoria agrestis* Sacc. has been reported on *Agropyron intermedium* (Host) Beauv. and on wheat by Zaprometoff (120) from Central Asia.

*Septoria agropyrina* Lobik (67) has large spores  $30-60 \times 2.5-4.5 \mu$ , which are pointed at the apex, but otherwise similar to *Stagonospora arenaria* Sacc. These forms will not be considered in this article, other than to be briefly discussed under *S. infusans* (Ell. and Ev.) Spr.

Because of nearly identical morphology and of interchangeable host range, *Septoria elymi* and *S. agropyri* are considered the same species, and since *S. elymi* (37, p. 132) is the older name, *S. agropyri* (38, p. 163) becomes a synonym. The differences between the fungus on *Elymus* spp. and that on *Agropyron* spp. are barely worthy of morphological note. The differences represent only strong racial differences. The fungus on *E. glaucus* appears to be a race that is somewhat distinct physiologically from the one on the midwestern *E. canadensis* and somewhat specialized on *E. glaucus* but capable of attacking *Agropyron* spp. in the Columbia River Basin.

The synonymy of *Septoria elymi* is as follows:

*Septoria elymi* Ell. and Ev., 1892 (37)

Syn.: *S. agropyri* Ell. and Ev. 1893 (38)

*S. agropyri* Brun., 1893 (14)

*S. agrestis* Sacc., 1895 (86, v. 11, p. 547)

*S. elymicola* Died., 1912 (32, p. 480)

*S. bromi* var. *elymina* J. J. Davis, 1924 (27)

A collection on *Agropyron repens* (O.S.C. 465) from 6 miles north of Eugene, Oregon, had 0- to 1-septate spores,  $11-19 \times 1.5-2.1 \mu$  (Figure 7, E). These occur in thin-walled ellipsoidal pycnidia (Plate 1, N) found in fuscous spots with pale centers. Cross sections of pycnidia show well formed walls composed of brown polyhedral cells giving rise to prominent, subulate pycnophores very similar to those of *Septoria elymi*. In pure culture, the fungus produces a yeasty growth, which later becomes shiny black. Spore exudates are gray-cream colored. The spores in culture are  $9-15 \times 2-3 \mu$ , but many

become swollen and variously distorted ( $7-35 \times 3-9 \mu$ ), however. The fungus is possibly near *Ascochyta elymi* Tehon and Daniels (104), or it may be the same as the inadequately described *A. graminum* Lasch.<sup>1</sup> The Oregon fungus is not a good *Ascochyta* because in pure culture its growth is typical *Septoria*, and the spores are narrow, even though scarcely ten times as long as broad (actually nine times). The culture of the fungus resembles *S. elymi* and it can possibly be assigned to this species.

The collection on *Elymus canadensis* var. *robustus* (*E. robustus* Scribn. and Smith) from Rockwell City, Iowa (Archer and Layton, No. 690) is assigned to *S. elymi*, but the 2-septate spores are larger than the typical spores for *S. elymi*. It is similar to Davis' *S. bromi* var. *elymina* (27, p. 292) (Figure 7, J), and to Hardison's material from Ann Arbor, Michigan. Material on *A. smithii* from Marshall, North Dakota, which was isolated in pure culture and proved similar to Oregon *S. elymi*, also had stout spores.

*Septoria cristata* Hollós (51, p. 6) may be the same as *S. gracilis* Pass. and both are apparently distinct from *S. elymi*. They have not been seen. Possibly they are species of *Selenophoma*.

The specimen on *Agropyron* from Silver Creek Falls, Oregon, has very narrow spores (Figure 7, K) and it may represent a semimicrosporous condition in *S. elymi*.

## SEPTORIA INFUSCANS (Ell. and Ev.) Sprague<sup>2</sup> on ELYMUS Spp.

### SYMPTOMATOLOGY AND DISTRIBUTION

*Septoria infuscans*, which is generally known as *Cylindrosporium infuscans* Ell. and Ev., was originally collected by Horner, on giant wild rye, *Elymus condensatus*, near Waitsburg, Washington. Since the date of description, 1902 (41), the fungus on this host has received scant attention, although it is often exceedingly common in late spring and during the summer months in the interior of Oregon and Washington. It produces fuscous brown to gray vague lesions, which in late spring, particularly following rains in May or June, sometimes give this grass a scorched appearance. Besides on the giant wild rye, the fungus is very common in summer and fall on *E. triticoides* in eastern Oregon and Washington. It occurs also on *E. glaucus*, in the vicinity of the Columbia Gorge just east of the Cascade Mountains, and was collected once in the John Day River Canyon, Gilliam County, Oregon, on

<sup>1</sup>In Rabenhorst, L., Klotzschii Herbarium vivum Mycologicum, sistens Fungorum per totum Germaniam crescentium collectionem perfectam. Cent. 12, No. 1155, 1847. (Reviewed by S[chlechtendahl] in Bot. Zeitung 6: 292-295. 1848. See p. 293.)

<sup>2</sup>In Cooke, Wm. Bridge, Mycobiota of North America, No. 113. 1940 (Exsiccati).

*Agropyron spicatum*, which was growing in the shade of *E. condensatus* that was heavily infected with the fungus.

During June 1939, a particularly heavy infection of *Septoria infuscans* was seen and collections made on *Elymus condensatus* from Wasco, Sherman, Gilliam, and eastern Umatilla counties, Oregon. Infection appeared to have started from macrospores still present on the old leaves of previous years. Most of the current crops of pycnidia contained microspores.

Outside of the Columbia Basin *S. infuscans* produces fuscous to chocolate mottling on the leaves and culms, or more often, the lesions become white in the center and finally stramineous. The lesions are particularly vague on *Elymus triticoides* in California, and on *E. condensatus* in Montana and Wyoming.

#### PURE CULTURE AND ARTIFICIAL INOCULATION STUDIES

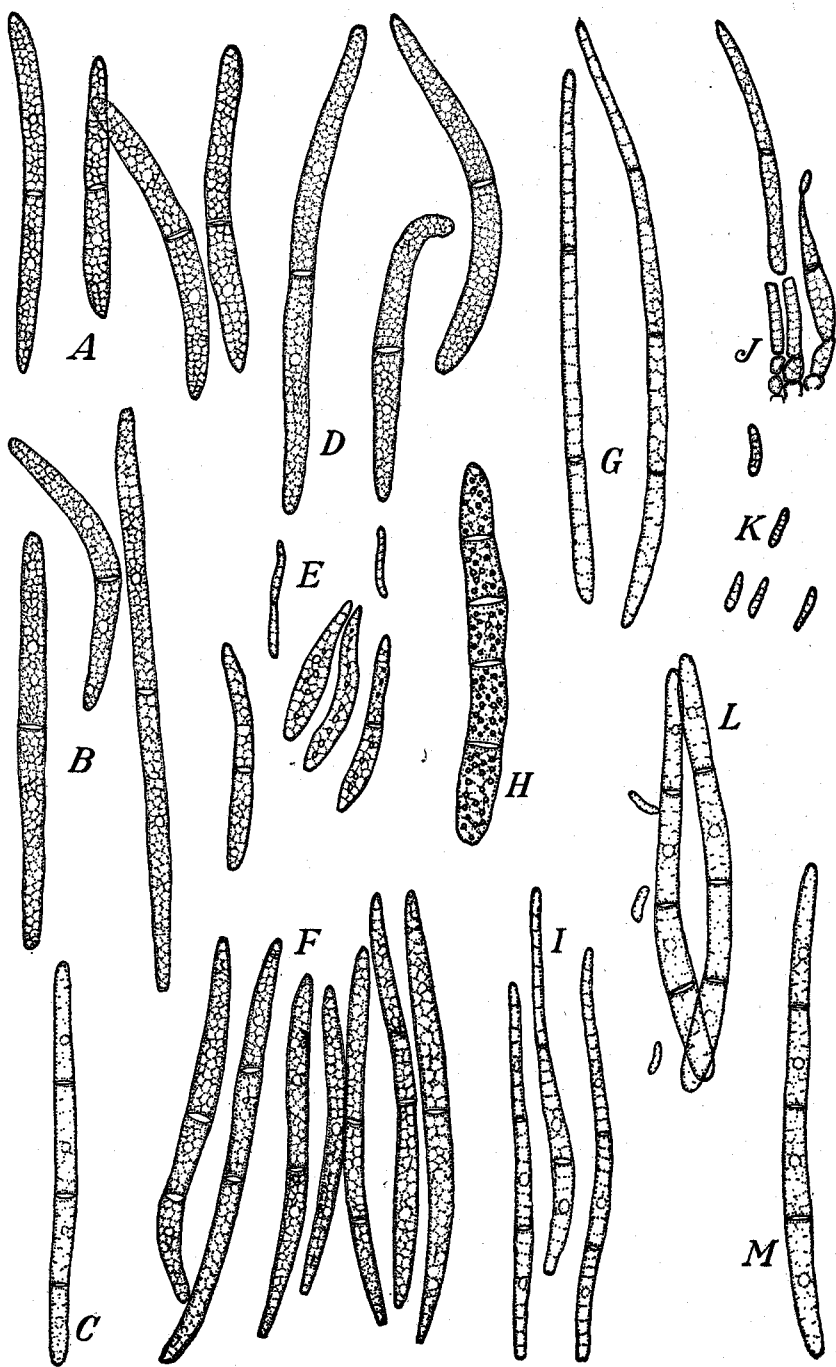
Isolations of *Septoria infuscans* from *Elymus triticoides* and *E. condensatus* from Sherman County, Oregon, and from *E. triticoides*, Davis, California, produced mounded, knobby colonies of a dull gunmetal gray. These colonies eventually produced pycnosporos, which oozed from the pycnidia as congo pink to flesh pink masses. The yeasty, initial conidial formation, typical for most species of *Septoria*, is lacking in this species to a very large extent. The spores in pure culture vary from normal appearing ones with one or two septa to aberrant forms with swollen cells and coarse granular contents. Others have as many as four septa (Figure 8, H). One isolate from *E. condensatus*, La Crosse, Washington, produced a weak mucose growth, which was cream colored, finally brown. This isolate was obtained from spores  $51-57 \times 2.1-2.3 \mu$ .

Inoculations with pycnosporos from pure cultures from *Elymus condensatus* were negative at Corvallis (February, 1939) on *E. condensatus*, *E. glaucus*, *E. mollis* Trin., *Agropyron repens*, *Poa pratensis*, *Holcus lanatus*, and *Triticum aestivum*. Inoculations in December 1939, produced typical lesions on *E. condensatus*, but none on *A. repens*, *P. pratensis*, *H. lanatus*, *Avena byzantina*, *Festuca rubra* L., *Agrostis* spp., *Triticum aestivum*, and *Hordeum vulgare* L.

#### MORPHOLOGY

**PYCNIDIA.** While *Cylindrosporium infuscans* was described (41) as an acervulus-producing species, examination of a considerable number of sections of available collections shows that the species invariably produces pycnidia (Plate 2, P). On *Elymus condensatus* in central Oregon and Washington, these are covered-cupuliform or elliptical in cross section. They measure

Figure 8. Pycnospores of *Septoria infuscans*: A, from *Elymus triticoides*, Warwick, Washington, June 26, 1937 (O.S.C. 8378); B, from *E. triticoides*, Warwick, Washington; collected September 25, 1937, with longer spores; C, from *Elymus* (?) *condensatus* collected by P. A. Young, Yellowstone National Park, June 27, 1925; D, from *E. condensatus* near Warwick, Washington, September 25, 1937 (O.S.C. 8392); E, microspores and malformed macrospores in pycnidia from *E. condensatus* near Biggs, Oregon, October 13, 1938; F, from *E. triticoides* near Moro, Oregon, June 17, 1939, showing some spores multiseptate; G, from *E. triticoides*, Davis, California, May 16, 1939; H, from pure culture isolated from *E. condensatus* near Biggs, Oregon; I, from *E. triticoides*, Klamath Falls, Oregon (O.S.C. 10,308); J, micro- and macropycnospores and attached pycnophores from *Elymus triticoides* near Wasco, Oregon, October 13, 1938 (O.S.C. 269); K, microspores from *E. condensatus* (O.S.C. 8392); L, from *E. condensatus*, Logan, Utah (B.P.I. 80,048); M, from *E. condensatus*, Kalispel, Montana, in linear white (faded) spots (B.P.I. 80,846) July 16, 1941. (All X1000)



70-110 x 75-180  $\mu$ . Very often they are flattened on top because they are not able to force the very stout host cells outward as do many other species of *Septoria*. Instead, the accumulation of hyphae produces a pseudoclypeus in some cases, or in other instances secondary thickenings form about the ostiole or from the inner surface of the ostiolar portion of the pycnidium. In the fungus on *Elymus glaucus* (O.S.C. 8444), the pycnidial wall was only 5 to 10  $\mu$  thick, but in those on the other hosts, it was thicker, 15 to 25  $\mu$ . It consisted of an outer layer of coarse, somewhat elongate cells made up of one (rarely) to three layers of brown cells, 6 to 13  $\mu$  thick. These contrasted abruptly with a hyaline inner layer of rounded to angular cells, giving rise to subspherical pycnophore initials from which the pycnophores (Figure 9, B) arise. The pycnophores were of two sorts. Those producing macrospores were botuliform to ampulliform, sometimes 1-septate, and varied in size from 3-8 x 1.5-3.5  $\mu$  (Figure 9, B, D). In some cases the pycnophores appeared to be poorly formed as though the spore grew directly from the ends of scarcely differentiated oblong hyphae.

Material of *Septoria elymi-europaei* Jaap on *Elymus europaeus* L. from Bavaria, which was used in comparing American material, has prominent subglobose pycnidia (Plate 1, B), many of which were found to be partly filled with prosenchymatous material (Plate 2, H) (compare with Plate 1, B). This seems to have formed by continuation of vegetative growth in the interior of the pycnidia following the production of pycnospores. A similar condition was noted in Tracy's collection of *Septoria* sp. on *Elymus virginicus* from Starkville, Mississippi.

A collection on *Elymus triticoides* from Klamath Falls, Oregon (O.S.C. 10,380) has large pycnidia, which measure up to 200  $\mu$  long and 130  $\mu$  deep. The walls were thin in comparison to the size of the pycnidia, measuring from 5.5 to 15  $\mu$  thick. They consisted of several layers of closely packed brown cells, which appear corky. The inner layer of cubical to polyhedral, hyaline cells produces the narrow pointed pycnophores. The pycnophores are very numerous, particularly on the somewhat flattened base of the pycnidium. They measure 4-6 x 1.1-2.0  $\mu$ . Collections on *E. triticoides* from Tudor, California, and Davis, California, May 1939, had thicker walls than the material from Klamath Falls, Oregon (Plate 1, E).

The pycnidia from the collection on *Elymus* (?) *condensatus* made by Young in Yellowstone National Park are golden brown, mostly 100-180 x 90-145  $\mu$  and have well developed ostioles (22-30 x 16-20  $\mu$ ), which are surrounded by brown pigmented cells (Figure 9, D). The pycnidia are more or less subglobose and with walls very thin in Young's specimen, as well as in those on *E. virginicus* from Starkville, Mississippi, and the one on *E. triti-*

*coides* from Klamath, Oregon. The walls are composed of two outer layers of oblong cells from which a single layer of hyaline hyphae produces tapering, sometimes curved, and occasionally 1-septate, pycnophores,  $5-9 \times 1.8-2.3 \mu$ .

The pycnophores that produced microspores, which can be termed micro-pycnophores, were tightly packed, narrowly ampulliform or fusiform,  $8-10 \times 1.0-1.5 \mu$  (Figure 9, C). On *E. condensatus* they are sometimes produced alone in globular pycnidia, which are about  $100 \mu$  in diameter, and which otherwise are identical in structure in pycnidia producing macrospores. In some cases, microspores are produced on what appear to be aborted macrospores (Figure 8, E). In other cases, microspores are produced just inside the ostiole (Figure 9, A). In still other cases, they are scattered among the macrospores. Apparently, the microspores are produced later than the macrospores as they appear to develop as a somewhat secondary condition of late "staling," following dry weather after heavy rains that had broken a previously rainless period, as in June 1937 (Figure 9, A).

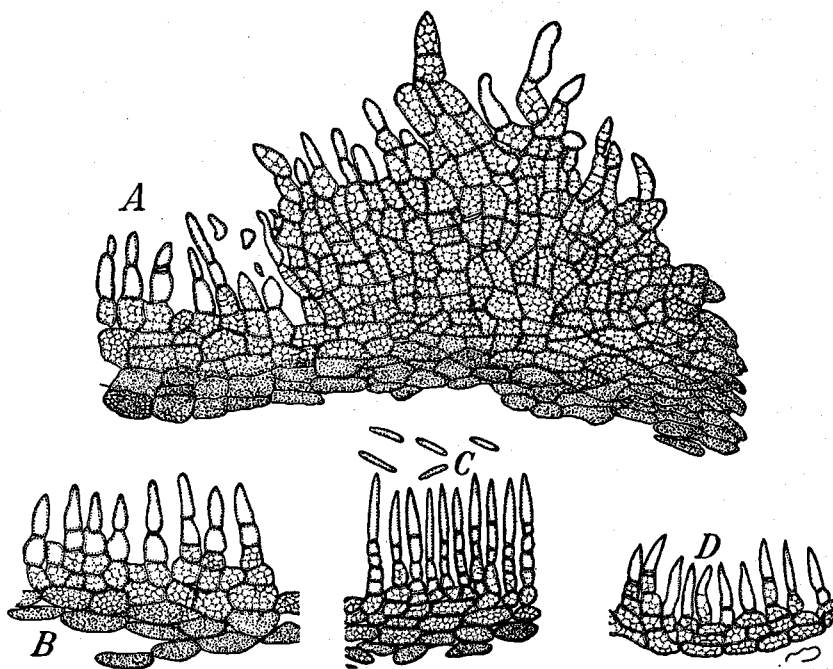
**PYCNOSPORES.** The macrospores, the typical pycnospores, on *Elymus condensatus* are blunt at the base and taper to a stubby point at the distal end and are stout clavate in outline with a tendency to bend at their one central septum (Figure 8, D). They measure  $28-50 \times 2.1-4.5 \mu$  in recently collected material. The type is stated to have nonseptate spores measuring  $44-55 \times 3-4 \mu$ . Their contents, which are hyaline, tend to stain as a network of protoplasmic granules. Collections on *E. glaucus* are restricted to a region immediately east of the Columbia Gorge. The spores on the latter host are variable, but resemble those on *E. condensatus*. The collection on *Agropyron spicatum* has large 1-septate spores.

Some collections on *Elymus triticoides* show spores that are identical with the clavate 1-septate spores of *Septoria infuscans* (Figure 8, A, B) on *E. condensatus*. One collection, made near Moro, Oregon, of the same form had spores showing more than one septum but otherwise similar (Figure 8, F).

Microspores have been noted on *Elymus condensatus*, *E. triticoides*, and *E. glaucus* in the Pacific Northwest. The hyaline nonseptate spores are very small,  $5-7 \times 1.0-1.5 \mu$  or sometimes smaller ( $4-7 \times 0.7-1.5 \mu$ ) and are narrowly ovate, short cylindric, straight, or often curved (Figure 8, E, J, K, L). Without careful study, they would never be recognized as part of the life cycle of the same fungus that produces the comparatively gigantic macrospores. There is no question as to their identity as genetic connection through mycelia can be traced from one spore form to the other in pycnidia. In some cases, the microspores appeared to develop almost saprophytically on the mature pycnidia (Figure 9, A) that had been checked by dry weather. In one

Figure 9. *Septoria infuscans*: A, Cross section of top of pycnidium from *Elymus condensatus* near Warwick, Washington (O.S.C. 8392), showing secondary development near ostiole (at right) accompanying microspore formation; normal thickness of peridium shown at the extreme left; B, cross section of pycnidial wall from *E. condensatus* at base of pycnidium showing macropycnophores, near Warwick, Washington (O.S.C. 8392); C, cross section of pycnidial wall from *E. condensatus* from same collection as in Figure 9, A, (O.S.C. 8392), showing development of micropycnophores and microspores; D, cross section of pycnidial wall from *Elymus condensatus*, Yellowstone National Park, P. A. Young, June 27, 1925. (All X1000)





collection made October 13, 1938, on *E. condensatus*, the contents of the pycnidia had broken up into microspores. These were produced in clusters, in chains, and on the ends of variously distorted macrospores (Figure 8, E), which ranged in length down to nearer the size of the microspores than is usually encountered.

*Septoria elymi-europaei* was described (58) as having pycnosporos 70 x 2-3  $\mu$ , while Jaap's collection from Bavaria, which is presumably the same species, was found to have pycnosporos 55-70 x 2-2.4  $\mu$ . The pycnosporos, however, are slightly plasmolyzed in the latter collection. They are hyaline, stiffly curved, narrowly obclavate, 2- to 4-septate (Figure 10, C).

Collections on *Elymus triticoides* from Oregon to California, which resemble *S. elymi-europaei*, are also stiffly curved to nearly straight, narrowly clavate, 1- to 4-septate, 40-75 x 1.7-2.7  $\mu$  (Figure 8, G, I). Young's collection on *E. (?) condensatus* has diamond-blue to clear-hyaline spores, 31-56 x 2.4-3.5  $\mu$  (average 40.6 x 3.0  $\mu$ ) (Figure 8, C). The bases of the spores are blunt with rounded or square corners. Mature spores from Young's collection are 3  $\mu$  or more wide, 3- often 4-septate, less often 1-septate, scarcely ever 2-septate. On the other hand, most of the spores from Tracy's collection from Mississippi are 2-septate, 44-51 x 1.8-2.9  $\mu$  (Figure 10, E).

The abundant but obscure material on species of *Elymus* and *Agropyron* from Montana and Utah east to the Dakotas and Nebraska have 1- to 3-septate spores similar to Young's material. Some spores reach 65  $\mu$  long (Figure 10, G) and are filiform obclavulate, often blunted at the base and pointed or blunted acuminate at the apex (Figures 8, L, M, 10, E, F, G, H, I, J). Isolations prove that some if not all of the material east of the Rockies is *Stagonospora arenaria* Sacc. or a *Septoria* similar to *Septoria agropyrina* Lobik. This material will not be considered further in this article. There is no direct evidence that *S. infuscans* extends east of the Rocky Mountains.

#### TAXONOMY

The fungus that Ellis and Everhart placed in *Cylindrosporium* unquestionably belongs in *Septoria*. The following disposition has been proposed: *Septoria infuscans* (Ell. and Ev.) Sprague

Syn.: *Cylindrosporium infuscans* Ell. and Ev., 1902 (41)

The very broad clavate 1-septate spores on *Elymus condensatus* clearly distinguish it from other species of *Septoria* on Gramineae. Multiseptate spores, however, in material from *E. triticoides* from northern Oregon show multiseptate tendencies, which become the rule in California, and on *E. condensatus* east of the Columbia Basin. It is our belief that the more or less aberrant form on *E. condensatus* that unfortunately is the type, is the same

fungus as the more slender, much more widespread form that resembles *S. elymi-europaei* Jaap (58). They act virtually the same in culture and there are all transitions between them, including symptoms, which range from mot-tles to true spots. To define clearly the limits of this group would require description of several subspecies. For instance, while specimens from Klam-ath Falls, Oregon, and Davis, California, are very similar to *S. elymi-europaei*, the blunter material, such as occurs in the Rocky Mountains, is more like *S. infuscans* (Figure 8, L, M), except that it is 1- to 3-septate on *E. condensatus*, and usually is produced in faded spots. Some material from Utah has 3-sep-tate, very stout spores (Figure 8, L). Whether the European *S. elymi-europaei* is different from the narrow multiseptate phase of *S. infuscans* is a point needing study. If the European material produces colonies similar to *S. infuscans* it is likely that it is the same as that species. Even the isolation from La Crosse, Washington, which produced a weak mucose growth, rather than small mounds, produced the typical aberrant spore forms ranging from true *S. elymi-europaei* types to microspores and 1-septate *S. infuscans* types. This species shows indications of Hansen's dual phenomenon (55).

### SEPTORIA PACIFICA Sp. Nov. on ELYMUS MOLLIS

A fungus, distinguished from all other species of *Septoria* on *Elymus* spp. by its very long pycnospores, occurs on *Elymus mollis* Trin. in Oregon.

#### SYMPTOMATOLOGY AND DISTRIBUTION

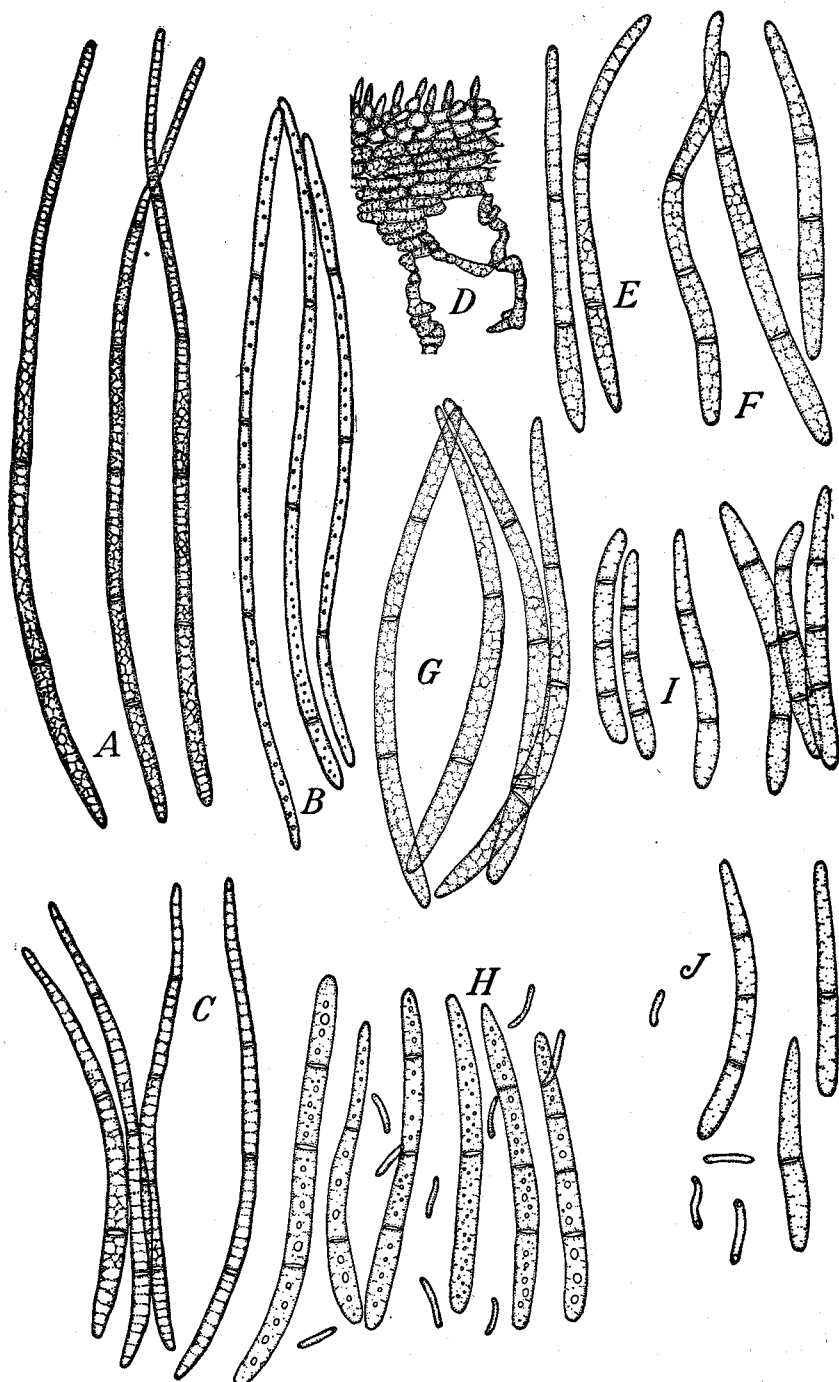
This fungus on *Elymus mollis* has been found only along the ocean beaches and dunes from Waldport, Oregon, north to the vicinity of Tillamook and Twin Rocks, Oregon. The fuscous lesions soon become straw-colored, leaving the prominent dark pycnidia as streaks on the coarse dead leaves of the host.

A fungus on *Elymus condensatus* and its var. *pubens* Piper, very similar to *Septoria pacifica*, was collected in central California in 1941 by H. W. Johnson. Recently it was found on *E. glaucus* in the plots at Mandan, North Dakota, on plants grown from western seed.

#### PURE CULTURE AND ARTIFICIAL INOCULATION STUDIES

Isolations were obtained with some difficulty from *Elymus mollis*. The colonies were pale caenstone-colored and eventually became covered with small, rounded, black, stromatic tissue, which exuded white spore masses. The colonies were very similar to those of *Septoria infuscans* except in the

Figure 10. *Septoria infusans*, *S. elymi-europaei*, *S. pacifica*, and *S. agropyrina* Lobik: A, Pycnospores of *S. pacifica* from *Elymus mollis*, 5 miles south of Newport, Oregon (O.S.C. 36); B, pycnospores of *S. pacifica* from *E. mollis*, 4 miles north of Waldport, Oregon, W. B. Cooke, February 25, 1938 (O.S.C. 421); C, pycnospores of *S. elymi-europaei* from *E. europaeus*, Bavaria near Obersdorf, August 10, 1917, collected and determined by Otto Jaap; D, cross section of pycnidial wall of *S. pacifica* on *E. mollis*, Waldport, Oregon (O.S.C. 421); E, pycnospores of *S. agropyrina* from *E. virginicus*, Starkville, Mississippi, S. M. Tracy; F, pycnospores of *S. agropyrina* from *Agropyron smithii*, Lincoln, Nebraska, September 12, 1940; G, *S. agropyrina* from *A. smithii*, Forsythe, Montana; H, *S. (?) agropyrina* from *A. repens*, Vermillion, South Dakota, September 14, 1940; I, *S. agropyrina* from *A. trachycaulum*, Tagus, North Dakota, July 17, 1940; J, *S. agropyrina* from *Elymus canadensis*, Leonard, North Dakota, October 1, 1940. (All X1000)



color of the spore exudate. All were characterized by their small pellet-like shape.

Pure culture inoculations with an isolation from *Elymus mollis* were negative in one trial, on *E. mollis*, *E. glaucus*, *Agropyron repens*, *Triticum aestivum*, *Lolium perenne*, and *Poa pratensis*. The fungus appears to develop only on mature plants in the Pacific Northwest and is apparently a very slow growing fungus.

#### MORPHOLOGY

**PYCNIDIA.** The pycnidia of *Septoria pacifica* on *Elymus mollis* are just beneath the epidermal layer of the host and are imbedded in the extremely glassy subepidermal layers of the leaf (Plate 2, K). They are nearly spherical or even slightly flask-shaped, are black with heavy walls (Plate 2, K). The outer portion of the wall contains five to eight layers of strongly pigmented oblong cells that terminate in a loose outer ramifying structure of branched mycelia that penetrates for some distance away from the pycnidium (Figure 10, D). Inside the outer layer of pigmented cell wall, and attached mycelia, are three or four layers of intertwined subcubical to polyhedral cells that give rise to narrowly flask-shaped pycnophores (Figure 10, D).

**PYCNOSPORES.** The pycnospores in winter collections are hyaline, fili-form, 1- to 8-septate,  $68-110 \times 1.6-3.5 \mu$  (Figure 10, A, B). In spring collections, the spores are smaller,  $60-85 \times 1.5-2.5 \mu$ . They vary from some that are nearly clear-hyaline to others that have small chlorinous droplets in the protoplasm.

#### TAXONOMY

*Septoria pacifica* has pycnospores distinctly longer and slightly narrower than *S. elymi-europaei* and the pycnidial walls are thicker. While it appears to be related to the later species, the differences between the two fungi necessitate segregation. The following, therefore, is proposed:

**SEPTORIA PACIFICA** sp. nov.

Maculis fuscis v. stramineis; pycnidiis prominulis, seriatim suberumpentibus, ostiolatis, globosis,  $110-150 \mu$  diam. nigris; peridiis parenchymaticis; pycnophoris filiformi-ampulliformibus; pycnosporulis filiformibus, hyalinis, 1- to 8-septatis,  $60-110 \times 1.5-3.5 \mu$ .

Hab. in foliis dejectis *Elymi mollis*, Oregon prope Marem Pacificem.

Spots fuscous soon bleaching to straw color; pycnidia black; seriately arranged, prominent, globose, sunken but erumpent, tardily ostiolate, walls heavy parenchymatous to pseudocorky,  $110-150 \mu$ ; pycnophores narrowly ampulliform, hyaline; pycnospores strongly 1- to 8-septate, filiform;  $68-110 \times 1.6-3.2 \mu$  (winter),  $60-85 \times 1.5-2.5 \mu$  (spring).

On necrotic leaves of *Elymus mollis* in Oregon along the Pacific Ocean. Type is O.S.C. 10,376, collected November 15, 1935, by R. Sprague and J. R. Kienholz at Waldport, Oregon.

*Septoria ammophilae* H. and P. Syd. on *Ammophila arenaria* (L.) Link has large, golden, hypophyllous pycnidia (Plate 1, A), with curved or hooked spores,  $48-60 \times 2 \mu$ . It is very distinct from *S. pacifica* and incidentally, does not resemble any species of *Septoria* on Gramineae seen in the Pacific Northwest. *S. arenaria* Rostr. (82) on *Psamma arenaria* Roem. and Schult. [*Ammophila arenaria*] has exceedingly narrow spores,  $60-100 \times 0.5-1 \mu$ . It has not been seen by the writer.

### SEPTORIA PASSERINII Sacc. on HORDEUM Spp.

*Septoria passerinii* Sacc. was collected on *Hordeum vulgare* L. by H. P. Barss at Corvallis, Oregon, May 7, 1921 (O.S.C. 10,523). Considerable search has failed to disclose the presence of the disease on barley during the past ten seasons. One collection was reported by the writer<sup>1</sup> on *H. nodosum* L. from Benton County, Oregon, 1938, and another collection on the same host was made by the writer in June 1939, also in the same county. The fungus has been reported from Idaho (3) although more recently Shade<sup>2</sup> did not include it in his list. Recently the writer has found *S. passerinii* very abundant and destructive on *Hordeum jubatum* L. in the Dakotas and on *H. nodosum* in eastern Montana, Wyoming, and Washington; it was once collected on *Hordeum brevisubulatum* (Trin.) Lk. in plots at Mandan, North Dakota.

### SYMPTOMATOLOGY

The fungus produces fuscous lesions on the leaves and sheaths. In severe attacks the leaves turn yellow, then brown after death. The pycnidia are only moderately conspicuous against the strongly fuscous lesions. The collection made in June 1939, on *Hordeum nodosum*, had strongly fuscous to dark brown lesions confined to the culms and sheaths.

### MORPHOLOGY

**PYCNIDIA ON HORDEUM VULGARE.** The pycnidia are creosote brown, mostly subglobose, scarcely erumpent, 90 to 140  $\mu$  in diameter and up to 100  $\mu$  deep (Corvallis material) (Plate 2, D). The walls are relatively thin,

<sup>1</sup>Sprague, R. Notes on diseases of cereals and grasses in Oregon and adjacent counties in Washington during the spring of 1938. Plant Disease Reporter 22: 174. 1938.

<sup>2</sup>See footnote on page 17.

5 to 10  $\mu$ , composed of strongly pigmented cells consisting of an outer layer of crushed, intertwined oblong cells and an inner layer of polyhedral cells. The pycnophores are somewhat filiform to subulate, 3.4-5 x 1.2-1.8  $\mu$  (in plasmolyzed material), and are mainly confined to the lower half of the inner pycnidial wall.

**PYCNIDIA ON HORDEUM NODOSUM.** Pycnidia are brown, ellipsoid, erumpent, thin-walled (3 to 8  $\mu$ ) (Figure 11, G, H) and measure 95-140 x 72-95  $\mu$ .

**PYCNOSPORES.** There are two kinds of pycnospores: macrospores and microspores.

The macrospores on *Hordeum nodosum* from Oregon are broadly filiform, obtusely pointed at both ends, rarely curved, 1-, sometimes 3-septate, 22-44 x 1.5-2.2  $\mu$ , with a mean size of 29 x 1.65  $\mu$  (Figure 11, A, F). Saprophytic overwintering spores on *H. nodosum* from 12 miles south of Sydney, Montana, are larger, 45-70 x 1.8-2.4  $\mu$ , but typical lesions on early season growth (May 22, 1941) on *H. nodosum* in Montana showed typical, curved spores 30-43 x 1.6-2.0  $\mu$ .

Microspores have been found on *Hordeum distichon* L. and *H. nodosum*. A collection (labeled *S. briosiana* Mor.) on *H. distichon* L. collected in the Kiev area in Russia by N. Gorscaruk, July 31, 1923, has typical bacteria-like microspores, 3-6 x 0.3-0.6  $\mu$  in pycnidia that are typical for *S. passerinii* (Plate 2, M). Microspores were found in large numbers on *H. nodosum* collected June 1939, in Benton County, Oregon.

#### TAXONOMY

This fungus, which was adequately discussed by Weber (118), who assigned it to *Septoria passerinii* Sacc., appears to be this species.

#### SEPTORIA PASSERINII Sacc. on SITANION HYSTRIX

One meager collection of a leaf spot disease was made in mountainous pine country west of Dufur, Oregon, at the edge of the Mt. Hood National Forest, May 5, 1933.

#### SYMPTOMATOLOGY

The pycnidia are clustered in fuscous to stramineous areas on dying leaves. The lesions, which are vague, often occupy the entire leaf.

#### PURE CULTURE STUDIES

Young colonies on potato dextrose agar were at first pale flesh colored, but the conidial masses soon became dirty pale brown and eventually, after



several weeks (5° C.), became coffee-brown. Finally, the spores germinated and a glistening creosote brown carbonaceous mass developed that eventually dried to dull black.

#### MORPHOLOGY

**PYCNIDIA.** The pycnidia are nearly spherical, black, sunken in the leaf tissue with a few fungus cells penetrating into the stomatal opening between the guard cells and are 77 to 120  $\mu$  diameter and 55 to 100  $\mu$  high (Plate 2, B). The peridium is about 7  $\mu$  thick, but is somewhat thicker (12  $\mu$ ) in places where the mycelium aggregates between the host cells. The mycelium is composed of dark brown polyhedral to elongate cells tightly packed and intertwined. The outer layers are elongated. The pycnophores vary from the small, slightly blunted ones, 2.1-5.0 x 1.2-1.6  $\mu$ , in prepared material, to somewhat larger ones that are a continuation of polyhedral cells arranged in tiers (Figure 11, C).

**PYCNOSPORES.** The pycnospores are 1- to 3-septate, narrowly obclavate to nearly filiform, 14-46 x 1.3-2.0 (mostly 40 x 1.4)  $\mu$  (Figure 11, E).

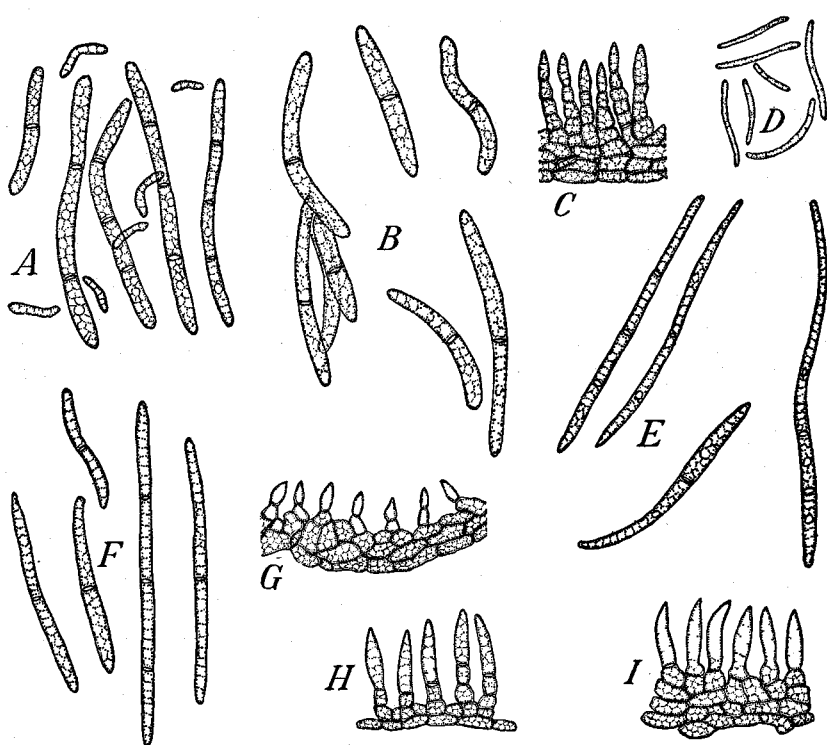
In pure culture, conidia were typically subcylindrical, curved, straight or sometimes sinuous, and measured 9-34 x 1.6-3  $\mu$  (average 23 x 2.2  $\mu$ ) in a 17-day-old culture (4-5° C.) (Figure 11, B). There were, in addition, various *Phoma*-like spores as well as distorted bodies of diverse sizes and shapes.

#### TAXONOMY

There are no species of *Septoria* listed on *Sitanion* but *Septoria microspora* Ell. was described (35) on *Hystrix patula* Moench. (*Asperella hystrix* Humb.), a related genus, and *S. passerinii* occurs on another related genus, *Hordeum*. *Septoria microspora* has small *Phyllosticta*-like spores (6-12 x 1.2  $\mu$ ) borne in pycnidia, 30 to nearly 78  $\mu$  in diameter (Figure 11, D; Plate 1, O). It is very likely that this is a microspore stage of the same fungus that occurs on *Sitanion hystrix*. Examination of material on *Hystrix patula* collected July 28, 1890, by Fisher in Indiana, was found to have bacillar spores, straight or sometimes curved, 9-12 x 0.7-1.2  $\mu$ . It is highly probable that this is a microspore summer stage of a *Septoria* and is referred to *S. passerinii*.

The fungus on *Sitanion hystrix* (Nutt.) J. G. Smith is assigned to *Septoria passerinii*, as it has the morphological characters of this species. The host range of possible races on *Sitanion*, *Hordeum*, and *Hystrix* has not been investigated.

Figure 11. *Septoria passerinii*, *S. microspora*, and *S. secalis*: A, Macrospores and microspores of *S. passerinii* Sacc. on *Hordeum nodosum* from near Lewisburg, Benton County, Oregon, June 13, 1939; B, conidia on 17-day-old culture on potato dextrose agar (5° C.) of *S. passerinii* from *Sitanion hystrix*; C, cross section of pycnidial wall of *S. passerinii* from *S. hystrix* (O.S.C. 10,382); D, microspores of *S. microspora* (Fisher, Indiana collection) (= *S. passerinii*); E, pycnospores of *S. passerinii* from *S. hystrix*, Mt. Hood, Oregon; F, pycnospores of *S. passerinii* from *H. nodosum*, near Corvallis, Oregon (O.S.C. 193); G, cross section of thin pycnidial wall of *S. passerinii* on *H. nodosum*, Corvallis, Oregon (O.S.C. 193); H, same collection as in Figure 11, G, showing very thin peridium and longer pycnophores; I, cross section of pycnidial wall of *S. secalis*, Pottawattamie County, Iowa, W. A. Archer, June 1, 1927. (All X1000)



SEPTORIA SECALIS Prill and Del. on SECALE  
CEREALE

*Septoria secalis* Prill. and Del. has not been reported from the far western United States, but is likely to occur in the scattered fields of rye (*Secale cereale* L.) in western Oregon and Washington. Because of this possibility, the disease was given brief study and some observations are reported here.

Weber reported on *Septoria secalis* in some detail (118). The fungus has hyaline, 3-septate, narrowly cylindrical spores averaging  $25-49 \times 2-3.5 \mu$ , mostly  $35 \times 2.7 \mu$ .

A collection by W. A. Archer made in Pottawattamie County, Iowa, shows thin structured, nearly globular pycnidia. The walls are composed of thick layers of light brown, rectangular cells giving rise to creeping hyaline hyphae terminating in prominent subulate to almost fusiform pycnophores, which are frequently bent or semisinuuous. They measured  $5.5-8 \times 1.9-2.2 \mu$  (Figure 11, I).

Another species, *Septoria secalina* (Jancz.) Sacc. (*Phoma secalina* Jancz.), has been described on rye. This has spores  $10 \times 0.5 \mu$  and is said to be near *S. briosiana* Mor. From the description and illustrations by Janczewski (60) this appears to be another instance of microspores in a species of *Septoria*. Janczewski mentions and illustrates that his *Phoma secalina* was associated with *S. graminum*, which in this instance was *S. secalis*. The writer assigns *S. secalina* to *S. secalis* Prill. and Del. A collection of *S. secalina* made by J. T. Rogers at Washington, D. C., November 4, 1920, also is referred to *S. secalis*. Rather fragmentary and plasmolyzed portions of this from prepared slides showed that rod-like microspores about  $0.6-0.8 \mu$  wide were in part associated with short but otherwise typical macrospores of *S. secalis*.

## SEPTORIA TENELLA Cke. and Ell. on FESTUCA Spp.

The *Septoria* diseases on the wiry, filiform leaves of *Festuca* spp. are of slight importance in Oregon, as far as have been noted.

## SYMPTOMATOLOGY AND GEOGRAPHIC DISTRIBUTION

Collections of *Septoria tenella* on *Festuca rubra* var. *commutata* Gaud. (Chewings fescue) were obtained at Bay City (O.S.C. 10,582) and Alpine, Oregon, (O.S.C. 187), and recently also on *F. rubra* at Corvallis, Oregon (Howard W. Johnson). Collections also have been obtained on *F. dertonensis* (All.) Aschers and Graebn. at Roaring River Hatchery, Linn County,

Oregon (O.S.C. 186) and on *F. idahoensis* Elmer and *F. ovina* L. in the Yellowstone National Park, Wyoming. In addition, innumerable collections have been made on *Festuca octoflora* Walt., which is universally attacked by *S. tenella* in the Northern Great Plains and westward into Idaho.

The collections on Chewings fescue contained small, vague, "greasy" brown spots on living leaves. On O.S.C. 186, the fungus occurs in straw-colored, indefinite areas. A collection of a species of *Phyllosticta* on *Festuca subulata* Trin. from Silver Creek Falls, Oregon, was also obtained.

#### PURE CULTURE AND HOST RANGE STUDIES

Pure cultures of *Septoria tenella* from Bay City (O.S.C. 10,582), Alpine (O.S.C. 187), Oregon, and of the *Phyllosticta* from Silver Creek Falls, Oregon, were obtained. The first two produced cream white, soon flesh pink, eventually slimy, cocoa-brown masses of conidia. These masses of conidia eventually became somewhat carbonized by development of stromatic hyphae. Sometimes transfers developed black stromatic mounds from the start, but water dilution cultures usually resulted in masses of conidia. The writer at first thought that the cultures were either mixed or contaminated until repeated dilution plates showed that the fungus was in pure culture.

Pure culture isolations from *Festuca octoflora* from near Grassy Butte, North Dakota (May 22, 1941), produced mucose mounded flesh pink colonies similar in appearance to those produced by *S. tritici*.

The culture of *Phyllosticta* from Silver Creek Falls resembled, to a certain extent, some cultures of *Septoria elymi*. The *Phyllosticta* was slow-growing, yeasty, and later mounded into small compact colonies.

Inoculation trials with the conidia-producing cultures from Bay City and Alpine were negative on a large number of hosts in nine trials. No infection could be obtained on *Festuca myuros* L., *F. megalura* Nutt., *F. rubra*, *F. rubra* var. *commutata*, *F. idahoensis*, *F. ovina* L., *F. tenuifolia* Sibth., *Poa pratensis*, *P. secunda*, *P. trivialis*, *Holcus lanatus*, *Lolium* spp., *Agrostis* spp., *Deschampsia caespitosa* (L.) Beauv., *Elymus* spp., *Brachypodium pinnatum*, *Cynodon dactylon* (L.) Pers., *Avena sativa*, *Triticum aestivum*, *Phleum pratense* L., *Hordeum vulgare*, *Secale cereale*, *Dactylis glomerata* L. and *Koeleria cristata* (L.) Pers.

#### MORPHOLOGY

**PYCNIDIA.** The pycnidia are creosote-brown, 60-120 x 95-130  $\mu$  and more or less elliptical in cross section. They are composed of tightly crushed, oblong to polyhedral cells averaging 0.5 to 3  $\mu$  (rarely coarser) wide. The

spores are produced on cylindrical, very narrowly subulate pycnophores that average about  $1\ \mu$  wide and up to  $4\ \mu$  long. In some cases, the pycnophores are not distinguishable and the spores are found on hyphae with slight differentiation from the hyphae growing from the wall of the pycnidia. Usually, however, the pycnophores can be distinguished and the small globose to angular pycnophore initials are traceable into the structure of the wall. This species is characterized by the small size of the cells composing the pycnidial wall and by the smallness of the pycnophores (Figure 12, E, K).

The pycnidia of the *Phyllosticta* on *Festuca subulata* measured  $48$  to  $120\ \mu$  in diameter. They were strongly erumpent, thin-walled, light golden, with the outer strands of the pycnidial wall radiating towards the ostiole.

**PYCNOSPORES.** The spores are exceedingly variable, measuring from  $5-70 \times 0.8-2.1\ \mu$ . The common shape is filiform, somewhat curved, 0- to 2-septate and  $25-45 \times 1-1.5\ \mu$  (Figure 12, A, B, D, M). On *Festuca dertonensis* (O.S.C. 186), the same fungus has spores  $28-41 \times 0.8-1.2\ \mu$  and  $7-17 \times 1.0-1.5\ \mu$  in adjacent pycnidia and typical *Ascochyta* spores in others, which measure  $9-12 \times 1.4-1.7\ \mu$  (Figure 12, F, G, J). On *F. rubra* var. *commutata*, all spore types are intermingled and are found to some extent in the same pycnidia.

In pure culture also, the spores are variable (Figure 12, C, H), measuring  $4-53 \times 0.6-4.6\ \mu$ . Many of them are typical for *Ascochyta*, others from the same single spore isolation are filiform *Septoria* spores. In addition, there are many sizes and shapes of spores including many monstrosities.

The spores from the collection on *Festuca subulata* were typical of *Phyllosticta* (Figure 12, I) but were slightly shorter ( $4.5-11 \times 1.4-2.0\ \mu$ ) than those in the *Phyllosticta* stages on *F. dertonensis* (O.S.C. 186) (Figure 12, J).

#### TAXONOMY

*Septoria tenella* Cke. and Ell. (24), which was inadequately described from undeveloped material as having spores  $40\ \mu$  long, appears to be the species on *Festuca octoflora* (*F. tenella* Willd.) in the plains country. Such collections as Brenckle's Fungi Dakotensis No. 618<sup>1</sup>, labeled "*S. festucae* Diet." (obviously in error for *S. festucae* Died.), which have spores  $40-60 \times 1.2-1.6\ \mu$ , are typical for *S. tenella* (Figure 12, B). *Septoria festucina* Tehon and Daniels (104) on *F. elatior* L. is the same species. Tehon very kindly furnished a mount from the type of *S. festucina* in lactophenol stained with cotton blue. This sample proved to be faintly 1- to 2-septate under critical

<sup>1</sup>This number filed in the Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming, as 119,972, is labeled in ink, "*Septoria festucae-octoflorae* Petr."

illumination (Figure 12, A). Recently the writer has collected material on *Festuca octoflora* Walt. in several localities in the Killdeer Mountains, North Dakota (B.P.I. No. 80,069) west to Wibaux, Montana. The pycnidia were stouter and the 0- to 2-septate spores  $44-67 \times 1.6-2.1 \mu$ , thus somewhat larger than those from Oregon material. The brown, usually basal, lesions were common, almost universal, on the green heading plants, May 21 to 23, 1941, in the Northern Great Plains. This fungus in North Dakota and Montana, therefore, appears to be a robust form of *S. tenella*, which, also on the basis of pure culture differences, is at least racially distinct from the Oregon material.

The collections on *Festuca rubra* var. *commutata* appear to be a race of *Septoria tenella* similar to *S. festucae* Died. In Oregon, *S. tenella* seems to be somewhat polymorphic. On *Festuca dertonensis*, the one collection contains material referable to *S. tenella*, *S. festucae*, and *Ascochyta* spp. From the similarity of morphology, other than spore size, association in the same lesions, and action of similar fungi in pure culture, the writer believes that *S. tenella* is variable and is the only filiform species of *Septoria* on fescues in the United States and probably also in Europe, so far as known collections are concerned.

*Septoria tenella* is characterized by brown pycnidia with small cells, small narrowly fusiform pycnophores and variable, filiform pycnosporos, which range from *Phyllosticta*-like ones to those of true *Septoria* spores. The following synonymy is proposed:

*Septoria tenella* Cke. and Ell., 1879 (24)

Syn.: *S. festucae* Died., 1912 (32)

*S. festucae-silvaticae* Died., 1912 (32)

*S. festucina* Tehon and Daniels, 1927 (104)

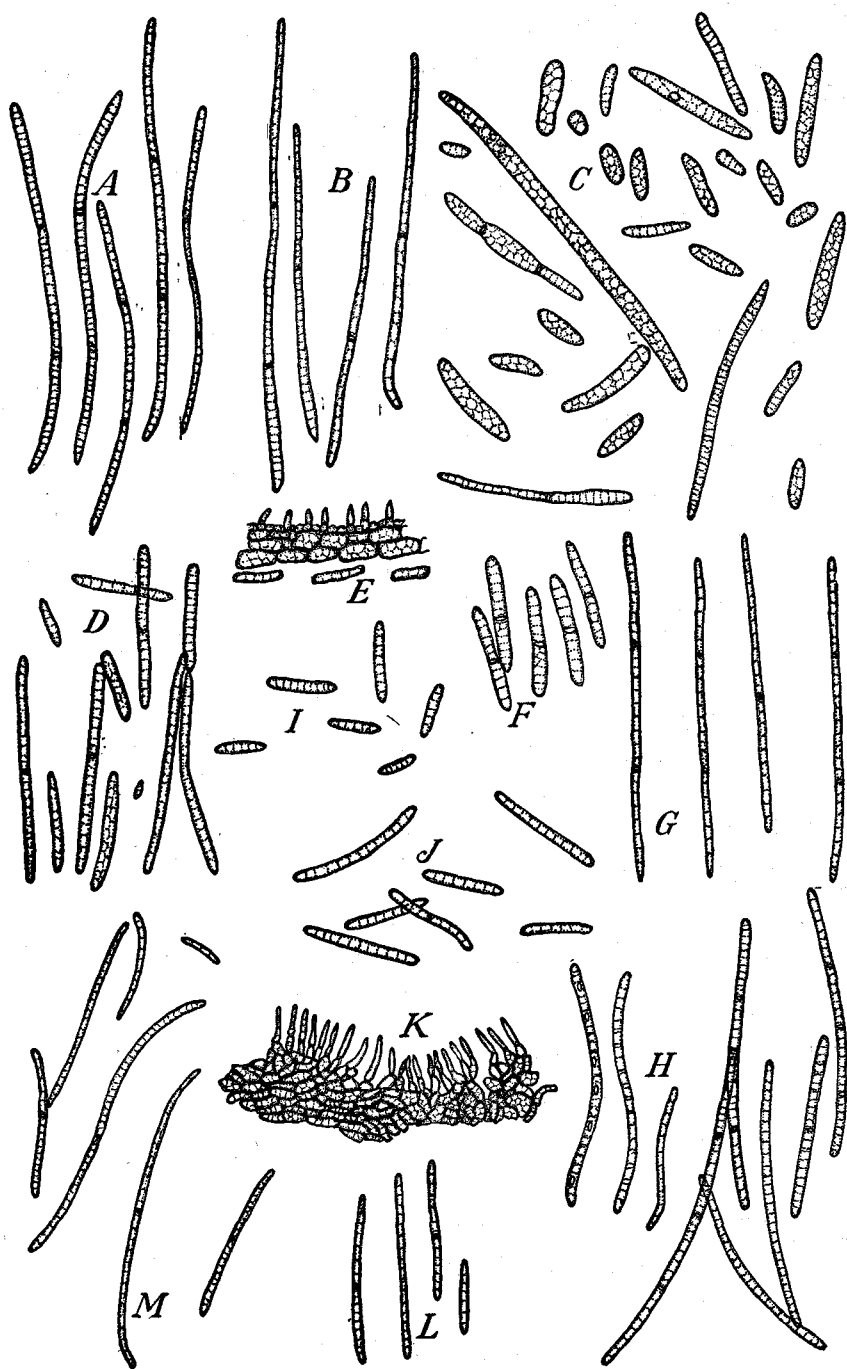
*S. vestergreniana* Allesch., 1903<sup>1</sup>

*Septoria festucae* Died., described on *Festuca gigantea* (L.) Vill. has light brown obscure pycnidia with very thin walls composed of loosely interwoven cells. The spores on *Festuca gigantea* commonly are small,  $10-25 \times 0.7-1.4 \mu$ , and needle-like to somewhat curved (Figure 12, L). The fungus is well within the variation noted on *S. tenella* in the United States, and while it may represent a variety on certain European grasses, it can be better assigned to synonymy under *S. tenella*. *Septoria vestergreniana* is the same as *S. festucae*. It is on the same host and differs only in having more prominent pycnidia than most collections on *F. gigantea*. *Septoria festucae-silvaticae* Died. is an even more obvious synonym of *S. tenella*. Another species, *S. vulpiellae* Maire ad int. (70, 16) on *Vulpiella incrassata* (Salzm.) Trabut [*F. in-*

<sup>1</sup>Vestergren, Micr. Rar. Sel. (Exsiccati) 614, 1903.

Figure 12. *Septoria tenella* on *Festuca* spp. (except I, which is *Phyllosticta* sp.): A, Pycnospores from type of *Septoria festucina* Tehon and Daniels (= *S. tenella*); B, pycnospores from *F. octoflora*, Fungi Dak. No. 618; C, conidia from pure culture S115 isolated from *F. rubra* near Bay City, Oregon; D, pycnospores from *F. rubra* var. *commutata* near Alpine, Oregon, April 14, 1938 (O.S.C. 187); E, cross section of pycnidial wall on *F. octoflora*, Stockton, Kansas; F, *Ascochyta*-like spores of *S. tenella* from *F. derionensis*, Fish Hatchery, Roaring River, Oregon, April 30, 1938 (O.S.C. 186); G, *Septoria*-like spores from same collection as Figure 12, F; H, pycnospores from spore exudate of culture S154 from O.S.C. 187, same collection as Figure 12, D; I, pycnospores of *Phyllosticta* sp. on *F. subulata*, Silver Creek Falls, Oregon, September 29, 1938. (This also may be a stage of *S. tenella*); J, an intermediate stage from the same lesions as the spores in Figure 12, F and G; K, cross section of pycnidial wall, on *F. rubra commutata*, near Alpine, Oregon (O.S.C. 187); L, pycnospores of *S. festucae* Died. (= *S. tenella*) on *F. gigantea* Fungi Pol. Ex. 232, June 29, 1917; M, pycnospores from *F. rubra*, Bay City, Oregon (O.S.C. 10,582). (All X1000)





*crassata* Salzm.] from Tunis, is not available. The description indicates that it belongs to *Selenophoma*.

The *Phyllosticta* on *Festuca subulata* appears to be near *Septoria* and is possibly a phase of the polymorphic *S. tenella*. Without additional material, it is better to leave the status of this collection unsettled.

### SEPTORIA POLIOMELA Syd.

One of the annual hair grasses, *Deschampsia danthonioides* (Trin.) Munro, in the Pacific Northwest, is attacked by a filiform spored species, *Septoria poliomela* Syd. In 1935, one collection was made in mixed oak-fir woods near Peoria, Oregon (O.S.C. 8491) and another under *Pinus ponderosa* near High Prairie, Klickitat County, Washington (O.S.C. 8130). Light tan to straw-colored lesions occurred on the lower leaves of the plants. The pycnidia were prominent.

Material of the same fungus was obtained on *Deschampsia caespitosa* near Granger, Oregon (O.S.C. 809). The evergreen perennial foliage was mildly parasitized at the leaf tips. The lesions are either terminal or extend for some centimeters along the sides of the leaves. The moderately prominent pycnidia are sometimes scattered over the leaf, more often are confined to the margin where dew accumulates.

### PURE CULTURE STUDIES

On potato dextrose agar, pure cultures of *Septoria poliomela* (S107), which were isolated from the High Prairie specimen, produced a white to pale cream-colored, slow growing, mounded, yeasty colony, which soon became covered with a short-nap, velvety-gray covering, a type of growth very similar to that produced by some cultures of *S. elymi*. The cultures did not resemble those of *S. tenella* isolated from *Festuca rubra* in Oregon.

No cross inoculation studies were made because the culture (S107) soon ceased to sporulate and was discarded.

### MORPHOLOGY

**PYCNIDIA ON DESCHAMPSIA DANTHONIOIDES.** Pycnidia are prominent, brown, somewhat gregarious, often coalesced, strongly erumpent, with the circular ostioles surrounded by dark pigmented cells. The structure is parenchymatous and from the outside the original hyphae are evident as definite strands growing from the base and converging toward the ostiole. The pycnidia measured 75-160 x 140-190  $\mu$  in the Peoria material and 40-108 x 72-150  $\mu$  in the collection from High Prairie. The pycnidia are elliptical in cross

section, substomatal, with the wall about  $10\ \mu$  thick. The wall of the pycnidium consists of 3 to 4 layers of compact, thin-walled, brown cells that surround an inner layer of delicate hyaline cells. An inner layer of creeping hyaline hyphae produces the narrowly fusiform pycnophores that are  $3.2\text{--}4.2 \times 0.9\text{--}1.1\ \mu$  (Figure 13, D).

**PYCNIDIA ON DESCHAMPSIA CAESPITOSA.** The pycnidia are ellipsoid, very strongly erumpent, ostiolate, vary from golden brown to creosote brown. The darker pycnidia, which are as large as  $200 \times 120\ \mu$  in diameter, are firmly formed except about the ostiole. The cells adjacent to the ostiole are radially arranged in the direction of the opening, which is somewhat fringed by the loose margin formed by these cells. In younger or lighter colored pycnidia, the entire structure is looser than in the larger, darker pycnidia. The pycnidia range from  $120 \times 50\ \mu$  to  $200 \times 120\ \mu$ , many being twice as long as wide.

**PYCNOPORES ON DESCHAMPSIA DANTHONIODES.** Pycnospores are clear hyaline, strongly curved,  $36\text{--}50 \times 1.4\text{--}1.6\ \mu$  and are 0- to 2-septate in the material collected at Peoria (Figure 13, A). The specimen on High Prairie had smaller spores, which were slightly curved or straight or sometimes moderately curved. These spores measured  $20\text{--}38 \times 0.8\text{--}1.3\ \mu$  (Figure 13, C).

**PYCNOPORES ON DESCHAMPSIA CAESPITOSA.** The spores are hyaline, 1- to 3-septate, needle-like, tapering towards each end or are slightly blunt at one end,  $33\text{--}47 \times 1.5\text{--}2.0\ \mu$ , mostly about  $40 \times 1.8\ \mu$ .

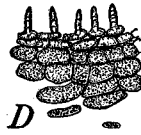
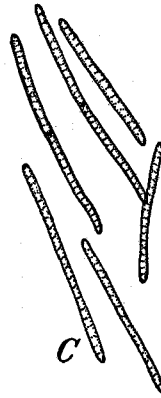
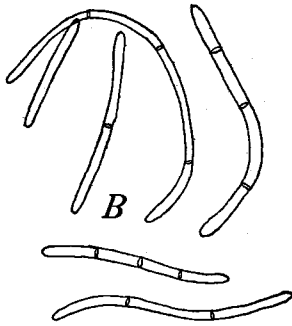
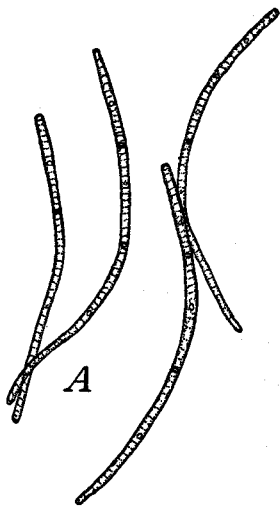
#### TAXONOMY

The only reference to a *Septoria* on *Deschampsia* that has been seen is that to *S. alopecuri* var. *airae* Grove (54) on *Aira caespitosa* L. [*D. caespitosa*]. This fungus has large, pale yellowish spores,  $60\text{--}75 \times 2.5\text{--}5.3\ \mu$ , and is distinct in most respects from the fungus on *D. danthonioides*, which has filiform spores.<sup>1</sup>

The material on *Deschampsia danthonioides* was first studied in comparison with *Septoria elymi* because it resembled this fungus in pure culture. The spores of *S. elymi* are  $21\text{--}50 \times 1.1\text{--}2.3\ \mu$  and fall within the range of *S. poliomela*. Spores from summer material (High Prairie) of the latter, however, fall below those of *S. elymi* in size. The spores of *S. elymi* are typically stouter. As mentioned previously, the pycnidial structure of *S. elymi* shows rather stout pycnophores while those of *S. poliomela* are rather diminutive as in *S. tenella*.

<sup>1</sup>What is probably the same fungus as *S. alopecuri* var. *airae* occurs with *S. poliomela* in collection O.S.C. 809 and has been seen in other collections from Oregon. It has twisted, worm-like, multiseptate, brownish spores and, therefore, is assigned to *Phaeoseptoria*. These fungi are being reported elsewhere, together with a number of related species on grasses (98, 99).

Figure 13. *Septoria poliomela*: A, Pycnospores from *Deschampsia danthomoides*, under oaks and firs, near Peoria, Oregon, May 8, 1935 (O.S.C. 8491); B, pycnospores from *Aira caryophyllea* (type); C, pycnospores from *D. danthomoides*, High Prairie, Washington; D, cross section of pycnidial wall, on *D. danthomoides*, near High Prairie, Washington, May 1, 1935, under ponderosa pines (O.S.C. 8130). (All X1000)



The culture of *Septoria poliomela* (S107) differed from those of *S. tenella* isolated from *Festuca rubra* var. *commutata* in the absence of masses of coffee-brown conidia.

While species of *Deschampsia* apparently have no described species of *Septoria* with filiform or narrowly obclavate spores, the closely related *Aira caryophyllea* L. has the recently described *S. poliomela* Syd. (101), which was collected in Madeira by G. Viennot-Bourgin in 1936. Pycnidia are 80 to 130  $\mu$  (Plate 1, G), and spores 15-30 (rarely 50)  $\times$  1.5-2.5  $\mu$  (Figure 13, B). The detailed description indicates that this species is similar to the Oregon and Washington material except that the spores are somewhat wider. Recently, Sydow kindly loaned a portion of the type for study. On this, the dark brown lesions are very prominent on the straw colored culms. The spores are slightly broader than those from Oregon and Washington, but otherwise the western material is assignable to *S. poliomela*. In the material seen by the writer, the spores of *S. poliomela* from Madeira were mostly 20-30  $\times$  1.5-2.2  $\mu$ .

Recently, Maire and Werner (72) listed *Septoria graminum* on *Aira caryophyllea* L. from Morocco, which no doubt is the same as *S. poliomela* Sydow (101, p. 280) on the same host.

#### SEPTORIA STIPINA Died. on STIPA COLUMBIANA var. NELSONI

The only specimen of a *Septoria* on *Stipa* from the far west is a fragmentary one made from herbarium sheets of *Stipa columbiana* var. *nelsoni* (Scribn.) Hitchc. collected by W. E. Lawrence in the Blue Mountains, Oregon, 1917 (O.S.C. 10,761). The fungus occurred on several basal leaves, which showed prominent, black pycnidia. The writer has not found this fungus in the Columbia Basin even after considerable search. It may be uncommon, as the needle grasses are usually late in starting growth in the spring in Oregon and, therefore, conditions of low humidity prevail almost from the beginning of their growth. A specimen was found in 1940 on *Stipa viridula* Trin. at Vermillion, South Dakota, which was described (96) as *Septoria secalis* var. *stipae* Sprague. In 1941, a specimen was found also on the same host in North Dakota and Minnesota and on *Stipa williamsii* Scribn. in plots at Mandan, North Dakota. These fungi resemble *S. secalis* Prill and Del. and do not have the thread-like spores of *S. stipina*.

#### MORPHOLOGY

**PYCNIDIA.** Pycnidia are prominent, dark brown, erumpent, ostiolate, and finally collapsed. They are 100-120  $\times$  150-200  $\mu$ . Structurally they con-

sist of compacted, creosote-brown crushed cells. Details of the inner fruiting surface were not discernible as the cells were plasmolyzed.

PYCNOSPORES. The spores are straight, very narrow, 1- to 4- (mostly 3-) septate,  $39-63 \times 0.8-1.1 \mu$  (average  $52 \times 0.95 \mu$ ) (Figure 15, O).

#### TAXONOMY

This fungus does not fit exactly the description of any species of *Septoria* on *Stipa*. It is nearest to *S. stipina* Died. (102), which was collected on *Stipa* sp. in Kashmir, India. *Septoria stipina* has dilute-brown pycnidia, 90 to  $120 \mu$  in diameter, with a prominent ostiole (Plate 1, D). It has filiform curved to flexuous hyaline spores,  $25-40 \times 0.5 \mu$ . The Oregon material has longer, stiffer spores borne in larger pycnidia. Until better material is available for study, the fungus from Oregon is tentatively assigned to *S. stipina*. While *S. stipina* from Oregon resembles somewhat *S. calamagrostidis* on *Trisetum*, it differs from the latter in having larger pycnidia and more septa in the spores.

*Septoria capillatae* Trott. (86, v. 25, p. 430) on *Stipa capillata* L., which replaces *S. stipae* Died. (33) (non Trabut), has narrow, curved spores,  $10-15 \times 1-1.5 \mu$  and is probably a species of *Selenophoma*. Grove states (54) that *S. stipae* Died. has irregularly bent spores allied to his falcate spored *S. lunata* Grove. *Septoria capillatae* is, therefore, very different from *S. stipina*. *Septoria stipae* Trab. (107, p. 49) was described in 1889 from Algeria and has superficial pycnidia containing bacillar, obtuse, flavid spores,  $18 \times 2 \mu$ . It is also entirely distinct from *S. stipina*. Furthermore, if *S. stipae* Trabut has pycnidia superficial as illustrated, it does not belong in *Septoria*. Except for its aseptate spores it is near *Septoriopsis* Gonz. Frag. (49).

#### SEPTORIA CALAMAGROSTIDIS (Lib.) Sacc. and S. TRISETI Speg.

These two species will be discussed together because of similarity of habitats.

#### HOST RANGE AND GEOGRAPHICAL DISTRIBUTION

*Septoria calamagrostidis* (Lib.) Sacc. is common in midwinter to early spring on seaside creeping bent (*Agrostis palustris* Huds.) in western Oregon. It is usually found along streams and in moist places in the Willamette Valley and adjacent coast valleys. It is of relatively minor importance except

in occasional attacks during moist weather. The fungus is sometimes found also on *A. exarata* Trin. in wooded areas, along streams and ditches, and has been collected in fir woods on *A. diegoensis* Vasey in Douglas County, Oregon. *Septoria calamagrostidis* is not uncommon on *Trisetum cernuum* Trin. and *T. canescens* Buckl. in the wooded hills of the coastal part and of the Cascade Mountains of Oregon.

*Septoria triseti* Speg. is more abundant than *S. calamagrostidis* (Lib.) Sacc., and even though very obscure, it causes a moderately important leaf spot disease in lawns and pastures in Benton, Washington, Lincoln, Polk, Clatsop, Columbia, Tillamook, Yamhill, Lane, Douglas, and Marion counties in Oregon, and occurs north at least to Puget Sound in Washington. *S. triseti* is most abundant on *Agrostis tenuis* Sibth., less so on *A. alba* L., and at Corvallis it has been collected also on *A. exarata* and *A. castellana* Boiss. and Reut.

#### SYMPTOMATOLOGY

*Septoria calamagrostidis* (Lib.) Sacc. causes gray to stramineous scattered lesions on the tips of blades and leaves of *Agrostis palustris* growing in moist locations. The pycnidia are obscure and often scattered. On *A. exarata* and *Trisetum* spp., the lesions are gray-green, later pale straw-colored, and the pycnidia are scattered, or less often are moderately abundant and more conspicuous than on *A. palustris*.

The symptoms caused by *Septoria triseti* on *Agrostis tenuis* are similar to those on *A. exarata* except that the gray lesions later become fuscous to nearly brown. *S. triseti* on *A. tenuis* causes more and larger lesions than *S. calamagrostidis* usually does on *A. palustris*.

#### PURE CULTURE STUDIES

*Septoria calamagrostidis* from *Agrostis palustris* usually produces a wet or slimy conidial mass that darkens to a coffee-brown. One culture from *Trisetum* and two from *A. exarata* produced brighter-colored spore masses with secondary gray, felty material covering all but sporulating sectors of the colonies. Other cultures from these hosts more nearly resembled the wet, slimy, later carbonaceous cultures typical of the fungus from *A. palustris*.

*Septoria triseti* showed considerable variation in culture. Material from early collections acted similarly to *S. calamagrostidis* on *Agrostis palustris* except that it tended to form the crustose, creosote-brown stroma sooner than *S. calamagrostidis*. Some later isolations produced small buff mounds (as S119) that later darkened to gray, finally dull black. The isolations from



Washington State were mainly of the slower growing race. The race on *A. alba* produced small mounded colonies as well. *S. triseti* from *A. exarata* var. *ampla* (Hitchc.) Hitch. produced the wet creosote to black colonies similar to the early Oregon isolations from *A. tenuis*.

#### INOCULATION STUDIES

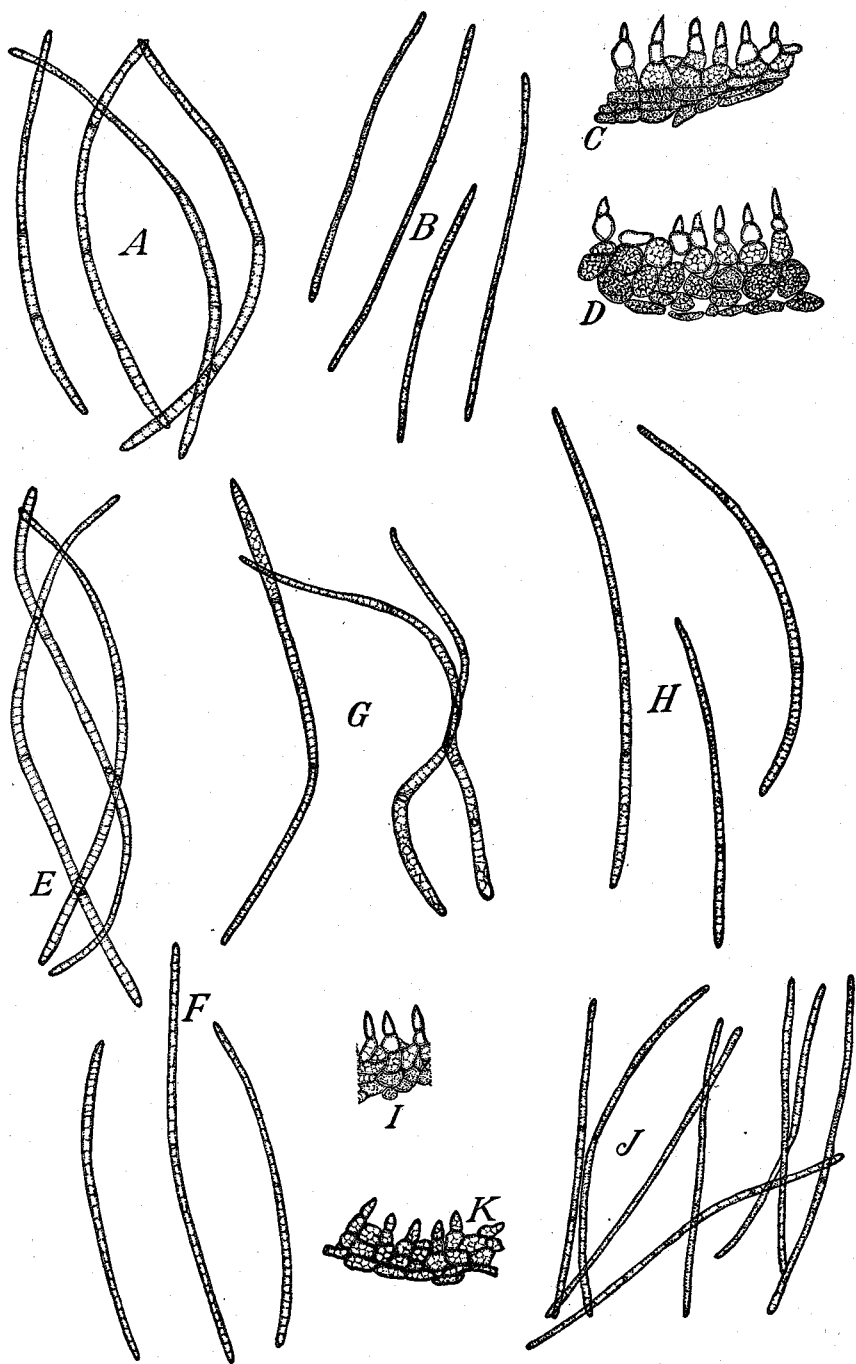
One inoculation with a culture of *Septoria calamagrostidis* (S36) was negative on *Agrostis palustris*, *A. tenuis*, *A. alba*, *A. exarata*, *Triticum aestivum*, *Avena sativa*, *Festuca dertonensis*, *F. ovina* L., and *Bromus carinatus* Hook. and Arn. Inoculations with *S. triseti* (cultures S113 and S114) produced slight infection on *Agrostis tenuis* in one trial out of four and were negative on *A. palustris*, *T. aestivum*, *A. sativa*, *F. rubra*, and *Lolium perenne*. Inoculations in the field at Corvallis, Oregon, in early March 1939, with viable material of *S. triseti*, gave moderate infection on *A. tenuis* and none on *A. palustris*.

In December 1939, a culture of *Septoria triseti* (S113) from *Agrostis alba* when the plants were incubated under cheesecloth out-of-doors in rainy weather, caused very heavy infection on 67 per cent of 450 leaves of *A. alba*, many of the plants being killed. On colonial bent (*Agrostis tenuis*) 10 per cent of the leaves were infected. The fungus produced no infections on sea-side bent (*Agrostis palustris*), *Phalaris arundinacea* L., *Poa nemoralis*, *P. pratensis*, *Festuca tenuifolia*, *F. rubra*, *F. rubra* var. *heterophylla* Mutel, *Lolium perenne*, *Brachypodium pinnatum*, *Cynodon dactylon*, *Dactylis glomerata*, *Triticum aestivum*, and *Phleum pratense*.

*Septoria calamagrostidis* isolated from *Trisetum canescens* (S229) and incubated and inoculated in the same way and at the same time as culture S113, mentioned above, produced 95 per cent leaf killing on 300 leaves of *T. canescens*. The fungus did not attack *Agrostis alba*, *A. tenuis*, *A. palustris*, *Calamagrostis nutkaensis* (Presl) Steud., nor any of the hosts listed in Table 1, all of which, except certain of the desert *Poa* spp., and *Koeleria cristata*, were inoculated. A smaller experiment under bell jar at the same time gave 90 per cent kill on *Trisetum canescens* and no infections on *Agrostis palustris* and *Calamagrostis nutkaensis*. Again in January 1940, heavy infection was obtained on *T. canescens*, but none on the common cereal and the grasses listed in Table 1.

*Septoria calamagrostidis* from *Koeleria cristata* (S171) produced 100 per cent infection on *Koeleria cristata* under bell jars and out-of-doors under cheesecloth in December 1939, but produced no infections on *Agrostis palustris*, *Poa secunda*, *P. pratensis*, *P. annua*, *P. juncifolia*, *Hordeum nodosum*, and *Festuca rubra*.

Figure 14. *Septoria calamagrostidis*: A, Pycnospores from *Agrostis palustris*, South Fork, Alsea River, Oregon, May 7, 1938 (O.S.C. 189); B, pycnospores from *Trisetum canescens*, Silver Creek Falls Park, Oregon, September 29, 1938 (O.S.C. 271); C, cross section of pycnidial wall, on *T. canescens*, Fourbit Creek, Crater Lake National Forest, June 3, 1926, D. C. Ingram (O.S.C. 8498); D, cross section of pycnidial wall, on *A. palustris*, near Corvallis, Oregon, Ray Kimmey, May 31, 1931 (O.S.C. 8490); E, pycnospores from *A. diegoensis* near Kellogg, Oregon, February 18, 1939 (O.S.C. 419); F, pycnospores from *T. cernuum*, Bergsvik Creek, Clatsop County, Oregon, May 16, 1938 (O.S.C. 198); G, pycnospores from *A. palustris*, Oak Creek, Corvallis, Oregon; H, pycnospores from *A. exarata*, Silver Creek Falls Park, Oregon, September 29, 1938 (O.S.C. 273); I, cross section of pycnidial wall from *A. palustris*, Oak Creek, Corvallis, Oregon (O.S.C. 53); J, pycnospores from *T. canescens*, 15 miles east of Sutherlin, Oregon, G. C. Fleischman; K, cross section of pycnidial wall from *A. diegoensis*. (All X1000)



At the same time and under the same prevailing conditions in which such severe infection was obtained with culture S113 from *Agrostis alba*, culture S109 from *A. tenuis* produced mild infection on 10 per cent of leaves of *A. alba*, trace on colonial bent (*A. tenuis*) and 8 per cent of leaves of Astoria bent (*A. tenuis*).

In the period January to March, 1940, potted plants were placed for several days upside down out-of-doors on a lawn of *Agrostis tenuis* heavily infested with *Septoria triseti*. Infection developed on 12 per cent of the leaf tips in several pots of *A. alba*, none on colonial bent (*A. tenuis*), and 6 per cent on Astoria bent (*A. tenuis*). A large number of cereals and other grasses also were inoculated, but with completely negative results.

It is indicated that *Septoria triseti* will not attack *Agrostis palustris* but will cause injury on *A. alba* and *A. tenuis*. It also appears that the race on *A. alba* is especially destructive to that host.

*Septoria calamagrostidis* on *Agrostis palustris*, *Koeleria cristata* and *Trisetum canescens* appears to have sharply delimited host ranges with no bridging hosts so far found.

#### MORPHOLOGY

**PYCNIDIA OF SEPTORIA CALAMAGROSTIDIS.** The pycnidia on *Agrostis palustris* are characteristically strongly flattened, subepidermal, dark brown, appearing black in leaf spots, 50-140 x 50-180  $\mu$  and are 50 to 85  $\mu$  deep. In midwinter the pycnidia are lighter colored, consisting of intertwined cells varying from 1.7 to 4  $\mu$  in diameter, of which the third or fourth layer of cells from the outside is bulbous, hyaline, and produces small, blunt, bottle-shaped pycnophores that seldom exceed 3.5 x 1.5  $\mu$  (Figure 14, I). Collections in late winter or spring had walls 7 to 9 cell layers thick. The cells were small, 2 to 3  $\mu$  in diameter, and closely packed. The outer layer was irregular with alternate strands of polyhedral cells overlapped to give a cobbled effect to the periphery of the cross sections (Figure 14, I). The pycnophores of *Septoria calamagrostidis* on *Trisetum canescens* are very similar to those on *A. palustris* (compare Figure 14, C, D; Plate 1, H).

A meager collection on *Agrostis diegoensis* has small, flattened to sub-globose pycnidia with relatively thin walls (Figure 14, K). The outer portion of the wall consists of fragmentary hyphae with elongated cells loosely enclosing 2 to 3 layers of polyhedral-globose cells, producing small, blunt, cuspidate pycnophores, 2.3-3 x 1.4-1.9  $\mu$ . Except for the smaller size of the pycnidia, the fungus on *A. diegoensis* has the same general structure as *A. palustris*.

The collection on *Agrostis exarata* collected in May 1937 (O.S.C.

10,377) has large, flattened pycnidia, which extended from the upper to the lower epidermis of the leaf, with the wall  $9\ \mu$  thick, made up of dark brown, closely packed cells, which enclosed 1 or 2 layers of somewhat globose, lightly packed, hyaline inner cells, which produced the small, obscure but numerous, pycnophores. The morphology of the fungus on *A. exarata* was scarcely different from that of *Septoria calamagrostidis* on *A. palustris*.

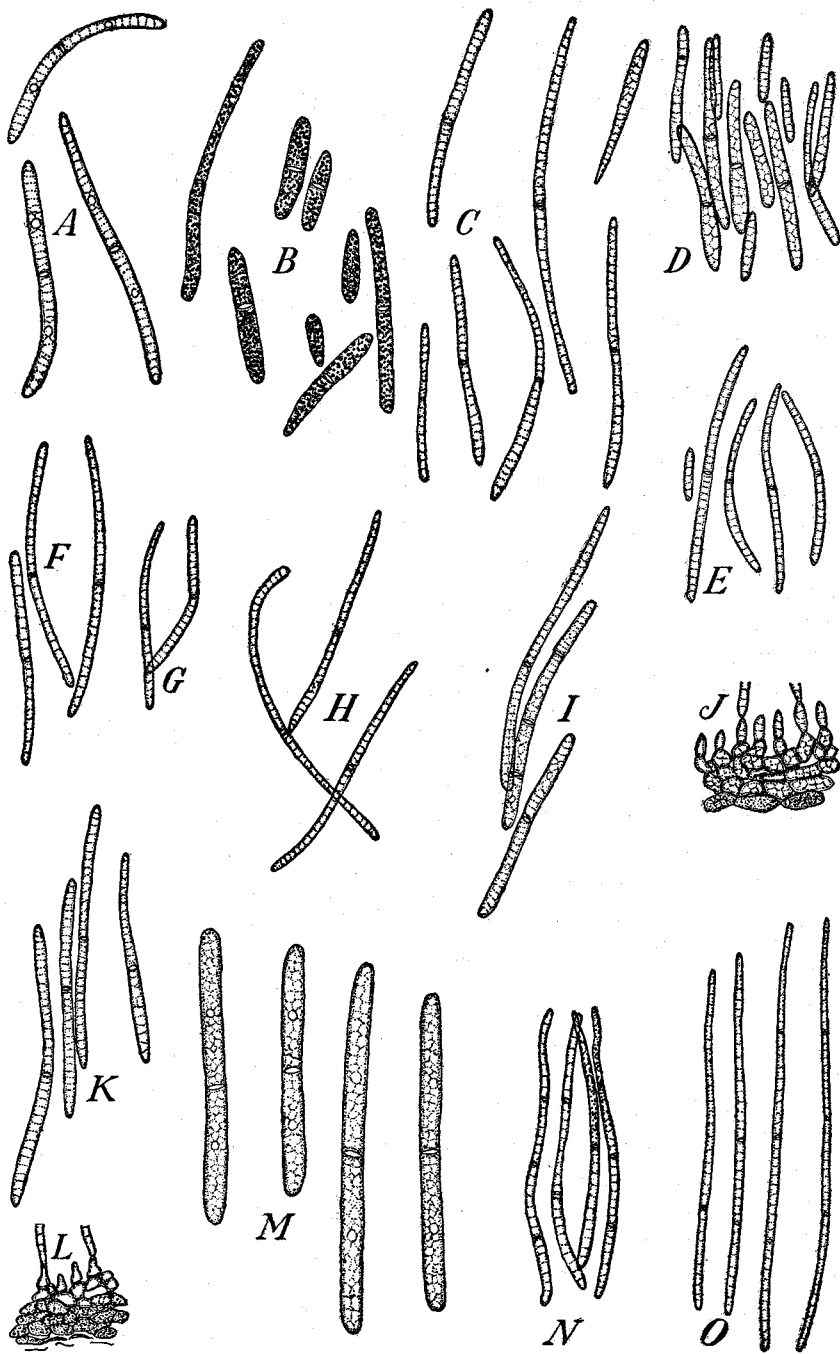
**PYCNIDIA OF SEPTORIA TRISETI.** The pycnidia of *Septoria triseti* are dark brown, subepidermal, and are usually globose. Sometimes they are flattened at the top when they are pressed against the inhibiting epidermis. They are small (Plate 2, L), mostly averaging 40 to  $85\ \mu$  wide and 40 to  $80\ \mu$  deep, but some reach a diameter of  $100\ \mu$ . The pycnidial wall is 6 to  $9\ \mu$  thick and the outer dark brown layer contrasts strongly with the inner hyphal hyaline layer. The strands of cells composing the wall are tightly wound over each other as in *S. calamagrostidis*. The strands of cells of the outer layer tend to converge towards the ostiole. The inner layers, as in *S. calamagrostidis*, are somewhat globulate but in some cases the small pyriform pycnophores arise from the ends of scarcely differentiated hyphae (Figure 15, J. L.).

**PYCNOSPORES OF SEPTORIA CALAMAGROSTIDIS.** The pycnospores on *Agrostis palustris* and *A. diegoensis* are filiform, distinctly 0- to 5- (mostly 3-) septate, curved and often strikingly sinuous,  $25-71\ (40-65) \times 1.0-2\ \mu$ , in winter collections (Figure 14, A, E, G). Most collections of *A. exarata* are generally distinguishable from those on *A. palustris* by the slightly stouter basal cells of the spores from *A. exarata* (but compare Figure 14, H and G).

On *Trisetum* spp., the pycnospores are distinguishable from those on *Agrostis palustris* by their being usually more stiffly curved or bent, scarcely ever strongly curved or sinuous, and are obscurely septate  $50-70 \times 1.2-1.5\ \mu$  (spring collections) (Figure 14, B, F, J; Plate 1, H). One collection on *T. canescens* made in early March in Douglas County, Oregon, however, had spores typically curved as usually found on *A. palustris*. The summer collections have very narrow pycnospores,  $31-73 \times 0.6-1.4\ \mu$ .

**PYCNOSPORES OF SEPTORIA TRISETI.** The spores are mostly 0- to 1-septate, filiform to narrowly fusiform and measure mostly  $18-43 \times 1.2-2.0\ \mu$  (Figure 15, A-I, K). Those on *Agrostis alba* (Figure 15, D) are particularly blunt and may represent a variety or form of *S. triseti* worthy of recognition. Material on *A. alba* collected in late summer (September 24, 1939) at Waldport, Oregon (O.S.C. 731) had very short spores,  $13-22 \times 1.4-1.7\ \mu$ . A collection of immature spores of *S. secalis* var. *stipae* Spr. on *A. hallii* Vasey (Figure 15, M) has spores much larger than those of *S. triseti*.

Figure 15. A-L, *Septoria triseti*: A, Conidia from young culture isolated from *Agrostis Stolonifera* (? hybrid), near Newport, Oregon (O.S.C. 16); B, Conidia from culture S127 from *A. tenuis*, which was staling, with the kind of spore frequently found in this species under these conditions; C, pycnosporos from *A. tenuis*, Corvallis, Oregon (O.S.C. 80); D, pycnosporos from *A. alba*, Fort Steilacoom, Washington, April 1, 1939; E, pycnosporos from *A. exarata* var. *ampla*, near Lewisburg, Oregon, June 13, 1931; F, pycnosporos from *A. tenuis*, Young's Bay, Clatsop County, Oregon, November 17, 1938; G, pycnosporos from *A. tenuis*, Alsea, Oregon, November 6, 1938 (O.S.C. 274); H, pycnosporos from *A. tenuis*, 4½ miles southeast of Hebo, Tillamook County, Oregon, March 7, 1938 (O.S.C. 155); I, conidia from pure culture S114 isolated from *A. tenuis*, Corvallis, Oregon, May 1938; J, cross section of pycnidial wall, on *A. tenuis* (O.S.C. 80); K, pycnosporos from *A. tenuis*, Oak Creek, Benton County, Oregon (O.S.C. 43); L, cross section of pycnidial wall from same collection as Figure 15, K; M, pycnosporos of *Septoria secalis* var. *stipae* on *A. hallii*, Helmick Park, Polk County, Oregon, June 24, 1937; N, pycnosporos of *Septoria phleina* Baudys et Pich. on *Phleum arenarium* Fungi Croatia V, 1925; O, pycnosporos of *Septoria stipina* Died. on *Stipa columbiana* var. *nelsoni*, Long Creek, Grant County, Oregon, W. E. Lawrence, July 28, 1917 (O.S.C. 10,761). (All X1000)



## TAXONOMY

Previous study (95) indicated that the narrow spored *Septoria* on *Agrostis palustris* was only a robust form of *S. calamagrostidis*. Additional study has strengthened this view; and *S. calamagrostidis* is now believed to occur on *A. palustris*, *A. diegoensis*, *A. exarata*, *Trisetum cernuum*, and *T. canescens* in Oregon.

The race on *Agrostis palustris* from western Oregon is assigned to Race 1. The specimens on *A. exarata*, which have slight morphological differences from Race 1, are designated Race 2. This study is not the first report of *Septoria* on *A. exarata*, as Seymour (91) lists both *S. graminum* and *S. grylli* Sacc. on *A. exarata*. His basis for this, we learn through the kindness of Dr. W. Lawrence White of the Herbarium of Cryptogamic Botany, Harvard University, is as follows: *S. grylli* was reported on *A. exarata* from Alaska by Saccardo, Peck, and Trelease (90, p. 19) and *S. graminum* on *A. exarata* and *Calamagrostis* also from Alaska by Anderson (2, p. 103). The Anderson specimen of the latter in the Mycological Collections of the Bureau of Plant Industry, U. S. Department of Agriculture, is reported as being on *C. langsдорffii*, which is *C. canadensis* var. *scabra* (Presl) Hitchc. in North American material (56). This specimen has no spores but the pycnidial walls suggest *S. arctica* Berk. and Curt.

Saccardo, Peck, and Trelease (90), in addition to reporting *Septoria grylli* on *Agrostis exarata*, with spores  $75-90 \times 1-1.2 \mu$ , also reported the same species on *A. scabra* var. *geminata* (Trin.) Swallen from Alaska, with spores  $60 \times 1 \mu$ . It seems very likely that both of these collections, as well as the one reported by Anderson (2) as *S. graminum* on *A. exarata*, referred to above, are *S. calamagrostidis* as described above. *Septoria grylli* was described by Saccardo (84) on *Andropogon gryllus* L. [*Chrysopogon gryllus* (L.) Trin.] from Italy as having filiform spores,  $75-85 \times 1 \mu$  borne in globose-lenticular, punctiform pycnidia.

The fungus on *Trisetum* appears to have developed some slight morphological differences and is named Race 3. This race is, however, scarcely morphologically distinguishable from Races 1 and 2. While generally the spores are less flexuous than in Races 1 and 2, there are collections that show strongly flexuous spores. It appears, therefore, conservative to leave these as one species. There are a number of species in the literature comparable to Race 3 of *Septoria calamagrostidis*. *Septoria caballeroi* Gonz. Frag., described on *T. ovatum* (Cav.) Pers. from Spain (48, p. 49), has pycnidia  $100 \times 140 \mu$  and spores  $35-55 \times 1.5 \mu$ . It is assigned to *S. calamagrostidis*. The form *S. caballeroi* f. *panicei* Gonz. Frag. (50) on *T. paniceum* Pers. North Africa is said to differ from the type in having eguttulate 1- to 3-sep-



tate spores. *Septoria graminum* was reported on *T. hispidum* Lange from Spain by Unamuno (111). *Septoria graminum* Desm. forma *triseti-loeflingianii* Cab. (17) has been described on *T. loeflingianum* (L.) Presl from Spain, having spores 29 to 50  $\mu$ , mostly 40  $\mu$  long. *Septoria triseti-hispidi* Unam. (113), which is clearly illustrated, has short, cylindric, aseptate spores, 15-20 x 3-3.5  $\mu$ , and is distinctly different from any available specimen on *Trisetum* in Oregon. The synonymy for *S. calamagrostidis* is as follows:

*Septoria calamagrostidis* (Lib.) Sacc.

Syn: *Ascochyta calamagrostidis* Lib., 1832

*S. caballeroi* Gonz. Frag., 1914

*S. caballeroi* f. *panicei* Gonz. Frag., 1917

*S. graminum* Desm. f. *triseti-loeflingianii* Cab., 1928

Seymour (91) also listed *Septoria graminum* and *S. nebulosa* Rostr. on *Trisetum spicatum* (L.) Richt. The spores of the Oregon material on *Trisetum* are very similar to those of *S. graminum*, which, it has been recently shown (95), was originally described on *Brachypodium sylvaticum*, but the pycnidia resemble those of *S. calamagrostidis*.

*Septoria calamagrostidis* Ell. and Ev. (39), which in 1902 became *S. everhartii* Sacc. and Syd. (86, v. 16, p. 973) is a species of *Selenophoma* and, therefore, will not be discussed in this paper.

Cocconi and Morini (22) list *Septoria bromi* on *Deyeuxia varia* (Schrad.) Kunth with filiform, clavulate, strongly curved spores, 50  $\mu$  long. *Deyeuxia* is now classed by Hitchcock (56) as a section of *Calamagrostis*, and on the basis of the description by Cocconi and Morini the fungus they call *S. bromi* (22) (No. 287) is here referred to *Septoria calamagrostidis* (Lib.) Sacc.

All of the collections on *Agrostis tenuis*, *A. alba*, one on *A. exarata* var. *ampla*, and one collection on a grass, probably *A. stolonifera*, are assigned to *Septoria triseti* Speg. Spegazzini (92) described this species on southern Argentina material collected on both *Trisetum phleoides* (Vill.) Trin. [*Koeleria phleoides* (Vill.) Pers.] and *A. magellanica* Lam., and it was said to have spores measuring 20-30 x 1-1.3  $\mu$  borne in pycnidia, 70-80  $\mu$ . Efforts to find the type have been unavailing, although Dr. Lindquist made a thorough search for it in the collections at the Institute Spegazzini (Museo de la Plata). The writer believes that the fungus on *A. tenuis* in Oregon is the same as *S. triseti*, which is considered distinct from *S. calamagrostidis*. It is distinct from the latter both in the size and septation of spores, and in having much smaller pycnidia. It shows affinity to *S. calamagrostidis* in development on potato dextrose agar and in the structure of the pycnidium. The

name *S. triseti* is retained but an emended description is necessary, as follows:

*Septoria triseti* Speg. (emended)

Lesions on leaves, indeterminate, sublinear to irregular, or on leaf tips, cinereous; pycnidia not prominent, black-brown, ostiolate, substomatal, globose to flattened at the ostiolar end where it is appressed against the leaf epidermis, 40-100  $\mu$  (mostly 40-80  $\mu$ ) in diameter, formed of irregular, oblong-polyhedral, parenchymatous cells, in strands, which converge in radii towards the ostiole, brown outer cells two layers thick (3  $\mu$ ) with 2 or 3 inner hyaline layers (3 to 5  $\mu$  thick) giving rise to narrowly bulbous-cylindric pycnophores, 2.5 to 3.5  $\mu$ . Pycnospores filiform to subbacillar or sometimes narrowly fusiform, straight, bent or less often moderately curved, 0- to 1-septate, 16-43 (18-35)  $\times$  0.8-2.0 (1.3-1.7)  $\mu$ .

On *Agrostis magellanica*, Staten Island, Fuegia, and on *A. tenuis*, *A. exarata* var. *ampla*, and *A. alba* in Oregon.

The writer questions if the material on *Koeleria phleoides* is the same as that on *A. magellanica* and until Spegazzini's specimens come to light he prefers to suspect that the material on *K. phleoides* is what has been described as *S. koeleriae* Cocc. and Mor. Emendation of *S. triseti*, therefore, is restricted to *Agrostis*. The specific name *triseti* is unfortunate.

*Septoria triseti* has not been found as yet on *Agrostis palustris*, although it is very common on *A. tenuis* growing in adjacent areas or intermingled with *A. palustris*. The specimens on *A. alba* are possibly morphologically distinguishable from those on *A. tenuis*, but at present the difference is considered racial. The common form on *A. tenuis* is Race 1, that on *A. alba*, Race 2. Another species, *S. phleima* Baudys and Picb. (4) (Figure 15, N) on *Phleum arenarium* L., in Europe, has spores slightly obclavate-filiform and averaging somewhat narrower than but otherwise similar to those of *S. triseti*.

### SEPTORIA CALAMAGROSTIDIS FORMA KOELERIAE (Cocc. and Mor.) Comb. Nov.

An obscure leaf spot occurs on *Koeleria cristata* (L.) Pers. in eastern Oregon, Washington, and Wyoming. W. E. Lawrence collected it in four locations in central Oregon (O.S.C. 570A; 10,363; 10,387; 10,844); William C. Cusick once, from the Blue Mountains, Oregon; the writer has found it three times in Klickitat County, Washington; and recently Fischer and Hardison sent specimens from Wyoming and Pullman, Washington, where it was common during the moist year 1941 (B.P.I. 80,078 and 80,079).

In addition to these collections, the fungus was collected January 26, 1939, in a cold frame at Corvallis, Oregon, on plants transplanted from High Prairie, Washington, in May 1938.

#### SYMPTOMATOLOGY

The collections from eastern Oregon and Washington did not show any specific symptoms. The few leaves that were infected were basal leaves that were dead and dried at the time of collection. The material at Corvallis shows definite circular to subcircular fuscous lesions on the leaves. The leaves later turn brown and the tips, or sometimes the entire leaf, die. The pycnidia are prominent.

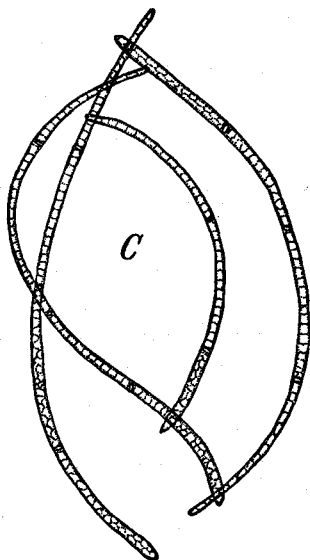
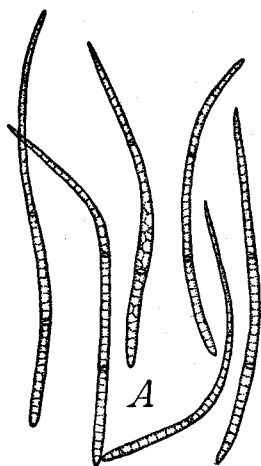
#### PURE CULTURE AND HOST RANGE STUDIES

The fungus produces slow-growing, yeasty colonies. They are tawny flesh, later dull brown, then olivaceous and finally black. They resemble cultures of *Septoria macropoda* var. *septulata*. Old cultures contain numerous pycnidia containing straight to strongly curved spores.

**PYCNIDIA.** The pycnidia are ellipsoid, often flattened at the top where they are pressed against the leaf epidermis, or are flattened at the base and rounded at the top. They are black-brown,  $80-140 \times 70-120 \mu$ . The pycnidia, like those of most species of *Septoria* that grow in the semiarid prairies and grasslands of the Columbia Basin, have strongly pigmented, tightly packed wall cells. A collection from east of Heppner, Oregon, although made in relatively humid middle March (Lawrence), shows this construction (Figure 16, D). The walls, which are 6 to  $10 \mu$  thick, have an outer brown layer of compacted, intertwined strands of cells, and on the interior is a thin layer of contrasting hyaline cells, 2 to  $3 \mu$  thick. The awl-shaped pycnophores, which arise from subbulbous cells, are  $2-4.8 \times 1.6-2.0 \mu$ . The collections made later in the year show that the cells are more strongly compacted into crushed layers resembling cork-tissue in higher plants. The collection from Corvallis, Oregon, made in midwinter under humid conditions, showed strongly pigmented walls consisting of small polyhedral cells, which were somewhat crushed on the outer portion of the wall. In cross section, the pycnidial wall has an almost rindlike appearance (Plate 2, C). The pycnophores in the Corvallis material are very numerous, small subulate,  $3-4.5 \times 1.2-1.7 \mu$  (Figure 16, B).

**PYCNOSPORES.** The collections from the Columbia Basin have needle-like spores, mostly  $40-60 \times 1.1-1.6 \mu$  (Figure 16, C). A collection by Lawrence from 5 miles south of Grass Valley, Oregon, has short, stiff spores,

Figure 16. *Septoria calamagrostidis* f. *koeleriae*: A, Pycnospores from *K. cristata*, Corvallis, Oregon, January 26, 1939; B, cross section of pycnidial wall, on *K. cristata*, Corvallis, Oregon; C, pycnospores from *K. cristata*, High Prairie, Washington; D, cross section of pycnidial wall, on *K. cristata*, east of Heppner, Oregon, W. E. Lawrence (O.S.C. 10,363). (All X1000)



12-44 x 1.4-1.7  $\mu$ . This collection is very evidently summer material of the same species as the others. The spores in this collection are essentially microspores. The collection from Corvallis has 0- to 2-septate spores, 35-55 x 1.3-2.0  $\mu$ , and the basal cell is slightly wider than the others, giving this collection the appearance of very slender spores of *Septoria bromi* (Figure 16, A), but more comparable with collections of *S. calamagrostidis* on *Agrostis palustris* and *A. exarata* made in winter in Oregon.

#### TAXONOMY

*Septoria koeleriae* Cocc. and Mor. was described on the annual grass, *Koeleria phleoides* (Vill.) Pers. from Bologna, Italy (21, p. 292) as having filiform nonseptate spores, 46-54 x 1.5  $\mu$ , borne in pycnidia, 40 to 45  $\mu$ . The size of the pycnidia compared to the length of the spores and of Cocconi and Morini's drawings indicates that the very small size of the pycnidia indicated was in error. Bubak (15) also pointed this out and cited pycnidia 80 to 120  $\mu$ . *Septoria koeleriae*, from all material seen, has filiform to very narrowly filiform clavate spores, 0- to 2-septate 35-60 (10-60) x 1.1-2.0  $\mu$ , commonly nonseptate, filiform, 45-55 x 1.2-1.5  $\mu$ , borne in dark brown ellipsoid to globose pycnidia, 80 to 140  $\mu$ .

*Septoria koeleriae* has been reported from Italy (21), Spain (112), Africa (50), Asia (15), and from the Pacific Northwest.

The species is assigned to *Septoria calamagrostidis* f. *koeleriae* (Cocc. and Mor.) comb. nov., as the spores are comparable with those on *Agrostis*, particularly on *A. exarata*, and *Trisetum* from Oregon. The pycnidia and particularly the pycnophores are very similar. There is less tendency to form bulbous pycnophore initials than in the species and the compacted pycnidial wall is more or less distinctive on *Koeleria*. Host range trials indicate specialized pathogenicity as well.

### SEPTORIA QUINQUESEPTATA Sp. Nov.

Maculis nullis, pycnidiis sparsis, erumpentibus, brunneis, apicis nigris, globosis, v. depressis, ostiolatis parvis tarduis, 98-115  $\mu$ ; pycnosporulis filiformibus, basis obtusis, apicis subacutis, 5-septatis hyalinis, rectis v. subcurvulis, 48-58 x 1.9-2.4  $\mu$ .

Hab. in foliis emortuis *Sphenopholis obtusatae* Mandan, North Dakota.

Spots none or associated with *Darluca filum* (Biv.) Cast. and *Cercospora agrostidis* Atk. in moldy and rusted leaves. Pycnidia very scarce somewhat in lines, widely spaced, erumpent, globose or subglobose, brown, black about the ostiole, which is small and late to open; pycnospores filiform, blunt at the base, subacute at the apex, 5-septate, hyaline, straight or stiffly curved, 48-58 x 1.9-2.4  $\mu$ .

Hab. in leaves of *Sphenopholis obtusata* (Michx.) Scribn. type No. 80732, Mycological collections of the Bureau of Plant Industry, Soils, and Agricultural Engineering collected by J. T. Sarvis, at the Northern Great Plains Field Station, Mandan, North Dakota, August 31, 1915.

This fragmentary material has mature pycnidia and spores that appear to be different from any other species of *Septoria* seen on Gramineae. Whether it is of any parasitic importance is not known. Morphologically *S. quinquesepata* is closest to *S. andropogonis* and to *S. mississippiensis*, but differs in distinguishably narrower 5-septate, as contrasted with 3-septate, spores and the tardily ostiolate pycnidia. It has stiffer, less curved, much shorter spores than *S. andropogonis* var. *sorghastri* Greene and Sprague.

### SEPTORIA SECALIS var. STIPAE Sprague on AGROSTIS Spp.

Recently the writer collected a *Septoria* on *Agrostis scabra* Willd. (*A. hiemalis* Auet.) Ft. Totten, North Dakota, that is scarcely distinguishable, morphologically, from *S. secalis* var. *stipae* Spr. (96), which was described originally on *Stipa viridula*. In the above collection on *Agrostis scabra*, the prominent, thin-walled (*Stagonospora*-like) pycnidia were scattered widely on the sheaths and culms. The spores were essentially identical with those of the type of *S. secalis* var. *stipae* on *Stipa viridula*, that is, 3-septate, hyaline,  $42-62 \times 2.8-3.2 \mu$ , as compared with 3-septate, hyaline, and  $37-54 \times 2.6-3.1 \mu$  for the type. Small pycnidia, in addition, containing minute bacterialike microspores were associated with the large ones containing the macrospores in such a way as to suggest strongly that both were stages of the same fungus. This connection seems the more likely since microspores are known to occur also in *S. secalis* on rye as mentioned previously.

In pure culture on potato dextrose agar, the fungus on *Agrostis scabra* was at first white, fragile, and slow-growing, finally forming a circular, pale buff compact mat 1 inch across in slant cultures. The agar was colored deep amber. There were no fruiting bodies. This development in artificial culture is typical of the species of *Septoria* with narrow cylindrical (bacillar) spores while the species with filiform spores tend to produce mucose, later stromatic growth on agar. Species of *Stagonospora* also produce the former type of growth. This fungus, although somewhat intermediate between *Septoria* and *Stagonospora*, is not a *Stagonospora* because its spores are approximately sixteen times as long as broad. With everything considered, the fungus is referred to *Septoria secalis* var. *stipae*. No cross-inoculations on *A. scabra* and *Stipa viridula*, however, with the fungus from these hosts have been made.

What appears to be an immature stage of *Septoria secalis* var. *stipae* was collected by the writer on *Agrostis hallii* near Helmick State Park, Oregon, June 24, 1937. The spores from this collection are uniformly long-cylindric, hyaline, and 1-septate (Figure 15, M). They measure 33-38 x 2.8-3.4  $\mu$ , with a mean size of 37 x 3  $\mu$ . While the spores from this collection are slightly shorter than those of the type of *S. secalis* var. *stipae*, and also are 1-septate instead of 3-septate as in the type, it should be added that, during the summer of 1941, collections were made at Spiritwood, Guptill, and Mandan, North Dakota, and Webster, South Dakota, of immature *S. secalis* var. *stipae* on *Stipa viridula*, which had 1-septate spores predominating. The material of this species on *Stipa williamsii* mentioned under *S. stipina* was also of the 1-septate phase.

It seems fairly clear, therefore, that the fungus on *Agrostis hallii* with 1-septate spores is an immature stage of *S. secalis* var. *stipae*, the spores of which are normally 3-septate.

The spores of the fungus on *Agrostis hallii* are slightly narrower than those of *Septoria avenae* Frank (43) (conidial stage of *Leptosphaeria avenaria* Weber) which were described originally as 2- to 4-septate, 28-43 x 3.5  $\mu$ , and listed by Weber (116) as 25-45 x 3-4  $\mu$  (mean 38 x 3.5  $\mu$ ). They are larger than those of the fungus known variously as *S. nodorum* Berk. (117), *Macrophoma hennebergii* (Kuehn) Berl. and Vogl. (9), and *Stagonospora hennebergii* (Kuehn) Petr. and Syd. (80), which are 0- to 3-septate, 16-30 x 2-3  $\mu$ .

A collection made on *Agrostis exarata* of another fungus with cylindrical spores was referred to *Septoria de-gasperiana* Sacc. in an addition to a check list of the diseases on Oregon Gramineae.<sup>1</sup> Recently this material was examined again and in the interim, the faintly chlorinous spores of the fresh material had become definitely brown on aging in the herbarium. This phenomenon is not unusual in dematiaceous fungi. The fungus is therefore a species of *Hendersonia*. The spores are cylindrical to slightly curved, 2- to 3-septate with large guttulae and measure 28-48 x 3.5-4.4  $\mu$ . *Septoria de-gasperiana* itself may well be an immature stage of *Hendersonia*. Saccardo's description ("minute pluriguttulatis, spurieque 1-septatis") indicates that the type is not mature (86, v. 25, p. 426). He states that it is related to *Septoria bellunensis* Speg. The latter (86, v. 3, p. 563), which occurs on *Molinia caerulea* (L.) Moench., has 0- to 2-septate, cylindrical spores 20-30 x 3-4  $\mu$ , borne in minute pycnidia (80-90  $\mu$ ).

<sup>1</sup>Sprague, R. Additions to the check list of the parasitic fungi on cereals and other grasses in Oregon. U. S. Department of Agriculture, Bureau of Plant Industries, Plant Disease Reporter 21: 414. 1937. [Mimeographed.]



SEPTORIA BROMI Sacc. and S. JACULELLA Sp. Nov.<sup>1</sup>  
on BROMUS Spp.

## GEOGRAPHIC DISTRIBUTION

The species of *Septoria* most widely collected in the West and Middle West and Tennessee (Lefebvre) on *Bromus* spp. is *S. bromi* Sacc., which attacks *B. commutatus* Schrad., *B. latiglumis* (Shear) Hitchc., *B. racemosus* L., *B. secalinus* L., *B. inermis* Leyss., *B. mollis* L., and *B. japonicus* Thunb. In Oregon, it is common but seldom of any economic importance, as most of its hosts are cheat grasses that are less than desirable forage grasses in the state.

*Septoria jaculella* Sprague is very common west of the Rockies on the polymorphic host species, *Bromus carinatus* (*B. marginatus* Nees, *B. polyanthus* Scribn.). It has been collected also on *B. ciliatus* L. in the Bradshaw Mountains of Arizona (Toumey), on *B. laevipes* Shear in California (Heller) and on *B. rigidus* Roth in Oregon and Washington, and on *B. tectorum* L. in Washington. Recently a fragment sent by John A. Stevenson from a collection made in "Nova California" in 1832 by the early explorer and collector, David Douglas, is very clearly *S. jaculella* on *Bromus carinatus*. This fragment represents one of the earliest mycological specimens from the Pacific coast and is fairly conclusive evidence that *S. jaculella* was a prehistory inhabitant of the west coast.

## SYMPTOMATOLOGY

The symptoms caused by *Septoria bromi* are obscure. The infected leaves turn yellow, then dry up, becoming brown. Elongate to elliptical spots sometimes occur. The pycnidia are obscure but are discernible to the naked eye.

The pycnidia of *Septoria jaculella* are large and black and borne in vague chlorotic patches on the leaves, or sometimes occur in the still green tissue of the leaf. Infected parts eventually die, sometimes as long streaks involving half to all of the width of the leaf blade.

## PURE CULTURE AND INOCULATION STUDIES

*Septoria bromi* was readily isolated from *Bromus* spp. collected from several locations in western Oregon. It produced slow-growing, flesh-colored, yeasty conidial masses, which became very dark, almost black, carbonaceous, and thus distinguishable from that of *S. tritici* and *S. annua*. The organism appeared to stale more readily than *S. tritici*.

<sup>1</sup>In Cooke, Wm. Bridge, *Mycobiota of North America*, No. 114. 1940. (Exsiccati.)

Several attempts to isolate *Septoria jaculella* were unsuccessful, although fresh and mold-free dilutions were readily available and were tried under conditions identical with those used with successful isolations of other species of *Septoria*. The latest attempt (February-March 1939) with material from both *Bromus carinatus* and *B. rigidus* from Lane County, Oregon, resulted in germination of spores. They produced irregularly spiraled germ tubes from both ends of the spore. After 18 days in culture, these measured about 100  $\mu$  long, but were not visible to the naked eye. Many of them apparently died after the contents of the spores had become exhausted, but others continued to grow, and after 20 days the mycelia had started to branch. The mycelium was diamond-blue color, the same as the spores. After 30 days, growth (5° C.) had ceased.

One inoculation trial with fresh material of *Septoria jaculella* was negative on *Bromus carinatus* and on various grasses and cereals including *B. secalinus*, *B. rigidus*, *B. mollis*, *Triticum aestivum*, *Poa pratensis*, and *Avena sativa*, out-of-doors in early March 1939 at Corvallis, Oregon.

Inoculation trials with *Septoria bromi* (S49) from *Bromus secalinus* were weakly positive on *B. secalinus* in one of two trials (1933), negative on *B. inermis* in one trial (1934), negative on *B. tectorum* and *B. carinatus* in two trials (1938), and positive on *B. commutatus*, and *B. secalinus*, but not on *B. carinatus*, *Poa pratensis*, *Triticum* spp., *Agrostis* spp., *Avena* spp., *Festuca* spp., *Phleum pratense*, *Arrhenatherum elatius*, *Phalaris arundinacea* and *Brachypodium* spp. in a final trial (December 1939).

#### MORPHOLOGY

**PYCNIDIA OF SEPTORIA BROMI SACC.** The black-brown pycnidia are spherical or sometimes flattened in large specimens. They are extremely variable in size with a few pycnidia reaching 240  $\mu$  in diameter. Most of them, however, are 60 to 120  $\mu$  in diameter.

In vertical cross section, the pycnidia are usually nearly circular and composed of two, more or less merging, layers of tissue (Plate 2, J). The outer, dark brown hyphae have rectangular, closely intertwined cells, which have a pseudo-polygonal aspect, in some instances due to their close packing. This layer is usually 4 to 10  $\mu$ , sometimes 10 to 12  $\mu$ , thick. Inside this, the cells of the second layer (4 to 10  $\mu$  thick) gradually become progressively hyaline and more interwoven. Near the inner periphery, the cells just below pycnophore initials are arranged in rows parallel to the long axis of the pycnophores. On the initials, the narrowly ampulliform, subcylindric pycnophores are produced, interspersed by sterile hyphae. The pycnophores are 5-7 x 1.5-2.0  $\mu$  and are sometimes 1-septate. In some cases, cylindrical hyphae

develop from cells of the inner peridial wall and appear to be elongate and form spores, which absciss later. Details of the pycnidia are shown in Figure 17, C, E, J, L, M.

**PYCNIDIA OF SEPTORIA JACULELLA.** The pycnidia are very large (100 to 310  $\mu$ ) (Plate 1, M), dark brown to black, carbonaceous, and suberumpent. Their outer periphery is composed of oblong cells that merge with hyaline cubed to polyhedral cells on the inside of the peridium. The walls are 4 to 20  $\mu$  thick at the base of the pycnidium and 8 to 11  $\mu$  near the ostiole. Some pycnidia, which have thin walls, are composed of a few layers of loosely woven strands of cells. In others, in the same collection, the pycnidia appear to be filling with prosenchymatous material (Plate 2, G). No perithecial stage, however, has been noted.

The ostioles are prominent, and, in old specimens, because of the collapse of the roof of the pycnidia, are sometimes 20 to 30  $\mu$  in diameter.

Collections made in midwinter near Coburg, Oregon, showed an unusual development. Mycelia aggregated between the mesophyll leaf cells and gradually pried them apart. The center of the irregular mass became the sporulating area. Eventually large subglobose pycnidia formed that had interrupted cell walls in which host cells were sometimes actually incorporated in the poorly constructed peridium. The fungus, in such cases, approached *Cylindrosporium*, but even in this material the fruiting body represents a very poorly formed pycnidium in an interrupted thinly formed stroma (Plate 2, A).

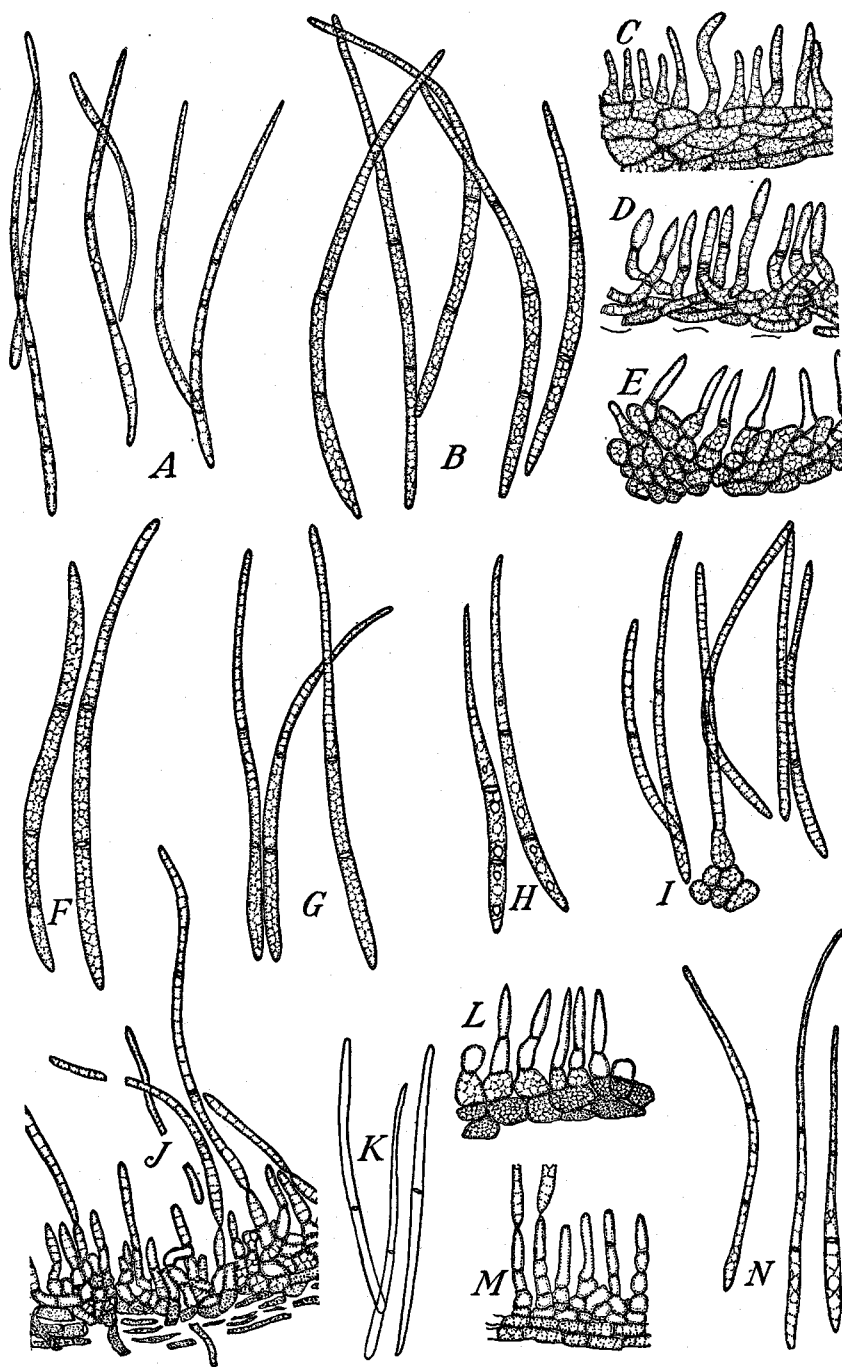
The pycnophores vary from prominent, bottle-shaped structures to short, nipplelike ones and rise from the inner layer of hyaline tissue (Figure 18, C, D, E, F, G, H). Material from freshly collected tissue killed and fixed in Hoggan's solution showed somewhat fusiform or subulate pycnophores, 4.8-7 x 1.6-2.4  $\mu$ . They arose from creeping hyphae with a flattened pad or bulbous cells just beneath the pycnophore. In some instances, the spores are produced without evident pycnophores. The material on *Bromus ciliatus* collected by Toumey in the Bradshaw Mountains of Arizona appears to have only very short pycnophores as the spores arise almost directly from the hyaline cells on the inside of the inner surface of the peridium. In cross sections of the pycnidia, the pycnophores and spores are closely packed in palisade arrangement.

**PYCNOSPORES OF SEPTORIA BROMI.** The pycnospores are characteristically whiplike, usually 2-septate, 33-65 x 1.2-2.5  $\mu$  (Figure 17, A, B, F, G, H, I, K, N). Winter collections on *Bromus mollis* show spores that are

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See Figure 17 on p. 117.

Figure 17. *Septoria bromi*: A, Pycnospores from *Bromus japonicus*, W. A. Archer, Romney, West Virginia; B, pycnospores from *B. secalinus* west of Alsea, Oregon, May 25, 1937 (O.S.C. 8299); C, cross section of pycnidial wall from *B. latiglumis* (= *B. altissimus*), Bruce, Wisconsin, J. J. Davis (See Figure 18, K); D, cross section of pycnidial wall of *S. bromi* var. *phalaricola* on *Phalaris arundinacea*, Astoria, Oregon (O.S.C. 10,370); E, cross section of pycnidial wall from *B. secalinus*, B. F. Dana, Temple, Texas (O.S.C. 8198); F, pycnospores from *B. mollis*, same collection as Figure 17, J; G, pycnospores from *B. commutatus*, near Alderwood Park, Lane County, Oregon, May 10, 1938; H, pycnospores from *B. mollis*, near Stevenson, Washington; I, pycnospores and one attached pycnophore from *B. mollis*, Oakville Church, Linn County, Oregon, May 9, 1938 (O.S.C. 190); J, cross section of pycnidial wall, on *B. mollis*, Bellfountain, Oregon, April 18, 1938 (O.S.C. 167); K, pycnospores from *B. latiglumis* (*B. incanus*), Couderay, Wisconsin, J. J. Davis; L, cross section of pycnidial wall, on *B. secalinus*, near Alsea, Oregon, May 25, 1937 (O.S.C. 8300); M, cross section of pycnidial wall, on *B. secalinus*, near Corvallis, Oregon, February 28, 1934 (O.S.C. 10,402); N, pycnospores from *B. mollis*, K. Keisler, Nieder Osterreich, May 1921. (All X1000)



somewhat stouter than those in spring or summer collections on this and related species of *Bromus*.

PYCNOSPORES OF *SEPTORIA JACULELLA*. The pycnospores are not whip-like but javelin or lancelike (hence *jaculella*) to clavate, hyaline, 2- to 5-septate,  $45-90 \times 1.9-4.0 \mu$  (Figure 18, A, B, I, J, K). They approach *S. bromi* only in winter material of the latter, but are decidedly stouter, stiffer, more septate, and, under white critical illumination, are faintly diamond-blue color. They often contain coarse granular material and the nuclei are prominent.

Collections made by W. E. Lawrence at Fossil and Fox Valley in eastern Oregon, by F. D. Bailey at Astoria, Oregon (O.S.C. 10,736), by the writer at Tangent, Oregon (O.S.C. 10,983), and by A. A. Heller at Bennett Springs, California, on *Bromus leavipes*, showed microspores. What appeared to be pycnidia filled with bacteria, on examination of prepared slides, proved to be microspores of *Septoria jaculella*. While a few macrospores were present, in the pycnidia most of the cavity was filled with microspores radiating in broken strands, usually from minute pycnophores. The microspores, which were  $2-4 \times 0.6 \mu$  (Figure 18, L) (Heller's collection had spores  $3-7 \times 0.4-0.5 \mu$ ), arose from micropycnophores, which varied from those nearly as large as macropycnophores to ones that were differentiated from the bacterially-like spores only by slight basal enlargements. The micropycnophores arose from small pycnophore initials, which composed a tightly packed, very thin-walled layer inside the brown, corky portion of the pycnidial wall. The entire fruiting layer showed considerable heteromorphic hyperplasia, but with only slight thickening of the peridium at places where the semilocules, which sometimes occur in this species, protruded into the cavity of the pycnidium.

#### TAXONOMY

*Septoria bromi* Sacc., which was described in 1878 (84, p. 194) (86, v. 3, p. 562) on *Bromus mollis* from Italy, has filiform obclavate spores said to be curved and minutely pluriguttulate,  $50-60 \times 2 \mu$ . *Septoria smithiana* Trott. (86, v. 25, p. 427) (*S. bromicola* A. L. Sm.) and *S. bromicola* Speg. (93) are narrow-spored specimens of *S. bromi* Sacc.

*Septoria bromivora* Speg. has arcuate, bacillar spores,  $30 \times 2 \mu$ . An examination of the type specimen showed an illustration of an ox-horn-shaped spore, sketched by Spegazzini, but critical examination of the type material revealed smaller spores (Figure 18, M). In any event, *S. bromivora* does not enter further into consideration here.

*Septoria bromigena* Sacc. (89, p. 123) has falcate spores, belongs in

*Selenophoma* (*Selenophoma bromigena* (Sacc.) Sprague and A. G. Johnson) (100) and is very distinct from both *S. bromi* and *S. jaculella*.

*Septoria bromi* Sacc. var. *septulata* Unamuno was described on *Bromus rigidus* (*B. maximus* Desf.) from Spain in 1931 (112). While this is on one of the hosts for *S. jaculella*, the description indicates that *S. bromi* var. *septulata* (112) is closer to *S. bromi* than to *S. jaculella*. Since *S. septulata* Beach (6) already exists, raising this varietal name to specific rank is not possible.

*Ascochyta graminicola* Sacc. var. *diedickeana* Baudys et Picb. (5) on *Bromus tectorum* has 1-septate, cylindrical spores, 11-17 x 2.5-3.1  $\mu$  and is, therefore, very distinct from *S. bromi*. Material of *A. graminicola* var. *diedickiana* has been seen from two Oregon collections of *B. carinatus*.

*Septoria affinis* Sacc. and *S. graminum* Desm. have been reported on brome grasses (84, 86, v. 3, p. 563, 565), but the former has narrowly bacillar spores while the latter is much narrower than the fungi under consideration, and actually (95) is known to occur only on *Brachypodium*.

Grove (53, p. 210) reported a fungus on *Bromus arenarius* Labill., sent to him by Dr. F. Stoward from Australia, which he (Grove) stated "approached *S. ophioides* Sacc., if not identical with it." The collection had spores up to 100  $\mu$  long in pycnidia 150 to 250  $\mu$ . Grove failed to give the width of the spores. *Septoria ophioides* Sacc. has large, black pycnidia, 250 to 330  $\mu$ , with spores 75-105 x 2  $\mu$  (85, p. 143). Saccardo described *S. ophioides* as occurring on an unnamed grass associated with *Astragalus* in Persia. Since the type is not available and possibly never will be, the writer is forced to reject this species from consideration. It is possible, however, that Stoward's collection on *B. arenarius* from Australia is *S. jaculella*. *Bromus arenarius* is sometimes found in the semiarid portions of Oregon but no species of *Septoria* has as yet been found on it there.

Apparently *Septoria jaculella* is an undescribed species, which has escaped detection because of its superficial resemblance to *S. bromi*. While it is abundant in the far west, it appears to be less common elsewhere.

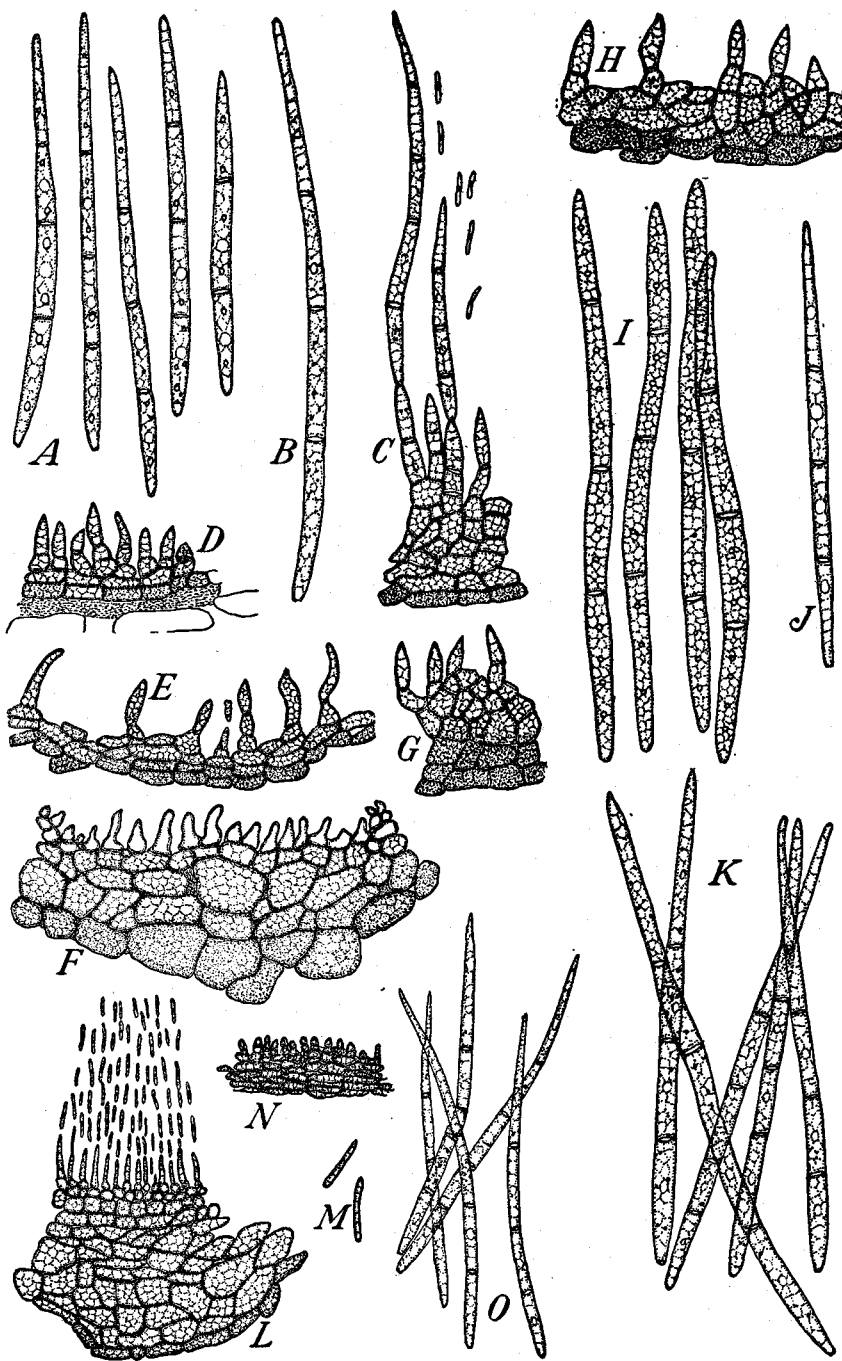
*Septoria jaculella* sp. nov.

Maculis griseis v. isabellinis, margine aureo; pycnidiis prominulis, nigris, numerosis, globosis v. lenticularibus, ostiolatis, 90 to 310  $\mu$  diam.; pycnosporulis rectis, obclavati-filiformibus, hyalino-caeruleis, 2 to 5 septatis, 45-90 x 1.9-4.0  $\mu$  (55-75 x 2.1-3.0  $\mu$ ). Micropycnosporulis bacillaribus 2-7 x 0.4-0.6  $\mu$ .  
Hab. in foliis et vaginis *Bromi carinati*, *B. ciliati*, *B. laevipidis*, *B. rigidi*, *B. tectori*; Oregon, Washington, California et Arizona.

Lesions vague chlorotic gray to isabelline, margins yellow to indefinite, pycnidia scattered, sometimes in green or yellow-green tissue, prominent, black, numerous, globose to lenticular, ostiolate 90 to 310  $\mu$  diam.; pycnosporules lance-like, straight, obclavate-filiform, hyaline (diamond-blue), 2- to

Figure 18. A-L, *Septoria jaculella*: A, Pycnospores from *Bromus carinatus*, A. A. Heller, Pacific Grove, California, April 4, 1903; B, pycnospore from *B. carinatus*, W.E. Lawrence, Fox Valley, Oregon (O.S.C. 10,395); C, cross section of pycnidial wall from same collection as preceding, showing macrospores attached to stoutly formed pycnophores, and microspores floating free; D, cross section of pycnidial wall, on *B. carinatus*, F. D. Bailey, Astoria, Oregon (O.S.C. 10,736) with resinous products between pycnidial wall and host cells; E, cross section of pycnidial wall, on *B. carinatus*, Fossil, Oregon; F, cross section of pycnidial wall, on *B. carinatus*, H. S. Jackson, Corvallis, Oregon, March 14, 1912. The walls in this early spring material have large cells, while the pycnophores are poorly developed and scarcely differentiated from the hyphal layer. In some cases, the spores grow directly from the hyphae, later breaking off and leaving papillate pycnophores; G, cross section of pycnidial wall, on *B. rigidus* (O.S.C. 8070); H, cross section of pycnidial wall, on *B. tectorum*, near Lyle, Washington; I, pycnospores from type of *S. jaculella* near Corvallis, Oregon; J, pycnospore from *B. ciliatus*, J. W. Toumey, Bradshaw Mountains, Arizona; K, pycnospores from *B. rigidus* near Lyle, Washington, February 26, 1935 (O.S.C. 8070); L, microspores from *B. carinatus*, W. E. Lawrence, Fox Valley, Oregon (O.S.C. 10,812); M, pycnospores found in the type of *S. bromivora* Speg.; N, cross section of pycnidial wall of *S. brevispora* Ell. and Davis (type); O, *Septoria bromi* on *B. latiglumis* (*B. altissimus*), J. J. Davis, Bruce, Wisconsin. (All X1000)





5-septate, 45-90 x 1.9-4.0  $\mu$  (55-75 x 2.1-3.0  $\mu$ ); micropycnospores, bacillar, 2-7 x 0.4-0.6  $\mu$ .

In foliage and sheaths of *Bromus carinatus* (type), *B. ciliatus*, *B. laevipes*, *B. rigidus*, and *B. tectorum*.

Of all the collections examined from the United States and Europe, only one, *Septoria bromi* on *Bromus latiglumis* (Shear) Hitchc. (*B. altissimus* Pursh.) collected by Davis in Wisconsin, appears to be at all intermediate between *S. bromi* and *S. jaculella* (Figure 18, O). This was assigned to *S. bromi*. In extremely large, thin-walled specimens of *S. bromi*, the pycnidia are similar to those of *S. jaculella*, but the spores of these two species are clearly distinguishable.

It might be mentioned that *Septoria bromi* var. *alopecuri* Karst. has spores 58-65 x 2.5-3 (61), but this fungus occurs on *Alopecurus pratensis* L. and has relatively small pycnidia (80 to 100  $\mu$ ). It has been raised by Paul Sydow (103) to *S. alopecuri* (Karst.) P. Syd. on the basis of a collection on *A. fulvus* J. E. Smith [*A. aequalis* Sobol.]

*Septoria brevispora* Ell. and J. J. Davis (25) (*non* Zeller) was described on *Bromus ciliatus* from Racine, Wisconsin. It has not been found in the far west. It is characterized by flattened pycnidia producing clavate, 3-septate spores on very short papillae. From the appearance of pycnidia in cross section of material of the type furnished by the late J. J. Davis (Figure 18, N) and the shape of the spores, the fungus is near *Stagonospora* and also near *Septoria nodorum* Berk. In a later collection, Davis (26) reported 1-septate spores 15-30 x 2.5-4  $\mu$ . It is, at least, distinct from both species of *Septoria* on *Bromus* spp. in the far west.

## SEPTORIA BROMI Sacc. Var. PHALARICOLA Var. Nov.

In 1934, Reed Canary Grass (*Phalaris arundinacea*) was attacked by a species of *Septoria* in the plots of the John Jacob Astor Experiment Station, Astoria, Oregon. Collections were made September 25, 1934, but further observations (1935-1939) have failed to disclose additional material.

### SYMPTOMATOLOGY

The disease was confined to scattered basal leaves that were dead or dying. The lesions were elliptical, buff spots up to 1 cm. in diameter, or large vague spots which covered all of dead straw-colored leaves. The brown pycnidia were moderately prominent.

## INOCULATION TRIALS

No inoculations were tried with this fungus as pure cultures were not obtained. Two inoculation trials with *Septoria tritici* from wheat and with *S. bromi* from *Bromus mollis* were negative on *Phalaris bulbosa* L. and in one trial on *P. arundinacea*.

## MORPHOLOGY

**PYCNIDIA.** The pycnidia are large, 150-180 x 204-276  $\mu$ , brown, ostiolate, globose to slightly flattened, and have very thin walls. The wall consists of one or two layers of loosely intertwined light brown cells, which give rise to hyaline hyphae terminating in cylindrical to narrowly subulate pycnophores, 4.5-11 x 1.5-2.2  $\mu$  (Figure 17, D). These are variable, some being elongate (? paraphyses), 1-septate and blunted as in some collections of *Septoria bromi* Sacc. on certain annual brome grasses.

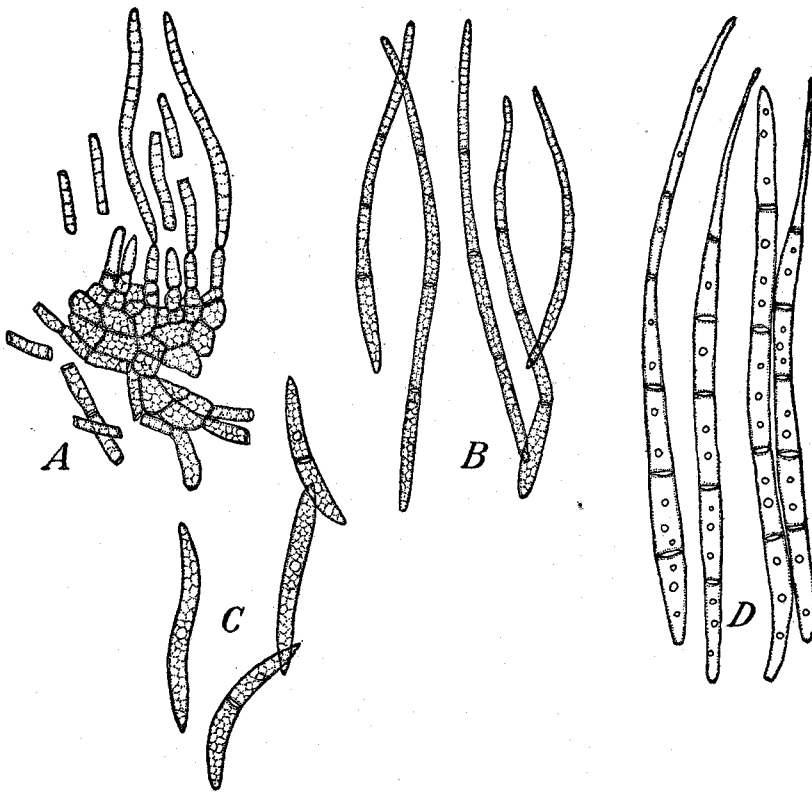
**PYCNOSPORES.** The pycnospores are hyaline, narrowly obclavate-filiform, commonly 3-septate, 34-66 x 1.7-2.9  $\mu$  (average 52.6 x 2.3  $\mu$ ) (Figure 19, B).

## TAXONOMY

*Septoria bromi* Sacc. was listed on *Phalaris arundinacea* by Saccardo (84, p. 194; 86, v. 3, p. 562) from Parma, Italy. He considered the fungus on *Bromus mollis* and that on *P. arundinacea* as the same species. Trail (108, p. 231) gave *S. bromi* var. *phalaridis* Trail on *P. arundinacea*, but Grove (54) placed this under *S. alopecuri* Syd. var. *phalaridis* (Trail) Grove. Trail gave the spore measurements as 53-65 x 3.5-4.0  $\mu$  with 8 to 15 septa.

The material from Astoria, Oregon, resembles *Septoria bromi* because of its globose to subglobose, thin-walled pycnidia, its somewhat whiplike spores, and its cylindrical pycnophores. It differs in having the spores typically 3-septate instead of the commonly 2-septate condition of *S. bromi* proper, and the spores are also less strongly obclavate than in *S. bromi*. The pycnidium represents an extreme in the thin-walled condition of *S. bromi*, as many collections of this fungus on *Bromus* spp. have coarser, more tightly packed peridia. Since the variations from *S. bromi*, however, are mainly relative, rather than specific, the fungus is considered a morphological variety of *S. bromi*. *Septoria phalaridis* Cocc. and Mor. (22, p. 392) described on *Phalaris brachystachys* Lk., has distinctly smaller spores (1-septate) (20-25 x 1.25  $\mu$ ) and also smaller pycnidia (96 to 105  $\mu$ ) than the Oregon material. For the Oregon fungus, therefore, the following is proposed:

Figure 19. A, Cross section of pycnidial wall of *Septoria munroae*, Yuma, Colorado, July 15, 1908; B, pycnosporos of *S. bromi* var. *phalaricola* (type); C, pycnosporos from type of *S. macrostoma*; D, pycnosporos of *S. arctica* on *Calamagrostis nutkaensis*, F. D. Bailey, Delmoor Bog, Clatsop County, Oregon, August 9, 1939. (All X1000)



*Septoria bromi* Sacc. var. *phalaricola* var. nov.

Maculis ochraceis, pycnidiis brunneis, globosis v. subglobosis, 150-190 x 204-256  $\mu$ , ostiolatis; pycnosporulis obclavato-filiformibus, 3-septatis, 34-66 x 1.4-2.9  $\mu$ .

On light buff lesions on leaves, pycnidia brown, globose to subglobose, 150-190 x 204-256  $\mu$ , ostiolate; walls thin, 6  $\mu$  consisting of one to two intertwined light brown parenchymatous layers of oblong cells from which hyaline hyphae arise, terminating in cylindrical to narrowly subulate pycnophores, 4-11 x 1.5-2.2  $\mu$ . Spores narrowly obclavate-filiform, somewhat whiplike, commonly 3-septate, 34-66 x 1.4-2.9  $\mu$ .

On leaves of *Phalaris arundinacea* L., Astoria, Oregon. Type: O.S.C. 10,370, deposited in the Mycological Herbarium at Corvallis, Oregon. Prepared slides of the pycnidia are also deposited in the Mycological Collections, Bureau of Plant Industry, Washington, D. C.

*Septoria macrostoma* Speg., which was described on *Phalaris canariensis* L. from Argentine, has curved 0- to 1-septate spores, 20-25 x 2  $\mu$  (Figure 19, C) and is, therefore, distinctly different from *S. bromi* var. *phalaricola*.

*Stagonospora foliicola* (Bres.) Bubak, which occurs on *Phalaris arundinacea* in the west, has 3- to 8-septate cylindrical spores 35-70 x 4.5-6.0  $\mu$  borne in elliptical to diffuse vinaceous lesions and is, also, very different from *S. bromi* var. *phalaricola*.

## SEPTORIA MUNROAE Ell. and Barth on MUNROA

*Septoria munroae* Ell. and Barth. on *Munroa squarrosa* (Nutt.) Torr. was described in 1902 from Rooks County, Kansas. The host, false buffalo grass, occurs in the western portion of the Great Plains area from Montana and North Dakota, south to Arizona and Texas. A collection by H. L. Shantz of *S. munroae*, from Yuma, Colorado (U.S.D.A. Ex. 60, 198) was used in studying the morphology of this species. The pycnidia are prominently and seriatly arranged on the straw-colored leaves. Virtually all of the leaves were infected. In cross section, the pycnidia are flattened-cupuliform to subspherical, 95 to 110  $\mu$  wide and 72 to 108  $\mu$  high. The walls are light golden brown, 11 to 14  $\mu$  thick. Hyphae (2  $\mu$  thick) from the outer portion of the peridium ramify into the adjacent host tissues. In the different layers of the peridium, there is a gradual transition, in the form of the cells, from cylindrical on the outside to subcubical to globose on the inside (Figure 19, A). The pycnophore initials are 2 to 2.5  $\mu$  in diameter, are subglobose with squared corners (polyhedral) and produce cylindrical pycnophores, which are obtusely rounded at the apex, and measure 5-9.5 x 1.5-2.1  $\mu$ .

The spores in the type are given as 80-110 x 2.5-3  $\mu$ , hyaline and with 1

to 3 septa near the broad end. Ellis and Bartholomew (36, p. 176) state that the pycnosporos resemble very much the conidia of *Cercospora*.

While no host range studies have been made, the writer believes that this species is distinct from other species on *Gramineae*.

### SEPTORIA ARCTICA Berk. and Curt. on CALAMAGROSTIS

The type of *Septoria arctica* Berk. and Curt. was collected, sometime between 1853 and 1856, on *Dupontia fischeri* R. Br. by Charles Wright on Arakam Island (Arakamtchetchene), also known as Kayne Island, which is on the Siberian side of Bering Strait. Abundant material of the same fungus was collected on the related grass, *Calamagrostis nutkaensis* (Presl) Steud., at Delmoor Bog near Seaside, Clatsop County, Oregon, by F. D. Bailey in August 1933. Subsequently Bailey and the writer collected considerable quantities of this leaf spot at Delmoor Bog at intervals from August 7 to October 29, 1939.

#### SYMPTOMATOLOGY

The large, strongly erumpent pycnidia are very prominent on the yellowed culms of *Dupontia fischeri*.

On *Calamagrostis nutkaensis*, numerous, prominent, seriatly arranged pycnidia occur in somewhat ill-defined brown to dull gray lesions that merge with the green surrounding tissue. They occur on the leaves, sheaths, and even on the glumes and pedicels. Under the favorable high humidity of the adjacent cranberry bog and sphagnum marsh, the fungus causes severe damage to the grass. Most of the leaves of plants seen in August were scorched severely by the streaking disease. After the death of the host, the lesions fade, leaving the pycnidia prominent.

#### PURE CULTURE STUDIES

The fungus from *Calamagrostis nutkaensis* germinates slowly on potato dextrose agar. The colonies when first visible are delicate, white cottony, and loosely textured. They continue to develop as a loose, cottony growth, which, after 6 months at 4-5° C., continues to be sterile.

#### MORPHOLOGY

**PYCNIDIA.** The pycnidia on *Dupontia fischeri* from the type are strongly erumpent, black, tardily ostiolate, globose with firm peridium, and reach 250  $\mu$  in diameter.

On *Calamagrostidis nutkaensis*, the numerous pycnidia are large, mostly 140 to 210  $\mu$  diameter, globose to slightly ellipsoid vertically, and characteristically semiloculated (Plate 2, N). Cross sections of pycnidia, particularly those made near the sides or off-center, show that they are irregularly lobed. The pycnidia, which are robust as in *Septoria jaculella*, grow irregularly, due probably to active secondary development in late fall whereby the fungus, in its irregular expansion, forces aside the host cells. The pycnidial walls are 8 to 12  $\mu$  thick, dark creosote-brown, composed of tightly packed corky cells with large, irregular polyhedral ones, included in some of the folds of the walls. The pycnophores are stout, varying from broadly to narrowly pyriform, and arise from subglobose initials. Spores are exuded in thick masses and are still visible in prepared material clustered about the ostiole.

Material from Delmoor Bog, collected in October, showed pycnidia nearly devoid of spores, but filled with a prosenchymatous growth as if a perithecial stage were forming.

PYCNOSPORES. The type is somewhat plasmolyzed and the reputed number of cross walls, 3 to 7, are not entirely discernible. The spores are hyaline, obclavate-scolecosporous, with tapering, rounded bases and sharply pointed ends, at least 2- to 3-septate, 60-80 x 2.8-3.6  $\mu$ . They are straight to stiffly curved, and in these respects they resemble those of *Septoria jaculella*.

On *Calamagrostis nutkaensis*, the spores (August 1939 material) are narrowly obclavate with rounded, tapering, finally blunted bases and abruptly tapered apices, which terminate as sharp elongated tips. Sometimes the basal cells are empty and shorter than usual. The spores were bluish-hyaline with no indication of coloring at the time they were collected in August. From their coarse granular contents, however, it was suspected that they might eventually develop color. The material collected in October showed some yellowing, although the spores were hyaline. The spores (August) were 3- to 7-septate with the more mature ones 70-89 x 3.5-4.6  $\mu$  (Figure 19, D). There were many shorter and narrower spores which, however, appeared to be immature or had the basal or terminal cells broken off.

A collection on *Calamagrostis epigeios* (L.) Roth, made by Lind in Jutland, Denmark, in 1903<sup>1</sup> is labeled *Septoria epigejos* but is assigned to *S. arctica*. It has hyaline 3-septate pycnospores, 40-65 x 2.2-2.8  $\mu$  with blunt bases and pointed apices.

#### TAXONOMY

*Septoria arctica* Berk. and Curt., which was described in 1858 (8), is very evidently the same species as occurs on *Calamagrostis nutkaensis* in

<sup>1</sup>Vestergren Micr. rar. sel. 941 (Exsiccati).



Oregon. Part of the complex on *Calamagrostis* in Europe, exclusive of the obviously different filiform-spored *S. calamagrostidis*, is referable to *S. arctica*. Collections from Europe and North America, however, which are not readily assignable to *S. arctica*, will be discussed as follows:

*Septoria epigejos* Thuem. (106) on *Calamagrostis epigeios*, which was collected in Kirghis, Imperial Russia, was described as having pycnidia disposed in lines, densely grouped, ellipsoid, large, and black; spores bacillar, sometimes curved, obtuse at the ends, 4- to 5-septate,  $45 \times 3.5-4 \mu$ . Unamuno (111) reported pycnidia of this species 79 to  $107 \mu$  with 4- to 5-septate spores,  $35-45 \times 3.5-4.0 \mu$ . Unfortunately, the type of *S. epigejos* is not available. Lind's collection made in 1903 and referred to above is assigned to *S. arctica*. Another collection by Lind from Jutland, however, is less typical for *S. arctica*. Lind (66, Plate VII, Figure 88) indicated brown spores for *S. epigejos* Thuem. on *Calamagrostis epigeios*. Specimens received from Harvard University of Westendorp's Crypt. Belg. No. 1055, labelled *S. calamagrostidis* (Lib.) Sacc., contained heavy-walled, subspherical pycnidia with pycnosporos with blunt bases, 4- to 10-septate,  $36-45 \times 3-4.5 \mu$ . These specimens also approach those of *S. epigejos*. They also resemble those of *S. rhizodes* Bres. and Krieg. (12) described on *C. halleriana* (Gaud.) Beauv. [*C. villosa* (Chaix) Mutel] from Saxony. This has yellow, subcurved-clavate, 7- to 10-septate spores,  $48-52 \times 3-4 \mu$ . In a collection on *C. nutkaensis* from Waldport, Oregon (O.S.C. 354), the spores have the same vermiform shape but are larger,  $55-71 \times 4.3-4.8 \mu$ . This resembles the description of *S. alopecuri* (Karst.) P. Sydow var. *calamagrostidis* Grove (54, p. 425) which is said to have spores linear, obtuse above and acute below, yellowish,  $40-100 \times 3-4 \mu$ , faintly curved with 3 to 13 distinct septa. Grove (54, Figure 25e) sketched a scoleospore with distinct constrictions at the cross walls. Material sent from Kew, England, collected at Goosehill Woods, did not contain spores. At the request of the writer, Miss E. M. Wakefield examined the rest of the same specimen at Kew and sent two slides to the writer. Slide A contained a few multiseptate, brown conidia,  $70-80 \times 4 \mu$ . These conidia resembled *S. epigejos* and, as Miss Wakefield pointed out, also resembled spores of *Cercospora*. The material from which these spores were found was overrun with *Cladosporium herbarum* and contained what appeared to be immature *Mycosphaerella tulasnei* and the "*Cercospora*" spores could not be determined as having come from a pycnidium. The spores were not indented at the septa as in Grove's illustration (54, Figure 25e). Slide B sent by Miss Wakefield contained spores similar to *Hendersonia mollis*, Grove,  $33-40 \times 4.0-4.3 \mu$ , and were nearer what Sydow calls *S. alopecuri* than

the long spores described by Grove for his variety *S. alopecuri* var. *calamagrostidis*. The large, thin-walled pycnidia ( $200\ \mu$ ) had small ostioles as described for *S. rhizodes*. The material on *C. nutkaensis* from Waldport, Oregon, is described elsewhere as *Phaeoseptoria calamagrostidis* Sprague (99).

In addition to these, Sydow's Myc. Germ. No. 2205, which as labeled *Septoria rhizodes* on *Calamagrostis lanceolata* (L.) Roth, has subcylindrical, clear-hyaline spores,  $27\text{--}35 \times 3.2\text{--}4.0\ \mu$ , borne in pale, thin-walled pycnidia very similar to *Stagonospora* and very different from the heavy-walled pycnidia of Lind's 1906 collection.

*Septoria calamovilfae* Petr. (80) has been collected recently in North Dakota, South Dakota, and Wyoming on *Calamovilfa longifolia* (Hook.) Scribn. Material collected at Faith, South Dakota, shows white spots on living leaves.

Another large-spored *Septoria* on *Sorghastrum nutans* (L.) Nash collected at Long Pine, Nebraska, September 13, 1899 (J. M. Bates 1294) should be mentioned as present in the region also. The spores are 3- to 9-septate, hyaline,  $56\text{--}100 \times 1.5\text{--}2.4\ \mu$ . They are filiform at the base and taper to a narrow yet rounded apex. This specimen, which was seen only recently by the writer, is the same as material collected by H. C. Greene and which is being described elsewhere as *Septoria andropogonis* var. *sorghastri* Greene and Sprague var. nov.

In a separate publication *Septoria andropogonis* forma *sporobolicola* Sprague is described on *Sporobolus heterolepis* (A. Gray) A. Gray with spores  $45\text{--}51 \times 2.4\text{--}3.4\ \mu$  from Lisbon, North Dakota (98). At the same time *Septoria mississippiensis* Sprague was described (98) on *Muhlenbergia mexicana* (L.) Trin. from Lake Itasca, Minnesota, with spores  $35\text{--}65 \times 2.1\text{--}3.1\ \mu$ . This fungus also occurs on *M. asperifolia* (Nees and Mey.) Parodi at New Rockford, North Dakota. These fungi and *S. andropogonis* J. J. Davis (spores  $33\text{--}51 \times 3.2\text{--}3.9\ \mu$ ), which Lefebvre collected at Manhattan, Kansas, on *Andropogon furcatus* Muhl. should be recognized as occurring in the area covered by this article.

#### SEPTORIA SPARTINAE (Trel.) Comb. Nov. on SPARTINA Spp.

*Septoria spartinae* (Trel.) comb. nov. on *Spartina gracilis* Trin. was collected July 14, 1940 at Logan, Utah, by George W. Fischer and on *S. pectinata* Link in June 1940 near Hecla, South Dakota, by the writer. The lesions on living leaves are elliptical to striate, straw to buff-colored, with obscure, tardily erumpent pycnidia.

## MORPHOLOGY

**PYCNIDIA.** Freezing microtome sections stained in cotton blue were very kindly sent by Fischer. These showed deeply immersed, scarcely erumpent, black, ellipsoidal pycnidia with stout walls. The walls were 10 to 14  $\mu$  thick, composed of several layers of polyhedral cells that ranged from deep brown around the ostiole to subhyaline at the base of the pycnidium. The pycnophores were prominent, cuspidate to narrowly pyriform, and arose from hyaline pycnophore initials along the floor of the pycnidium. The pycnidia were 100 to 140  $\mu$  wide and 70 to 90  $\mu$  deep. Because of the "glassy" host cells, this fungus has assumed a "*Rhabdospora*-like" stout-walled pycnidium such as noted in *Septoria pacifica*.

**PYCNOSPORES.** The hyaline, mostly 2-septate spores in Utah material are narrowly elongate-fusiform, tapering to a relatively sharp apex and a more gradually blunted or truncate base, 26-38 x 2.0-2.5  $\mu$ .

## TAXONOMY

*Ascochyta spartinae* Trel. produces small, rounded, yellow spots on leaves of *Spartina pectinata* Link in Wisconsin. The spores are hyaline, straight or slightly curved, usually slightly narrower at one end, 1- (1-3) septate and average 35 x 3  $\mu$ . It appears that the material from Utah, South Dakota, and Wisconsin are phases of the same species. The fungus is a species of *Septoria*:

***Septoria spartinae*** (Trel.) comb. nov.

Syn. *Ascochyta spartinae* Trel.

Emended as follows: Lesions straw to buff, elliptical to striate, pycnidia obscure, not rare, immersed, tardily erumpent, black, ostiolate, ellipsoidal, densely parenchymatous, epiphyllous and hypophyllous, 100-140 x 70-90  $\mu$ , pycnophores prominent, cuspidate to narrowly pyriform, 4-7 x 2.5-3.7  $\mu$ , pycnospores elongate-fusiform, straight or with the base curved, apex tapering to a point, base narrowly truncate, mostly 2-septate (Utah) or 1- to 3-septate (Wisconsin), 26-38 x 2-2.5 (Utah) -3.0  $\mu$  (Wisconsin).

On living leaves of *Spartina gracilis* Trin. in Utah and *S. pectinata* Link in Wisconsin and South Dakota.

The collection on *Spartina gracilis* from Utah, sent by Fischer, was the first specimen of a *Septoria* on a grass that the writer had seen from that state.

## KEY TO RELATED GENERA AND TO SPECIES OF SEPTORIA

In using this key, it should be emphasized that climatic factors may influence, to a considerable extent, the morphology of the pycnidia, pycnophores, and pycnospores. This key has taken cognizance of these facts, as much as possible, within the limitations of such keys. It should be recalled that the pycnophore dimensions are based to a considerable extent on those of prepared mounts and may, therefore, be smaller than those of fresh material. Discretion is necessary at all times in classifying the variable Fungi Imperfecti.

- I. Spores falcate, aseptate, pycnidia small, globose . . . *Selenophoma* spp. (not included in this paper).
- II. Spores cylindrical, multiseptate, predominantly less than 10 times as long as wide, pycnidia golden-brown, thin-walled, pycnophores typically short . . . *Stagnospora* spp. (not included in this paper).
- III. Spores filiform to narrowly obclavate 0- to multiseptate, predominantly at least 10 times as long as wide, pycnidia typically brown, pycnophores usually moderately long . . . *Septoria* spp.

	Page
A. Pycnospores 0- to 2-septate, less often 3-septate.	
1. Pycnidia prominent, as much as 180-250 $\mu$ in diameter.	
a. Spores filiform, 36-50 x 1.4-1.6 $\mu$ . . . <i>Septoria poliomela</i> .....	90
b. Spores obclavate-filiform, 33-65 x 1.2-2.5 $\mu$ . . . <i>S. bromi</i> .....	114
c. Spores obclavate, 28-50 x 2.1-4.5 $\mu$ . . . <i>S. infuscans</i> .....	67
2. Pycnidia intermediate, 100-180 $\mu$ in diameter.	
a. Spores filiform, 2-septate, 40-56 x 1.8-2.4 $\mu$ . . . <i>S. elymi</i> on <i>E. canadensis</i> var <i>robustus</i> .....	66
b. Spores elongate-fusiform 26-38 x 2-2.5 $\mu$ . . . <i>S. spartinae</i> .....	131
c. Spores, elongate fusiform, 25-42 x 2.5-4.0 $\mu$ , pycnidia sometimes less than 100 $\mu$ in diam . . . <i>S. calamovilfae</i> .....	130
d. Spores narrowly cylindrical 1-septate ( <i>Ascochyta</i> phase, 12-24 x 1.7-2.8 $\mu$ ) . . . <i>S. oudemansii</i> .....	57
3. Pycnidia small, obscure, 50-110 $\mu$ in diameter.	
a. Pycnidia typically 50-80 $\mu$ , spores 0- to 1-septate . . . <i>S. triseti</i> ....	101
b. Pycnidia typically 80-120 $\mu$ , spores 0- to 2-septate . . . <i>S. tenella</i> ....	85
B. Spores typically more than 2-septate.	
1. Pycnospores usually less than 50 $\mu$ long.	
a. Spores averaging more than 2 $\mu$ wide.	
(1) Spores bacillar.	
(a) Produces a pale colored leaf spot, spores 3-septate, 25-50 x 2.5-3.5 $\mu$ , on rye . . . <i>S. secalis</i> .....	84
(b) Produces a dark brown leaf spot, spores 3-septate, 25-50 x 2.7-4.1 $\mu$ , on <i>Lolium</i> . . . <i>S. loligena</i> .....	29
(c) Produces a pale colored leaf spot 1-3-septate, 37-62 x 2.6-3.4 $\mu$ , on <i>Stipa</i> and <i>Agrostis</i> , <i>S. secalis</i> var. <i>stipae</i> .....	111
(d) Produces a pale colored leaf spot, 3-septate (rare, see one- septate phase) 35-55 x 3-4 $\mu$ . . . <i>S. oudemansii</i> .....	55

	Page
(2) Spores narrowly obclavate, apex more or less pointed.	
aa. Pycnidia 100-140 $\mu$ , on <i>Sporobolus</i> . . . <i>S. andropogonis</i> f. <i>sporobolicola</i> .....	130
bb. Pycnidia 75-100 $\mu$ , on <i>Andropogon</i> . . . <i>S. andropogonis</i> .....	130
cc. Pycnidia 100-200 $\mu$ . . . <i>S. agropyrina</i> .....	64
b. Spores less than 2 $\mu$ wide.	
(1) Pycnidia golden-brown, ellipsoid.	
(a) Pycnophores 4-7 $\mu$ long, spores 35-40 x 1.3-1.6 $\mu$ . . .	
<i>S. macropoda</i> .....	43
(b) Pycnophores 3-4 $\mu$ long, spores 30-50 x 1.2-2.1 $\mu$ . . .	
<i>S. elymi</i> .....	60
(2) Pycnidia creosote-brown, subglobose to ellipsoid, spores 14-46 x 1.3-2.0 $\mu$ . . . <i>S. passerinii</i> .....	79
2. Pycnosporos frequently more than 50 $\mu$ long.	
a. Spores narrowly filiform, about 1 $\mu$ wide . . . <i>S. stipina</i> .....	94
b. Spores more than 1 $\mu$ wide.	
(1) Spores often more than 2.7 $\mu$ wide.	
(a) Spores averaging less than or approximately 65 $\mu$ long.	
aa. Spores strictly hyaline	
(aa) Spores 2- to 4-septate, stiffly curved, obclavate-filiform, pycnophores 4-9 $\mu$ long . . . <i>S. infus-cans</i> (in part) .....	67
(bb) As in (aa) but blunter, 3-septate <i>S. agropyrina</i> ....	64
(cc) Spores mostly 3-septate, somewhat whiplike, obclavate-filiform, pycnophores 5 to 11 $\mu$ long	
<i>S. bromi</i> var. <i>phalaricola</i> .....	123
bb. Spores somewhat chlorinous . . . <i>S. mississippiensis</i>	
(b) Spores averaging more than 65 $\mu$ long.	
aa. Pycnidia prominent, as much as 320 $\mu$ in diameter.	
(aa) Spores seldom more than 5-septate, lance-shaped, obclavate . . . <i>S. jaculella</i> .....	115
(bb) Spores 3- to 7-septate, obclavate, apex elongated . . . <i>S. arctica</i> .....	127
bb. Pycnidia smaller, commonly less than 150 $\mu$ in diameter.	
(aa) Pycnophores narrowly ampulliform, spores long-filiform . . . <i>S. pacifica</i> .....	78
(bb) Pycnophores cylindrical, spores obclavate-filiform . . . <i>S. munroae</i> .....	126
(2) Spores less than 2.7 $\mu$ , but more than 1.0 $\mu$ wide.	
(a) Pycnidia brown, cells compact, frequently elongated	
aa. Pycnophores awl-shaped, 2 to 5 $\mu$ long	
(aa) Spores very narrowly obclavate-filiform.	
aaa. On <i>Agrostis exarata</i> , <i>S. calamagrostidis</i> .....	100
bbb. On <i>Koeleria cristata</i> , <i>S. calamagrostidis</i> f. <i>koeleriae</i> .....	107
(bb) Spores filiform, less often very narrowly obclavate-filiform.	
aaa. Spores typically sinuous . . . <i>S. calamagrostidis</i> on <i>Agrostis palustris</i> .....	100

	Page
bbb. Spores usually slightly curved, but less often sinuous . . . <i>S. calamagrostidis</i> on <i>Trisetum</i> spp. . . . .	101
bb. Pycnophores short, papillate, 2 to 3 $\mu$ long . . . <i>S. macropoda</i> on <i>Poa howellii</i> . . . . .	50
(b) Pycnidia golden-brown, cells moderately compact, variable in shape, not uniformly elongated.	
aa. Spores seldom over 1.7 $\mu$ wide . . . <i>S. macropoda</i> var. <i>septulata</i> . . . . .	50
bb. Some spores more than 1.7 $\mu$ wide.	
(aa) Spores never as many as 8- to 9-septate	
aaa. Pycnophores 2 to 6 $\mu$ long . . . <i>S. macropoda</i> var. <i>grandis</i> . . . . .	51
bbb. Pycnophores 4 to 13 $\mu$ long.	
(aaa) Spores typically sinuous . . . <i>S. tritici</i> f. <i>avenae</i> . . . . .	27
(bbb) Spores variously curved but less often sinuous.	
aaaa. Microspores present, macrospores 25-90 x 1.4-2.6 $\mu$ on wheat, <i>S. tritici</i> . . . . .	18
bbbb. Microspores not known.	
(aaaa) Pycnosporos up to 85 $\mu$ long on <i>Lolium</i> . . . . .	
<i>S. tritici</i> var. <i>lolicola</i> . . . . .	28
(bbbb) Pycnosporos up to 105 $\mu$ long on <i>Holcus</i> . . . . .	
<i>S. tritici</i> f. <i>holci</i> . . . . .	36
(bb) Spores 3 to 9-septate, up to 95 $\mu$ long . . . <i>S. andropogonis</i> var. <i>sorghastri</i> . . . . .	130
(cc) Spores 5-septate, up to 60 $\mu$ long . . . <i>S. quinqueseptata</i> . . . . .	110

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# HOSTS, SPECIES OF SEPTORIA, AND OCCURRENCE IN THE WESTERN UNITED STATES

Hosts and species of <i>Septoria</i>		Occurrence	Page, Plate or Figure
<i>Agropyron inerme</i>	<i>Septoria elymi</i> .....	Oregon	58; Figure 7, G
<i>A. repens</i>	<i>S. elymi</i> .....	Oregon, Washington, North Dakota, South Dakota, Montana, Minne- sota, Iowa, Wisconsin	58; Plate 1, L, N; Figure 7, C, D, E, K, L
<i>A. repens</i>	<i>S. (?) agropyrina</i> .....	South Dakota	74; Figure 10, H
<i>A. smithii</i>	<i>S. elymi</i> .....	Minnesota, Iowa, Montana	58
	<i>S. agropyrina</i> .....	Nebraska, Montana	74; Figure 10, F, G
<i>A. spicatum</i>	<i>S. elymi</i> .....	Washington, Wyoming	58; Figure 7, O
	<i>S. infusans</i> .....	Oregon	67
<i>A. subsecundum</i>	<i>S. elymi</i> .....	Montana	58
<i>A. trachycaulum</i>	<i>S. elymi</i> .....	Minnesota, Iowa, Montana	58
	<i>S. agropyrina</i> .....	North Dakota	74; Figure 10, I
142 <i>Agrostis alba</i>	<i>S. triseti</i> .....	Oregon, Washington	96; Figure 15, D
<i>A. castellana</i>	<i>S. triseti</i> .....	Oregon	96
<i>A. diegoensis</i>	<i>S. calamagrostidis</i> .....	Oregon	96; Figure 14, E, K
<i>A. exarata</i>	<i>S. calamagrostidis</i> .....	Oregon	96; Figure 14, H
	<i>S. triseti</i> .....	Oregon, Washington	96; Figure 15, E
<i>A. hallii</i>	<i>S. secalis</i> var. <i>stipae</i> .....	Oregon	112; Figure 15, M
<i>A. scabra</i>	<i>S. secalis</i> var. <i>stipae</i> .....	North Dakota	111
<i>A. palustris</i>	<i>S. calamagrostidis</i> .....	Oregon, Washington	95, 96; Figure 14, A, D, G, I
<i>A. tenuis</i>	<i>S. triseti</i> .....	Oregon, Washington	96; Plate 2, L; Figure 15, A, B, C, F, G, H, I, J, K, L
<i>Andropogon furcatus</i>	<i>S. andropogonis</i> .....	Kansas	130
<i>Avena byzantina</i>	<i>S. tritici</i> f. <i>avenae</i> .....	Oregon, Washington	27
<i>A. fatua</i>	<i>S. tritici</i> f. <i>avenae</i> .....	Oregon, Washington	27
<i>A. sativa</i>	<i>S. tritici</i> f. <i>avenae</i> .....	Oregon, Washington	27; Plate 2, F; Figure 1, E
<i>Bromus carinatus</i>	<i>S. jaculella</i> .....	Oregon, California	113; Plate 1, M; Figure 18, A, B, C, D, E, F, I, L
<i>B. ciliatus</i>	<i>S. jaculella</i> .....	Arizona	113; Figure 18, J
<i>B. commutatus</i>	<i>S. bromi</i> .....	Oregon	113; Plate 2, J; Figure 17, G

<i>B. japonicus</i>	<i>S. bromi</i> .....	Washington, Wyoming	113
<i>B. laevipes</i>	<i>S. jaculella</i> .....	California	113; Plate 2, G
<i>B. mollis</i>	<i>S. bromi</i> .....	Oregon, Washington	113; Figure 17, F, H, I, J
<i>B. racemosus</i>	<i>S. bromi</i> .....	Oregon	113
<i>B. rigidus</i>	<i>S. jaculella</i> .....	Oregon, Washington	113; Plate 2, A; Figure 18, G, K
<i>B. secalinus</i>	<i>S. bromi</i> .....	Oregon, Texas, Idaho	113; Figure 17, B, E, L
<i>B. tectorum</i>	<i>S. jaculella</i> .....	Washington	113; Figure 18, H
<i>Calamagrostis nutkaensis</i>	<i>S. arctica</i> .....	Oregon	127; Plate 2, N; Figure 19, D
<i>Calamovilfa longifolia</i>	<i>S. calamovilfae</i> .....	North Dakota, South Dakota, Wyoming	130
<i>Deschampsia caespitosa</i>	<i>S. poliomela</i> .....	Oregon	90; Figure 13, B
<i>D. danthonioides</i>	<i>S. poliomela</i> .....	Oregon, Washington	90; Figure 13, A, C, D
<i>Dupontia fischeri</i>	<i>S. arctica</i> .....	Alaska (Siberia)	127
<i>Elymus canadensis</i>	<i>S. elymi</i> .....	North Dakota, South Dakota, Minnesota, Iowa	58; Figure 7, H
<i>E. condensatus</i>	<i>S. agrapyrina</i> .....	North Dakota, South Dakota	67; Figure 10, J
	<i>S. infuscans</i> .....	Oregon, Washington, Utah, Montana	67; Figure 8, D, E, H, K, L, M; Figure 9, A, B, C
<i>E. condensatus</i>	<i>S. pacifica</i> .....	California	75
<i>E. condensatus</i> var. <i>pubens</i>	<i>S. pacifica</i> .....	California	75
<i>E. glaucus</i>	<i>S. elymi</i> .....	Oregon, Washington, Michigan	58, 64; Figure 7, A, B, I, J, M, Q
	<i>S. infuscans</i> .....	Oregon, Washington	67; Plate 2, P
<i>E. mollis</i>	<i>S. pacifica</i> .....	Oregon	75; Plate 2, K; Figure 10, A, B, D
<i>E. triticoides</i>	<i>S. elymi</i> .....	California	58
	<i>S. infuscans</i> .....	California, Oregon, Washington	67; Plate 1, E; Figure 8, A, B, F, G, I, J
<i>Festuca dertonensis</i>	<i>S. tenella</i> .....	Oregon	84; Figure 12, F, G, J
<i>F. idahoensis</i>	<i>S. tenella</i> .....	Wyoming	85
<i>F. octoflora</i>	<i>S. tenella</i> .....	North Dakota, South Dakota, Montana, Colorado, Kansas, Oregon, Idaho	85; Figure 12, B, E

HOSTS, SPECIES OF SEPTORIA, AND OCCURRENCE  
IN THE WESTERN UNITED STATES—*Continued*

Hosts and species of <i>Septoria</i>		Occurrence	Page, Plate or Figure
<i>F. ovina</i>	<i>S. tenella</i> .....	Wyoming	85
<i>F. rubra</i>	<i>S. tenella</i> .....	Oregon	85; Figure 12, C, M
<i>F. rubra</i> var. <i>commutata</i>	<i>S. tenella</i> .....	Oregon	87; Figure 12, D, H, K
<i>Holcus lanatus</i>	<i>S. tritici</i> f. <i>holci</i> .....	Oregon, Washington	35; Plate 2, 0; Figure 3, A, C D, E, F, G, H, I, J
<i>Hordeum brevisubulatum</i>	<i>S. passerinii</i> .....	North Dakota	79
<i>H. jubatum</i>	<i>S. passerinii</i> .....	North Dakota, South Dakota, Iowa	79
<i>H. nodosum</i>	<i>S. passerinii</i> .....	Oregon, Montana, Wyoming, Washington	79; Figure 11, A, F, G, H
<i>H. vulgare</i>	<i>S. passerinii</i> .....	Oregon, Idaho, Iowa, North Dakota, South Dakota	79; Plate 2, D
<i>Koeleria cristata</i>	<i>S. calamagrostidis</i> f. <i>koeleriae</i> .....	Oregon, Washington, Wyoming	106; Plate 2, C; Figure 16, A B, C, D
<i>Lolium multiflorum</i>	<i>S. tritici</i> var. <i>lolicola</i> .....	Oregon	28; Figure 2, A, B, C, D
	<i>S. loligena</i> .....	California	28
14 <i>L. perenne</i>	<i>S. tritici</i> var. <i>lolicola</i> .....	Oregon	28; Plate 1, K; Figure 2, E, G
<i>Muhlenbergia asperifolia</i>	<i>S. mississippiensis</i> .....	North Dakota	130
<i>M. mexicana</i>	<i>S. mississippiensis</i> .....	Minnesota	130
<i>Munroa squarrosa</i>	<i>S. munroae</i> .....	Colorado, Kansas	126; Figure 19, A
<i>Phalaris arundinacea</i>	<i>S. bromi</i> var. <i>phalaricola</i> .....	Oregon	122; Figure 17, D; Figure 19, B
<i>Poa ampla</i>	<i>S. macropoda</i> var. <i>grandis</i> .....	Washington	42; Figure 6, H
<i>P. annua</i>	<i>S. macropoda</i> .....	Oregon, Washington	42; Figure 4, A, B, C, E, F
<i>P. arachnifera</i>	<i>S. oudemansii</i> .....	North Dakota	56
<i>P. arida</i>	<i>S. macropoda</i> var. <i>grandis</i> .....	South Dakota	41
<i>P. canbyi</i>	<i>S. macropoda</i> var. <i>grandis</i> .....	Montana	41
	<i>S. oudemansii</i> .....	North Dakota	56
<i>P. compressa</i>	<i>S. macropoda</i> var. <i>septulata</i> .....	Oregon, North Dakota, South Dakota	41; Plate 1, F, J; Figure 5 D, E
	<i>S. oudemansii</i> .....	Oregon, North Dakota	56
<i>P. cusickii</i>	<i>S. macropoda</i> var. <i>grandis</i> .....	Montana	42; Figure 6, C
<i>P. howellii</i>	<i>S. macropoda</i> .....	Oregon, Washington	55
<i>P. juncifolia</i>	<i>S. oudemansii</i> .....	North Dakota	56
<i>P. kelloggii</i>	<i>S. macropoda</i> .....	Oregon	50; Figure 4, D
<i>P. nervosa</i>	<i>S. macropoda</i> var. <i>grandis</i> .....	Montana	42; Plate 2, F
	<i>S. macropoda</i> var. <i>septulata</i> .....	Washington	51; Figure 5, G
<i>P. nevadensis</i>	<i>S. macropoda</i> var. <i>grandis</i> .....	Oregon, California	41; Figure 6, F



<i>P. pratensis</i>	<i>S. oudemansii</i> .....	North Dakota	54
	<i>S. macropoda</i> var. <i>septulata</i> .....	Oregon, Washington, Idaho, Montana, North Dakota, South Dakota, Minnesota, Wyoming, Iowa, Nebraska	41; Figure 5, A, B, C, F, H, I
	<i>S. oudemansii</i> .....	Oregon, Washington, Idaho, Wyoming, North Dakota, Nebraska, Minnesota, California, Michigan	52, 53
<i>Poa scabrella</i>	<i>Septoria macropoda</i> var. <i>grandis</i> .....	Washington, California	41; Figure 6, D
<i>P. secunda</i>	<i>Septoria macropoda</i> var. <i>grandis</i> .....	Oregon, Washington, Montana, North Dakota, South Dakota, Wyoming	41, 54; Figure 6, A, B, E, G, I, J
<i>P. secunda</i>	<i>S. oudemansii</i> .....	Washington, Wyoming	56
<i>P. vaseyochloa</i>	<i>S. macropoda</i> var. <i>grandis</i> .....	Washington	41
<i>Secale cereale</i>	<i>S. secalis</i> .....	Iowa	84; Figure 11, I
<i>Sitanion hystrix</i>	<i>S. passerinii</i> .....	Oregon	80; Plate 2, B; Figure 11 B, C, E
145 <i>Sorghastrum nutans</i>	<i>S. andropogonis</i> var. <i>sorghastri</i> .....	Nebraska	130
	<i>S. spartinae</i> .....	Utah	130
	<i>S. spartinae</i> .....	South Dakota	130
	<i>S. quinquesepata</i> .....	North Dakota	111
	<i>S. andropogonis</i> f. <i>sporobolcola</i> .....	North Dakota	130
	<i>S. stipina</i> .....	Oregon	94; Figure 15, 0
	<i>S. secalis</i> var. <i>stipae</i> .....	South Dakota, North Dakota, Minnesota	112
	<i>S. secalis</i> var. <i>stipae</i> .....	North Dakota	94, 112
	<i>S. calamagrostidis</i> .....	Oregon	96; Plate 1, H; Figure 14, B C, J
	<i>S. calamagrostidis</i> .....	Oregon	96; Figure 14, F
<i>Triticum aestivum</i>	<i>S. tritici</i> .....	Oregon, Washington, California, Idaho, Kansas, Montana, North Dakota, Minnesota, Iowa	16, 17; Plate 2, Q; Figure 1, A, B, D, F, H, I, L, N
<i>T. dicoccum</i> var. <i>farrum</i>	<i>S. tritici</i> .....	Oregon	17, 19; Figure 1, J, K
<i>T. spelta</i>	<i>S. tritici</i> .....	Oregon	17
<i>T. turgidum</i>	<i>S. tritici</i> .....	Oregon	17

# HOST INDEX<sup>1</sup>

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