AMERICAN JOURNAL OF BOTANY

Vol. VI — January, 1919 — No. 1

BIOLOGIC SPECIALIZATION IN THE GENUS SEPTORIA

Walter Spurgeon Beach

Introduction

The genus Septoria presents an excellent field for the study of biologic specialization on account of the very large number and the uncertain status of the described species, of which there are more than 1200. The morphological characters for the limitation of these are few, consisting chiefly of spore shape, length, thickness, and septation, and in some instances a slight tinting of the spore; pycnidium shape, size, and color; and ostiole size and character. The biological characters for the limitation of species are the size, shape, margin, zonation, and color of the disease spots, and their location and distribution upon the host. The specific descriptions in many cases are meager and really useless. The presence of a Septoria upon an unrecorded host is often made the basis of a new species.

By tabulating (10), according to spore length, all the "species" of Septoria given in Saccardo's "Sylloge Fungorum," it has been found that nearly 700 fall within the limits of 20 to 50 μ. Twenty-six species on grasses are between 20 and 40 μ. Yet in one case a Saccardian description gives a spore length ranging from 19 to 62 μ. There have been great inaccuracies in measuring spores and pycnidia, with tendencies to report the measurements in round numbers. Elliott (7) has shown the degree of personal error with our modern technique. Among eleven observers measuring many spores of Alternaria, he found that there was a variation of over 41 per cent from the highest measurement returned for maximum length, and that such a variation would make it impossible to distinguish the species of Alternaria on the basis of spore measurement. Septation is largely dependent upon the stage of maturity of the spores, is often difficult to see, and was ignored by early mycologists. Environmental conditions cause fluctuations in the size of spores and pycnidia. The value of disease characters is doubtful, for they commonly change with the age, the part, and the species of the host, as well as with weather conditions. The confusion that Cavara (4) met regarding these points in his attempt to distinguish *Septoria tritici* and *S. graminum* on wheat, led him to state that both forms probably belong to the same morphological species.

Little is known respecting the existence of biologic specialization in the genus Septoria. Except for a few instances (15, 22, 45), no cross-inoculations have been made to ascertain whether a Septoria, as found upon a particular host, is restricted to that host, or is more or less cosmopolitan and adaptive in its parasitism. In the literature at present one is confronted by two extremes of treatment: (*a*) closely similar species are described on the same host, *e. g.*, *Septoria lactucae* and *S. consimilis* on *Lactuca sativa*, (*b*) more widely variant forms on distantly related hosts are described as representing one species, *e. g.*, *S. graminum* on twelve or more genera of grasses, and a species of sedge. It is obvious that such practice is not consistent, and cannot adequately reflect the truth.

The facts as presented above are illustrative of the present unsatisfactory status of the species not only of Septoria but also of many other genera of the fungi imperfecti. More accurate knowledge regarding host characters, morphological variation, and biological specialization is greatly needed from the standpoint of classification. The genus is the more worthy of study on account of its high economic importance. To study such a large genus as Septoria in culture, either upon the living hosts or upon artificial media, would require the time of many investigators. The present paper is intended merely as a contribution to the general problem as suggested above, and the investigations were conducted with the following leading objects:

1. To determine the host range of as many species of Septoria as possible in order to ascertain (*a*) whether morphologically similar forms from different hosts vary in host range, and (*b*) whether morphologically unlike forms ever have the same host range; or in other words to ascertain whether any of the species available for study consist of a number of biologic forms, and whether any now listed as distinct species are identical.

2. To compare disease characters, *i. e.*, the host response to infection, when produced (*a*) by a single species of Septoria upon dissimilar hosts, or (*b*) by different species of Septoria on the same host.

3. To note any morphological changes in the size and shape of spores and pycnidia as a result of change of host or the condition of the host, or of other environmental factors.

4. To determine the susceptibility of different parts of the same host and of these at different stages of maturity, and to note whether any distinctions in disease characters are correlated with host structure and condition.

Historical Review

The literature dealing with biologic specialization is extensive. A comprehensive review cannot be undertaken here, yet a brief summary of the essential points, especially as brought out by the investigations of rusts and powdery mildews, will be useful in the interpretation of the results to be presented. It may be well to mention that biologic specialization is also spoken of as "adaptive parasitism," and biologic forms are referred to as "biologic species," "biologic races," "physiological races," and "adapted races."

Eriksson (8) called attention definitely to the nature of biologic specialization through the results of his cross-inoculation experiments with *Puccinia graminis* in Sweden. He found that, although this rust upon the cereals and grasses represented the same morphological species, the form upon one host-species was not always identical with the form upon another; since, for example, oat rust would transfer to oats, but not as a rule to other species of Gramineae. He showed that this fungus embraces at least six distinct forms distinguished by their dissimilar powers of infection with respect to the species of the grass family. In a subsequent paper (9) Eriksson showed that the trend of specialization may be different in isolated localities. This was illustrated by the fact that the form on rye, *Puccinia graminis secalis*, has a relatively vigorous development in Sweden, but a relatively weak one in North America. In the case of *Puccinia graminis tritici* on wheat, the more vigorous development is in the latter country.

Ward (46), experimenting with *Puccinia dispersa* upon Bromus, discovered "bridging species." The nature of a "bridging species" is described by this statement of the author: "Although it is generally true that the adapted races of *Puccinia dispersa* are restricted to groups of closely allied species, there do occur species which serve as intermediaries in the passage of the fungus from one section of the genus to another."

Stakman and Piemeisel (43) claim that the biologic forms of *P. graminis* can be distinguished from one another morphologically as well as biologically, by the size, shape, and color of the urediniospores. Regarding susceptibility they state: "All gradations in susceptibility occur from complete immunity to complete susceptibility to the various biologic forms. The following reactions may be made to inoculation: no visible effect, appearance of small flecks, production of very small uredinia without flecks, production of very small uredinia in small or large flecks, production of large uredinia surrounded by small dead areas or by apparently healthy tissue."

Arthur (1), Hitchcock and Carleton (13), Carleton (2, 3), and Stakman (42) have also carried out valuable investigations upon biologic specialization in rusts.

Neger (21) and Marchal (17) were early workers upon adaptive parasitism in the powdery mildews. Salmon, however, has done the most extensive work in this field, and has published a long series of papers (30–39). He proved that several biologic forms of Oidium parasitize the species of Bromus, that an individual species may be the meeting place of several biologic forms, and that "bridging species" exist. An additional discovery is best stated in his own words (35, p. 57): "The inter-relations of the biologic forms with certain of their host-plants become complicated by the existence of 'biologic forms' of the host-plants." Salmon found that in *Bromus mollis* there is a susceptible and an immune race with respect to four separate biologic forms of the mildew.

G. M. Reed (24–29) has corroborated the results of Salmon and others, and has carried out extensive cross-inoculation experiments with *Erysiphe graminis* (27, 28, 29) in which he has shown considerable variation in susceptibility among the species and varieties of Triticum, Hordeum, Avena, and Secale, a few of which are immune. In *Erysiphe cichoracearum* upon Cucurbitaceae (25) he found but one biologic form, capable of growing upon various members of this host family.

The more important instances of biologic specialization reported in other groups of fungi are as follows: by Stäger in Claviceps (41), by Diedicke in Pleospora and its conidial stage Helminthosporium (5), by Gilbert in *Plowrightia morbosa* (11), by Müller in *Rhytisma acerinum* (20), and by Hesler in *Sphaeropsis malorum* (12). Shear and Wood (40) found that the races of *Glomerella cingulata* from different hosts vary somewhat in the vigor of their attack upon other hosts. Tests by Westerdijk (47) indicate the absence of biologic specialization among similar races of *Sclerotinia libertiana*. Rands (23) has proved by cross-inoculation that the Alternaria of Datura and that of potato are not identical as some have supposed.

With species of Septoria only a few investigators have worked. Levin (15) inoculated several plants akin to the tomato with *Septoria lycopersici*. Definite small black spots without pycnidia appeared on potato, but no effect was seen on other plants. Norton (22) performed similar experiments in humid inclosures, and obtained infection upon several species of Solanum. A further discussion of this author's results will be given in a subsequent section. Stone (45) proved by infection that *Septoria ribes* and likewise its perfect stage *Mycosphaerella grossulariae* taken from *Ribes nigrum* will infect *R. grossularia*, *R. rubrum*, and *R. oxyacanthoides*.

Montemartini (18) has concluded that parasitic fungi are extremely sensitive to the chemical composition of the nutritive medium on which they live, and that under its influence they acquire characters of adaptation, which attain to a certain fixity. In consequence fungi may become unable to flourish on species different from those to which they have accustomed themselves, or even on other portions of the same plant which they inhabit, or in different developmental stages of such plant or organ. This problem is further complicated by atmospheric conditions, and the influence thereof upon sensitivity to attack as well as upon the virulence of the infecting bodies.

The review here given serves to illustrate the intricate nature of biologic specialization, and to remind one of the various factors to be considered in the interpretation of the results of inoculation experiments.

Experimental Methods and Material

The species of Septoria for investigation were with few exceptions collected in the vicinity of Urbana, Illinois. During the growing season spore-bearing material was gathered in the field from naturally infected plants. In fall and winter spores were obtained in most cases from pure cultures isolated before the first frost. In preparation for inoculation, spore suspensions were made with distilled water and were concentrated enough to contain fifty to one hundred spores per loop.

The experiments were begun in June and were continued to the following April. In summer the work was conducted in the field upon plants growing in their natural state. Freedom from disturbance and as far as possible from natural infection governed the selection of suitable individuals. After the first frost the experiments were continued in the greenhouse upon potted plants transplanted from nature or grown from seed.

The method of inoculation was somewhat varied. In the field an atomizer was most convenient, for the spore suspension could be carried safely in the glass container. In the greenhouse a wire loop was more commonly used to spread drops of the suspension over the leaf surface. Where a bloom or other epidermal structures made it difficult to secure good contact, especially with leaves of grasses, the suspension was rubbed on with the clean finger tips with proper care. Consistency of method was followed in a single series to secure comparable results. The entire surface of certain leaves was inoculated, while adjacent leaves of the same plant or of near-by plants were used as checks to detect foreign infection where there was danger of this. Inoculations were made upon individuals of the original host to afford a check upon the viability of spores, or upon unfavorable environmental conditions.

In providing conditions favorable for infection, covers made of paraffined paper bags were found to give the most satisfactory results. Some use was also made of bell jars. The inoculated leaves, or the entire plant, were covered for periods varying from three to five days. In cases in which disease spots without pycnidia resulted, the bags were replaced over the plants for a second period to promote the growth of the fungus, and to induce if possible the development of spore-bearing bodies. If this failed, the spotted leaves were detached and put into a sterile moist chamber. In this manner pycnidia were obtained and infection proved in some cases in which results would otherwise have been in doubt. This was especially necessary in instances in which spore suspensions were made from natural material, and the spores of other fungi might have been present to cause the spots.

In the following accounts the results of the inter-inoculations with each species of Septoria are presented graphically by means of diagrams, and in more detail in a few representative cases by means of tables. The arrows in the diagrams indicate infection, and the lines ending in bars non-infection.

The denominators of the adjacent fractions state the total number of leaves inoculated, and the numerators the number of leaves having one or more infected spots. The total number of spots formed is given in the tables where this is required for a closer comparison of susceptibility. In the second column of each table the letter *f* indicates that the experiment was conducted in the field or out of doors, and *g* that it was carried on in the greenhouse. The letter *b* with the accompanying figure records the number of days the plant was bagged immediately following inoculation.

The lists of hosts given were compiled partly from Saccardo's "Sylloge Fungorum," and partly from data furnished by the herbaria of the New York Botanical Garden and the United States Department of Agriculture.

SEPTORIA POLYGONORUM DESM.

All collections of Septoria made from species of Polygonum at Urbana were determined as *Septoria polygonorum* Desm. This fungus has been reported upon the following species of Polygonum, which are arranged in groups:

A. Infected by the author

P. persicaria
" *pennsylvanicum*
" *lapathifolium*
" *orientale*

B. Inoculated but not infected

P. amphibium
" *hydropiper*
" *convolvulus*

C. Not used in experiments

P. bistorta
" *sieboldii*
" *mitis*
" *hydropiperoides*
" *muhlenbergii*
" *dumetorum*

D. Synonymous

P. incarnatum = *P. lapathifolium*
" *nodosum* = *P. lapathifolium*

The members of group *C* are foreign, or were not found growing in this vicinity. The species of group *B*, as well as others that gave negative results when inoculated, apparently had sufficient opportunity to become infected in nature; for infected plants of smartweed were usually growing in close proximity to the uninfected kinds. Yet repeated search for material resulted in finding *Septoria polygonorum* upon only *Polygonum persicaria*, *P. pennsylvanicum*, and *P. lapathifolium*, upon which the form in this locality appears to be specialized. The plants of *P. orientale* were few and apparently escaped infection by being isolated. It remains an open question whether the forms of *Septoria polygonorum* reported upon *P. amphibium*, *P. hydropiper*, and *P. convolvulus* of group *B* are differently specialized or whether the hosts are resistant in this region. The former case is likely if the fungi and their hosts were correctly determined.

TABLE I

Infections with Septoria polygonorum Desm.

Date	Conditions	Plants Inoculated	No. of Leaves Infected and Inoculated	No. of Spots	Check Infections on Original Host
		Spores from *Polygonum pennsylvanicum*			
June 28	f-b 2	*Polygonum persicaria*	12/16	many	8/10
Aug. 30	f-b 2	" "	11/20	"	
Sept. 6	f-b 3	" "	8/12	45	
Sept. 14	f-b 3	" "	10/15	26	
			41/63		
Aug. 30	f-b 4	*Polygonum lapathifolium*	3/10	34	6/6
Sept. 14	f-b 4	" "	5/5	many	6/6
			8/15		
Sept. 14	f-b 4	*Polygonum orientale*	6/6	28	6/6
June 9	shaded	*Polygonum erectum*	0/10		4/5
June 28	f-b 3	" "	0/11		8/10
			0/21		12/15
June 28	f-b 0	*Polygonum convolvulus*	0/8		8/10
June 28	shaded	*Polygonum hydropiper*	0/45		8/10
Sept. 7	shaded	*Polygonum acre*	0/12		
Sept. 21	f-b 4	" "	0/20		plus
			0/32		
Sept. 21	shaded	*Polygonum scandens*	0/25		plus
June 28	shaded	*Polygonum amphibium*	0/7		8/10
		Spores from *Polygonum persicaria*			
July 10	shaded	*Polygonum pennsylvanicum*	0/10		10/15
Oct. 3	g-b 5	" "	5/5	many	
			5/15		
Sept. 9	f-b 4	*Polygonum lapathifolium*	7/10	many	10/10
Sept. 20	f-b 4	*Polygonum orientale*	7/7	many	
July 10	shaded	*Polygonum convolvulus*	0/20		10/15
Mar. 3	g-b 3	" "	0/5		
			0/25		
July 10	shaded	*Polygonum hydropiper*	0/30		10/15
Sept. 28	f-b 4	" "	0/25		plus
			0/55		
July 10	f-b 3	*Polygonum erectum*	0/25		10/15
Sept. 7	shaded	*Polygonum acre*	0/10		
Sept. 21	f-b 4	" "	0/20		
			0/30		
		Spores from *Polygonum lapathifolium*			
Sept. 11	f-b 3	*Polygonum pennsylvanicum*	2/5	15	
Sept. 21	f-b 3	*Polygonum persicaria*	6/12	15	8/8
Mar. 10	g-b 3	" "	3/4	13	
			9/16	28	

TABLE I—*Continued*

Date	Conditions	Plants Inoculated	No. of Leaves Infected and Inoculated	No. of Spots	Check Infections on Original Host
		Spores from *Polygonum lapathifolium*			
Sept. 21	f-b 3	*Polygonum orientale*	7/7	many	8/8
Sept. 21	f-b 4	*Polygonum hydropiper*	0/25		8/8
Sept. 21	f-b 4	*Polygonum acre*	0/20		8/8
Sept. 21	shaded	*Polygonum scandens*	0/20		8/8
Oct. 7	g-b 4	*Polygonum convolvulus*	0/12		
Dec. 3	moist chamber	*Polygonum convolvulus* (leaves detached)	3/7	5	
Oct. 7	g-b 4	*Fagopyrum esculentum*	0/10		
Dec. 3	moist chamber	*Fagopyrum esculentum* (leaves detached)	0/7		
Dec. 3	moist chamber	*Rumex crispus* (leaves detached)	0/7		

Septoria polygonorum was isolated, and the growth characters were alike in the fungus as isolated from each of the four hosts in group *A*. No distinctions in biological characters, as shown by their powers to infect, were apparent among these four stocks of the same Septoria from as many different hosts, at least in the light of the experiments thus far conducted.

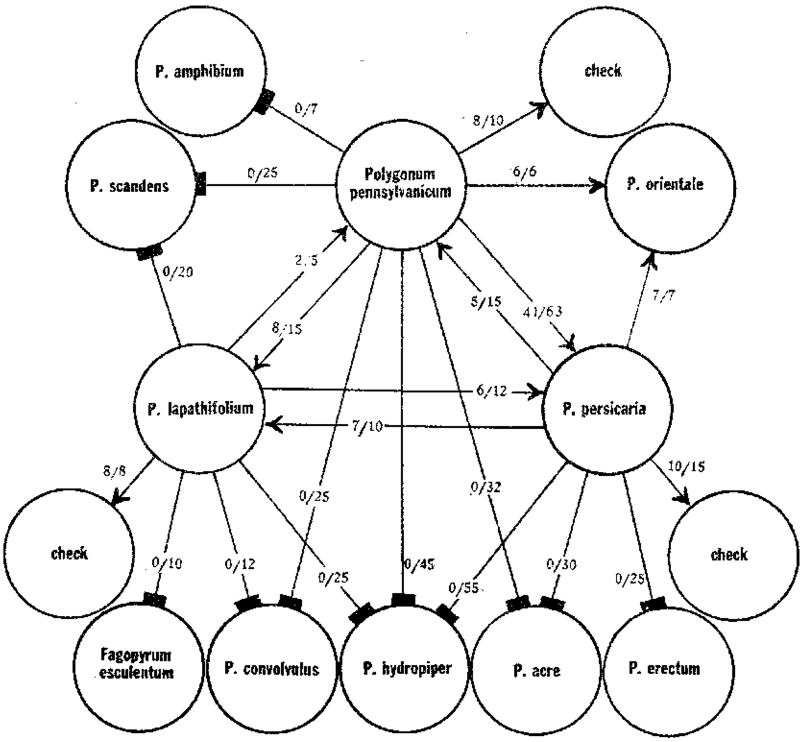

DIAGRAM I. Infections with *Septoria polygonorum* from *Polygonum pennsylvanicum*, *P. persicaria*, and *P. lapathifolium*.

Although a vigorous parasite upon the few species of Polygonum, the form of *Septoria polygonorum* dealt with here is not at all cosmopolitan in its parasitism. A special attempt was made to infect a plant of *P. convolvulus* kept constantly covered with a paraffined paper bag to insure a humid atmosphere and provide partial shading, but with negative results. One hundred leaves of *P. hydropiper* also gave negative results. The fungus was induced to attack detached leaves of *P. convolvulus* kept in a moist chamber in the moist laboratory, spots and pycnidia developing in seven days; but it would not attack *Rumex crispus* or *Fagopyrum esculentum* in a similar way. Thus *Septoria polygonorum* appears as a species with fairly fixed infection-powers, possibly embracing forms differently specialized in addition to the one experimented with here.

The disease spots are not the same on the various species of Polygonum. The distinctions are illustrated in Plate I, figures 1–4. The specimens were selected as representing the usual character of the spots. Specimens of the same species might have been selected showing scarcely distinguishable spots. Upon *P. pennsylvanicum* the spots attain the greatest size, often become irregular in outline, have but a very narrow, dark brown border, and have pycnidia uniformly distributed throughout their area (fig. 1). The spots upon *P. persicaria* are intermediate in size, and are chiefly characterized by a rather wide, dark reddish-brown border. The spots seldom lose their orbicular shape, and the pycnidia are grouped nearer the center (fig. 2). Upon *P. lapathifolium* the spots range smallest in size, and are yellowish-brown in the fresh leaves, with a border of the same color, but in the dry specimens the spots become reddish-brown (fig. 3). In size and shape the spots on *P. orientale* resemble those on *P. pennsylvanicum*, but are yellowish-brown in the fresh leaf. The reddish-brown border appeared when the leaf was put into a moist chamber for a day. The variability in the biological or host characters shown here illustrates the untrustworthy nature of these characters when used to distinguish species.

Septoria lactucicola Ell. & Mart.

Septoria lactucicola has been reported upon *Lactuca floridana*, *L. scariola*, and *L. canadensis*, but in most instances on the last-named plant. The results in diagram 2 show that this Septoria is somewhat adaptive in its parasitism, being able to attack three genera and five species. Were the experiments conducted on a broader scale, the host range would probably be enlarged. There is a gradation in susceptibility passing from *L. canadensis* through to *Sonchus oleraceus*. Although the fungus attacked *L. sativa* and *L. scariola* rather readily, with 16 spots on 30 leaves and 10 spots on 35 leaves respectively, the infection was slight compared with 23 spots on 7 leaves of the original host. Moreover, there were but few fruiting bodies on these new hosts. The most of the 17 spots on *Prenanthes* sp. were very small, and *Sonchus oleraceus* was a very uncongenial plant for the fungus. The comparison will be more clear with a description of the spots.

Septoria lactucicola produces upon *L. canadensis* round, reddish-brown to black spots, usually from 3 to 15 mm. in diameter, and frequently with concentric zones of lighter and darker color. *L. scariola* was the only new host in which these characters were preserved, and here the spots were lighter-colored, probably on account of the thinner leaves. Upon *L. sativa* the spots were spreading, with an indefinite border, and several times larger than those on *L. canadensis* where the border is very definite. They were colored light brown in the center, gradually changing to yellow and then to the green of the normal tissue. No pycnidia were observed in the greenhouse, but they developed in two days upon leaves detached and put into a moist chamber. For a further comparison of the spots on these first three hosts compare Plate I, figures 7–9. The spots upon *Prenanthes* sp. were 1 mm. to 3 mm. in diameter, dark brown, more or less angular, and usually surrounded by a greenish-yellow zone. Pycnidia were seen upon the plant, but spores developed only in the moist chamber. The spots upon *Sonchus oleraceus* were 1 mm. to 5 mm. in diameter, grayish brown, and more or less limited by the leaf veins. A small number of pycnidia with spores characteristic of *Septoria lactucicola* were obtained upon two of several infected leaves placed in a moist chamber.

That the biologic characters change with the host is clearly shown. Such variation has doubtless led to erroneous determinations, or to the useless multiplication of species in many instances. Environment may likewise cause alterations of these characters, for the spots on *L. canadensis* tended to lose their concentric zones and become spreading if kept long in a moist atmosphere.

SEPTORIA LACTUCAE PASS.

The following hosts are reported for *Septoria lactucae: Lactuca sativa*, *L. scariola*, *L. virosa*, *L. canadensis*, and *Chrondrilla muralis*. The fungus appears to cross readily between *L. sativa* and *L. scariola*, and causes upon both of these hosts marked disease. The passage of the fungus from either of these hosts to *L. canadensis* apparently takes place only under very favorable conditions of heat and moisture, for it was necessary to cover the plants for a prolonged time with bags, and to atomize them frequently with water to secure infection. A considerable degree of infection was secured in this way, yet it is probable that this Septoria does not occur commonly on *L. canadensis* in nature. The disease characters on *L. canadensis* were different from those seen upon *L. sativa* or *L. scariola;* the spots were smaller, had no tendency to spread, were darker in color, and commonly had a yellow zone for a border. They were angular in outline, usually 1 mm. to 5 mm. broad, and the central area was brown to black. Pycnidia and spores were present.

Especially favorable conditions were also provided in order to infect *Sonchus asper;* still the transfer of the fungus to this more distantly related host was not difficult, for almost 25 percent of the inoculated leaves were more or less diseased. Such infection raises a question of identity between *Septoria lactucae* and certain of the species of Septoria described upon the

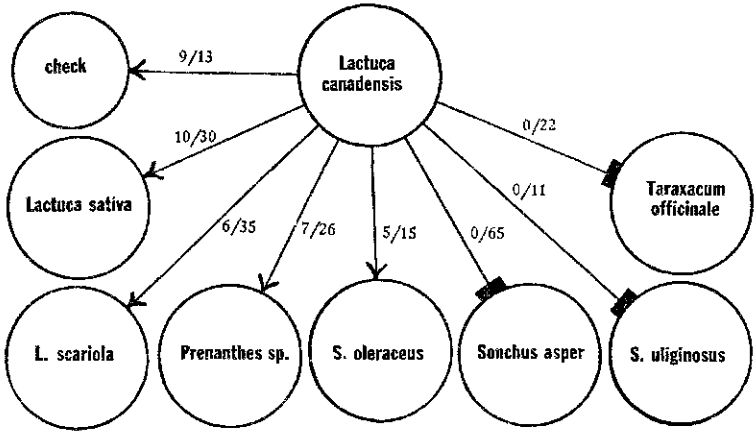

DIAGRAM 2. Infections with *Septoria lactucicola* from *Lactuca canadensis.*

genus Sonchus. An examination of exsiccati showed a close similarity between *S. lactucae* and *S. sonchifolia,* but more extensive data is needed to prove their identity. The spots formed upon *Sonchus asper* by *S. lactucae* were grayish-brown to black, angular in outline, 1 mm. to 5 mm. in width, and contained reproductive bodies.

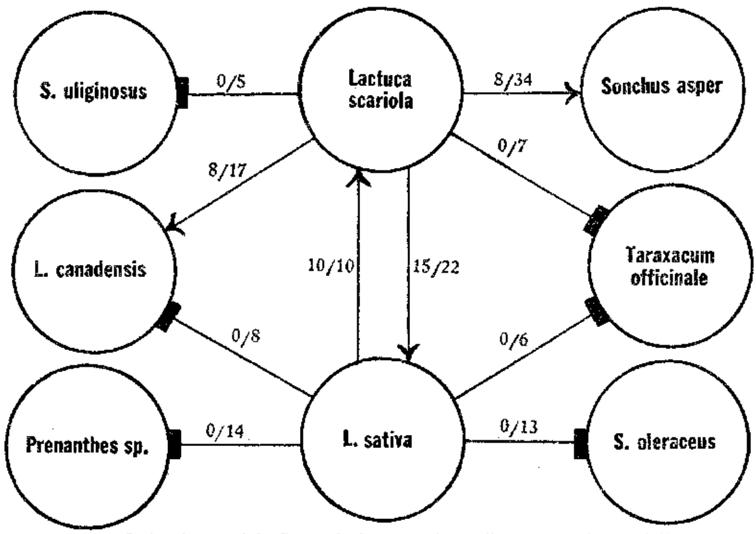

DIAGRAM 3. Infections with *Septoria lactucae* from *Lactuca sativa* and *Lactuca scariola.*

If *Septoria lactucae* is compared with *S. lactucicola*, it is found that the two species are different in their adaptation to their hosts as well as different morphologically, although the host ranges of the two almost coincide. Each infects *Lactuca sativa*, *L. scariola*, *L. canadensis*, and can pass over to the genus Sonchus. Yet *Septoria lactucae* is best adapted to *Lactuca sativa* and *L. scariola*, grows less readily upon *L. canadensis*, and infects *Sonchus asper* somewhat, while *Septoria lactucicola* is best adapted to *Lactuca canadensis*, grows less readily upon *L. sativa* and *L. scariola*, and infects *Sonchus oleraceus* slightly.

Septoria tritici Desm.

There was some uncertainty regarding the name of the species of Septoria from wheat used in these experiments. In the literature two species are frequently mentioned as associated on *Triticum vulgare:* viz., *Septoria tritici* Desm., described in 1842, and *S. graminum* Desm., described in 1843. To the latter is usually ascribed the damage done to winter wheat and other cereals by Septoria. Cavara (4, p. 41) in studying the forms of Septoria on wheat was confronted by so much disagreement that he revised the descriptions of Desmazières as follows:

"Die *Septoria tritici* Desm. (Pl. Cryptog. no. 669), welche anfangs gelbe, dann rostbraune, und endlich weissliche Flecke durch die Zerstörung des Parenchyms bildet, hat gewöhnlich gefächerte Sporen von 50 bis 60 x 1.5–2 μ; sie sind von fadenförmiger Gestalt mit häufig ein wenig aufgetriebener Mitte. Die Scheidewände sind von Desmazières nicht bemerkt worden. Die *Septoria graminum* Desm. (Pl. Cryptog. no. 728) besitzt Perithecien die dem blossen Auge nicht wahrnehmbar und kleiner und dichter gestellt als bei der vorigen Art sind; sie bilden durch ihre Vereinigung längliche grau nebelige Flecke. Die Sporen sind etwas feiner als bei *Septoria tritici* und ein Ende ist dicker als das andere; sie messen 40–50 x 1–1.5 μ, sind nicht gefächert, zeigen aber mehrere Tröpfchen."

Upon the basis of this revision Cavara compared all the exsiccati available to him. His comparisons led him to make this statement (4, p. 22): "Wenn man sich nun Rechenschaft von der grossen Veränderlichkeit der Charaktereigenschaften giebt, wie Form und Farbe der Flecke, Grösse der Perithecien, Vorhandensein oder Fehlen der Scheidewände bei der Gattung Septoria, so wird es sehr wahrscheinlich das *S. graminum* und *tritici* nur Formen einer einzigen mycologischen Art sind und die sich ergebenden Differenzen vielleicht nur der Verschiedenartigkeit der Wirtspflanze zuzuschreiben sind."

The collections of Septoria from wheat used in the present investigation were made from one plot of Turkey Red winter wheat at the Illinois Experiment Station. In June, at a time when the grain had fully headed, nearly all the leaf blades were more or less infected. After harvest, volunteer clumps of wheat came up from heads scattered on the ground, and in

October the leaves in these clumps were badly attacked by Septoria. Collections for purposes of inoculation were made at this time, and also in December and January. After the ground froze the clumps were cut out, allowed to thaw slowly, and were then kept in a closed collecting can in the greenhouse. In a few days the pycnidia were forming spores abundantly.

The spores from this source, collected either in summer or winter, were septate, and the pycnidia were brownish-black, round to elliptical when viewed from above, usually arranged in rows between the leaf veins, and were often visible to the naked eye. The spores from the leaves of the plants that had been frozen and then treated as mentioned were much longer but somewhat more slender than spores from material collected in other ways. Septation was difficult to detect and seemed to be absent in some cases, but proper staining made it apparent in most of the spores. The pycnidia under these same conditions were often more than double their ordinary size, but were unchanged in shape. Infections obtained upon wheat seedlings by inoculation with these longer types of spores always resulted in pycnidia of normal proportions, and in shorter spores with more definite septa, typical of the fungus found on the leaves of wheat in summer or fall. A more comprehensive description of these morphological variations will be given in a subsequent section.

Whether one base his conclusions upon Cavara's revised descriptions, or upon his assertion that *Septoria tritici* and *S. graminum* are probably identical, the fungus at hand must be designated *S. tritici* Desm., in one case on account of morphology, and in the other on account of priority. Yet circumstances indicate that the organism is the same as that often reported as injuring wheat and other cereals and called *S. graminum* (4, 14, 16, 19). It is well to note, however, that all the inoculation experiments, the results of which are summarized in diagram 4, were made with spores taken from the leaves of volunteer wheat collected in late fall or winter.

Seedlings grown in flower pots were used exclusively for inoculation with *Septoria tritici.* Following inoculation, the bags were placed over the pots for three days, but were removed temporarily each day to atomize the leaves with water. On the fifth to the sixth day yellow spots began to appear on the leaves of wheat. These spots enlarged and coalesced until half or more than half of the blades were yellow and drooping. Unless the plants in the greenhouse were covered with bags for a second period or set in a large moist chamber, the yellow blades would dry and no pycnidia would develop. The first pycnidia were observed on the twelfth day, and were distributed in "greenish islands" of tissue, which fact showed that the yellowing of the entire leaf surface was not all due directly to the attack of the Septoria.

That the Septoria of wheat under consideration is limited in its host range to the varieties of *Triticum vulgare* appears conclusive from the results of the infection experiments given in diagram 4. In some instances, especially with the other species of Triticum, and with barley, oats, and rye, there was blanching of the inoculated leaves, but this progressed uniformly backward from the leaf tips and was not due to a parasite. This reaction was also subsequent to the appearance of the irregular yellow spots on the leaves of *Triticum vulgare.* No pycnidia were ever detected upon any plant except upon those in which positive infection is recorded. It is

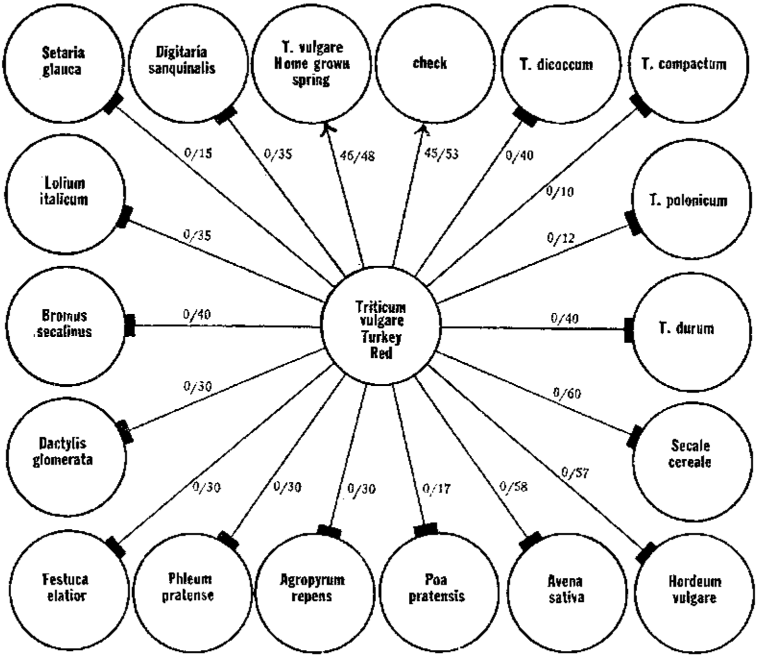

DIAGRAM 4. Infections with *Septoria tritici* from *Triticum vulgare.*

interesting to note that the fungus could not infect hosts closely related to *Triticum vulgare* such as *T. durum*, *T. compactum*, and *T. dicoccum.* If the forms of Septoria upon the species of Gramineae listed below are all morphologically alike, as there is reason to believe, it is evident that *Septoria tritici* consists of more than one, possibly of several, biologic forms. To determine the infection-powers of the form on each of these grasses presents a profitable field for further experiment.

Hosts reported for Septoria graminum	*Hosts reported for Septoria tritici*
Triticum vulgare	*Triticum vulgare*
Hordeum vulgare	*Triticum caninum*
Avena sativa	*Glyceria fluitans*
Secale cerale	*Brachypodium*
Poa annua	*Festuca*

Poa compressa
Poa pratensis
Bromus sterilis
Calamagrostis epigeios
Calamagrostis langsdorfii
Digitaria sanguinale
Panicum scribnerianum
Paspalum orbiculare
Alopecurus agrestis
Avena planiculmis
Carex riparia

Two series of inoculations were conducted to ascertain whether there was any variation in susceptibility among the varieties of *Triticum vulgare.* In the first series, Turkey Red, Minnesota Reliable, Red Cross, Red Hussar, and Home Grown spring wheat were about equally infected. Pesterboden and Malakoff were infected to a less degree than the above named varieties, while Hungarian was but slightly attacked. In the second series, detailed data were recorded. In terms of percentage, Turkey Red and Beloglina gave each about 52 percent infection if the leaves that had one or more spots of infection were counted. Pesterboden and Malakoff gave 43 percent and Hungarian only 25 percent. This is not a correct basis of comparison, however, for the individual leaves of Turkey Red and Beloglina had the largest and most numerous spots with pycnidia in the greatest number. In Hungarian, often but two or three pycnidia were present on a leaf, while with Pesterboden and Malakoff the condition was intermediate.

SEPTORIA MALVICOLA ELL. & MART.

A Septoria determined as *S. malvicola* Ell. & Mart. was collected upon *Malva rotundifolia* near Hutchinson, Minn. The common mallow is the only host reported for this fungus. The fact that this Septoria gave almost 100 percent infection (diagram 5) when transferred to *Althaea rosea,* the hollyhock, suggests that the fungus may be identical with *Septoria fairmani* E. & E. described on this plant. The identity appears evident when the spot characters produced upon the hollyhock by the mallow Septoria are compared with those of *S. fairmani* as described and as found in exsiccati. The spots on the mallow are smaller and are commonly surrounded by a broad yellow zone. When the fungus was transferred to the hollyhock this yellow zone did not appear, but instead only the narrow black border coincident with the limiting leaf veins was present, features given for *S. fairmani.* When these spots obtained by the inoculation of the hollyhock were compared with *S. fairmani,* North American Fungi no. 3557, there was agreement in all essential points. In the morphology of the fungus the specimens showed no distinctions beyond the limits of variation, and the morphological differences given in the literature are within the range of personal error. The ease with which the fungus passed from the mallow to the hollyhock indicates that this may happen in nature. The plants inoculated in the open were somewhat shaded, and were covered three days with a bell jar. The evidence is sufficient to prove the identity of *S. malvicola* and *S. fairmani.* Leaves of both *Althaea rosea* and *Malva rotundifolia* infected by inoculation with spores from the latter host are illustrated in Plate I, figs. 5 and 6.

Septoria scrophulariae Peck

Verbascum thapsus was the only host outside the genus Scrophularia to which *Septoria scrophulariae* would transfer, and in this case spots without pycnidia developed. These spots are believed to represent a real cross-infection, since the spores applied were from a pure culture, and the disease was confined to the area inoculated on each leaf. The results of inoculations indicate that *Verbascum blattaria* can be infected to a slight extent, but this was not definitely proved.

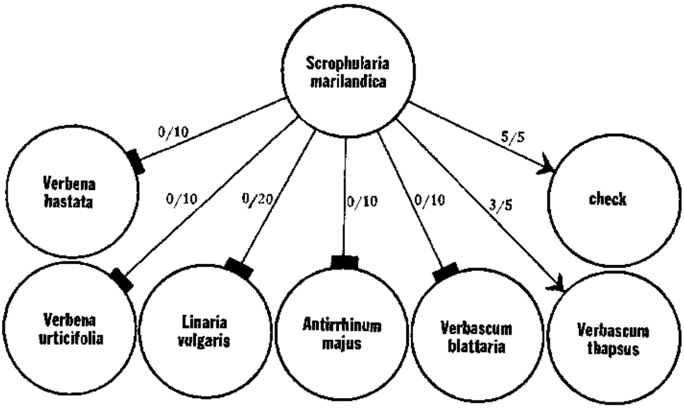

Diagram 6. Infections with *Septoria scrophulariae* from *Scrophularia marilandica.*

A resemblance in many respects between *Septoria scrophulariae* and *S. verbascicola* will be discussed in a following section.

Septoria convolvuli Desm.

Septoria Septulata sp. nov.

In the Saccardian description of *Septoria convolvuli* Desm., both *Convolvulus arvensis* and *C. sepium* are given as hosts, but the following distinctions in morphology are noted in the forms from the respective hosts:

"In forma *Conv. arvensis* observavi sporulas 35–50 x 1–1.5, aciculares minutissime 5–6 guttulatas v. septulatas hyalinas; in forma *Calystegiae* sporulas 35–40 x 1–1.5, continuas, hyalinas utrinque obtusiusculas. An differentiae constantes?" (Saccardo, Sylloge Fungorum, 3: 536.)

The forms of Septoria collected at Urbana upon *Convolvulus arvensis* and *C. sepium* fitted respectively the characterizations of the above-named forms as quoted. One hundred spores from *C. arvensis* had an average spore length of 44 microns, whereas a like number of spores from *C. sepium* averaged only 35.5 microns. There was a difference in average spore length whatever the conditions under which the two forms were compared. The distinctions mentioned regarding spore tips is not evident, but the spores from *C. arvensis* were always the more definitely septate. With respect to host characters there is little by which the forms can be distinguished.

The results of the infection experiments (tables 2 and 3) proved that the forms of Septoria from these two bindweeds are likewise distinct in

TABLE 2

Infections with Septoria septulata sp. nov. from Convolvulus arvensis

Date	Conditions	Plants Inoculated	No. Leaves Infected and Inoculated	No. of Spots	Remarks
Oct. 22	g-b 3	*Convolvulus arvensis*...	15/20	many	Check, most of the leaves killed
Nov. 14	g-b 3	" " ...	4/5	"	
Mar. 2	g-b 3	" " ...	20/20		
			39/45		
June 26	g-b 0	*Convolvulus sepium*.....	3/20	11	Pycnidia and spores but spots very small
Oct. 22	g-b 3	" "	3/3	12	
Nov. 14	g-b 3	" "	2/7	5	
Mar. 18	g-b 4	" "	1/9	1	
			9/39	29	
Nov. 14	g-b 3	*Ipomoea purpurea*......	0/5		
Mar. 2	g-b 3	" "	0/10		
			0/15		
Oct. 22	g-b 3	*Ipomoea batatas*........	0/10		
Nov. 14	g-b 3	" "	0/7		
			0/17		
Mar. 2	g-b 4	*Ipomoea learii*.........	0/10		
Mar. 2	g-b 4	*Ipomoea setosa*.........	0/4		

their powers of infection, for each can cause vigorous infection only upon its original host. The fungus from *C. arvensis* does infect *C. sepium* to some degree, with 9 out of 39 leaves inoculated showing a few small disease spots, but this is to be compared with 39 out of 45 leaves upon the original host, on which the spots were ordinarily so numerous and so spreading that the leaves were entirely killed. When *C. arvensis* was inoculated with the

TABLE 3

Infections with Septoria convolvuli Desm. from Convolvulus sepium

Date	Conditions	Plants Inoculated	No. Leaves Infected and Inoculated	No. of Spots	Remarks
Sept. 10	f-b 4	*Convolvulus sepium*	6/7	21	Check, spots large
Oct. 10	g-b 4	" "	5/5	12	
Nov. 14	g-b 4	" "	5/6	16	
Mar. 18	g-b 4	" "	1/5	4	
			17/23	53	
Sept. 10	f-b 4	*Convolvulus arvensis*	0/7		Few minute spots, no pycnidia, infection doubtful
Sept. 25	f-b 4	" "	0/12		
Nov. 14	g-b 4	" "	0/25		
Mar. 18	g-b 3	" "	0/35		
			0/79		
Nov. 14	g-b 4	*Ipomoea purpurea*	0/5		
Mar. 18	g-b 4	" "	0/5		
			0/10		
Oct. 22	g-b 4	*Ipomoea batatas*	0/5		
Nov. 14	g-b 4	" "	0/10		
			0/15		
Mar. 18	g-b 4	*Ipomoea learii*	0/20		
Mar. 18	g-b 4	*Ipomoea setosa*	0/5		

fungus from *C. sepium*, no disease spots with pycnidia were obtained upon any of 79 leaves inoculated, although minute brown spots, usually less than 1 mm. broad, were often formed. The significance of these spots is unexplained, though they may represent incipient infection.

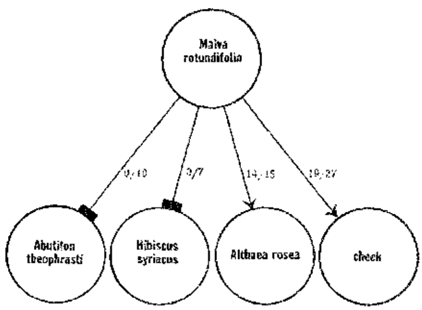

DIAGRAM 5. Infections with *Septoria malvicola* from *Malva rotundifolia.*

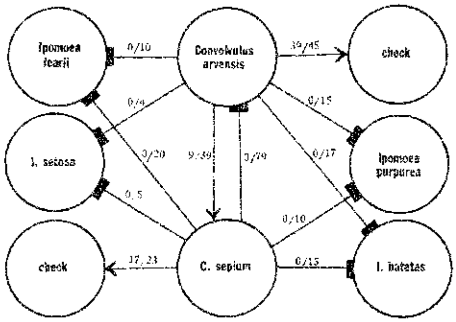

DIAGRAM 7. Infections with *Septoria septulata* from *Convolvulus arvensis* and *S. convolvuli* from *C. sepium.*

Septoria convolvuli is reported upon *Ipomoea purpurea*, but all attempts to infect species of Ipomoea were futile.

Were the two forms of Septoria under consideration to be accepted as belonging to a single species, here would be a well established case of biologic specialization. But since the forms have been proved to be different both morphologically and biologically, they should each have specific rank. The name *S. convolvuli* is reserved for the form on *Convolvulus sepium* upon

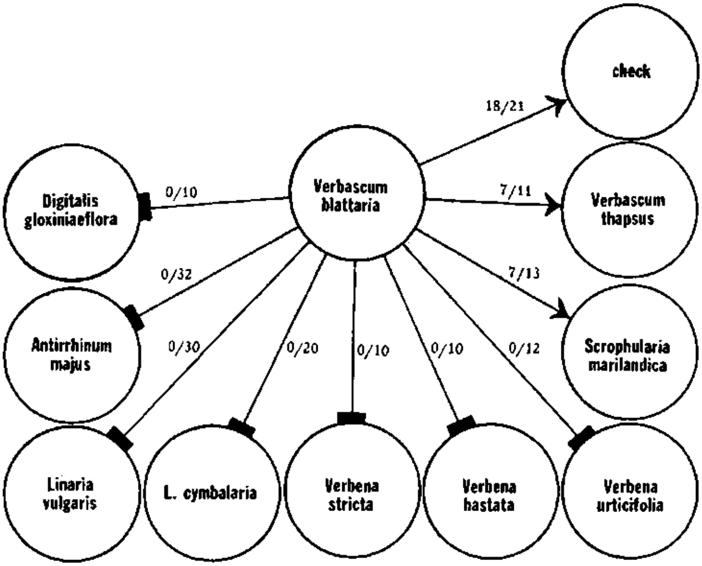

DIAGRAM 8. Infections with *Septoria verbascicola* from *Verbascum blattaria.*

which host the type of *S. convolvuli* was described (6). For the form upon *Convolvulus arvensis* the following new species is proposed:

Septoria septulata sp. nov.

Spots orbicular, then irregular and confluent, light brown to dark brown; pycnidia mostly epiphyllous, innate, globose, 60–90 μ, protruding with a prominent ostiole, 20–30 μ; spores curved or flexuous, one end narrow with a more acute tip, 3–5 septate, 30–50 μ long by 1–2 μ wide. Habitat: old or fading leaves of *Convolvulus arvensis.*

This species appears to be the equivalent of the form on *C. arvensis* described in Saccardo's Sylloge Fungorum, 3: 536.

SEPTORIA VERBASCICOLA BERK. & CURT.

Septoria verbascicola appears to be somewhat adaptive in its host relations. The infection of *Scrophularia marilandica* was as vigorous as that on the original host when conditions were made favorable for the fungus. This was done by keeping the inoculated plant constantly covered with a bell jar for ten days, and by atomizing the leaves daily with water following the application of the spores. At the end of this period under cover disease spots began to appear. The plant used seemed to retain its full vigor notwithstanding the rather unusual conditions provided in the experiment. The infection of *Scrophularia marilandica* secured without these special conditions was slight. When the fungus was transferred back to *Verbascum blattaria*, the original host, there was heavy infection, though the inoculated plant was inclosed no more than two days.

The disease spots formed upon *Scrophularia marilandica* were essentially like those upon *Verbascum blattaria.* Upon either host the central area of the spots was ashen in color, while the border was reddish-brown to purplish. Under humid conditions a dull green zone appeared outside the reddish-brown ring, indicating the destruction of new tissue by the encroaching fungus, or the entire area of the spot would be dull green to black. This latter phenomenon was to be seen chiefly upon the original host. Pycnidia were numerous upon both hosts under the humid conditions.

Septoria scrophulariae Peck, which is common upon *Scrophularia marilandica* in nature, forms spots scarcely distinguishable from those above described. The most important distinction is the scanty number of pycnidia; not more than a half dozen are often to be seen in a spot. The spores and pycnidia of *S. verbascicola* and *S. scrophulariae* from material collected near Urbana were so similar that it was suspected that the forms were identical. The fact that the former infected *Scrophularia marilandica* readily made such identity probable, but this view was shown to be questionable when it was found that the latter infected *V. blattaria* slightly if at all. It was discovered, moreover, that the two fungi can be separated easily in culture, as *S. verbascicola* produced pycnidia and spores upon all media used, while *S. scrophulariae* seldom did; the growth of the first was chocolate-colored, that of the second buff.

Septoria verbascicola attacked *Verbascum thapsus* readily, but few spore-bearing structures developed. The spots attained a size as great as those upon *V. blattaria*, were angular in outline, and purplish in appearance. It seems probable that this host is infected in the field, although no proof of this was secured. Leaves of mullein were collected with similar disease spots, some of which were very large, but as no pycnidia were found it cannot be stated that the injury was caused by Septoria.

The rather constant formation of small brownish spots upon the species of Verbena following inoculation with *S. verbascicola* would appear to indicate incipient infection, yet the failure to obtain pycnidia, and to prove that the spots were not due to other causes, leaves the matter in doubt.

SEPTORIA CIRSII NIESSL.

Upon *Cirsium arvense*, *Septoria cirsii* is an active parasite, both in the field and when brought into the greenhouse. In the field it attacks chiefly the lower leaves and causes large, usually irregular, brown, dry spots, mostly along the leaf margins, but often the whole leaf is involved. In the greenhouse growth is similar, but more rapid and extensive. Inoculated leaves are generally completely destroyed. The fungus is also reported upon *Cirsium discolor*.

According to the infection experiments conducted, *Septoria cirsii* can make a weak attack upon both *Cirsium discolor* and *C. lanceolatum*. The spots formed upon these hosts resemble those upon *C. arvense*, but are smaller and very few in number. The difference in the vigor of attack upon these hosts is also well demonstrated by the length of the incubation period and the rate of development. Upon *Cirsium arvense* spots appeared in thirteen days after inoculation, pycnidia were observed in fifteen days, and in four weeks the whole plant was dead from the spread of the disease. Upon *Cirsium lanceolatum* spots were first visible in twenty days, and in four weeks they had attained a breadth ranging from 3–8 mm. Pycnidia and spores were found at this time. The plant had to be kept in a moist atmosphere to bring about the formation of many spores. The incubation period and rate of development were similar in *Cirsium discolor*. There were no noticeable differences in the morphology of the fungus upon the various hosts.

The relation of maturity of the spores to the presence of septa was often noticed in this species. Where spores were made to develop abundantly in a moist chamber, septa could not be seen at all, or could be seen only

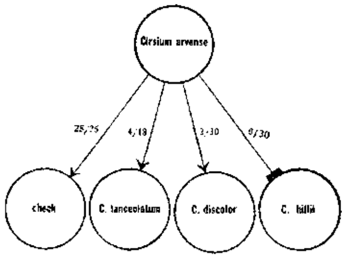

Diagram 9. Infections with *Septoria cirsii* from *Cirsium arvense*.

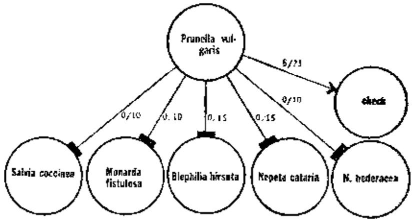

Diagram 10. Infections with *Septoria brunellae* from *Prunella vulgaris*.

faintly after staining with iodine. In old spots, or where the growth had been slow, the septa were plainly seen. Spores obtained from an old culture upon corn meal agar had septa that were strikingly definite. Plants inoculated with spores from this culture were heavily infected.

Septoria brunellae Ell. & Halst.

The inoculations with *Septoria brunellae* gave negative results in all cases except upon the original host, which facts indicate that the fungus is probably limited to *Prunella vulgaris* in its host range. Upon this one host it is a marked parasite; frequently the whole surface of some leaves is discolored by the confluent spots.

SEPTORIA LYCOPERSICI SPEG.

The inoculations with *Septoria lycopersici* gave results in agreement with those published by Norton (22) who inoculated several plants related to the tomato in humid atmospheres. He states that spots developed better and spores were larger on potato and *Solanum carolinense* than on tomato, while on Datura the spots were slow-growing, light-colored, and small-spored. In the present experiments the spots on potato were darker in

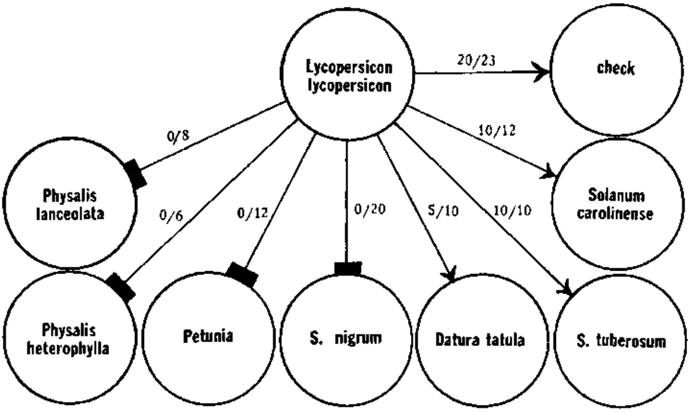

DIAGRAM 11. Infections with *Septoria lycopersici* from tomato.

color and smaller than those on tomato, while those on *Solanum carolinense* were likewise darker in color, but larger, and often coalesced until the leaves were destroyed. The spots on Datura were very similar to those described by Norton. Spores developed upon the potato and *Solanum carolinense* produced full infection of tomato leaves.

SEPTORIA LEPIDIICOLA ELL. & MART.

Septoria lepidiicola is reported upon only *Lepidium virginicum* and *L. apetalum*. The data in diagram 12 show that the fungus on these two hosts is identical biologically as well as morphologically. The negative results obtained when plants belonging to other genera of Cruciferae were inoculated indicate that the fungus is confined to the species of Lepidium. No data are at hand to show whether it will attack more than the two species of the genus. The failure to obtain signs of incipient infection, such as spots without spore-bearing bodies, upon species outside the genus Lepidium proves that the fungus has little adaptability. It may be possible, however, to obtain growth in some form upon the remaining species of Lepidium that have not been inoculated experimentally.

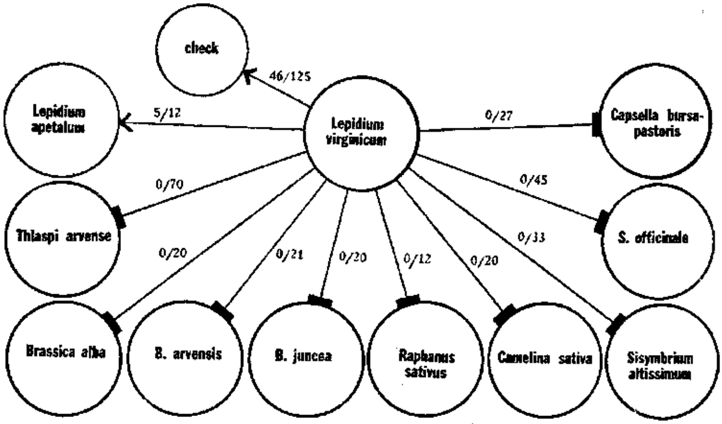

DIAGRAM 12. Infections with *Septoria lepidiicola* from *Lepidium virginicum*.

SEPTORIA HELIANTHI ELL. & KELL.

The following plants have been reported as hosts for *Septoria helianthi:*

1. *Helianthus grosseserratus*	5. *Helianthus petiolaris*
2. " *annuus*	6. " *lenticularis*
3. " *doronicoides*	7. " *strumosus*
4. " *californicus*	8. " *laevis*

In the vicinity of Urbana this Septoria was a common parasite of *H. grosseserratus*, upon the lower or shaded leaves of which it causes grayish-black spots that often become more than a centimeter in breadth. It was less commonly found upon *H. tuberosus*, upon which the spots were smaller, and rarely upon *H. annuus* and *H. rigidus*.

In three separate trials *H. grosseserratus* was readily infected with its own form of Septoria without maintaining a humid atmosphere beyond three days. The other species of Helianthus infected by the Septoria from *H. grosseserratus* are shown in diagram 13. Except for *H. tuberosus*, which grew naturally in the greenhouse yard, all these cross-infections were upon seedlings grown in the greenhouse. Proof of infection was obtained only by detaching spotted leaves and laying them in a moist chamber to induce the development of pycnidia. For this reason, as well as on account of the attack of insect pests, no accurate data could be secured concerning the degree of susceptibility of certain of the hosts, consequently some of the records are wanting. It is clear, however, that the original host is the only one that is congenial for this Septoria from *H. grosseserratus*, for on its own host alone spore-bearing bodies developed naturally under the ordinary greenhouse environment. The infection of small shoots of *H. tuberosus* covered, out of doors, with a bell jar was relatively feeble. Numerous spots developed, but the author could not satisfy himself that they were entirely due to Septoria, on account of the scanty appearance of pycnidia, and because a Phyllosticta, apparently saprophytic however, often appeared when the leaves were placed in a moist chamber.

TABLE 4

Infections with Septoria helianthi Ell. & Kell. from Helianthus grosseserratus

Date	Conditions	Plants Inoculated	No. Leaves Infected and Inoculated	Remarks
Sept. 16	g-b 3	*Helianthus grosseserratus*...	5/5	Check, leaves mature, 32 spots
" "	g-b 3	*Helianthus occidentalis*.....	0/6	Leaves mature
" "	g-b 3	*Helianthus rigidus*.........	0/5	" "
" "	g-b 3	*Helianthus mollis*..........	0/5	" "
" "	g-b 3	*Helianthus tuberosus*.......	0/5	" "
" "	g-b 3	*Helianthus annuus*........	3/8	Seedlings, pycnidia in moist chamber, 10 spots
" "	g-b 3	*Silphium integrifolium*.....	0/5	
" "	g-b 3	*Bidens cernua*...........	0/20	
July 5	g-b 3	*Helianthus grosseserratus*...	7/7	Check, leaves young, 26 spots
" "	f-b 4	*Helianthus tuberosus*.......	4/10	Many spots, but few with pycnidia
" "	f-b 4	*Helianthus mollis*.........	0/7	Leaves young
" "	f-b 4	*Helianthus rigidus*.........	0/10	" "
" "	f-b 4	*Silphium integrifolium*.....	0/5	
Jan. 5	g-b 4	*Helianthus rigidus*.........	plus	Seedlings, only spots formed
" "	g-b 4	*Helianthus argyrophyllus*...	4/20	Seedlings, pycnidia in moist chamber
" "	g-b 4	*Helianthus cucumerifolius* .	6/20	As above
Mar. 2	g-b 4	*Helianthus grosseserratus*...	plus	Check, seedlings
" "	g-b 4	*Helianthus californicus*.....	plus	Seedlings, pycnidia in moist chamber
" "	g-b 4	*Helianthus annuus nanus flore pleno*..............	plus	As above
" "	g-b 4	*Helianthus annuus double primrose queen*..........	plus	As above
" "	g-b 4	*Helianthus maximilianus*...	0/10	
" "	g-b 4	*Coreopsis lanceolata*........	0/20	
" "	g-b 4	*Rudbeckia laciniata*........	0/10	
Spores from *Helianthus tuberosus*				
July 24	f-b 4	*Helianthus tuberosus*.......	4/10	Check, pycnidia and spores
" "	g-b 4	*Helianthus grosseserratus*...	0/5	
" "	f-b 4	*Helianthus rigidus*.........	0/10	
" "	f-b 4	*Helianthus mollis*..........	0/10	
" "	f-b 4	*Helianthus annuus*........	0/5	
" "	f-b 4	*Silphium integrifolium*.....	0/5	
Spores from *Helianthus rigidus*				
Sept. 18	f-b 5	*Helianthus grosseserratus*...	0/8	No check, but spores germinated well in laboratory tests
" "	f-b 5	*Helianthus tuberosus*.......	0/5	

It appears significant that the Septoria from *Helianthus rigidus* did not infect *H. grosseserratus* when the plant, inoculated in the field, was bagged five days, and that the form from *H. tuberosus* did not give ready infection of *H. grosseserratus* in the greenhouse. The failure of infection in the series of inoculations made upon mature plants of various species of Helianthus on September 16 (table 4) in the greenhouse, and also on similar hosts in the field in summer, in which spores from *H. grosseserratus* were used, may have been due to the age of the leaves, yet checks on the original host gave positive results. A corresponding set of hosts were inoculated at these same periods with spores from *H. tuberosus* with negative results, but these were not shown by diagram as no checks were used. Still, in these cases the spores germinated well in laboratory tests.

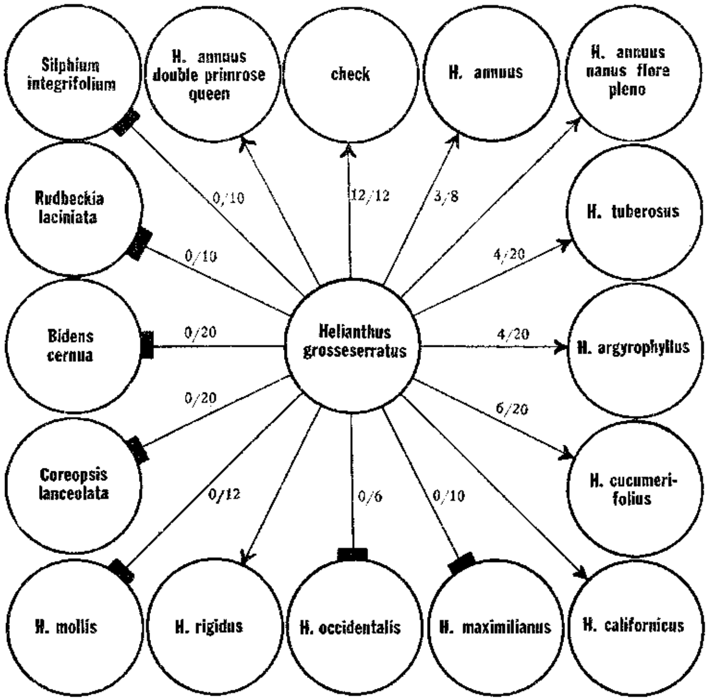

DIAGRAM 13. Infections with *Septoria helianthi* from *Helianthus grosseserratus*.

All the data obtained respecting *Septoria helianthi* indicate that the forms used in inoculation are not vigorously parasitic except upon their original hosts. These data are scarcely ample for definite conclusions, yet the results are in harmony with what was observed regarding the host range of this Septoria in the vicinity of Urbana. If there are no fixed biologic forms, nevertheless there appears to be a degree of specialization upon the different species of Helianthus, possibly of a temporary nature such as Montemartini (18) claims for rusts.

Septoria rubi West.

Septoria rubi was collected frequently at Urbana upon *Rubus occidentalis*, the black raspberry, but was never found upon any species of Rubus belonging to the blackberry, or Eubatus, section of the genus. Since plants of the blackberry were often growing in close enough proximity to *R. occidentalis* to enable them to become inoculated with the Septoria, it appears that the species of blackberry were not susceptible to the fungus on the black raspberry. During July thirty leaves each of *R. occidentalis* and a species of blackberry were inoculated with spores of Septoria from the former host. Both of these plants inoculated were young, and were growing close together in a shaded place. In two weeks all the thirty leaves of *R. occidentalis* were thickly spotted with Septoria, but no trace of infection could be found upon the blackberry.

No definite conclusions can be drawn from the above-described observations and the accompanying experiment. The facts may indicate that *Septoria rubi* is split into biologic forms, or that the species of blackberry in this locality are permanently resistant to the Septoria. This fungus is reported, however, upon twenty-eight or more species of Rubus, distributed among all sections of the genus, a fact that makes it appear probable that all members of the genus are parasitized. If this be true, the brief data above indicate the existence of biologic forms in *Septoria rubi*. The large number of species in the genus Rubus, of which so many are known to be hosts of Septoria, makes them an attractive field for a further study of biologic specialization.

Septoria atro-purpurea Peck

The presence of disease spots without pycnidia is the only indication that *Septoria atro-purpurea* from *Aster cordifolius* can infect *A. ericoides* and *A. laevis*. This infection was obtained under prolonged humid conditions, and it is improbable that it occurs often in nature. These asters have not been reported hitherto as hosts for the fungus. This parasite, according to specimens in the Herbarium of the United States Department of Agriculture, attacks *Solidago latifolia* and *Machaeranthera aspera*. The data indicate that this Septoria is able to adapt itself to related hosts to a considerable degree.

The disease spots on *A. cordifolius* are nearly orbicular, with a central area of reddish-brown and a margin of light green. In the larger and older spots a gray area appears within the reddish-brown. Upon *A. ericoides* the spots were a bright reddish color, with a margin of yellow, and a ragged and indefinite outline. The spots on *A. laevis* were very small and brown, indicating that the fungus was less well adapted to this host than to *A. ericoides.* As the spores for inoculation were from pure culture, and adjacent leaves not inoculated showed no symptoms of disease, it appears certain that the spots in question were due to the Septoria applied.

General Discussion

Age incidence. In the field Septoria spots are more frequently observed upon the old or fading leaves of plants, but this is often due to the fact that the young leaves have recently expanded, and have not had time to become infected. The immature foliage is sometimes the more susceptible, but this varies with hosts. From the results of the infection experiments the leaves of *Lepidium virginicum* appear to be equally susceptible at all ages. Old leaves of *Lactuca scariola* in which the edges are cracked and drying are infected without difficulty, but the spots remain small. Partially grown leaves of this host are more easily infected, and the spots become larger. The older leaves of *Convolvulus arvensis* and *C. sepium* are the most heavily attacked, while inoculation of the immature leaves seldom produces infection.

The influence of age upon susceptibility is very well shown in *Malva rotundifolia* and *Althaea rosea.* Disease first develops on the oldest leaves; in those of intermediate age the incubation period has greater length, while those partially grown are resistant. A plant of *Althaea rosea* with seven leaves was thoroughly wetted with a suspension of spores of *Septoria malvicola*, and kept under a bell jar four days. In ten days the five mature leaves were spotted, the oldest having the heaviest infection. It was nearly three weeks before the sixth leaf showed disease, and the seventh or youngest leaf inoculated continued healthy. In two trials with the mallow there were similar results, which are in accord with what one sees in the field, for there only old shaded leaves are badly attacked.

Susceptibility of different leaf surfaces. Equal areas of the upper and the lower surfaces of separate lots of leaves of a number of plants were inoculated, and other factors made as comparable as possible. In *Lactuca scariola* the upper surface gave the heavier infection. In *Polygonum persicaria* 39 spots, 1–5 mm. in diameter, resulted on the top side as compared with six spots, 1–2 mm. in diameter, on the lower. The leaf surface of *Erigeron annuus* in 150 separate areas, 75 above and 75 below, was inoculated with loop-drops of a suspension of spores of *Septoria erigerontis*, and 14 infections from above and six from below were obtained. In contrast to these experiments, the inoculation of the lower surfaces of leaves of *Solanum carolinense* with *Septoria lycopersici* gave abundant infection, while leaves inoculated above remained free of disease. No explanation of the above-described results can now be given, but the number of stomata, the character of the cuticle, the ease with which the suspension makes contact with the surface, and the light exposure may be factors.

Effect of the mass of inoculum. The effect of varying the concentration of the spore suspension was tested. One hundred areas upon *Erigeron annuus* were inoculated with loop-drops containing approximately 100 spores, and an equal number of areas with loop-drops averaging 1–3 spores. In the former case there were 35 areas infected, and in the latter 15, but in the 35 areas over 80 points of infection were noted, while in the 15 areas only 18 were present. Infections were obtained upon *Lactuca scariola* with loop-drops containing only 1–3 spores in 11 percent of the inoculations.

Effect of wounding. Certain leaves of young potted plants of *Malva rotundifolia* were perforated with a fine needle in numerous places. All the leaves of each plant were inoculated over the entire upper surface, and bagged for four days. Only the perforated leaves became infected. Either the wounding had the effect of overcoming the resistance that may have been present in the cell contents of the young foliage, or the pierced epidermis afforded an easy entrance for the germ tubes of the spores.

Variations in the morphology of the fungus. The more detailed studies of morphological variations were made with *Septoria tritici* and *S. verbascicola*, and the chief results obtained are shown in graph i by curves which represent the ranges of spore length in these fungi under a number of different conditions. No investigation was made of the factors causing these variations, but apparently they are due to differences in humidity. An increase in spore length when infected leaves were kept in a moist chamber for a period was apparent in many other species of Septoria.

There was no alteration in spore length when *S. verbascicola* was transferred from *Verbascum blattaria* to *Scrophularia marilandica* under comparable conditions, as *E* and *F* of graph 1 show. Norton (22) reports that the spores of the tomato Septoria become longer upon the potato and *Solanum carolinense*, but shorter upon *Datura tatula* than they were upon the original host, when the inoculations were made within humid inclosures. It is not stated whether he took account of environmental relations other than the change of host, but the lesser spore length upon *Datura tatula* makes it appear that the host has a definite effect on morphology. Still, in the numerous crosses recorded in the tables of the present paper, no changes of spore length were observed for which environmental factors such as humidity might not account, at least in all cases in which the fungus and host were in compatible relations.

If all the species of Septoria have a corresponding relation to the environment, and if all have a broad range between the maximum and minimum spore length, as in *S. tritici* and *S. verbascicola*, it is obvious that many of the measurements now given in specific descriptions are far from accurate. The range of 19 to 62 microns reported for *S. sisymbrii* is not of greater width than that shown for the fungi in graph 1, and indicates care in measurement. It is not proper to compare dry herbarium specimens with material freshly collected, especially if it has been allowed to form spores in a moist chamber. It is well to make a record of the source of the material collected, and the conditions under which it was found. (*Cf.* graph 1, *C*, *D*, *G*, and *H*.)

Host limitations. The experimental results thus far obtained indicate that the species of Septoria do not have a broad host range. Each can infect vigorously one or a few closely allied plants, and can infect to a less degree a number of hosts that stand in rather immediate relation to the vigorously infected ones. In some cases this host range does not extend beyond the limits of a genus, and in other cases includes but two or three related genera. Although some of the fungi studied have been found to have approximately the host range previously reported for them, in many instances the host ranges established by the experiments have been much more narrow than the reports on hosts would lead one to conclude, a few forms being limited to the species upon which they were collected. Notable illustrations of this are the forms of Septoria on wheat, *Convolvulus sepium*, and possibly upon *Rubus occidentalis* and *Helianthus* sp. Further infection experiments would doubtless reveal more cases of identity both morphological and biological among forms now classed as separate species, while at the same time some of the present species would be shown to consist of more than one morphological form, or species.

The value of disease characters. The variable nature of disease characters, as manifested by the host, has been well demonstrated. These variations are dependent upon the species, the age, and the part of the host as well as upon environmental conditions. On this account these characters lose much of their value in taxonomy, but inasmuch as the host ranges of the species of Septoria are not broad, and the number of forms parasitizing a single host is very few, such characters may be of some use in distinguishing the parasites on individual hosts. For these same reasons the host itself will continue to be a valuable key in the determination of the fungus.

Biologic specialization. The experiments herein described have not been broad enough to include forms from all the hosts reported for any species, especially with such fungi as *Septoria rubi* upon numerous members of Rubus, *S. graminum* or *S. tritici* upon several different genera of Gramineae, and *S. polygonorum* upon various species of Polygonum. Great difficulty will inevitably be met in bringing together even a major portion of the respective forms for comparative study, such as would be necessary to establish firmly the existence of biologic specialization, and to ascertain the number of biologic forms. Still, such data as the present investigations furnish indicate clearly that biologic specialization exists in many species of Septoria. This is shown by the fact that in many instances the Septoria from one host either fails to infect, or infects to only a slight degree, certain hosts upon which morphologically similar forms of Septoria are known. In illustration of this, the species of Septoria from wheat, from *Rubus occidentalis*, and from certain species of Helianthus and Polygonum furnish examples.

Conclusions

1. The results of the present investigations indicate that certain species of Septoria are differentiated into biologic forms.

2. Although some forms show a degree of adaptability in host relations, in general the species studied are limited to one or to a few closely related hosts which they can vigorously infect.

3. In some cases the host range does not extend beyond the limits of a genus, while in other cases two or three related genera are included.

4. In many cases the host ranges established by the experiments have been more narrow than the host indices indicate.

5. Disease characters, as manifested by the host, vary with the host and with environmental conditions, and are therefore unreliable in taxonomy.

6. Certain species of Septoria have been shown to vary considerably in morphological characters under different environmental conditions, and hence the value of measurements now given in specific descriptions is questionable.

7. Inoculation experiments show that *Septoria malvicola* E. & M. and *S. fairmani* E. & E. are identical.

8. Similar experiments show that the form of *S. convolvuli* Desm. described upon *Convolvulus arvensis* is biologically as well as morphologically distinct from the type form of *S. convolvuli* described upon *C. sepium*, and is entitled to specific rank.

The writer takes pleasure in making acknowledgment to Dr. F. L. Stevens, Professor of Plant Pathology, University of Illinois, for helpful suggestions and guidance in the preparation of this thesis. The writer also wishes to express his appreciation of the valuable assistance given by Prof. William Trelease, Head of the Department of Botany, University of Illinois, in the solution of questions of taxonomy. Thanks are due Fred J. Seaver, Curator at the New York Botanical Garden, and Vera K. Charles, Mycologist, U. S. Department of Agriculture, for furnishing data upon the host ranges of various species of Septoria.

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EXPLANATION OF GRAPH 1

This graph represents variations in spore length in *Septoria verbascicola* B. & C. and *S. tritici* Desm. under a number of different conditions. The measurements of spores are indicated in microns by the base line, each space representing one micron. The frequency is indicated on the perpendicular lines, each space representing one spore. The measurements are at intervals of 2.4 microns, and for each curve 200 spores were measured.

A and *B* represent ranges in length of spores from a single culture of *S. verbascicola* upon onion agar; in *A* the spores were from the lower portion of the colony which was moistened by the small amount of water on the agar, while in *B* the spores were from the upper edge of the colony where the agar was drying. *C* represents spores from spots of leaves of *Verbascum blattaria* in the field where the light exposure was intense; *D*, spores from shaded rosette leaves of the same host in the field; *E*, spores from the same host kept under very humid conditions in the greenhouse; *F*, spores of the same fungus growing upon *Scrophularia marilandica*, conditions as in *E*.

G represents the range of spore length of *S. tritici* upon the upper stem leaves of naturally infected wheat plants in the field in July; *H*, spores of the fungus from the same field taken from the basal leaves of volunteer wheat in January. The plants of wheat were dug up and kept for a few days in a closed collecting can in the greenhouse.

EXPLANATION OF PLATE I

Preparatory to photographing, the leaves were treated with hot alcohol to remove the chlorophyll, but this process produced no apparent change in the character of the disease spots. The leaves were then softened in 50 percent glycerine and pressed.

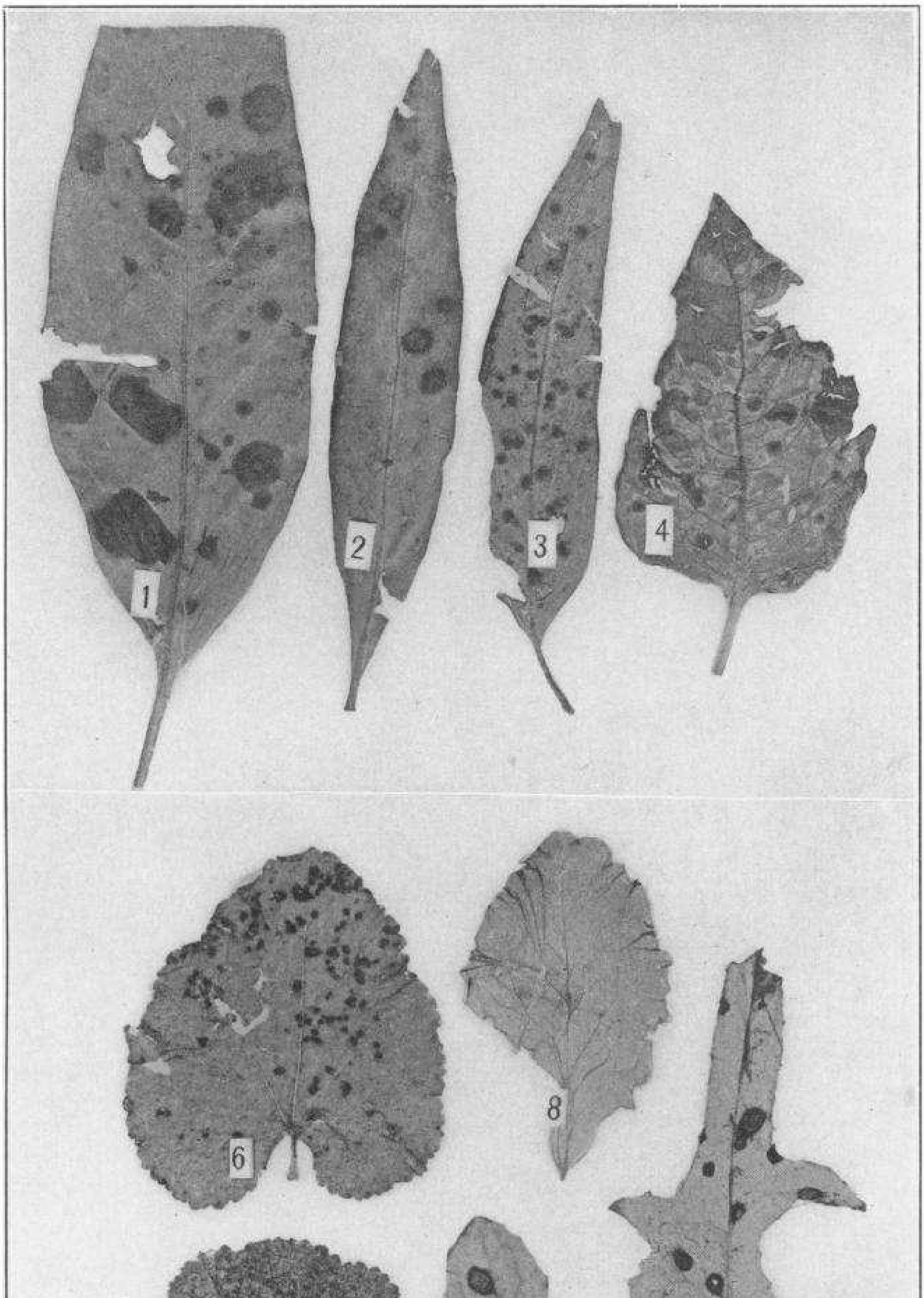
FIG. 1. Disease spots of *Septoria polygonorum* Desm. upon *Polygonum pennsylvanicum*. Natural infection.

FIG. 2. Disease spots of the same fungus upon *P. persicaria*. Natural infection.

FIG. 3. Disease spots of the same fungus upon *P. lapathifolium*. Natural infection.

FIG. 4. Disease spots of the same fungus upon *P. orientale*. Artificial inoculation.

FIG. 5. Disease spots of *Septoria malvicola* E. & M. upon *Malva rotundifolia*. Artificial inoculation.



BEACH: SPECIALIZATION IN SEPTORIA.

FIG. 6. Disease spots of *S. malvicola* upon *Althaea rosea.* Inoculated with spores from *Malva rotundifolia.*

FIG. 7. Disease spots of *S. lactucicola* E. & M. upon *Lactuca scariola.* Inoculated with spores from *L. canadensis.*

FIG. 8. Disease spot of *S. lactucicola* upon *Lactuca sativa.* Inoculated with spores from *L. canadensis.*

FIG. 9. Disease spots of *S. lactucicola* upon *Lactuca canadensis.* Natural infection.