

SOME GRAMINICOLOUS SPECIES OF HELMINTHOSPORIUM: I¹

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INTRODUCTION

Although the genus *Helminthosporium* includes a large number of forms thriving saprophytically on the bark, leaves, and stems of both woody and herbaceous plants, it has become familiar to plant pathologists and perhaps, in a large measure, to students of fungi generally, through a relatively moderate number of parasitic species. Undoubtedly the most widely known of these parasitic forms are those affecting graminaceous hosts, as considerable losses to important cereal crops, including especially barley, corn, rice, oats, wheat, and sorghum, in various parts of the world, have continued for several decades to encourage a desire for knowledge leading to some sort of effective control. Besides these economically important forms, many parasitic species of *Helminthosporium* have been recorded as thriving on various members of the grass family, but have remained more or less obscure because either the hosts affected were of little economic value, or, being important, the parasitism occasioned little or no observable damage.

However, as is not uncommon in the case of large genera, publication of an increasing number of descriptions of presumably new species, thriving on related or even identical hosts, has injected a large degree of uncertainty into the specific taxonomy. In many instances, writers have failed to compare their organisms with congeneric forms, or have used for such comparison herbarium material which had already undergone the degenerative changes in structure incident to the death of the spores. It was in an effort to define the more distinctive differences between the forms parasitic on barley and oats, and those found on a few of the more common uncultivated or wild grasses that the present study was undertaken. This paper, which it is hoped may be followed by others dealing with the very considerable variety of species of *Helminthosporium* growing on grasses in the United States, is offered as a comparative mycological account of some of the more readily available species. No attempt is made here to deal with the intimate pathological aspects, as these have been for some years the subject of intensive study by other workers, both in this country and abroad.

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APPEARANCE OF AFFECTED PLANTS

Although the symptoms produced by a species of *Helminthosporium* on some particular host are generally quite well defined, the different members of the genus considered collectively bring about a considerable variety of changes. These may be briefly considered under a number of categories.

SPOTBLOTCH, FOOTROT, EYESPOT

Perhaps the most easily recognized type of lesion is represented by the discoloration resulting from the attack, for example, of *Helminthosporium sativum* P. K. & B. on barley (*Hordeum* spp.), wheat (*Triticum* spp.), and quack grass (*Agropyron repens* [L.] Beauv.). Here each foliar infection produces a fairly well-defined, more or less longitudinal spot ranging in color from light brown to nearly black. An entirely similar type of leaf injury is characteristic of the diseases of Kentucky bluegrass (*Poa pratensis* L.) and of barnyard grass (*Echinochloa crus-galli* [L.] Beauv.), attributable to two congeneric parasites that are newly described in this paper as *H. vagans* and *H. monoceras*, respectively. When the leaf sheaths also are affected, the discoloration often becomes increasingly diffuse downward, so that the base of the stem may be quite uniformly discolored—a condition that in the case of wheat, where it is usually complicated with more or less injury to the roots, has become widely known as footrot. Similar dark foliar spots characterize the incipient attack of *H. leersii* Atk. on white grass (*Leersia virginica* Willd.), of *H. giganteum* H. & W. on goose grass (*Eleusine indica* [L.] Gaertn.), and Bermuda grass (*Cynodon dactylon* L.), and of *H. oryzae* B. de H. on rice (*Oryza sativa* L.). Later, however, the central areas lose their dark color, the older and larger spots being finally represented by a dark brown ring surrounding a central straw-colored area. The term "eyespot," which has been applied (73)³ to a disease of sugar cane (*Saccharum officinarum* L.) caused by *H. sacchari* Butl., is perhaps most accurately descriptive of the latter type of foliar lesions.

NETBLOTCH

A second category of discoloration very characteristic, though less common, is caused by *Helminthosporium teres* Sacc. on barley, as well as by a fungus on *Festuca elatior* L. described in this paper as *H. dictyoides*. The affected leaves, while still green and living, show abundant brownish discoloration in irregular pattern, within which may be recognized a network of darker longitudinal and transverse linear streaks. With the withering of the leaf these reticulate markings become less pronounced, and are finally more or less completely obliterated.

STRIPE

Helminthosporium gramineum Rabh. causes an unusual type of injury to barley, the leaves previous to heading time becoming variegated with yellow bands extending frequently the whole length of the leaf. On the premature death of the plants the foliar organs split along these longitudinal markings, giving them a ragged or shredded appearance. This type of injury has been shown to be contingent on continued development of the parasite in the growing tissues in a manner not unlike the development of certain smut fungi.

³ Reference is made by number (italic) to "Literature cited" pp. 731-739.

WHITE BLAST

Helminthosporium turcicum Pass. produces on maize (*Zea mays* L.) a type of injury that is probably more common than might be supposed, as it is likely to escape detection. The green color of the affected tissue disappears completely, leaving a chlorotic area that increases in size until it may be several inches long and perhaps one inch in width. Owing to the large size of the corn leaf blade, the desiccated areas, which may be surrounded, moreover, by a narrow, brownish, marginal zone, contrast sharply with the surrounding green tissue and are quite readily recognizable as due to the agency of a parasite. However, with the larger number of graminaceous hosts, having much smaller leaves, proportionately large segments of the blade are involved at once; withering usually starts at the tip and proceeds downward, thus simulating the appearance of withering due to drought. It may be mentioned that the parasitic nature of species of *Helminthosporium* not associated with dark discoloration or conspicuous pathological changes in the mechanical properties of the plant tissues involved manifestly can not be ascertained definitely by observation alone. *Helminthosporium dematioideum* Bub. and Wrob. on the leaves of sweet vernal grass (*Anthoxanthum odoratum* L.) may be cited as an example of a considerable number of fungi, the relation of which to their host or substratum is certainly not as obvious as might be desired.

OTHER TYPES OF INJURY

Differing quite markedly from all of these forms of injury is that caused by a species of *Helminthosporium* attacking young plants of a species of *Paspalum*, provisionally identified as *Paspalum boschianum* Fluegge, which will be further discussed as *H. micropus*. The first evidence of infection appears as a water-soaked area, the tissue of which has lost all its rigidity. The condition suggests an injury such as might have been brought about by the application of a few drops of boiling water. The affected area frequently dries and shrivels, often leaving the surrounding tissue quite normal; or if the affected spot is large enough to interrupt the vascular communications the more distal portion of the leaf blade may gradually wilt without any further advance of the fungus.

In the attack of *Helminthosporium ravenelii* Curtis on *Sporobolus indicus* (L.) R. Br. it is quite impossible to notice either wilting or discoloration. The fructifications of the fungus grow directly out of the inflorescence in a dense, dark, brownish green, velvety layer, the latter being so conspicuous and abundant as to have suggested the term "smut grass" as common name for the host. The infection undoubtedly is altogether local, for even when the larger portion of the panicle has been overgrown with the fungus, the exposed parts present an appearance not greatly different from that of an entirely healthy inflorescence. The fungus discussed in this paper as *H. oryzae*, when developing on the inflorescence of rice, shows an approach to *H. ravenelii* in the crowded habit of its sporophores.

TAXONOMIC CHARACTERISTICS

The definition of the genus *Helminthosporium* Link (85) as recognized in the large works of Saccardo (128, v. 4, p. 402) and Lindau (83) has been very generally adopted by mycologists. The genera *Brachysporium*

Sacc. (128, v. 4, p. 403) and *Napicladium* Thüm. (150) are distinguished from *Helminthosporium*, the former in possessing relatively short spores, the latter in having spores tapering toward the apex. Naturally, these distinctions are based on no fundamental differences, and may readily be supposed to have been advanced primarily to serve in dividing in some way a large group of organisms into a number of smaller groups. As it is not always possible to determine definitely whether the spores of a certain species are in the main to be regarded as longish, or short, or tapering, the advantage accruing from erection of these genera on artificial distinction has been at least partly counteracted by the confusion occasioned by different writers assigning the same form to different genera. Indeed, certain of the forms included in the present paper have been assigned by some writers to one or the other of the genera allied to *Helminthosporium*, and a few other forms might perhaps be thus assigned with equal cogency.

The imperfect fructifications characteristic of the genus *Helminthosporium* consist of sporophores emerging from the substratum singly or in clusters, or more rarely arising as a dense, velvety layer. After attaining a certain length and becoming usually one-to-several-septate, depending somewhat on the species, a spore is developed at the tip. After the latter has reached a certain degree of maturity the sporophore continues to grow near the point of attachment of the first, pushing aside the first spore, and producing another spore a little farther on. A number of spores are thus produced, which, with the exception of the last one, usually fall off or are blown off in nature, their places of attachment being marked by a series of geniculations bearing a dark scar at the apices. In most foliicolous species, the sporophores as collected in the field show branching in only relatively infrequent instances, although a few forms exhibit a more readily demonstrable tendency toward ramification. In *H. ravenelii* branching of the sporophore is, however, very abundant and accounts in a measure for the dense, velvety texture of the crust. Length, width, color, frequency of septation, and general habit of the sporophore, while of considerable value in the diagnosis of some species and consequently always to be given consideration in specific descriptions, in general leave much to be desired in distinctiveness.

The mode of emergence from the epidermis of the host is usually not especially characteristic. In the case of those grasses having small leaves provided with a relatively delicate epidermis emergence usually takes place in an altogether miscellaneous manner, either from the stomata or between epidermal cells. In the case of those grasses of which the epidermis is mechanically somewhat stronger, as in barley or barnyard grass, the sporophores, especially in the beginning before the leaf tissue becomes distorted by shriveling, show a tendency to emerge from the stomata, although emergence between epidermal cells is never uncommon. The only instance observed by the writer where the sporophores appear to be entirely confined to the stomata is that of *Helminthosporium turcicum* on corn leaves, the localization here being readily attributable to the character of the epidermis, which in this host is of unusual mechanical strength, the stomata on the other hand being large and uniformly distributed. Sporophores may appear singly, or in clusters ranging in numbers from 2 to 5, 6, or even 7. Small clusters usually are proliferated nearly simultaneously. However, where the number runs up to half a dozen, some of the sporophores are usually younger,

having been developed after the first two or three had perhaps commenced to proliferate spores.

By far the most distinctive characteristics for taxonomic purposes are to be found in the spore. Within the genus these structures show an unusual range of difference with regard to size. Those of *Helminthosporium giganteum*, for example, which are among the largest reproductive bodies produced by any group of fungi, exceed those of the smaller species like *H. dematioideum* about twice in width and ten times in length, although the latter can not be regarded as especially small. The length of the spore, particularly in the case of those species in which this body is nearly colorless and straight cylindrical like *H. tritici-repentis* Died., *H. bromi* Died., *H. teres*, and *H. giganteum*, is subject to great variation, the length of the smaller ones often scarcely exceeding their width. For this reason the magnitudes approaching the maximum are to be regarded as the more characteristic of the species. The width of the spores of any particular species on the other hand is much more apt to be nearly uniform, regardless of considerable differences in length.

With respect to coloration, the spores represented in the genus exhibit all gradations between the subhyaline condition present, for example, in *Helminthosporium giganteum* and *H. tritici-repentis*, to the dark olivaceous hue characteristic of *H. sativum* and a considerable number of closely related congeneric forms. Most of the species are intermediate between these extremes—yellowish, yellowish brown, and brown. A few species have spores with subhyaline end cells, all the other cells being uniformly dark; or the middle cells may be dark, with the color becoming perceptibly fainter toward the ends.

The spores of most forms of *Helminthosporium* are characterized by some peculiarity in shape by which they can be often recognized with a high degree of certainty. The general contour may be straight cylindrical as in *H. avenae* Eidam, curved ellipsoidal as in *H. sativum*, or tapering toward the tip as in *H. dictyoides*. The basal end is usually most characteristic. In *H. teres*, the proximal cell is hemispherical; in *H. bromi*, hemi-ellipsoidal; in *H. tritici-repentis*, elongate conical with rounded apex, thus crudely suggesting in outline the top or bottom aspect of a snake's head. In *H. monoceras*, the basal half tapers gradually toward the basal end, which is abruptly rounded off; in *H. turcicum* the tapering is more abrupt and continues to the insertion of the hilum. The same is true in *H. micropus* except that here the extreme basal end is drawn out somewhat, the contour being slightly concave near the hilum. In this connection, it may be stated that the hilum—that is, the more or less calloused region at the base of the spore, marking the place of attachment to the sporophore—may be represented by a conspicuously protruding modification as in the two species last mentioned; or, as is much more frequently true, it is visible as a dark spot situated altogether within the contour of the spore wall. In a few species the hilum is not at all conspicuous, as in *H. giganteum*, where it appears as a small wedge-shaped basal prolongation, with a delicate single-contoured confining membrane.

As a good deal of the taxonomic literature based on dead herbarium material gives a wrong impression of the structure of the spore, particularly with reference to its walls and septa, a few remarks may be justified here. The developing spore remains nonseptate during the earlier stages of growth, usually until its definitive size has been largely

attained. Cross walls then appear, the first formed segments being further reduced in size by later successive divisions. Although at the time a segment has just undergone division, the appearance under the microscope is that of a thin line extending across the spore, the protoplasts thus delimited soon round up along the zones where cross walls are in contact with the external wall. The latter in the hyaline-spored forms seems to undergo no readily perceptible increase in thickness; in the dark-spored forms the subsequent apparent increase in thickness is quite considerable. In the process of maturation the individual segments appear to deposit a membrane of their own, the matured spore thus consisting of the original outer spore wall, inclosing a row of more or less independent segments, like peas in a pod. In some species, as for example, *Helminthosporium leersii*, where the outer wall is relatively delicate, these segments may be removed readily from their enveloping membrane by tapping or gently pressing on the cover glass. The process often results in no injury at all, each segment being capable of germinating independently and promptly.

The mode of germination characteristic of a species usually bears a more or less apparent relation, both to the shape of the spore and the structure of its wall. In most of the forms with cylindrical hyaline spores, where the peripheral wall is everywhere uniformly thin, germ tubes are produced more or less indiscriminately from all segments, basal, apical, and intermediate. In the species with tapering spores, as *H. dictyoides*, for example, one germ tube usually arises from the distal cell, and one or two from the larger basal cell, the intermediate segments rarely participating directly in the process. The germ tubes are not polar in position, but arise from undifferentiated regions usually laterally or obliquely at some distance from the hilum or the extreme apex. The fully matured spores of *H. sativum* and closely related species have two perceptibly thin places in the peripheral wall, these being located at the tip and at the base of the spore, in the latter case occupying a narrow zone adjacent to and surrounding the hilum. These areas may be clearly seen, for example, in *H. monoceras*. Here normal germination takes place by the production of one germ tube from the thin-walled region at the tip, or from that near the hilum, or more often from both; never from the intermediate segments, unless, as has been mentioned, the latter have been partly exposed or completely liberated from the enveloping wall by manipulation or mechanical injury. In some other forms like those later discussed under the names *H. halodes*, *H. rostratum*, and *H. oryzae*, germination of entirely mature spores takes place as in *H. sativum* and *H. monoceras*, but not infrequently newly proliferated, subhyaline spores, the walls of which have not become thickened, can be seen to produce, in addition to the two polar germ tubes, one or more tubes from the middle cells as well.

A modification of the septa, visible in the spores of some species, and undoubtedly present in others, may be not without significance in germination. If the cross walls of large, subhyaline-spored forms, like *Helminthosporium teres* or *H. giganteum*, are closely examined a small circular spot having perhaps one-fifth or one-fourth the diameter of the spore may usually be distinguished. It is difficult to determine whether this represents an open communication between the segments or merely two opposed pits in the adjacent segment walls. The appearance of these walls in plasmolyzed dead spores would suggest that the latter alternative is the more probable one, a suggestion that is supported by the fact that

each segment suffers death independently of the others. There can be little doubt, however, that this modification provides means of communication between adjacent living segments. Such a communication would manifestly be of importance especially in those species in which germ tubes are produced only from the two end cells. There are, it may be mentioned, peculiarities in the germination of some species that can not be definitely ascribed to the structure of the septa or of the peripheral wall, or indeed to any demonstrable structural feature; as, for example, the production of three germ tubes from the basal cell of *H. dematioideum*, or the proliferation of clusters of tubes from the end cells or middle cells in *H. giganteum*.

It is interesting to note that if leaves bearing actively sporulating fructifications of forms possessing thin-walled, hyaline spores, like *Helminthosporium teres* or *H. bromi*, are examined under the microscope by reflected light, it will be seen that the mature spores lying about in some abundance are badly distorted and their walls utterly collapsed. When these spores are mounted in water, most of them instantly become turgid, and at a suitable temperature begin to germinate within 30 minutes, showing that the collapsed condition is by no means an indication of death. Dead spores or dead segments of partly living spores, also present in a preparation, recover their former size and shape very largely, although not wholly, but are readily recognized by their abnormally swollen membranes and coarsely granular contents made familiar by the drawings and descriptions of many authors, who unfortunately regarded them as normal. Although some authors report germination of spores exhibiting such swollen walls presumably in all segments, either as a result of age or the application of reagents, the writer has never observed an instance of viability in such material.

Germination is usually accompanied by conspicuous protoplasmic changes beginning in the segments concerned, and finally involving all the segments of one spore. The contents lose their uniform hyaline structure, becoming minutely granular or uniformly vacuolate, or more usually both granular and vacuolate. The germ tubes and mycelium in general vary somewhat with the different species. All the species seem to thrive on the culture media commonly employed in laboratories, which fact, together with the large size of the spores, makes the members of the genus among the fungi most easily isolated and cultivated. Not all of the species, however, can be made to sporulate in pure culture, those possessing hyaline spores—*Helminthosporium bromi*, *H. tritici-repentis*, etc.—being especially refractory in this respect. The majority of forms with dark spores, on the other hand, sporulate quite readily and even abundantly, although the spores thus produced may depart somewhat in shape and size from those produced under ordinary field conditions. This is particularly true of *H. sativum*, where the spores, instead of being long and slender-allantoid, become shorter, thicker, and nearly straight. When media containing a large amount of nutrient is employed, an abundant development of mycelium usually takes place and sporophores are produced in great numbers. Growth, however, soon comes to a standstill, leaving the sporophores short, and bearing only a few spores, the latter frequently being abnormally short. In such cases more satisfactory results can be obtained by the use of media containing little nutrient, as corn-meal-decoction agar or tap-water agar. If such cultures are protected from evaporation, the relatively small number of sporophores will continue to grow for several months, producing scores of

fairly characteristic spores in a dense racemose cluster. Sporophores thus produced may show a tendency to branch, not usually observable in material collected in the field.

A process quite analogous to germination may be observed in the proliferation from the spores of *Helminthosporium gramineum*, of short sporophores in the regions where ordinarily germ tubes appear. These bear a variable number of secondary spores that may usually be distinguished from the primary spores by their smaller dimensions. When this takes place while the latter are still attached to the sporophore, the whole apparatus may bear a partial resemblance to an *Alternaria* fructification. A somewhat similar condition appears to obtain quite normally also in *H. catenarium*, the fungus parasitic on wood reedgrass (*Cinna arundinacea* L.), where, however, the secondary spores more often are borne directly at the tip of the primary one, which thus comes to bear two hila. When grown in culture, this species develops ramifying fructifications in which a series of spores alternating with short sporophoric hyphae bear short sporophoric processes from the end cells. In fructifications of this type, the distinction between sporophore and spore is at least partly obliterated, the two types of structures merging into one another. This miscellaneous type of growth may be observed when *H. teres*, *H. cyclops*, and even *H. sativum* are grown on artificial media. This growth is apparently encouraged by moist conditions, although, as has been indicated, it appears to occur in nature in the case of *H. catenarium* and *H. gramineum*.

It may not be out of place to mention a peculiarity in the growth of the mycelium of most species of *Helminthosporium* which, although perhaps not confined to this genus, may not be without significance. If, for example, a number of spores of *H. bromi* are mounted in water and two come to lie in contact with each other, it will be seen that usually one or more pairs of germ tubes are proliferated from approximately opposite positions and immediately anastomose, thus uniting the two spores by several short hyphal connections. (Pl. 8, Dc.) This tendency toward anastomosis is expressed even more strongly in the mycelium that develops somewhat below the surface of agar cultures, and may be studied conveniently by cultivating the fungus on poured plates, the anastomosis occurring abundantly near the lower surface of the agar. Some of the cells involved in these hyphal fusions swell into subglobose bodies and proliferate short irregular processes of inflated segments, the whole resulting in small, dark brown, knotty masses of mycelium. Some of these continue to increase in size, developing into the subspherical sclerotia, readily visible to the naked eye, the profuse occurrence of which in culture is a distinguishing mark of this species. Although the writer has not succeeded in cultivating these sclerotia further, there can be little doubt that they represent immature perithecia, as they are entirely similar to the immature perithecia found on leaves of the natural host in fall. The inference is further strengthened by the fact that other species of *Helminthosporium*, *H. teres* and *H. tritici-repentis*, of which ascigerous conditions are known, show these structures in abundance. The writer is inclined to believe that in whatever species such sclerotia or abundant anastomoses (resulting in the production of complexes of lobulate segments) are found to occur, perithecia may be sought with considerable prospect of success.

Ascigerous forms have been reported for a relatively small number of species of *Helminthosporium* parasitic on grasses. These are all readily referable to the genus *Pyrenophora* [Rab.] or to *Pleospora* [Fries], depending on the presence or absence of bristles on the perithecium—a basis for generic distinction, which, while regarded by Winter (159, p. 493) with considerable justification as inadequate, has been recognized as valid by Saccardo (128, v. 2, p. 238) and Lindau (82, p. 429). *Helminthosporium bromi*, *H. tritici-repentis*, and *H. teres* have associated with them in this country ascigerous forms belonging to the genus *Pyrenophora* that occur in great abundance on dead host material in spring, *Pyrenophora teres* (Died.) (= *Pleospora teres* Died.) being found on the spike and culm of barley straw, *Pyrenophora tritici-repentis* (Died.) (= *Pleospora tritici-repentis* Died.) on the culm, and in slight measure on the decaying leaves, of quack grass, while *Pyrenophora bromi* (Died.) (= *Pleospora bromi* Died.) is very abundant on the leaves of awnless brome grass, *Bromus inermis* L. In the latter two species the perithecia usually reach perfect development, asci and ascospores reaching maturity early in May near Madison, Wis. Material collected at that period exhibited abundantly the preliminary swelling and circumscissile rupture of the ascus preceding the simultaneous expulsion of the spores from near the base of the dehiscing structure—a mode of discharge observed by Porter (110) in species of *Pleospora*, and in the species under consideration by Diedicke (28) as well as by Atanasoff (2).

tr./

Pyrenophora teres, on the other hand, probably does not form altogether normal ascospores, if the observations made in the spring of 1919 and 1920 may be taken as typical. The ascus may remain undeveloped, showing no trace of young ascospores; or ascospores may be delimited, but become arrested in their development before or after septation has occurred; or certain segments of the spore may develop normally, the others eventually collapsing, giving rise to the unsymmetrical spores shown in Plate 3, D. As Diedicke (29) and Noack (95) have shown, the developing perithecia or sclerotia begin to proliferate conidiophores with the advent of suitable conditions; and a perithecium involved in the production of conidiophores is not likely to show any further development of its ascospores. The production of conidia usually is large in the case of the sclerotial form on barley; moderate in the case of *Pyrenophora tritici-repentis*; and small in the case of *Pyrenophora bromi*. The latter species is probably the only one in which the production of ascospores plays an essential part in the resumption of growth in spring; for, as a rule, in the forms on quack grass and barley, the conidia produced on the sclerotium or immature perithecium would appear to play a relatively larger part in effecting early dissemination on the young host plants. In the case of the forms with dark, thick-walled spores, as for example, *H. sativum* and *H. vagans*, with which neither sclerotia nor perithecia are known to be associated, the conidia are found to germinate readily in spring, since exposure in winter does not bring about any very decided diminution in viability. Conidia of *H. sativum*, *H. oryzae*, and *H. ravenelii* will germinate well one year after their formation, whereas those of *H. bromi*, *H. tritici-repentis*, and *H. teres* are mostly dead within one or two months. The absence of an ascigerous stage from the life history of the former species, and its presence in the latter, are probably not without significance in relation to the longevity of the conidia.

HELMINTHOSPORIUM GRAMINEUM RAB.

Brachysporium gracile (Wallr.) Sacc. var. *gramineum* (Rab.) Sacc. 1886, in *Sylloge fungorum*, v. 4, p. 430.

Napcladium hordei Rostrup 1893, in *Sydomme hos landbrugsplanter foraarsagede af Snyltesvampe*, p. 130-132.

Helminthosporium gramineum (Rab.) Erikss. 1885, in *Fungi par. scand. exs.*, no. 187. *Heterosporium gramineum* of Oudemans, not Rabenhorst.

The binomial *Helminthosporium gramineum* was applied by Rabenhorst⁴ to a fungus occurring on leaves of barley (*Hordeum vulgare* L.) collected at Poppelsdorf, Germany, June, 1856, and distributed as No. 332 of the Herbarium Mycologicum. The pieces of leaves and stem that constitute the specimen deposited in the Herbarium of the Office of Pathological Collections are too small to show any possible characteristic pathological effect; and the fructifications of the fungus are in a condition that would appear to make its identification with any particular one of the three congeneric species now known to occur on barley a matter of great uncertainty. Rabenhorst regarded the fungus as related to *Helminthosporium gracile* Wallr. but differing from the latter in that its spores were solitary, elongated-cylindrical, and 3 to 6 septate. Apparently, in accordance with this view, Saccardo (128, v. 4, p. 430) at first reduced the form to a variety of Wallroth's species, which, moreover, he transferred to the genus *Brachysporium*. Later, however, he listed it as an independent species (128, v. 10, p. 615).

In 1886, Eriksson⁵ distributed as *Helminthosporium gramineum* (Rab.) Erikss. specimens of diseased barley collected near Stockholm, Sweden, during the preceding season. The label includes a short revision of the specific diagnosis:

Hyphi conidiophori solitarii vel 2-4 aggregati, subflavi 1-5 septati, denique saepe angulato anfracti. Conidia subflava, recta, elongato cylindracea, 1-5 septata, 50-100 μ longa, 14-20 μ lata.

Although this characterization applies better to the parasite causing the stripe disease than to that responsible for net-blotch, Eriksson apparently did not distinguish between the two. At any rate, the specimen in the herbarium of the Office of Pathological Collections shows lesions of both diseases; and in an account (37) of the "leaf spot disease" (*blad fläckensjukdom*) he reported most of the plants to have been affected more or less, while a relatively small proportion (1 to 5 per cent) were affected so badly that no heads were developed. It may readily be supposed that the less severely diseased plants were mainly affected with net-blotch instead of with stripe, a supposition supported by the description of the foliar lesions as elongated dark brown spots with light margins.

Von Post (111), working independently of Eriksson, in 1886 published an account of the "brown stripe disease" (*brunrandsjukdom*) of barley, that had been very destructive at Ultuna, Sweden. The longitudinal yellowish streaks, characteristic of all the leaves of attacked individual plants, suggestive of the variegation of ribbon grass, and later changing to brown or yellowish brown; the dying of the plants before the development of spikes, the systemic distribution of the fungus (indicative of seed transmissal and seedling infection) provide conclusive evidence that this investigator was dealing exclusively with the stripe disease.

⁴ RABENHORST, G. L. KLOTZSCHII HERBARIUM VIVUM MYCOLOGICUM SISTENS FUNGORUM PER TOTAM GERMANIAM CRESCENTIUM COLLECTIONEM PERFECTAM . . . Ed. II, Century III, no. 332. 1856.

⁵ ERIKSSON, J. FUNGI PARASITICI SCANDINAVICI EXSICCATI NO. 187. *Helminthosporium gramineum* (Rab.) Erikss. Stockholm, Sweden. July, 1885.

The conidial form that von Post observed developing on the brown areas of affected leaves he identified with *Helminthosporium gramineum* Rab. as defined and distributed by Eriksson.

Rostrup (123), in 1888, described a disease characterized by symptoms and development similar to those described by von Post, which had been doing considerable damage in certain sections of Denmark, and which he attributed to a new species of *Napicladium*, *N. hordei*.

In 1892, Pammel (102) reported a destructive disease of barley from Iowa, which obviously was identical with that described by von Post, being evidenced long before heading time by the presence on all the leaves of affected individual stools, of pale yellow streaks extending from base to tip, premature death, and subsequent tearing of the foliage into shreds. Pammel identified his fungus with the one distributed by Eriksson as *Helminthosporium gramineum* Rab.

Publications by Ritzema Bos (120) and Frank (43) are evidence that the same type of malady appeared and caused losses during the next few years in Holland and in Germany. However, Ritzema Bos' figures of the foliar lesions as well as of the 8-septate spore, and the description of the symptoms in Frank's earlier account (42) leave a suspicion that, like Eriksson, these authors were dealing not with stripe alone, but also with net blotch, and failed to distinguish between the two diseases and causal organisms.

Rostrup (125) appears to have been the first investigator to recognize that barley was affected by two different diseases caused by two distinct related fungi. However, as he associated Rabenhorst's binomial with the cause of the less destructive "leaf spot disease" (*bladpletsyge*) instead of with the "stripe disease" (*stribesyge*), and attributed the latter to a different although related genus of fungi, the prevailing taxonomic confusion was not immediately settled. Indeed, it was not until the appearance of Ravn's detailed papers (115, 116) that the ambiguity, which Eriksson's publications had originally introduced, was disposed of effectively. Ravn assigned the parasite causing stripe to *Helminthosporium gramineum* Rab., reduced *Napicladium hordei* Rostrup to a synonym, and distinguished the fungus very clearly, with regard to morphology and pathogenicity, from the congeneric forms causing net blotch of barley and leaf spot of oats.

While Ravn's papers (115, 116) thus left no further occasion for confusing *Helminthosporium gramineum* with *H. teres*, it did nothing to distinguish it from *H. sativum*, a species later described from the United States, but the occurrence of which as a third congeneric form parasitic on barley has not been recognized in Europe. As will be pointed out in another connection, the European literature is not devoid of ambiguous accounts, of which Masee's treatment (90) of barley leaf blight may be taken as an example, indicating that *H. sativum* is certainly not altogether absent, but usually is mistakenly recognized as *H. gramineum*. And a similar condition obtains in the writings of investigators in America and other countries.

Yet after allowances for erroneous diagnoses are made, stripe remains one of the most important and widespread diseases of barley. In Europe it has been reported not only from Sweden (111), Denmark (115), Germany (42), and Holland (120), but also from England by Prain and Percival (112) and by Biffen (13), from Ireland by Johnson (72), and from Russia by Jachewski (66). According to the records of the Plant Disease Survey, it is found in most of the States of the Union, apparently wherever

barley is grown to any extent, the damage varying from a relatively small amount to approximately one-fifth of the crop. From Canada the disease has been reported by Güssow (48) and by Fraser (45). Hauman-Merck (52) noted the prevalence of *Helminthosporium gramineum* on barley in Argentina to an extent unknown in Central Europe. Yoshino (161) and Ideta (65) have recorded the disease in Japan, where Hori (63), in 1918, observed an unusually severe outbreak. Chou (20) notes *Pleospora graminea* Died. on barley among the pathogenic fungi prevalent in the locality of Nanking in China. In India, the stripe disease has been studied by Butler (19), who states that the damage caused in that country is less than that recorded in European literature.

The symptoms of the stripe disease were described correctly by von Post (111), Pammel (102), and Rostrup (124), and in an especially detailed manner by Ravn (115). The first evidence of infection may often be recognized in the unfolded leaves of young seedlings by the presence of small pale spots, although generally at this stage the manifestations of abnormality are not pronounced. Later, usually about 6 weeks after sowing, after a number of leaves have become fully developed, these organs begin to show longitudinal, etiolated, yellowish stripes, often extending from the base of the blade to the tip. A single broad blade may show from 5 to 7 of these stripes although a smaller number is much more common. Not infrequently the stripes are interrupted and are thus replaced by numbers of elongated yellowish streaks. In any case, the similarity to ribbon grass then constituting one of the most striking characteristics of the disease, is soon modified by the appearance of dark brown discoloration in longitudinal elongated streaks. These brown discolored streaks are most apt to occur especially at the margins of the yellowish stripes, the tissues of which have now become dry and brittle, but often extend also as brown lines beyond the base of the blade, into the upper portions of the sheath. Often the brown streaks are separated from the remaining healthy parts by a yellowish zone within which the chlorophyll has largely disappeared. At this intermediate stage, especially when the brown streaks are short and relatively wide, the disease is apt to be mistaken for netblotch or spotblotch. Later the likelihood of a wrong identification is again diminished, for finally the remaining green tissues are also involved, the yellow and brown discolorations gradually fade into a uniform dark gray or brownish gray, the dead, rather brittle tissues split freely, and a dark efflorescence consisting of the abundant fructification of the parasite makes its appearance on the longitudinal foliar strips. (Pl. 1, A.) As the mechanical rigidity of the diseased leaf tissue becomes greatly lessened during the later stages, the leaf blades or their shredded remains (Pl. 1, Ab-e) usually droop or hang down in a characteristic way.

The effect of the parasite on the stem is equally pronounced. The elongation of this organ incident to heading, especially of the uppermost internodes, is considerably reduced or sometimes almost entirely suppressed. As a result the height of the plants is correspondingly reduced, diseased specimens generally not attaining much more than half the height of healthy individuals. Most frequently the spike never becomes visible, but remains entirely enclosed in the basal portion of the upper leaf sheath. In other instances, the inflorescence is thrust into the upper part of the upper leaf sheath, and, failing to emerge normally, protrudes partly from the opening on the side of the latter. (Pl. 1, A.) This abnormal mode of emergence generally involves some distortion of the awns, as

these tend to remain wedged in the sheath, from which, indeed, they may fail to become completely liberated. The condition thus brought about is in a measure characteristic of the disease, although Hegyi (57) reports a similar type of malformation due to the attack of aphids and to a period of cold weather at a critical time just before heading. In a relatively small proportion of plants, the inflorescence emerges from the sheaths, but for a smaller distance than in normal plants. However, even then the ovaries rarely develop anything beyond abortive seeds, the enveloping lemmas and paleas showing a decided brownish tinge. Viable seed certainly is not generally produced, the few instances recorded by Ravn being apparently more or less exceptional.

In southern Wisconsin, the life of diseased plants usually comes to an end between June 20 and June 25, depending to a large extent on the earliness or lateness of the season. Although at first readily distinguishable in the field, the dead plants are soon hidden as a result of the continued growth of the healthy individuals. By harvesting time, ordinarily soon after the middle of July, they have usually collapsed to such an extent that their remains are not found without special search. Owing to the production of immense numbers of fructifications during the several intervening weeks, particularly on the dead foliar parts, the spores of the fungus may be distributed to the floral parts of healthy plants. The experimental work of Ravn showed that the reappearance of the disease in successive seasons is due to the resultant contamination or infection of the seed with spores of the fungus. When seed thus naturally inoculated germinates, the seedling tissues are immediately infected. As the growth of the fungus keeps pace with that of the host, the parasite maintains itself in the growing point and, indeed, in all parts of the plant, even when at the time no outward symptoms are visible. The development of the disease, including its eventual manifestation toward flowering time, thus presents a striking analogy to that of the systemic smut diseases, and is brought about by a similar mode of parasitism of the fungus concerned. To this manner of development also must be attributed the fact observed by von Post (111), Rostrup (124), Pammel (102), Ravn (115), and others that the affected single individual plants or affected stools are quite uniformly diseased in all their parts, and are, with possible rare exceptions, totally destroyed. The use of terms like "moderate," "slight," "more or less," while not inappropriate in describing the extent to which a barley crop may be affected by stripe, is altogether inapplicable in describing the severity of attack of individual plants, and can in such connection be interpreted only as evidence indicating an erroneous diagnosis.

While in morphology *Helminthosporium gramineum* exhibits no striking characteristics, the writer is of the impression that its similarity to other congeneric species, particularly to those occurring on the same host, as well as on other cereals, seems to have been somewhat exaggerated. It is certainly conspicuously different from *H. sativum*, and is usually not so difficult to distinguish by microscopical examination of its fructifications from *H. teres* and *H. avenae* as Ravn's statements might lead one to believe. The sporophores occur usually in clusters of 2 to 6, fascicles of 3 to 5 being common (Pl. 1, E_a-E_e), whereas the corresponding clusters of *H. teres* (Pl. 2, E_a-E_c) and *H. avenae* (Pl. 4, De-D_g) rarely include a larger number than 3. Although, just as in the latter two species, the basal segment is considerably distended, the width of the sporophores of *H. gramineum* is perceptibly smaller in the

distal portion, measuring usually approximately $6\ \mu$ as compared with 7 to $9\ \mu$ for those of *H. teres* and *H. avenae*.

The spores vary from subhyaline when newly proliferated to yellowish brown when fully mature, never, however, becoming dark olivaceous, like those of *H. sativum*. They are (Pl. 1, Ba-h) typically straight or very slightly curved; subcylindrical, but quite frequently widest in the basal portion and tapering more or less toward the apex. Both apical and basal ends are rounded off, abruptly presenting a hemispherical contour. The peripheral wall is relatively thin as in other species having subhyaline or light-colored spores. The septa vary from 1 to 7 in all the material the writer has had occasion to examine, and are only infrequently associated with perceptible constrictions (Pl. 1, Bf, h), while in the spores of *H. teres* (Pl. 2, Ca) constrictions are more common and often moderately pronounced. Germination takes place promptly when the spores are mounted in water, usually within 30 minutes. Germ tubes are proliferated usually from both end segments and from several intermediate segments, the numbers produced from the basal segment varying from 1 to 3, while the other segments rarely give rise to more than one (Pl. 1, Ca-d).

A phenomenon undoubtedly related to germination is the production in nature of secondary spores or short secondary fructifications from primary spores, that in this species occurs to a greater extent than in the other congeneric forms parasitic on cereals, and which suggests comparison, for example, to *H. catenarium*. The secondary spores are not generally produced directly on the apex, but on a sporophoric process arising from the apex (Pl. 1, Dc, e) or obliquely from the apical cell (Pl. 1, Da, d) or less frequently laterally from the basal segment (Pl. 1, De). Not infrequently the process remains short and gives rise to only a single spore (Pl. 1, De), while again it grows out into a sporophore bearing half a dozen spores (Pl. 1, Dc). Evidently such secondary development may take place after the primary spore has become detached from the sporophore on which it was borne, as it usually is associated with a collapse of some or all segments of the primary spore involved (Pl. 1, Da). The secondary spores (Pl. 1, Dca-cc, Dda) may be nonseptate or show 1 to 3 cross walls; they are, in general, decidedly smaller than the primary ones, the minimum dimensions approximating 11 by $20\ \mu$ (Pl. 1, Dca-cc, Dda). As the smaller individuals of the one order can not be readily distinguished from the larger individual of the other, all gradations may be found between these magnitudes and the maximum dimensions of the primary spores, $20\ \mu$ for width, $105\ \mu$ for length. The maximum measurement for spore length of *H. gramineum* is thus barely two-thirds as large as that of *H. teres*—a fact of great importance in identifying the species by microscopical examination.

Diedicke (29), in 1903, reported from Germany the discovery of an ascigerous stage of *Helminthosporium gramineum* in a species of *Pleospora*, which he found to correspond fairly well to *P. trichostoma* (Fr.) Winter. However, as the latter appeared to include a number of forms parasitic on different hosts but not interchangeable in their host relations, he regarded it as a collective species, and separated it first into a number of biologic races (28) which later he recognized as individual species (29). The perithecial form collected on old barley straw in a field that had been affected severely with the stripe disease was accordingly referred to a newly derived species, *P. graminea*. On inoculating barley leaves with sclerotia of the fungus, typical symptoms of stripe

are reported to have appeared in a number of cases, thus presumably establishing its identity. Diedicke's findings were confirmed by Noack (95) who, working independently, studied apparently the same ascigerous fungus collected on barley stubble in Hesse, Germany. Using conidia, ascospores, and sporulating material of host leaves, Noack secured infection by inoculating the first leaf of barley seedlings when it had attained a height of only several centimeters; and also on plants about 4 weeks older. The symptoms induced in the young seedlings were systemic, whereas on the older plants local infections manifested by the appearance of brownish spots were obtained.

The work of both Diedicke and Noack is open to the criticism that it was not done in connection with parallel infection experiments carried out with *Helminthosporium teres*, and that consequently these authors were, perhaps, not so capable of distinguishing between the pathological effects of the two related fungi as might have been desired. It may be mentioned that their fungus was obviously very similar to the form discussed in this paper as *Pyrenophora teres* (Died.) collected by the writer near Madison, Wis., where it occurred in abundance in spring on barley stubble apparently regardless as to whether or not the crop of the preceding year had been seriously affected with stripe. Recently, Paxton (106) has reported the occurrence of the mature perithecial stage of *H. gramineum* on two-year-old barley straw in California. Transfers of ascospores to corn-meal agar resulted in the production of conidia, which when used to inoculate barley gave rise to typical stripe lesions. According to Van Poeteren (109), perithecia of the parasite have been found on the glumes of germinated grains of barley, the seedlings of which exhibited the symptoms of stripe. This author suggests incubating seed in a moist warm atmosphere for three days in order to determine in advance from the appearance or nonappearance of perithecia whether it will give rise to diseased or healthy plants.

Of all the diseases due to species of *Helminthosporium*, the stripe disease undoubtedly has been made the subject of the largest amount of investigation aiming at effective methods of control. As the effective inoculum is presumably very largely, if not entirely, borne on the seed, the disinfection of the latter by the use of various fungicides and by the application of heat has not been without a considerable measure of success. Copper sulphate was found effective by Riehm (119) when applied in 1 or 0.5 per cent solution for 30 minutes; by Lind and Ravn (81) when applied in 0.5 per cent solution for 4 hours; and by Müller and Molz (93) when applied in the same solution for 16 hours. Lind and Ravn (81) obtained satisfactory results by the application of formaldehyde in 0.2 per cent solution for 6 hours; Schander (129) in 0.2 per cent solution for 30 minutes; and Johnson (70) in 0.16 per cent solution for 3 hours at 20° C., in 0.25 per cent solution for 2 hours at 10°, and 0.25 per cent solution for 1 hour at 25°. According to Lind and Ravn (81) treatment with mercuric bichloride in 0.1 per cent solution for 1 to 2 hours gives good results. Riehm (119) found 0.2 per cent mercury chlorphenol applied for 15 minutes effective. The hot-water treatment of seed for the control of stripe was found by Lind and Ravn (81) less effective than chemicals and of value only for lightly infected seed; Johnson (68), however, found a modified treatment with hot water 5 hours cold, and 15 minutes at 52° C., quite valuable. A variety of intermittent hot-water treatments have been devised, consisting in dipping the seed in hot water for relatively brief periods alternating with

longer periods of exposure to cooler water. Müller and Molz (93), as well as Lind and Ravn (81), found hot-air treatment worse than useless for stripe, as it tended to increase the proportion of diseased plants; Atanasoff and Johnson (3), on the other hand, found that such treatment markedly reduced the disease without materially injuring the seed. As the disinfection of barley seed usually involves a number of diseases, the choice of any particular treatment often is contingent on its effectiveness in controlling smut, netblotch, spotblotch, and the bacterial blight as well as stripe.

Owing to the successful control of stripe by seed treatment, not much attention has been devoted to other methods of combating the disease. The various reports already mentioned, of the occurrence of an ascigerous stage, and the statement by Paxton that 16-year old herbarium specimens of cultivated barley affected with *Helminthosporium gramineum*, when placed in a moist chamber, produced conidiophores and viable conidia from the dormant mycelium, suggest the possible value of measures involving sanitation. Indeed, Frank (43), Weiss (157), and later Jaczevski (66) recommended rotation of crops, though perhaps more on general principles than because of possible experimental evidence or knowledge of the presence in fields of an overwintering stage playing an important part in establishing the parasite on successive crops. Ferraris (40) recommended burning the stubble in addition to seed disinfection. The removal and destruction of diseased plants found effective in Scotland (134) would obviously constitute a method of eradication too laborious to be seriously considered in the United States. The observations of various investigators, notably of Hori (63) and of Lind and Ravn (81), show that the proportion of diseased plants is increased when the seed germinates in soil at a low temperature. Müller and Molz (93), however, did not find late sowing in a warmer seedbed advisable; for, although less disease developed, the delay brought about a decrease in the yield.

Von Post (111) observed considerable differences in susceptibility to stripe between varieties of barley. Ravn (115) found the six-rowed varieties as well as the *erectum* types more heavily attacked, in general, by *Helminthosporium gramineum* than the *nutans* types, a condition exactly the opposite of that he found to obtain with reference to attack by *H. teres*. Kiessling (76), while unable to confirm Ravn's findings regarding the comparative susceptibility of the nodding and the erect types, noted pronounced differences in the proportions of diseased plants present in the stands of different varieties. It is worthy of note that some of Kiessling's strains, representing genetically pure lines, manifested with fair consistency moderate susceptibility, while other pure lines exhibited a high degree of resistance. This author urged, very justifiably, that the plant breeder ascertain the measure of resistance to stripe inherent in any varieties of barley with which he may be dealing and reject those lines showing marked susceptibility.

HELMINTHOSPORIUM TERES SACC.—PYRENOPHORA TERES
(DIEDICKE)

Helminthosporium hordei Eidam 1891, in *Der Landwirt*, Bd. 27, p. 509.

Pleospora teres Died. 1903, in *Centralbl. f. Bakt. Abt. 2*, Bd. 2, no. 2, p. 52-59.

The binomial *Helminthosporium teres* was applied by Saccardo (126, pl. 833) to a fungus collected on leaves of barley near Padua, March, 1881, and figured in the "Fungi Italici" as having 3-septate conidio-

phores arising in a group of five from a green substratum and bearing at the tip a single conidium. The latter were represented as dark green structures, thick walled, 4 to 5 septate, ellipsoidal or subcylindrical, tapering perceptibly toward the rounded ends. A part of a leaf, showing a green region interspersed with uniform brown elliptical areas marked with short, black, longitudinal lines, was doubtless intended to represent the pathological habit of the fungus. In 1882 (127), a brief diagnosis of the species was published:

Maculis oblongis amphigenis, olivascentibus; hyphis fasciculatis, 100-130=12, cylindraceis basi subincrassatis, fuliginosis; conidiis acrogenis cylindraceis, rectis utrinque rotundatis, 110-115=18, 4-5 septatis, non constrictis, obscure olivaceis.

Neither the figures nor the text make it possible to identify definitely Saccardo's fungus with any one of the three species of *Helminthosporium* parasitic on barley. The number of sporophores in a fascicle, and the number of septa in the spore, suggest the form causing stripe; the thick wall, tapering ends, color, and absence of constrictions in the contour of the spore, suggest that causing spot-blotch; while the excessive width of the sporophore and the relative straightness of the spores suggest that responsible for net blotch. Although size of spores and appearance of lesions clearly point away from the stripe fungus, the former is nearly equally applicable to the other two species, while the latter is scarcely characteristic of any.

Nearly a decade later Briosi and Cavara⁵, in an account of the fungus causing leaf spot of oats, recognized it as a form of Saccardo's species. Oudemans (100), after examining Rabenhorst's specimens of *Helminthosporium gramineum*, concluded that the latter fungus was identical both with the one redescribed by Eriksson (37) under the same name and with *H. teres* Sacc. Ravn (115), however, did not accept Oudemans' views in their entirety, but in distinguishing two diseases of barley applied Rabenhorst's binomial to the fungus causing stripe, and Saccardo's to the causal organism of barley "Helminthosporiosis" or net blotch. In making these dispositions he took into consideration the destructive character of the parasite described by Rabenhorst in contrast to the local foliar lesions which, while figured and described very poorly by Saccardo, he was nevertheless able to identify with those characteristics of "Helminthosporiosis" by an examination of Saccardo's original specimens. The Italian mycologist, moreover, confirmed Ravn's opinion that his *H. teres* was the species responsible for "Helminthosporiosis."

The disease itself had not escaped earlier observation by other students. As was pointed out in another connection, Eriksson's specimens of *Helminthosporium gramineum* Rab. showed typical lesions of net blotch as well as of stripe; and his note on the "bladfläckensjukdom" indicates that the former was moderately abundant in the field. Kirchner (77), in 1891, had published an account of the "brown-spottedness" (Braunfleckigkeit) of barley leaves, observed in southern Germany during the preceding two seasons. The spots were described as blackish brown in color, narrow, often over 1 cm. in length, and surrounded by a narrow yellow zone while the leaf is still green. With the multiplication of the spots the leaves were observed to wither and give rise to the fructifications of the fungus. Material was submitted to Eriksson, who pronounced the fungus identical with that distributed by him, although

⁵ BRIOSI, G. et J. CAVARA. I FUNGI PARASSITI DELLE PIANTE COLTIVATE OD UTILI. No. 80. Pavia, Italy, 1889.

Kirchner called attention to the fact that up to eight septa were present in the spores. This fact, together with the relatively mild nature of the disease, indicates that he was most probably dealing with net blotch. In 1898 Rostrup (125) had discussed a disease of barley which he designated as a "leaf-spot disease" (*Bladpletsyge*), characterized by the presence, largely on the lower, less vigorous leaves, of elongated dark brown spots, surrounded by a narrow yellow margin. This malady, which was not observed to be very destructive, Rostrup attributed to *H. gramineum* Rab. Apparently the same trouble had been investigated later also in Silesia by Eidam (35), who attributed it to a new species of *Helminthosporium*, *H. hordei*, which he found was not transmissible to oats and consequently different from the congeneric parasite causing leaf spot of the latter host.

The disease is evidently widely distributed in the United States, the records of the Plant Disease Survey containing reports of its occurrence in 21 States, including all the barley-growing districts of any importance. In this connection it may be mentioned, however, that although often responsible for appreciable loss, net blotch is of relatively minor economic importance compared to stripe or spot blotch. It is true that in Bakke's paper (6), which contains the first published record of the disease in this country, *Helminthosporium teres* is represented as probably the most serious parasite of barley. As Bakke failed to distinguish between the disease under consideration and the much more serious trouble attributable to *H. sativum*, the exaggerated account of the destructiveness, as well as the somewhat inaccurate morphological treatment of *H. teres*, both of which unfortunately appear to have been incorporated in Butler's handbook (19), are readily explained.

The course of development of netblotch has been described in detail by Ravn (115). In the vicinity of Madison, Wis., where in 1919 the writer had occasion to observe the progress of the disease, the regular crops exhibited the characteristic symptoms in small measure during the earlier part of the season. Later the lesions sparingly present on scattered leaves were completely obliterated by the blotches due to *Helminthosporium sativum*, that began to appear in great profusion at the heading stage about June 20. A much more favorable opportunity to study the disease presented itself with its development on volunteer plants from the latter part of August until the beginning of November, when netblotch was present in considerable abundance, to the practical exclusion of both stripe and spotblotch. The writer is informed that a somewhat suppressed manifestation of the trouble on the regular crop, and its extensive distribution on the volunteer crop, is, in general, not altogether uncharacteristic of its seasonal occurrence in our northern latitudes.

According to experiments reported by Ravn (115), the disease is propagated by seed infected or contaminated by the fungus. When such seed germinates at a relatively low temperature, as, for example, 10° to 15° C. or less, there results a local infection of the first seedling leaf which he designated as primary *Helminthosporiosis*. This is in contradistinction to secondary *Helminthosporiosis* resulting from infection by conidia developed on the dead tissues involved in the primary or in subsequently developed secondary lesions. On the other hand, when germination took place at a temperature of 20° C. or above, primary *Helminthosporiosis* failed to develop even though the seed was infected or contaminated. That such thermal relations are effective

in the development of primary lesions in the field was shown by the virtual absence of such lesions from the first leaf of plants resulting from sowings made in July and the first half of August, in contrast to a high percentage of infection secured from sowings made in March and April. The prevalence of netblotch on volunteer barley in the northern latitudes of our Middle Western States, where the temperature in midsummer ordinarily is at least as high as in Denmark, is accordingly on *a priori* grounds not to be attributed to seed infection. And, indeed, the abundance of the lesions on the first few leaves of a large proportion of volunteer seedlings in the fields kept under observation by the writer in 1919 indicated secondary infection due to spores from stubble and other remains of the regular crop.

Barley leaves affected with netblotch usually are not difficult to distinguish from leaves attacked by stripe or spotblotch. The presence of the parasite in the living foliar tissues is manifested by the appearance of dark brown spots or streaks which at first may be barely perceptible, measuring perhaps not above 1 mm. in length, but later increasing considerably in size, although not frequently measuring more than 20 to 25 mm. in a longitudinal direction. The increase in width usually is relatively small. A variegated appearance simulating that of the foliage of ribbon grass, due to alternately placed green and yellow stripes, is never produced, although the brown streaks characteristic of the later intermediate stages of stripe may sometimes be approximated in leaves affected by *Helminthosporium teres*. The most distinctive feature of the discolored areas involved in netblotch lesions is to be found, however, in the irregular distribution of the brown pigment, the latter being accentuated in very narrow lines, some oriented longitudinally, others transversely or obliquely to the axis of the leaf. As a result, a more or less irregular dark brown reticulate pattern may be distinguished within the areas of diffused brown. (Pl. 2, A, B.) Indeed, the pigmentation of the interstices within the reticulate pattern may become so reduced that the discoloration is present almost exclusively as a sharply defined network of brown lines. (Pl. 2, B.) The resulting macroscopic appearance, utterly different from that characteristic of stripe or spotblotch, and duplicated (as far as the writer is aware) only in leaves of meadow fescue affected by *H. dictyoides*, led Johnson (3) to apply to the disease the descriptive name "netblotch," which has since been generally adopted in the United States. The parts of the leaf immediately adjacent to the discolored tissue usually shows more or less etiolation that becomes manifest in the appearance of a narrow yellowish zone surrounding the spots. (Pl. 2, B.) Sometimes, especially in incipient lesions in which the reticulate character is pronounced, the measure of etiolation is apparently small, and the dark brown netlike lines are found in leaf tissue apparently very little changed. Later, however, all the lesions show yellow margins, which eventually become extended until the whole leaf blade is involved and withers from the tip to the base. (Pl. 2, Ad, Ae.) At this stage the spots, which may number several score on a single leaf and often become more or less confluent, begin to fade from a dark brown to a more diffused dull brownish gray. Not much later the fructifications appear as a light efflorescence extending usually from the brownish spots over the surrounding yellowish gray portions of the dead foliar organ.

The injury due to *Helminthosporium teres*, like that occasioned by most of its foliicolous congeners is thus the result of the destruction of

leaf tissue. As long as weather conditions are suitable, each successive leaf to be unfolded sooner or later becomes infected and in time may be killed. Plate 2, A, showing a volunteer seedling with five leaves, the first (Pl. 2, Ae) entirely withered, the next three (Pl. 2, Aa-b) exhibiting increasingly earlier stages, and the fifth (Pl. 2, Aa) apparently healthy, drawn from material collected September 2, 1920, represents a rather severely affected specimen. It may be mentioned that after September 15 the production of new lesions was much slower, with the result that, on November 3, the upper leaves of the plants, then about 24 inches tall, were entirely free from the disease, although fresh lesions could be found on the leaves lower down, while the lowermost withered foliage was covered with an abundance of profusely sporulating conidial fructifications.

The brown or olivaceous conidiophores (Pl. 2, Ea-d), emerging from the stomata or between epidermal cells, singly or in groups of 2 or 3, vary usually from 120 to 200 μ in length, and above the swollen basal cell, from 7 to 9 μ in diameter. They are thus somewhat stouter than those of *Helminthosporium gramineum* and *H. sativum*, besides being less closely septate, the septa occurring at intervals varying usually from 15 to 60 μ , and averaging approximately 35 μ . The writer has not observed them in fascicles of 5 and 6, indicating that their occurrence in groups of such number is at least less common than in the case of the stripe fungus. On the other hand, the conidiophores of *H. teres* appear to be quite indistinguishable from those of *H. avenae* in all respects.

Although *Helminthosporium teres* has been confused with both *H. gramineum* and *H. sativum*, the spores of the netblotch fungus are certainly not readily mistaken for those of the latter species. The writer's material, collected near Madison, Wis., October 28, 1919 (after a protracted period of damp, cloudy weather under conditions apparently nearly optimum for sporulation) showed these structures (Pl. 2, Ca-f) to vary from 30 to 175 μ in length and from 15 to 22 μ in width. In respect to spore length, therefore, the species is altogether superior to the two congeneric forms occurring on barley and inferior to *H. bromi* in approximately the same degree as the latter is inferior to *H. giganteum*. From 1 to 10 septa were found present, the septa, after the delimited segments have partly rounded up, being associated usually with perceptible constrictions in the contour of the spore. As the constriction at the proximal septum is especially pronounced and constant, and the basal, as well as the apical end, is rounded off in a hemispherical form, the basal segment is given a subglobose shape as characteristic for the species as are the basal segments of *H. tritici-repentis* and *H. bromi*.

The spores are subhyaline in color, like those of the latter two species, when newly proliferated, but become greenish fuliginous or yellowish when older, usually, however, not assuming a tinge quite as dark as the brownish yellow of fully matured spores of the stripe fungus, and consequently never approximating the dark olivaceous color of those of *H. sativum*. Associated with this light color is a thin peripheral wall, the drawings of Saccardo (126) and some other authors showing the outer wall as a thick structure being apparently based on dead material. While the spores of *H. gramineum* usually are entirely straight, those of the netblotch fungus not infrequently exhibit slight irregular crooks (Pl. 2, Cf), in which respect as well as in the general subcylindrical shape and location of the hilum within the contour of the basal end, a similarity to *H. bromi* and *H. tritici-repentis* again is evident.

When the spores are mounted in water, they germinate promptly, germ tubes being produced laterally or obliquely from intermediate as well as end segments, the protoplasm changing from a uniform to a regularly vacuolate structure. (Pl. 2, Da-d.) Like those of related species they are relatively short lived, a considerable proportion of the segments dying during the first 10 to 15 days of exposure, and probably few surviving after two months. It appears very probable that Bakke's account (7) of the longevity of *Helminthosporium teres* was based on material not of this species, but of *H. sativum*.

On media containing little organic food material, like tap-water agar (tap water 1,000 cc., agar-agar 20 gm.), or Beyerinck's agar (distilled water 1,000 cc., ammonium nitrate 0.5 gm., dipotassium phosphate 0.2 gm., magnesium sulphate 0.2 gm., calcium chloride 0.1 gm., ferrous sulphate trace, agar-agar 15 gm.), aerial growth, although sparse, often consists almost entirely of conidial fructifications bearing spores similar in structure and color to those developed in nature, but usually much shorter and containing only 2 to 3 septa. A strong tendency toward production of secondary spores is apparent also in artificial cultures, giving rise to conditions like those illustrated by Ravn (115).

On media containing a large amount of organic food material, a profuse white aerial growth results, consisting partly of fluffy mycelium, and partly of more or less compact erect columnar masses. The submerged mycelium shows abundant anastomosis with the formation of numerous complexes composed of dark brown inflated or lobulate segments. (Pl. 9, Fa-b.) The latter apparently represent incipient stages of sclerotia which on sterilized barley straw may become readily visible to the naked eye, often exceeding 0.5 mm. in diameter. Ravn, although failing to observe any indication of ascus formation in these cultivated bodies, nevertheless interpreted them as immature perithecia of a Pyrenomycete, probably related to *Pleospora polytricha* (Wall.). This interpretation was justified by Johnson's (69) discovery in Wisconsin of the ascigerous stage of the netblotch parasite in a fungus he referred to the genus *Pleospora*, the specific identity of the stages in the pleomorphic forms being supported by apparently conclusive inoculation and cultural studies. The same ascigerous form was collected by the writer on barley straw and stubble from fields near Madison, Wis., late in March, 1919, as well as in March and April of the following year. As Diedicke (29) and Noack (95) recognized a similar ascigerous form as the perfect stage of *H. gramineum* in Germany, it may not be superfluous to mention that the Pyrenophora fructifications found on barley stubble in Wisconsin do not seem to be confined to weak culms such as might conceivably represent the remains of plants affected with stripe, but are found very abundantly on culms which, because of their manifest normal size and attachment to a perfectly developed head, can not easily be supposed to be derived from "striped" plants. (Pl. 3, A.) Previous to the publication of Noack's paper, Diedicke (29) had suggested the binomial *Pleospora teres* for the ascigerous stage of *H. teres*, at that time unknown, and consequently somewhat hypothetical.

The perithecia on barley straw (Pl. 3, B) are of the same type as those of *Helminthosporium bromi* and *H. tritici-repentis*. In general, however, they are perceptibly larger, measuring usually about 0.5 mm. in diameter. Although the lateral wall may sometimes taper toward the top, a distinct ostiolar beak usually is not present, and in most instances the ostiole is represented by a mere opening in the apical portion of the fruiting body. Setae may be altogether absent, or present in moderate number not

usually near the ostiole but on the lower portion of the wall. They (Pl. 3, Ca) differ from the sporophores (Pl. 3, Cb, Cc) usually produced in large numbers on the upper surface of the fruiting body in spring, in being dark olivaceous rather than of a brown color, in being more closely septate, and in tapering toward the tip to about one-half their basal diameter. Although material of *Pyrenophora tritici-repentis* and *P. bromi* collected near Madison, Wis., in the spring of 1919 and 1920, showed asci and ascospores in excellent condition, the development of corresponding structures in *P. teres* did not go beyond a more or less abortive stage. In most instances the asci remained small; if ascospores were delimited, they usually failed to grow to normal dimensions, and frequently showed no cross walls. Plate 3, D represents approximately the least abnormal conditions found in the season of 1920, showing each of the asci with several obviously normal spores, the remainder being either more or less misshapen, or having one or several or all of the segments collapsed. The space in the interior of the imperfectly developed fruiting body not occupied by asci, is filled with colorless vertically oriented, more or less filamentous pseudoparenchyma. As has been indicated in another connection, the failure of the asci to develop normally may be attributed to the advent of weather conditions in the spring encouraging the production of the numerous conidiophores (Pl. 3, B), the initiation of which appears to involve a cessation in the development of the internal parts of the perithecium. As abundant moisture and a relatively high temperature appear to favor the conidial stage, it is not illogical to expect that a long protracted period of cold, dry weather in spring might result in the production of more nearly normal asci.

Judging from the more satisfactory material examined, the asci of *Pyrenophora teres* are subcylindrical throughout most of their length, the proximal portion tapering toward the short stipitate base, and the wall of the apical end modified by a ring-like thickening. They measure 30 to 36 by 220 to 250 μ , and contain 8 spores in distichous arrangement. Normal specimens of the latter are light brown in color; measure approximately 18 to 22 by 52 to 60 μ ; and show three transverse septa associated with perceptible and often pronounced constrictions. One or both middle segments may, in addition, be divided by a longitudinal wall. The protoplasmic contents appear more or less granular and vacuolate. Germination takes place promptly when the spores are mounted in water, in a manner entirely similar to that of the two related ascigerous forms discussed in this paper.

It is difficult to estimate the measure of importance to be attributed to the ascospores and conidia developed by the perithecia in reestablishing the fungus at the beginning of successive seasons. The abundance of these fructifications, however, indicates that they constitute a source of inoculum that ought not to be overlooked, and certainly provides an additional reason for crop rotation, or such sanitary measures as turning under or otherwise disposing of the stubble of the preceding season. Most of the investigations relating to the control of netblotch have been carried out as subsidiary to control studies of the more destructive diseases affecting barley, particularly stripe, loose and covered smuts (*Ustilago nuda* and *U. hordei*), and spotblotch. In general, the seed treatments effective against stripe and spotblotch have also been found to reduce materially the number of primary infections of netblotch. Nevertheless the literature does not seem to indicate any treatment for the disease quite equalling in efficacy, for example, the various formalde-

hyde treatments that have been devised against stripe, or the hot-air treatment described by Atanasoff and Johnson (3) against spotblotch. Moreover, as the plant is subject to attack at any stage of growth, and the fungus can spread from a small number of diseased seedlings to other plants, reduction of primary lesions by methods aiming at the disinfection of the seed is of relatively less value than in the case of diseases, the occurrence of which is contingent on seed contamination and infection during the germination period.

HELMINTHOSPORIUM AVENAE EIDAM

Helminthosporium teres Sacc. forma *avenae-sativae* Briosi & Cavara 1889, in I fungi par. delle piante colt. od utili, no. 80.

Helminthosporium avenae-sativae (Br. & Cav.) Lindau in Rabenh. Krypt. Fl. V. Deutschland. Ed. 2, Bd. 1, Abt. 9, p. 34.

Helminthosporium avenae (Br. & Cav.) Ravn, 1900, in Bot. Tidsskr. v. 23, p. 212-213.

Helminthosporium gramineum of Ritzema Bos, Frank, Fraser not Rabenhorst.

In 1889 Briosi and Cavara⁶ distributed specimens of a fungus collected near Pavia, Italy, where it was found parasitic on the leaves of oats, *Avena sativa* L., producing narrow, oblong, longitudinally elongated, olivaceous foliar spots, with dark margins. The infection was described as starting ordinarily at the tip of the leaf, where the first spots appear, and from whence the mycelium gradually invades the leaf parenchyma, until the entire blade withers and dies. The injury to the foliage thus occasioned was reported to interfere with the full development of the seeds. Briosi and Cavara designated the fungus itself as *Helminthosporium teres* Sacc. forma *avenae-sativae*, differing from the typical species by the greater length of the conidiophores, the occurrence of the latter singly instead of in fascicles, and the somewhat smaller dimensions of its spores. In the brief diagnosis of the form, accompanied by figures, the conidiophores are described as scattered, stout, cylindrical, many-septate, fuliginous, measuring 150 to 200 by 9 to 12 μ ; the spores as acrogenous, olivaceous, cylindrical, or slightly swollen in the middle, rounded at the ends, 4 to 6 septate, and measuring 80 to 110 by 15 to 16 μ . Their representation of the septa and spore wall as thick structures indicates that Briosi and Cavara used dead material for their studies, a circumstance to which may be attributed, perhaps, the inexact description of the color of the spore, and their failure to mention the more distinctive features of the fungus.

Eidam (35), in 1891, published an account of a leafspot of oats occurring in Silesia and affecting usually the first leaf, but sometimes also the second and third leaves of the host. He recognized the causal parasite as a new species, *Helminthosporium avenae*, distinct from his *H. hordei* (= *H. teres* Sacc.) because of the negative results obtained in his attempts to infect barley with the former, and oats with the latter. Ritzema Bos (121) later described an attack upon oats by *H. gramineum* Rab., the resulting foliar spots differing from those occurring on barley in being short, somewhat round, and associated with a reddish color of the diseased leaves. Ravn (115), as the result of comparative cultural and biometrical studies of the parasites causing stripe, netblotch of barley, and the "Helminthosporiosis" of oats, concluded that the latter represents an independent species.

It is of some slight nomenclatorial interest to note that Ravn, apparently in the belief that Briosi and Cavara's priority in recognizing the

⁶ Op. cit., p. 657

parasite as a separate taxonomic entity necessitated the perpetuation of their form name as the specific name, adopted the combination *H. avenae* (Br. & Cav.). The last portion of the form name—*sativae*—he omitted purposely on the ground that it was unnecessary. Lindau (83, p. 34-35), presumably because of the patent irregularity in altering a name in such manner, recognized Briosi and Cavara's form name without alterations as the proper specific name, and consequently listed the fungus as *H. avenae-sativae* (Br. & Cav.). However, as the use of an earlier varietal name to replace a specific name (when the variety is raised to specific rank) is not sanctioned by present usage, it is obvious that both Ravn's and Lindau's combination are equally unauthorized, and that the proper combination is evidently the one established by Eidam.

In this connection, it may be mentioned that Cooke (23), in 1889, described as *Helminthosporium avenaceum* Curtis Herb., a fungus occurring on straw in the United States (oat straw according to Saccardo) the conidia of which were characterized as cylindrical to subfusoid, pale honey-colored, and measuring 75 to 85 by 15 μ . Harkness (50) mentioned *H. avenaceum* Curt. as having been found on Avena, at San Francisco, in April. Atkinson (4) records having collected a fungus to which he applies the same name, in Mississippi, on June 26, 1891. It is not impossible that these authors were dealing with the fungus originally described from Italy, inasmuch as the brief diagnosis published by Cooke is not greatly at variance with that of Briosi and Cavara, and in purely morphological details nearly as satisfactory for the parasite causing leaf spot of oats as the latter. Since in none of the American writings was the fungus associated with any lesions in the living plant, such possible identity can not readily be established. The question is further complicated by the occurrence of forms of *Helminthosporium*, associated with sclerotia appearing saprophytically in considerable quantity on oat straw in spring, and evidently representing immature perithecia of *Pleospora* or *Pyrenophora*. The writer has investigated two such forms collected near Madison, Wis., in 1919 and 1920, one of which seems to be similar to or identical with *H. avenae*, while the other is entirely different, its small, dark olivaceous, strongly curved, 5-septate spores germinating by the production of 2 polar germ tubes. Further details may be published in a later paper.

In 1895, Harvey (51) published a brief account of a disease of oats found in Maine during the preceding two seasons, manifested apparently by premature yellowing of the foliage, and the subsequent production of dark brown spore masses that appeared as small dark dots or lines upon the affected leaves. The fungus in question was a species of *Helminthosporium*, which Ellis, to whom material was sent, identified as *Helminthosporium inconspicuum* C. & E. var. *britannicum* Grove. Unfortunately, however, as the only statement regarding the host relationship of Grove's variety in the diagnosis given by Saccardo (128, v. 4, p. 411-412) refers to fading grass leaves without any mention of species or genus, it is quite impossible, with the paucity of morphological detail, to identify it with any one of a considerable number of fungi.

Ellis's identification might be supposed to indicate that the Maine fungus corresponded in some measure with the diagnosis of the Warwickshire form:

Effusum bruneolum, hyphis subflexuosis, vix nodulosis, 4-5 septatis, pallide brunneis, 160-180=10 μ ; conidiis longis, diaphanis, endochromate brunneolo diviso, dein 3-5 septatis, 60-100=18-22 μ .

That the correspondence is not especially close is indicated by Harvey's statement that the spores of his fungus were somewhat shorter, measuring 40 to 80 by 15 μ , and sometimes less frequently septate, namely, 1 to 5 times. And his figure of the spore, showing this body as an ellipsoidal, comparatively closely septate structure does not suggest any close resemblance either to *H. inconspicuum* C. & E. or to *H. ieres*, between which Grove's variety was reported as occupying a median position. Nor is it any more suggestive of *H. avenae*. On the assumption that only one parasitic species of *Helminthosporium* occurs on cultivated oats, Harvey's fungus might perhaps nevertheless be supposed to be identical with the one distributed by Briosi and Cavara. An examination of specimens of diseased oats collected near Bloomington, Ill., in June, 1920, bearing conidiophores and conidia of a type somewhat different from that generally found characteristic of the oat leaf-spot fungus, has, however, made the writer inclined to believe that such an assumption might probably prove to be incorrect.

The disease caused by *Helminthosporium avenae* is widely distributed. It was reported early from Germany (35), Austria (56), Denmark (115), Belgium (88), Holland (121), and Italy. Fraser (45), in 1913, found the "stripe disease of barley" severely affecting oats in Quebec. Anderson (1, p. 105) reported *H. avenae* from Alaska. According to records of the Plant Disease Survey the *Helminthosporium* leaf spot of oats appears to have been observed in New York, Pennsylvania, Indiana, Wisconsin, Louisiana, Iowa, Minnesota, Nebraska, Montana, Idaho, and Washington. Undoubtedly, it occurs at least in all the northern States to a greater or less extent; the writer, for example, has found it quite abundant in Connecticut and Maine during the season of 1921, apparently wherever the host was cultivated. Yoshino (161) reported *H. avenae* as occurring in Japan, and Butler (19) records leaf spot as being very common in India, especially on young plants.

Ravn's investigations have shown that, in general development, the disease follows the same course as netblotch of barley. The infection of the seedling during the germination period results in the production of primary lesions on the first leaf; from the primary lesions the fungus spreads to the foliage, is disseminated later by successive generations of spores, and finally the maturing fruit is infected or contaminated to propagate the trouble the next season. The local symptoms of infection, on the other hand, however, are quite different. Instead of numerous spots exhibiting an irregular reticulate pattern of short accentuated lines or streaks, the affected oat leaves rarely show more than 3 or 4 brown spots. (Pl. 4, A.) It is true that the colored figure in Butler's manual shows a large number of lesions on a single leaf. Such a heavily spotted condition certainly has never been observed by the writer, and, perhaps, may be associated with a more severe manifestation of the disease in India.

The spots may be broad and irregular, or long and narrow; in any case, the margins are frequently poorly defined, merging gradually into yellow, reddish, or orange shades which eventually spread over a large portion of the leaf blade. The gradual extension of diffused yellow and reddish discoloration appears to be coincident with the progress of the fungus in the affected tissue. In the absence, usually, of extensive brown conspicuously abnormal spots, the morbid decline of the leaf, due to the development of the parasite, simulates withering occasioned by weather conditions or maturation much more closely than in any of the three *Helminthosporium*

rium diseases of barley. As a result, the damage to the oat crop due to leafspot, although undoubtedly not of major importance, is much more likely to be considerably underestimated than that caused by the majority of related diseases of other cereals. Thus, during the latter part of June, 1920, the oats observed by the writer growing in isolated patches in the eastern half of Long Island bore only meager evidence of being affected by leafspot. Nevertheless, four weeks later, microscopical examination revealed the fructifications and spores of *H. avenae* on more than half of the mature plants, sometimes in considerable quantity.

After the death of the affected leaf, the red and orange pigmentation very largely disappears, being replaced by a pale-yellow or gray color, and even the brown discoloration usually loses some of its intensity. At this point the conidiophores of the fungus make their appearance. As Ravn has pointed out, these structures (Pl. 4, Da-g) are very similar to those of *Helminthosporium teres* in all respects—color, dimensions, septation, and mode of emerging from the epidermis—although exhibiting sometimes a slightly greater tendency toward occasional branching (Pl. 4, Dc, De). The spores also resemble those of *H. teres* very closely, having approximately the same range in size and number of septa; and showing the same irregularly cylindrical shape, hemispherical ends, subhyaline to light fuliginous coloration, and mode of germination by the production from intermediate as well as end segments, of laterally or obliquely oriented germ tubes.

The writer was unable to confirm Ravn's finding that the conidia of *H. avenae* slightly exceed in length those of *H. teres*. In general, the dimensions of the two species appeared quite equal, and whatever slight inequality in length and width was observable was rather in favor of *H. teres*. It must be mentioned, however, that the fresh material used by the writer in the study of the two forms was not developed under comparable conditions, that of *H. teres* having been collected late in October during a damp, cool period seemingly especially favorable for sporulation; while the material of *H. avenae*, collected late in July, had manifestly developed at midsummer temperature. Perhaps the two fungi might better be regarded as biological forms of the same species, in the same sense in which such forms are recognized in *Puccinia graminis* and in the mildews. Whatever slight morphological differences, demonstrable in the conidial stage by biometrical methods, may exist between the two fungi, they could scarcely be of a larger magnitude proportionally than the differences between various biological forms of, for example, the stem rust fungus. A study of the ascigerous form of *H. avenae*, which, as has been suggested, the writer believes he has collected, although in very poor condition, ought to cast some light on its taxonomic relationship. For the present, it is advisable to follow Eidam and Ravn in regarding the parasite on oats as distinct from *H. teres*. Certainly the idea, proposed by Briosi and Cavara, of placing it as a morphological "forma" of *H. teres* is not tenable.

It may not be amiss to call attention to an error apparently caused by a partial misinterpretation of Ravn's paper, and more particularly of his widely copied but, perhaps, insufficiently representative figures of the conidia and conidiophores of *Helminthosporium gramineum*, *H. teres*, and *H. avenae*. In some general treatises, the impression is conveyed that the possible morphological difference between *H. avenae* and *H. teres* is approximately of the same order as the difference between *H.*

teres and *H. gramineum*. The differences between the latter two species are, in reality, altogether much larger. For example, while the largest spores of the fungi causing netblotch and leafspot of oats, seen by the writer, have measured between 170 and 175 μ , the longest spores of the stripe fungus have not been found to exceed 105 μ in length. The number of septa in the spore of the stripe fungus very rarely exceed 7, while in the other two species 8 and 9 cross walls may be found quite readily and even 10 or 11 occur in a small proportion of instances. Production of secondary spores, common in *H. gramineum*, is rare in *H. avenae* or *H. teres*. In short, *H. gramineum* is not closer to either *H. avenae* or *H. teres* than a moderate number of other congeneric species.

As leafspot usually is not a serious disease, and in the United States not very conspicuous in its manifestations, little attention has been paid to its control. Atanasoff and Johnson (3) have found the hot-air seed treatment effective in reducing the disease. The value of methods of control based on seed disinfection would appear to be contingent, at least to some extent, on the absence of a possible sclerotial or ascigerous stage, or the relative ineffectiveness of such a stage as a factor in the propagation of the fungus.

HELMINTHOSPORIUM TRITICI-REPENTIS DIEDICKE—PYRENOPHORA TRITICI-REPENTIS (DIED.)

Helminthosporium gramineum Rab. f. sp. *tritici-repentis* Diedicke olim 1902, in Centbl.

Bakt.[etc.] Abt. 2, Bd. 9, p. 317-329.

Pleospora tritici-repentis Died. 1903, in Centbl. Bakt.[etc.] Abt. 2, Bd. 11, p. 52-59.

Pleospora trichostoma (Fr.) Wint. f. sp. *tritici-repentis* Noack 1905, in Ztschrif Pflanzenkr., v. 15, p. 193-205.

Helminthosporium tritici-repentis as recognized by Diedicke (28), first, as a biological or form species of *H. gramineum* Rab. and later (29), as an independent species, distinct from *H. teres*, *H. bromi*, *H. gramineum*, and *H. avenae*. It appears to be widely distributed, its perithecial form occurring very abundantly in our northern latitudes on the dead culms of quack grass, *Agropyron repens*. The visible effects resulting from the attack of the fungus on growing plants of quack grass are usually not at all conspicuous, any dark discoloration like that induced by the parasitism of *H. sativum* on the same host, being absent. The affected leaf gradually loses its green color and withers from the tip downward, changing at the same time first to a pale yellowish, and later to a gray color. As the foliage of the host developed after the earlier stages of growth is relatively rigid, the mechanical distortion associated with the death of any except the lower and more delicate leaves (Pl. 5, A) usually is not very noticeable.

According to Diedicke, the disease resembles barley stripe in affecting the whole plant, usually suppressing the development of the inflorescence, or preventing its emergence from the enveloping sheath. Although this opinion is not without some plausibility, anatomical evidence regarding the distribution of the fungus in the tissues of the plant would appear to be necessary before the disease can be regarded as systemic in the same sense as stripe. Some differences in the manifestations of the two diseases certainly are apparent. The symptoms do not become evident simultaneously in all the leaves of individual quack-grass plants, but are manifested first in the basal leaves, and later may appear in successively higher foliar organs. Nor do diseased leaves of *Agropyron repens* exhibit anything similar to the longitudinal variegation char-

acteristic of the foliage of barley infected with *H. gramineum*. The conidial fructifications of *H. tritici-repentis*, moreover, make their appearance scattered sparsely here and there over the surface of the dead leaves, not crowded on the affected parts like those of the stripe fungus. It is evident, therefore, that at least in some respects, the development of *H. tritici-repentis* on the host presents closer analogies to types like *H. dematioideum* and *H. siccans* than to *H. gramineum*.

The dark olivaceous usually 3 to 6 septate sporophores of *Helminthosporium tritici-repentis* (Pl. 5, Da-f) emerge from the stomata, or, more frequently, from between epidermal cells. Above the somewhat swollen basal segment, they vary in width from 7 to 9 μ , being thus perceptibly inferior in this dimension to the homologous structures of *H. bromi*. In length they vary from 80 to 220 μ . The conidia (Pl. 5, Ba-m) are typically subhyaline, straight-cylindrical, from 1 to 9 times septate, from 12 to 21 μ in diameter, and 45 to 175 μ in length. As in *H. teres*, the septa usually are associated with slight but perceptible constrictions in the contour of the thin peripheral spore wall.

The most distinctive peculiarity in the spores of this species is found in the shape of the basal segment, the proximal portion of which usually tapers abruptly in the manner of a cone to be rounded off or flattened near the hilum. In profile the basal segment thus is remotely suggestive of the horizontal aspects of the head of a snake, while the distal end usually is rounded off in a hemispherical form (Pl. 5, Ba, e, j, k). It may not be superfluous to add that departures from this type are not infrequent. The 2 or 3 terminal segments may taper appreciably toward the distal end (Pl. 5, Bb, c, d, m) or the width of the different segments may vary considerably (Pl. 5, Bg, m) or the axis of the spore may be somewhat curved (Pl. 5, Bc). Germination begins within an hour after the spores are mounted in water. Each segment is capable of producing a germ tube, the larger spores (Pl. 5, C) thus producing from 6 to 8 or more germ tubes, although usually one or several cells may remain seemingly inert.

The ascigerous stage of this species of *Helminthosporium*, as mentioned before, occurs in great abundance on the dead culms of *Agropyron repens* and to a small extent also on the leaves, particularly on the sheaths, (Pl. 6, Ba-b.) Although the black perithecia are readily discernible in autumn, their subsequent maturation appears to be rather slow. In the vicinity of Madison, Wis., mature perithecia have been collected from early in April until well toward the end of May. When developing in the looser tissue of the leaf, especially after some decay has taken place, the imbedded portion usually is distinctly subspherical, from 0.2 to 0.35 mm. in diameter, and tapers into a short, well-defined beak as shown in Plate 6, A. However, when developing in the harder tissue of the culm, the perithecium usually is much more irregular in shape and the beak less readily recognizable as a special modification. In any case, the beak usually bears near the ostiole a number of dark-brown sterile setae which may be straight or flexuous, continuous or several times septate, occasionally branched, and varying in number from several to over a score. As Diedicke pointed out, under certain conditions a large number of conidiophores and conidia may be produced from the upper side of the perithecium, the further development of the ascospores, if not complete, then often being checked altogether. This tendency toward conidial production usually is well expressed in the case of those perithecia found on the upright culms; on the other hand, when the host material is loosely

covered with leaves or other rubbish, it often is entirely suppressed. There can be little doubt that the environmental factors of temperature and moisture are of primary importance in this connection.

Diedicke recognized this perithecial form as a new species, *Pleospora tritici-repentis*, which he distinguished from *Pleospora bromi* largely because of the smaller dimensions of its perithecia, asci, and spores, and because of the failure of reciprocal inoculations to produce infection. Noack (95) did not accept the taxonomic dispositions made by Diedicke but regarded the perithecia on *Bromus asper* and *B. inermis* as not different morphologically from those on *Agropyron repens*, or from the perithecia on barley presumably associated with the stripe fungi. He consequently reduced the parasites on quack grass and on the two species of *Bromus* to biological forms of *Pleospora trichostoma* (Fr.) Wint., which, like Diedicke earlier, he identified as the ascigerous stage of *Helminthosporium gramineum*. The fungi under consideration were accorded a dubious status in the general works published subsequently, like those of Lindau (83) and of Stevens (139).

A comparison of material collected by the writer near Madison, Wis., in the spring of 1920, showed the general correctness of Diedicke's statements regarding the relative sizes of the perithecia and asci of *Pyrenophora tritici-repentis* and *Pyrenophora bromi*. As the diameter of the perithecia of the parasite on quack grass appears to vary from 0.20 to 0.35 mm. the inequality in size between the fruiting bodies of the two forms certainly is not pronounced. In *Pyrenophora tritici-repentis*, especially when developing on decaying leaves, the ostiolar beak usually is narrower, less massive, and consequently a somewhat more distinctive structure than in *Pyrenophora bromi*. The asci (Pl. 6, C) of *Pyrenophora tritici-repentis*, measuring usually from 170 to 215 by 43 to 50 μ , are similarly somewhat smaller than those of *Pyrenophora bromi*.

It may be mentioned that measurements of asci in fully matured living material are dependent to a considerable extent on the amount of moisture present, as these structures under dry conditions usually are found contracted tightly over the spores, while under moist conditions they swell until the space inside of the fruiting bodies is completely occupied. In any case, on being crushed out of the perithecia, they undergo very considerable swelling preliminary to the rupture of the ascus wall and the discharge of the eight ascospores. The latter, of a brownish color and measuring usually 18 to 28 by 45 to 70 μ , are uniformly three times transversely septate, often with one or both of the middle segments further divided by a longitudinal wall. The septa are associated with constrictions in the peripheral wall of the spore, which frequently is found enveloped in a gelatinous covering. (Pl. 6, Da, Db, Eb.)

Germination takes place promptly by the production of a germ tube from several or all segments. (Pl. 6, Da-b.) On media ordinarily employed in laboratories, like potato agar, a fairly compact mass of white aerial mycelium is produced, corresponding in all respects to the growth obtained by the use of conidia. Anastomosis with the resultant production of groups of inflated lobulate segments is abundant in the submerged mycelium, but large sclerotia or imperfect perithecia of a size readily visible to the naked eye, like those produced by *Helminthosporium bromi*, have never been observed in pure cultures of *H. tritici-repentis*.

The parasite on quack grass consequently is to be regarded not as a biological race of *Helminthosporium gramineum* but as an independent morphological species. While the ascigerous stage bears a strong resemblance to *Pyrenophora bromi*, as well as to a number of other congeneric forms found on graminaceous hosts, it is readily distinguishable at least from *Pyrenophora teres*. On the other hand the conidia which, like those of *H. teres* and *H. avenae*, show a range in length intermediate between the range of this dimension in *H. gramineum* and *H. bromi*, can not possibly be mistaken for the conidia of any of these species because of the characteristic contour of the basal segment.

HELMINTHOSPORIUM CATENARIUM, N. SP.

During the latter part of September, 1920, the writer kept under observation a stand of wood reed grass (*Cinna arundinacea* L.) near Brooklyn, N. Y., on the northern coast of Long Island. Although the season had not been a dry one, the grass, nevertheless, showed symptoms suggesting drought injury. The distal portions of most of the leaves had withered completely (Pl. 7, A) and, in some instances, the injury involved more than half of the blade. Less frequently, the foliar organs exhibited longitudinally elongated dry areas or spots within healthy green parts. No indication of any discoloration, either at the margins of the lesions or in the dried portions, was ever observed. As the disease presented many of the characteristics of white blast, quite common on sweet corn in the trucking district in the vicinity of New York City, some of the affected leaves were collected and examined in the laboratory. The microscope revealed an abundance of *Helminthosporium* fructifications on the affected leaves, particularly on those parts that had apparently been dead for some time.

As in other species of *Helminthosporium* occurring on graminaceous hosts possessing foliage with a relatively firm epidermis, the sporophores of the fungus on *Cinna arundinacea* are found to emerge very largely from the stomata. (Pl. 7, Ea-c.) Beyond being conspicuously thin walled, and rather unusually strongly geniculate at the points of attachment of the conidia, they exhibit no especially distinctive features.

The spores, which are colorless to light yellowish, however, show such a large measure of variability in shape and apparent development, that the fungus is easily recognized as one of the more aberrant and peculiar members of the genus. A considerable proportion of the spores are of moderate length, straight and tapering (Pl. 7, Ba, d, j), and perhaps could not be readily distinguished from those of *Helminthosporium dictyoides*, although the latter eventually become more deeply tinged with yellow. Usually only the shorter spores appear both straight and uniformly tapering. Generally, those in excess of 80 μ are very perceptibly curved or bent in an irregular manner, and, in addition, the diameter of the different segments varies to a very considerable extent. The longer spores often show a decided median constriction. (Pl. 7, Bb, e.)

Frequently, a secondary spore (Pl. 7, Bi) is found attached at the tip of a primary one (Pl. 7, Bh), being characterized by smaller dimensions and, if immature, by the absence of septa. That the formation of secondary spores is not an unusual occurrence is indicated by the presence of a dark conspicuous scar at the tip of many spores, quite similar to the basal hilum and often associated with a peculiar prolongation of the distal

portion of the terminal segment, giving the spore a general contour crudely suggesting that of a rifle cartridge with contracted tip. (Pl. 7, Bc, f.) It thus will be seen that while the smaller spores resemble those of *H. dictyoides*, and in a measure those of *H. gramineum*, the larger ones are of a length not attained by the spores of any of these species, approximating most closely that of the spores of *H. tritici-repentis*. (Pl. 7, Bb.) The spores of the parasites on *C. arundinacea* and on *Agropyron repens*, moreover, show additional similarity in respect to coloration and general shape, both being subhyaline, as well as more or less irregularly curved and of variable width. The spores of *H. tritici-repentis*, however, have not been observed to show an apical hilum or apical attenuated prolongation; nor has the fungus on wood reed grass exhibited the peculiar modification of the basal segment characteristic of *H. tritici-repentis*.

In pure culture, on potato agar or corn-meal agar, the parasite on *Cinna arundinacea* grows readily, producing a white mycelium, both in the form of erect compact tufts 2 to 5 mm. in height and usually developed at the point of inoculation, or of minute superficial flecks scattered sparsely over the surface. In any case, the hyphae usually remain sterile for a number of days before the spores begin to develop terminally. After this stage is reached the sporophore, instead of developing by alternately elongating and proliferating spores, as is usual in the genus, usually develops in the manner somewhat similar to that characteristic of members of the genus *Alternaria*. The tip of the primary spore (Pl. 7, Dba) may bud to produce a sessile secondary spore (Pl. 7, Dbc) and this may produce a tertiary spore in the same way. Not infrequently, however, the tip of the spore (Pl. 7, Dbc) grows out into attenuated segments (Pl. 7, Dae) having approximately the diameter of the primary sporophore and obviously of a similar nature. These segments usually never attain any great length before proliferating a terminal spore (Pl. 7, Dbf); and as growth continues, fructifications result, consisting of superimposed spores and sporophoric segments, that may exceed 0.5 mm. in height. As the basal and distal segments of the spores not infrequently produce short sporophoric branches directed at oblique angles to the main axis (Pl. 7, Dab, ac, ad, af) and bearing one or more spores (Pl. 7, Dbd, be, bg), the fructifications usually are further complicated by the presence of a number of lateral sporiferous processes. It may be mentioned in this connection that the distinction between spore segment and sporophoric segment is not always well defined, but often may be partly obliterated, the fructification then being represented by a process of segments varying from 6 to 18 μ in thickness, and disarticulating at certain constricted septa marked by the presence of hila.

As far as the writer is aware, the parasite on *Cinna arundinacea* has not been described in literature. Atkinson (4), it is true, reported *Helminthosporium turcicum* as occurring on the leaves of this host in Alabama. While it is not impossible that Atkinson may have been dealing with the same fungus that causes injury to maize, there would seem to be much more probability in the assumption that this writer was confronted with the fungus under consideration, although with the exception of the pathological effects occasioned by them, the similarity between the two parasites can hardly be said to be a close one. Because of its tendency toward the formation of chains of spores in nature as well as in pure culture, the fungus on wood reed grass is named *H. catenarium*.

DIAGNOSIS

Helminthosporium catenarium, n. sp.

Attacking the foliage of *Cinna arundinacea*, L., where it causes the premature death of large areas of tissue, the tip and margin being usually most commonly affected.

Sporophores brown or olivaceous; emerging usually from the stomata, singly or in groups of 2; measuring 5 to 8 by 60 to 200 μ ; producing the first spore at a distance of 25 to 60 μ from base, and successive spores at intervals of 15 to 30 μ , the point of attachment marked by scars at the apices of pronounced geniculations.

Spores 1 to 10-septate, the septa sometimes associated with slight constrictions or irregularities in the contour of the thin peripheral wall; subhyaline to light yellowish, 14 to 18 by 30 to 200 μ , measured at their maximum diameter; the shorter ones usually straight, widest at the basal or second segment, tapering uniformly to approximately half the maximum diameter at tip; the longer ones often perceptibly crooked, irregular in diameter, frequently showing both a basal hilum and an apical scar, the apical scar marking the attachment of a secondary spore, and usually associated with a peculiar modification of the distal portion of the terminal segment, consisting in the prolongation of the latter at a uniform diameter representing the minimum width of the spore. Secondary spores or spores of a higher order of the same diameter, but usually considerably shorter, less frequently septate, or continuous. Both types germinating normally by production of 1 or 2 lateral germ tubes from basal segment, and a single lateral or oblique tube from terminal segment. Contour of basal end hemi-ellipsoidal, of distal end hemispherical; hilum and apical scar not protruding.

In pure culture on potato glucose agar, aerial mycelium white or dirty yellowish, present as dense erect tufts 2 to 5 mm. high at point of inoculation and as small flecks scattered sparsely over the surface; in either case consisting of sterile hyphae and an increasing number of conidial fructifications; the latter arising on the expanded terminations of hyphae not otherwise much modified, and consisting of a series of successively proliferated spores that may be either sessile or separated by intercalary, narrower sporophoric segments. The fructification frequently branching, as a result of the proliferation of lateral or oblique sporophoric processes from the basal or terminal segment of individual spores; and, less typically, sometimes consisting of miscellaneous processes of segments varying from 6 to 18 μ in thickness, and disarticulating at constricted septa marked by the presence of scars or hyla.

HABITAT.—Parasitic on *Cinna arundinacea* L. collected at Douglaston, N. Y., September, 1920.⁷

HELMINTHOSPORIUM BROMI DIEDICKE—PYRENOPHORA BROMI (DIED.)

Helminthosporium gramineum Rab. f. *bromi* Diedicke *olim* 1902, in Centbl. Bakt. [etc.] Abt. 2, Bd. 9, p. 317-329.

Pleospora bromi Died 1903, in Centbl. Bakt. [etc.] Abt. 2, Bd. 11, p. 52-59.

Pleospora trichostoma (Fr.) Wint. f. sp. *bromi* Noack 1905, in Ztschr. Pflanzenkr. v. 15, p. 193-205.

The occurrence in Germany of a species of *Helminthosporium* parasitic on *Bromus asper* Murr. was recorded by Diedicke (28) in 1902. Krieger⁸ later collected and distributed the same fungus on the leaves of *Bromus inermis* Leyss. It undoubtedly is on the latter host that the parasite is found most commonly in the United States, observations made by the writer in the vicinity of Madison, Wis., during the spring of 1920, pointing toward its general prevalence on this widely distributed host. Diedicke described the disease symptoms occasioned by the fungus so adequately that little can be added except in the way of corroboration.

Helminthosporium bromi is probably one of the earliest of all parasites affecting the grasses of our northern latitudes, to appear in spring, as

⁷ Type specimens of all species described in this paper as new have been deposited in the following herbaria: Office of Pathological Collections, Bureau of Plant Industry, United States Department of Agriculture, Washington, D. C.; Cryptogamic Herbarium, Harvard University, Cambridge, Mass.; herbarium, New York Botanical Garden, New York City; herbarium, Department of Botany, University of Wisconsin, Madison, Wis.

⁸ KRIEGER, W. FUNGI SAXONICI. No. 1941 *Helminthosporium bromi* Died. [exsiccatil]. 1903, 1905.

the first leaves that arise from the overwintering rootstock of *B. inermis* have barely completed their development before they begin to show the scattered spotting characteristic of its attack. (Pl. 8, Ab-c.) Each spot originates as a minute dark brown or black speck about which the chlorophyll gradually appears to break down, producing a yellowish or nearly colorless halo. Both the central spot and the surrounding zone usually increase considerably in extent, especially in a longitudinal direction, until the former may occupy an area 2 mm. in width and 6 mm. in length. On badly infected leaves the yellowed zones frequently run together as shown in Plate 8, B. Even more moderate infection, however, leads to a premature withering of the leaf (Pl. 8, Ad), beginning at the tip and proceeding downward, until the whole structure may be involved; for although the sheath is much less frequently spotted, it is not entirely immune, especially while the plant is still very young. After the leaf has become withered the sporophores make their appearance, first on or near the darkened areas, but later quite generally over the entire leaf. Emerging singly or in clusters of two (Pl. 8, Ea-c), most frequently between epidermal cells without much reference to the stomata, they measure 7 to 10 μ in diameter and usually 100 to 150 μ in length, although sometimes attaining a maximum length of 250 μ . From 2 to 6 septa usually are present. The geniculations associated with the production of successive spores are not generally very pronounced.

In the account given by Diedicke (28) the spores are described as 4 to 6 septate, 108 to 150 μ long, 13 to 20 μ in diameter, and exactly similar to those described and figured by Ravn (115), the supposed similarity presumably applying to *Helminthosporium teres*. Such a statement of the morphological features of the spores of the two species, it is quite impossible to substantiate by a comparison of American material, which reveals instead very decisive differences. The contrast in length between the two species is especially conspicuous, the spores of *H. bromi* measuring from 45 to 265 μ in length, examples exceeding 200 μ in length being of not uncommon occurrence. (Pl. 8 Ca-f.) Some difference in diameter also is perceptible, although this is much less pronounced, the spores of *H. bromi* varying commonly from 14 to 26 μ . As the number of septa in the spores of both species varies from 1 to 10, it is apparent that the individual segments in the spores of *H. bromi* exceed in length those of *H. teres* in approximately the same measure as do the spores. In *H. teres*, moreover, the spore often is conspicuously constricted at the septa, a modification absent or less strongly pronounced in those of *H. bromi* (Pl. 8, De). Related to these features are the specific peculiarities in the contour of the basal cell that have been mentioned in another connection, this contour being approximately hemi-ellipsoidal in *H. bromi* and hemispherical in *H. teres*.

In the conidia of *Helminthosporium bromi*, the hilum is represented by a scar, not especially conspicuous, and included entirely within the contour of the peripheral wall. As the peripheral wall consists of a relatively thin membrane, it is not surprising that the conidia show little resistance to unfavorable conditions. Even in actively sporulating material, microscopic examination reveals one of several dead segments in most of the spores, and when material is kept in the laboratory the proportion of dead segments or dead spores is very greatly augmented in the course of a week. When mounted in water, viable spores germinate

very promptly, producing lateral or oblique germ tubes indiscriminately from middle and end cells, the number of tubes originating from any particular segment not usually exceeding two. Anastomoses of newly proliferated germ tubes are not infrequent, the germination of spores lying in juxtaposition, thus often yielding scalariform figures united by several hyphal connections. (Pl. 8, Db-c.) As has been pointed out previously, when the fungus is cultivated on potato agar media, anastomosis of hyphae is associated often with the production, below the surface of the substratum, of numerous groups of inflated segments. Of the latter, a small proportion develop into subspherical sclerotia, usually from 0.2 to 0.5 mm. in diameter, the presence of which in agar cultures (Pl. 9, C) is characteristic of the fungus, and which, judging from their size and structure, doubtless represent immature perithecia.

In Germany, Diedicke (28) noted the appearance on *Bromus asper* of the sclerotia or young perithecia as early as July 26. This date corresponds quite closely with their appearance in southern Wisconsin. When fully matured, they consist of a subglobose portion imbedded within the somewhat distended leaf tissue, usually from 0.3 to 0.4 mm. in diameter and tapering into an irregular ostiolar beak protruding approximately 0.1 mm. above the broken epidermis. A variable number of septate, tapering, sterile bristles usually are to be found near the tip of the ostiolar modification; and although it is not improbable that in some seasons conidiophores may be produced abundantly from the perithecium as in *Pyrenophora tritici-repentis* and *P. teres*, only a sparse production was observed during the season of 1920.

The development of the asci appears to be delayed until spring, beginning evidently with the warmer weather usually experienced in our northern latitudes late in February or early in March, and proceeds slowly, until toward the middle of April they readily discharge their spores when mounted in water. In all morphological details the asci closely resemble those of *Pyrenophora tritici-repentis*, although they usually seem to be somewhat larger. The difference, which is not pronounced, becomes, perhaps, most evident during the process incident to spore discharge, as the asci of the parasite on brome grass appear to undergo perceptibly greater distention before the outer membrane is burst than the asci of the congeneric parasite on quack grass. Plate 9, D, representing an ascus partly distended, measuring 300 μ in length and 65 μ in diameter, shows the 8 spores in distichous arrangement immersed in granular epiplasm, the thickened ringlike modification at the apex, and the short well-defined stipe common to both species.

The ascospores, light brown in color and measuring 20 to 30 μ by 45 to 72 μ , are uniformly divided by 3 transverse septa. Longitudinal septa may be absent, or one or both of the middle segments may be further divided by a longitudinal wall. Germination takes place by the production of a germ tube from several or all of the segments. Cultures of the fungus derived from ascospores differ in no particular from those derived from conidia.

Because of the distinctive and extraordinarily large conidia characteristic of the parasite and its production of sclerotia on various kinds of agar media, the writer agrees with Diedicke in regarding the fungus as an independent species. In this connection it may be mentioned that Diedicke (28) first reported it as a biological species of the stripe fungus, a disposition which Noack (95), who recognized *Pleospora trichostoma* as the ascigerous stage of *Helminthosporium gramineum*, later sought to

maintain. The ascigerous stage, it must be admitted, is morphologically not readily distinguished from related congeneric forms. The fungus, in any case, would seem to be referable to *Pyrenophora* rather than to *Pleospora*, if, indeed, the former is to be maintained as a separate genus.

HELMINTHOSPORIUM GIGANTEUM H. & W.

Heald and Wolf, in 1911, described (54) and later also (55) figured a species of *Helminthosporium* on Bermuda grass (*Cynodon dactylon* L. = *Capriola dactylon* [L.] Kuntze) collected at Falfurrias, Tex., where it was found associated with a disease—

characterized by the presence of numerous yellowish or pale straw-colored spots, 0.5 to 1 mm. wide, by 1 to 4 mm. long, longitudinally elongated, and with a narrow brown border. The spots are generally absent from the leaf sheath, and when numerous they may become confluent on the lamina and thus cause somewhat extended dead areas.

The fungus, which was named quite appropriately *Helminthosporium giganteum*, was further characterized as follows:

The conidiophores are dark brown, many-septate, 9 to 12 by 200 to 400 μ , with a slightly bulbous base; the spores are elongated, cylindrical with slightly tapering ends, 5-septate, pale brown, densely granular contents, 15 to 21 by 300 to 315 μ .

The writer collected the same parasite on Bermuda grass at various times during the months of February, March, and April, 1921, near Fort Myers and Wauchula, Fla. During February and March, especially in the vicinity of Fort Myers, the fungus occurred in considerable abundance, old spots bearing sporophores being found scattered generally over the foliage of the host. Fresh lesions providing material suitable for study were almost entirely absent at that time, a circumstance attributable apparently to the condition of the host; for the latter, although green, was not actively growing and the foliage, moreover, was everywhere severely affected by *Puccinia cynodontis* Desm. and *Helminthosporium cynodonti* Marignoni. About the middle of April, several weeks after the resumption of active vegetative growth, the more recently unfolded leaves of *Cynodon dactylon* began to show newly developed lesions associated with conidiophores and conidia in a living state. At nearly the same time altogether similar foliar spots made their appearance on goose grass (*Eleusine indica* [L.] Gaertn.). Microscopical examination revealed no morphological difference in the fructifications present on the two graminaceous species.

On July 13, 1922, a stand of Bermuda grass near Bladensburg, Md., was observed to be attacked by the fungus with unusual severity. Many of the leaves had been killed altogether, and of those that remained functional nearly all bore scores of discrete or confluent spots, or extensive whitened areas which often involved altogether from one-fourth to one-third of the tissues of the individual foliar organs. Plants of *Agropyron repens* distributed in the Bermuda grass likewise bore a sprinkling of the foliar spots characteristic of the fungus, although in smaller quantity. On microscopical examination the similarity of the abundant fructifications on both Bermuda and quack grass collected in Maryland to those of the Florida parasite was readily apparent. *Agropyron repens* and *Eleusine indica*, therefore, represent additional hosts of the interesting fungus described by Heald and Wolf (55).

The foliar lesions bear a good deal of resemblance to those produced, for example, by *Helminthosporium leersii*. They first become visible as minute brown spots in green and otherwise healthy tissue. (Pl. 10, A.)

Soon these spots increase in length and width, the center in the meantime fading to almost white or light straw color. In this way the appearance described by Heald and Wolf (54) is brought about. (Pl. 10, A, B.) At this stage the lesions are of the simple "eye-spot" type. Under certain conditions, apparently when the parasite is thriving most luxuriantly, the diseased areas become greatly enlarged, sometimes occupying the entire width of the leaf blade of Bermuda grass for a distance of one centimeter or more. When such development occurs the dead areas usually show a number of roughly concentric brown markings, evidently corresponding to successive positions of the margin, and giving the areas a distinctively zonate aspect. With the multiplication of the smaller lesions and the extension of the larger ones, a large proportion of the leaves are killed outright long before the end of the season. Previous to this the sporophores of the fungus make their appearance singly or in pairs over the larger dead regions always at some distance from the margin of the surrounding green tissue. The conidiophores are distributed rather sparsely in comparison with the crowded spacing of the homologous structures of many congeneric forms, although not actually few in number.

The sporophores of *Helminthosporium giganteum* (Pl. 10, Ea, b) are the largest of those of any species studied by the writer, the measurements of the Florida material agreeing well with those given in the original specific description. The septa are mostly spaced with considerable regularity, at intervals varying commonly from 25 to 40 μ . Usually the scar marking the point of attachment of the first spore is found 140 to 250 μ from the base, and successive scars associated with geniculations, usually not pronounced, occur at intervals of approximately 40 μ .

The conidia (Pl. 10 Ca-d), which are produced in relatively small numbers, are easily the most massive of those of any species of *Helminthosporium* hitherto described, and are probably among the very largest produced by any group of fungi. Individual spores were found exceeding considerably in length even the generous measurements given by Heald and Wolf, the one figured in Plate 10, Cc, for example, measuring 385 μ in length and 21 μ in diameter. The volume of a spore of such dimensions is several hundred times greater than the volume of spores of molds that are not by any means regarded as minute fungi, while on comparison with some of the smallest types, like species of *Actinomyces*, ratios approximately 1 to 300,000 may be obtained. The writer has found it possible, after staining with eosin, to make out with the naked eye, spores approaching the dimensions given.

Besides being the largest, the conidia of *Helminthosporium giganteum* also, perhaps, are the shortest-lived conidia of any species of *Helminthosporium* discussed in this paper. If the spores from a group of fructifications which are still actively proliferating new conidia are mounted in water, a large proportion will be found to contain one or more dead segments. After spore production in a group of fructifications ceases all of the conidia will contain dead segments, and in a relatively brief period, probably not exceeding two weeks, only a small number will still show living segments. To this lack of longevity, together with the production of spores in small numbers, the comparatively restricted occurrence of the parasite probably may be attributed.

The spores of *Helminthosporium giganteum*, while alive, are altogether hyaline, colorless, and filled with homogeneous protoplasm. The characterization of these structures by Heald and Wolf in the words, "pale

brown, densely granular contents," would seem to indicate that these authors very probably drew their description from dead material. The peripheral wall is thin as in other species with subhyaline spores, and sometimes shows a perceptible constriction at the septa, the latter varying in number usually from 2 to 6 and delimiting segments ranging up to 80μ in length, and from 16 to 25μ in diameter. The ends of the spores are rounded off abruptly, showing usually a hemispherical or hemi-ellipsoidal contour. The basal end is modified by the presence of a minute dark apical projection at the apex of a small, faintly delimited, obtusely conical part, which, while the spore is still attached, fits into a depression in the center of the scar on the sporophore.

When the spores are placed in water they germinate very promptly, the germ tubes being proliferated sometimes singly and indiscriminately from end or middle segments (Pl. 10, Da, c); or more typically in groups of 3 or 4, usually from both basal and apical ends (Pl. 10, Db), or less commonly from one or more intermediate segments (Pl. 10, Dc). In any case the germ tubes are of unusual width, measuring 6 to 10μ in diameter, and grow with remarkable rapidity. Germination is associated with a change in the protoplasm from an apparently homogeneous to an abundantly vacuolated structure. It may not be superfluous to add that the spores filled with "densely granular contents" never germinate, and segments exhibiting such structure, always together with a swollen peripheral wall, similarly remain inert.⁹

HELMINTHOSPORIUM DICTYOIDES, N. SP.

During the latter part of June, 1920, the writer observed a disease on meadow fescue (*Festuca elatior*, L.) which seemed to be widely prevalent in the region about Washington, D. C., scarcely any stand of this grass being entirely free from it. As meadow fescue, although not one of our most highly prized forage plants, is nevertheless of not inconsiderable economic importance, and is besides very generally distributed, an effort was made to determine whether the disease occurs also in other sections. In the vicinity of New York City, from early in July to the end of August, it was found to be so common on *F. elatior* that the very characteristic and conspicuous lesions could, in the absence of an inflorescence, be quite safely used to distinguish this species of grass from grasses having somewhat similar foliage as, for example, *Bromus inermis* or *B. secalinus* L. Especially severely affected material was found near Port Washington on Long Island, where the dampness of the atmosphere incident to proximity to the sea, may have favored the progress of the malady. Other collections of diseased material were made at Stamford, Conn., August 2, 1920; Norwood, Mass., November 7, 1920; Lisbon Falls, Me., July 24, 1921; Annapolis, Md., October 15, 1921; and at numerous stations in Maryland, Virginia, and the District of Columbia near Washington, D. C., from early in August until late in October, 1921. Indeed, the writer has never failed to find the disease present to a greater or less extent on meadow fescue in all the localities in the New England and Middle Atlantic States that he has had occasion to visit.

The symptoms of the trouble, a brief account of which was published in 1922 (32), are very similar to those induced by *Helminthosporium*

⁹ Since this account was written the writer has had opportunity to study the mode of development of the fungus in greater detail and on a considerable number of additional hosts. The results have been partly indicated in a brief note (33), and will be published in more complete form in a later paper.

teres on barley. The newly affected green tissues show abundant brownish discoloration in irregular patterns, within which may be recognized a network of darker longitudinal and transverse linear streaks. (Pl. 11, A, C.) The minute reticulate design formed by the latter is, in well developed cases, more extensive and pronounced than in any specimens of barley affected with netblotch which the writer has ever seen. After a considerable portion of the leaf blade has been involved, it gradually withers and dies, the withering beginning at the tip and proceeding toward the base. (Pl. 11, A.) In 1920, in the neighborhood of New York City, such destruction of foliage continued throughout nearly the entire season, and caused an amount of damage that appeared to be far from trivial. Indeed, the writer is inclined to believe that the malady, which may conveniently be designated like that caused by *H. teres*, as netblotch, is the most serious parasitic trouble affecting meadow fescue in our northern latitudes.

On examining the withered portions of affected leaf blades, the cause of the disease is readily recognized as a species of *Helminthosporium*. To *H. teres*, however, the fungus shows no close similarity, the spores of the barley parasite having dimensions so much greater as to preclude any possibility of confusing the two forms. It shows a much greater degree of similarity to *H. gramineum*. The sporophores, as in the stripe fungus, are found in groups larger than in most congeneric species, the number in a group varying usually from 2 to 6 (Pl. 11, Ea-i). On the other hand, the basal enlargement characteristic of the sporophores of *H. gramineum* appears to be less pronounced in the homologous structures of the form on meadow fescue. The spores of the two fungi possess some characteristics in common, but exhibit quite distinctive specific differences as well. Thus they agree in color, in both species varying from subhyaline and colorless when newly proliferated, to distinctly yellowish when fully mature; and on measuring show an approximately equal range in length. However, the spores of *H. gramineum* are appreciably greater in diameter, and, while manifesting a tendency to taper toward the apex, do not depart very greatly from a straight-cylindrical type, whereas those of the parasite on *Festuca elatior* (Pl. 11, Ba-q) more frequently show a very pronounced diminution in diameter from the base to the tip, and in only relatively few instances approach an approximately cylindrical shape. In germinating the conidia of the fungus on meadow fescue do not generally produce germ tubes indiscriminately from both the end and the middle segments, but typically give rise to a lateral or oblique germ tube from one or both end segments (Pl. 11, Dc-k), although, less frequently, one or more germ tubes may be produced from a middle segment (Pl. 11, Da-b). It also may be mentioned that the spontaneous development from primary spores of short sporophores bearing secondary spores, characteristic of the barley stripe fungus, has not been observed in any material of the parasite on meadow fescue.

Another congeneric form with which the species of *Helminthosporium* on *Festuca elatior* might possibly be confused is the one described in this paper as *H. siccans* that occurs on *Lolium multiflorum* Lam. and *L. perenne* L. The latter on comparative examination, however, is readily distinguished by the appreciably larger dimensions, conspicuously darker coloration, and less tapering form characteristic of its conidia. These conidia when altogether mature possess, moreover, a considerably thicker peripheral wall, and, in germinating, typically produce two germ tubes from each of the end segments instead of one.

The literature contains, as far as the writer is aware, only two references to the occurrence of a species of *Helminthosporium* on *Festuca elatior*. The earliest is that of Diedicke (29), who recorded his discovery of a parasitic form that produced a local infection similar to the type of infection brought about by *H. bromi*, *H. teres*, and *H. avenae*. As this writer gave no further details concerning either the fungus or the disease, it is not possible to determine whether or not he was dealing with the parasite found widely distributed in the Middle Atlantic States. In a later reference by Pammel, King, and Bakke (104), is reported from Iowa the occurrence on *F. pratensis* (= *F. elatior* L.) of a species of *Helminthosporium* having spores similar to those of *H. sativum* and producing on its host a leaf spot closely resembling late blight of barley, although less severe. Material deposited by these authors in the Office of Pathological Collections, Bureau of Plant Industry, was examined by the writer. This examination revealed no reason why the fungus should not be referred to *H. sativum*. At any rate the Iowa fungus represents an entirely different organism from the one under consideration, which would appear to merit recognition as a new species. On account of the reticulate pattern characteristic of the foliar lesions the specific name *dictyoides* is suggested.

DIAGNOSIS

Helminthosporium dictyoides, n. sp.

Occurring on *Festuca elatior* L., on which it causes a moderately destructive disease of the foliage, with symptoms very similar to those of barley attacked by *Helminthosporium teres*; newly infected leaves showing irregular brownish areas marked with dark longitudinal and transverse streaks forming a delicate reticulate pattern. Affected leaves later withering, the withering beginning at the tip and progressing to the base of the blade.

Sporophores dark brown or olivaceous; emerging singly or in groups of 2 to 6 from stomata or between epidermal cells; measuring usually 6 to 8 μ in diameter and 70 to 150 μ in length; 3 to 6-septate, the septa generally occurring at intervals of 10 to 30 μ ; producing first spore usually at a distance of 50 to 100 μ from base; points of attachment of successive spores marked by moderately or strongly pronounced geniculations.

Conidia subhyaline and nearly colorless when newly proliferated, to yellow when fully matured; typically straight; maximum diameter usually at basal segment, 14 to 17 μ ; tapering uniformly and very perceptibly to apical segment, the latter in long spores frequently not exceeding 8 to 9 μ in diameter, in short ones usually of greater diameter; more rarely approximately cylindrical, or short ellipsoidal. Length 23 to 115 μ , usually 50 to 70 μ , 1 to 7 septate, typically 3 to 5 septate, the septa not associated with perceptible constrictions except occasionally, and then constrictions most frequently present only at the basal septum; length of segments 7 to 24 μ , typically 12 to 15 μ . Contour of basal end hemispherical, of apical end hemispherical or hemi-ellipsoidal; peripheral wall or exospore uniformly thin, and entirely including the hilum within its contour. Germinating typically by two germ tubes, one from each end segment and produced usually at right or oblique angle to axis of spore; rarely by one or more germ tubes from intermediate segments.

HABITAT.—Collected at Brooklyn and Port Washington, N. Y.; Stamford, Conn.; Norwood, Mass.; Lisbon Falls, Me.; Washington, D. C.; Kensington and Annapolis, Md.; and Falls Church, Va. Apparently found wherever the host occurs in the Middle Atlantic and New England States.

HELMINTHOSPORIUM SICCANIS, N. SP.

In the latter part of June, 1922, the writer observed that the Italian rye grass, *Lolium multiflorum* Lam, in the experimental farm at Arlington, Va., was very generally affected by a leaf spot disease. The trouble was found to occur on the foliage of both young and more nearly mature plants, being manifested by the appearance of minute, longitudinally

elongated, dark brown spots, measuring usually 0.1 to 0.3 mm. in width and 0.2 to 1.0 mm. in length, although sometimes apparently as a result of coalescence, attaining dimensions several times larger. Many of the more severely affected leaf blades bore more than a hundred of these localized discolorations and frequently more than a dozen could be distinguished on the sheath, mostly near its juncture with the blade. (Pl. 12, Ab.) Owing to the large number of spots often present on a single foliar organ, an appearance somewhat suggestive of netblotch is brought about, but as distinct transverse markings have not been observed, the reticulate pattern characteristic of leaves of barley and meadow fescue attacked by *Helminthosporium teres* and *H. dictyoides*, respectively, is not evident. It may be mentioned that the most distinctive sharply defined discolorations have usually been found on leaves of younger plants, while on the leaves of plants attacked after the heading stage the discoloration frequently appeared to be somewhat suppressed. In any case, however, the organs attacked soon turned yellow at the tip and withered, the withering eventually involving the sheaths as well as the blades.

Microscopical examination of leaves that had succumbed to the malady revealed an abundance of fructifications typical of the genus *Helminthosporium* emerging from the dead tissues. Although the symptoms of the disease caused by it are quite different from those of the stripe disease of barley, the fungus shows a strong resemblance to *H. gramineum*. The spores of the two species are nearly similar in shape, being usually straight and cylindrical or tapering toward the tip. The tendency toward tapering, to be sure, is more pronounced in the conidia of the parasite on Italian rye grass, which, moreover, when fully mature, are of a brown or brownish olivaceous color, appreciably darker than the yellow fuliginous hue characteristic of the spores of the stripe fungus. With this deeper coloration is associated a peripheral wall, decidedly thicker than the spore wall of subhyaline-spored types but inferior to that of species possessing olivaceous spores of the type of *H. sativum*. The conidia of the form on *Lolium multiflorum* are perceptibly longer than those of *H. gramineum*, and a proportional inequality obtains in regard to the spore segments of the two species.

Germination in water normally takes place in a manner very similar to the germination in *H. gramineum*; that is, by the production typically of one or two germ tubes from both apical and basal segments and a single tube from several or all intermediate segments, although occasionally two tubes may be proliferated from an intermediate segment. The production of sporophoric processes by conidia under natural conditions, while not uncommon, is not as frequent in the fungus on *L. multiflorum* as in the stripe fungus, and apparently usually comes to an end with the production of a single secondary conidium.

The form on Italian rye grass shows considerable resemblance to *Helminthosporium dictyoides* on meadow fescue, not only in general pathological habit but in morphological details as well. The conidia are largely of the same straight cylindrical or tapering form. They are noticeably larger, however, more frequently septate, and when fully mature darker and provided with a thicker peripheral wall. The mode of germination also shows some difference, the parasite on *Lolium multiflorum* being usually more profuse in the production of germ tubes. With the form described in this paper as *H. stenacrum* occurring on *Agrostis stolonifera* the fungus is not readily confused, being distinguished

by its smaller dimensions, thicker peripheral wall, and absence of attenuated apical prolongation.

Although not much importance can be attributed to the length of the conidiophores as a diagnostic characteristic, it may not be superfluous to mention that in the species under consideration these structures show a rather usually wide range in this dimension. This variability apparently is less due to differences in length of intervals between the points of insertion of successive spores than to pronounced differences in length of the sterile portion below the insertion of the first conidium. It is not difficult to suppose that changes in environmental conditions are responsible for either greater or lesser development of the sporophore preliminary to the proliferation of the first conidium, resulting in conditions like those illustrated in Plate 12, Fe-j, on the one hand, and like those figured in Plate 12, Fa-d, on the other.

A fungus quite indistinguishable from the form on Italian rye grass was found to occur abundantly in Virginia and Maryland on the closely related host, *Lolium perenne*. An examination of numerous specimens of diseased perennial rye grass collected near Annapolis in May, 1921, and in the vicinity of Washington, D. C., during the months of May and June, 1922, revealed no constant or significant morphological characteristics by which the form parasitic on this forage crop could be distinguished from the parasite on Italian rye grass. In the absence of any cross-inoculation work the writer is inclined to regard the fructifications on the two hosts as belonging to the same species of *Helminthosporium*. It must be noted, however, that the attack of the fungus on *L. perenne* is usually not associated with the conspicuous spotting of the leaves readily observed on affected foliage of *L. multiflorum*, the discoloration being generally less evident and in many instances scarcely demonstrable. In the latter event, the withering of the foliage due to the parasite is, without microscopical examination, not very easily distinguished from the vegetative decline associated with drought or normal ripening.

As a large proportion of the leaves of the two species of *Lolium* are killed prematurely, it is safe to assume that the parasite interferes with the development of the plants sufficiently to cause appreciable economic loss. According to the writer's observations, the leaf disease attributable to the parasite constitutes the most destructive fungus trouble affecting the two valuable forage grasses in Maryland, Virginia, and the District of Columbia. That it has hitherto apparently escaped the attention of American pathologists is indicative more, perhaps, of neglect of diseases destructive to the graminaceous forage crops than to a possibly limited distribution.

It is interesting to note that in 1903 Diedicke (29) made mention of the occurrence of a species of *Helminthosporium* on *Lolium perenne*, causing a local infection similar to that occasioned, for example, by *Helminthosporium bromi* or *H. teres* on their respective hosts. No further description was given, and this investigator, after failing to connect the fungus with any ascigerous stage, apparently paid no further attention to it. Whether the American fungus is the same as that observed by Diedicke in Germany is a question open to conjecture. In any case, it appears not to have been described; and it evidently is distinct from the other species parasitic on grasses studied by the writer. It appears expedient to recognize it as a species, for which, because of its pathological effect on the foliage of its hosts, the specific name *siccans* is proposed.

DIAGNOSIS

Helminthosporium siccans, n. sp.

Occurring on *Lolium multiflorum* Lam. (type) and *L. perenne* L., on which hosts it causes a moderately destructive disease of the foliage, producing typically numerous dark brown longitudinally elongated spots, usually measuring 0.1 to 0.3 mm. in width by 0.2 to 1.0 mm. in length that by coalescing often appear as discolored areas several times larger. Affected leaves later dying, the withering beginning at the tip of the blade and eventually involving the sheath wholly or in part.

Conidiophores olivaceous, emerging usually singly, less frequently in pairs, and rarely in groups of three from stomata or more especially from between epidermal cells on the vascular ridges; measuring 7 to 9 μ in diameter by 50 to 300 μ in length; 1 to 9 septate, the septa inserted at intervals of 15 to 90 μ ; producing first conidium at a distance of 50 to 250 μ from base; points of attachment of successive conidia at angles of geniculate irregularities occurring at intervals of 5 to 30 μ .

Conidia subhyaline or light fuliginous when newly proliferated, later becoming yellow, brownish, or brownish olivaceous, never dark olivaceous like *Helminthosporium sativum*; when fully mature provided with a moderately thick peripheral wall; typically straight or slightly curved; measuring usually 14 to 20 μ in diameter by 35 to 130 μ in length; usually subcylindrical, or tapering slightly or more markedly toward apex, the distal segment often not exceeding 10 μ in diameter, or rarely greater in diameter at the distal end than at the base. Apical and basal ends abruptly rounded off, the contours at the ends being approximately hemispherical. Hilum moderately conspicuous included within contours of peripheral wall. Germinating by the production of germ tubes from intermediate as well as end segments, the basal and distal segments both usually participating in the process by the proliferation of 1 or 2 lateral or oblique germ tubes. Of the intermediate segments one, several, or all may produce one or rarely two lateral germ tubes. Under natural conditions germination by the production of one or less frequently two sporophoric processes, each bearing usually a single conidium, is not uncommon.

HABITAT.—Collected in May and June near Annapolis, Md.; Baltimore, Md.; Rockville, Md.; Kensington, Md.; Washington, D. C.; Arlington, Va.; Mount Vernon, Va.

HELMINTHOSPORIUM STENACRUM, N. SP.

On specimens of *Agrostis stolonifera* L. collected at various times in September, October, and early November, 1920, in southwestern Connecticut, especially in the vicinity of Stamford and Norwalk, the writer found a well characterized species of *Helminthosporium* occurring with some regularity. The fructifications were found on dry withered leaves that formed a considerable proportion of the foliage. Owing to the relatively small size of the foliar organs concerned, and the absence of any pronounced discoloration, it was not possible to determine definitely whether the dying of the leaves was due to the presence of the fungus or to other causes. In general, the distribution of the conidiophores on the dead tissues suggested a course of events somewhat similar to that exemplified by the parasitism of *H. turcicum* in ordinary seasons—development of the fungus on leaves already reduced in vitality as a result of normal maturation, followed by the production of fructifications some time after their death.

The sporophores distributed rather sparsely over the surface of the withered leaves are moderately large structures of the same general type as those of *Helminthosporium teres*, although usually more abundantly septate and less frequently occurring in groups. (Pl. 13, Ca-d.) In width, color, character of peripheral membrane, general shape, and mode of germination, the spores show some similarity to those of *H. gramineum*, *H. teres*, and *H. avenae*. (Pl. 13, Aa-r, Ba-c.) In length, however, they are decidedly superior to the spores of *H. gramineum*, and in an approximately equal degree inferior to those of the other two species. While in newly proliferated spores the peripheral wall may exhibit slight constrictions at the septa, the contour of fully mature spores usually is

altogether smooth, a detail in which the species shows more similarity to *H. siccans* and *H. gramineum* than to the barley net-blotch fungus. No tendency toward the production of secondary spores, such as is manifested in *H. gramineum* and *H. catenarium*, has ever been observed. As in *H. catenarium*, however, the distal portion of the spore is frequently produced into a somewhat constricted apical prolongation. Apparently such modification is the result of development taking place subsequent to the proliferation of the spore in its original condition, and thus, in a sense, is of secondary origin. In any case, the apical extension is characterized by a conspicuous paucity of septa, such cross walls as are found present usually appearing to have developed tardily, as the delimited segments frequently have not contracted away from one another along the edge of the plane of contact.

In pure culture on artificial substrata the fungus produces abundant, although not especially characteristic, growth. Normal sporulation on the media ordinarily employed in laboratories has not been observed, although on tap water agar a relatively sparse production of somewhat small, atypical fructifications was brought about. The imbedded mycelium shows abundant anastomosis resulting in numerous complexes of inflated cells similar to those produced, for example, by *Helminthosporium teres*, *H. bromi*, and *H. tritici-repentis*; and, if the analogy is not misleading, pointing toward the existence of an ascigerous stage.

The fungus appears to be quite distinct from any graminicolous species of *Helminthosporium* hitherto described; as well as from several undescribed forms which the writer has collected on both wild and cultivated members of the genus *Agrostis*. Because of the somewhat attenuated distal prolongation characteristic of many of the spores, the specific name *stenacrum* is suggested.

DIAGNOSIS

Helminthosporium stenacrum, n. sp.

Occurring on withered leaves of *Agrostis stolonifera* L.

Sporophores dark olivaceous, emerging singly or in pairs, usually between adjacent epidermal cells; measuring 7 to 10 μ in diameter, and 80 to 250 μ in length; 3- to 10-septate, the septa occurring at intervals of 10 to 35 μ ; producing the first spore usually 80 to 150 μ from the base, the points of attachment of successive spores occurring at well-defined geniculations.

Spores subhyaline to yellowish when fully mature; 15 to 23 by 53 to 135 μ ; sub-cylindrical with hemispherical or hemi-ellipsoidal ends, or widest somewhat below the middle and tapering moderately toward the ends; the apical portion sometimes produced into a somewhat narrowed distal prolongation; 1 to 11 septate, the septa not associated with constrictions, or marked by barely perceptible constrictions. The peripheral wall thin and including the dark hilum within its contour. Germinating by the production of germ tubes from several or from all segments, the intermediate segments proliferating usually not more than one tube, the end segments occasionally giving rise to two or even three tubes.

HABITAT.—Collected near Stamford, Conn., and Norwalk, Conn., in September, October, and November, 1920.

HELMINTHOSPORIUM DEMATIOIDEUM BUBÁK & WRÓBLEWSKI

In 1916, Bubák and Wróblewski (18) described as *Helminthosporium dematioideum* a fungus occurring in Galicia on the glumes and paleas of sweet vernal grass, *Anthoxanthum odoratum* L.

Caespitulis minutis, dispersis, pulverulentis, atris. Mycelio dematioideo, repente, atrobrunneo. Conidiophoris cylindricis, 25-60 μ longis, 5-6 μ latis, subtorulosis, septatis, brunneis.

Conidiis cylindraceo-oblongis, 38-42 μ longis, 9-13 μ latis, maturis 3 septatis, utrinque late rotundatis, flavobrunneis, crasse tunicatis, levibus.

The description applies moderately well to a fungus found occurring in abundance on dead leaves of sweet vernal grass collected near Washington, D. C., June 20, 1920, and at various times throughout July, 1920, near Port Washington, N. Y. On the inflorescence, the fungus, it is true, also was present, but in much smaller amounts than on the foliage. It was also found on withered foliage of *Agrostis alba* L. (= *A. palustris* Huds.) and *Agrostis perennans* (Walt.) Tuckerm., collected during July and August, 1920, near Brooklyn, N. Y., and Norwalk, Conn., not infrequently on the same leaves that bore also fructifications of one or another of the two apparently undescribed larger-spored species of *Helminthosporium* occurring on these grasses. As the presence of the fungus was in no case associated with local discoloration of the foliar tissue that served as substratum, it was not possible to determine definitely its relationship as a saprophyte or possible parasite. It may be said, however, that the organism, although fairly common on the different species of *Agrostis* mentioned, was not present in sufficient quantity to justify the belief that it was the main cause of the premature withering, abundantly observed during the season of 1920. On the other hand, the manner of its occurrence on *Anthoxanthum odoratum* is not such as to exclude the possibility of a parasitic relation. For in some collections every leaf appears to bear fructifications of the fungus, sometimes, indeed, in great abundance and not infrequently to the approximate exclusion of other fungi. Owing to the small size of the leaves of sweet vernal grass, and the consequent difficulty in recognizing possibly pathological withering from the withering normally taking place during the later stages in the life of the plant, the presence or absence of a parasitic relation could be established perhaps only by well controlled infection experiments.

The principal circumstance that might suggest a possible lack of identity of the European and American forms, is the recorded occurrence of the former only on the inflorescence of *Anthoxanthum odoratum*, while the latter, although not absent from the inflorescence, is certainly much more abundant on the foliage. As sweet vernal grass is an early maturing species and as the material from which the description of the Galician fungus was drawn appears to have been collected in October, it is not improbable that the leaves of the plant were rather poorly represented in the type specimens if, indeed, not altogether missing. Thus the American fungus may at least provisionally be referred to *Helminthosporium dematioideum*, although a few remarks concerning its morphology may not be out of place, especially in view of the brevity of the diagnosis given by Bubák and Wróblewski.

The sporophores (Pl. 14, Da-c), as indicated in the original description by these authors, measure only 5 to 6 μ in width and, compared to most graminicolous congeneric species, are generally decidedly short, although not infrequently exceeding 60 μ in length (Pl. 14, Db, c), and even in some instances measuring three times as much (Pl. 14, Da). They usually are found singly or in pairs, rarely in larger groups; are septate usually at intervals of 10 to 25 μ ; and often can be collected bearing 6 to 8 spores *in situ*. (Pl. 14, Db.) The spores (Pl. 14, Ba-h) are distinctly yellowish when fully mature, from 2 to 6 times septate, and measure 8.5 to 14 by 18 to 48 μ , although the range in septation and in dimensions given by Bubák and Wróblewski may be regarded as typical. In shape they are generally subcylindrical or tapering perceptibly toward the base. The proximal septum is frequently, but not constantly, associated with a

constriction; the basal, like the distal end, usually presents a hemispherical contour within which the small dark hilum marking the point of attachment may be readily recognized. Germination normally proceeds by the production of one to three germ tubes from the basal cell, at positions approximately midway between hilum and basal segment, not usually immediately adjacent to the hilum. (Pl. 14, Ca, Cc-g.) Other modes of germination, as, for example, the production of a germ tube from the apical segment (Pl. 14, Cb), may be regarded as abnormal and usually are attributable to the death of the basal segment as evidenced by the concave contour of the cross wall in contact with the adjacent living segment.

HELMINTHOSPORIUM TRISEPTATUM, N. SP.

In collections of velvet grass (*Notholcus lanatus* [L.] Nash [= *Holcus lanatus* L.]) made near Port Washington, Mineola, Douglaston, and other localities on the western end of Long Island during the months of July and August, 1920, a fungus related to the plants usually referred to the genus *Helminthosporium* was found occurring quite commonly on withered or withering leaves. (Pl. 14, E.) As the form is of a type somewhat different from the majority of the species of *Helminthosporium* on grasses, and does not appear to have been described hitherto, a brief account of it may not be out of place.

The sporophores (Pl. 14, Ha-c) are scattered relatively sparsely between the long hairs that constitute the abundant pubescence characteristic of velvet grass. They are distinguished not only by being relatively long, but also by the presence of ring-like thickenings of the peripheral wall immediately below the points of attachment of the successive spores. The upper portion of the sporophore may thus present a more or less distinctly moniliform contour, within which the lumen maintains an approximately uniform diameter.

Compared to the other species of *Helminthosporium* discussed in this paper, the spores (Pl. 14, Fa-f) of the fungus on velvet grass show perhaps the greatest degree of constancy with regard to morphological features. Associated with the dark olivaceous color is a peripheral wall not exceeded in thickness by that of any of the related forms described in this paper. At the basal end, however, it decreases uniformly in thickness toward the hilum, where the curved inner and outer contours appear to become tangent to each other. This condition is present also in other forms as, for example, in *Helminthosporium monoceras*, where, however, the wall is similarly attenuated at the apical end, a difference reflected in mode of germination characteristic of the species. For, whereas *H. monoceras* germinates from both ends, in the form under consideration only the basal segment normally participates directly in the process. (Pl. 14, Ga-e.)

The fungus appears to be mainly, if not wholly saprophytic. It is referred to the genus *Helminthosporium* rather than to *Brachysporium*, as in well developed spores (Pl. 14, Fe) the length is somewhat greater in proportion to the diameter than generally appears to be true in fungi assigned to the latter genus. The specific name *triseptatum* is suggested because of the number of septa characteristic of typical spores.

DIAGNOSIS

Helminthosporium triseptatum, n. sp.

Fructifications scattered sparsely on withering leaves of *Notholcus lanatus* (L.) Nash (= *Holcus lanatus* L.); usually not visible macroscopically or associated with visible alterations in the substratum.

Sporophores arising singly or in pairs, dark olivaceous, 6 to 8 by 200 to 400 μ ; usually 6 to 11 septate, the septa occurring at intervals 18 to 40 μ in length, averaging approximately 25 μ ; producing first spore approximately 175 μ from base. Proliferation of spore associated with conspicuous local thickening of peripheral wall resembling ring or band; these thickenings occurring in series, giving upper portions of sporophore a more or less moniliform contour.

Spores dark olivaceous; ellipsoidal or short cylindrical with hemispherical ends, sometimes tapering more or less toward basal end; regularly 2 to 3 septate, the septa not associated with constrictions in the peripheral wall; the latter unusually thick, although somewhat thinner at the distal end, and at the basal end diminishing markedly in thickness toward the hilum; the hilum not projecting beyond contour of proximal end. Measuring 15 to 21 by 35 to 50 μ ; germinating by the production of one or two germ tubes at positions adjacent to or in close proximity to hilum.

Habitat.—Collected during July and August, 1920, near Port Washington, Mineola, Valley Stream, Rosedale and Douglaston, N. Y.

HELMINTHOSPORIUM VAGANS, N. SP.

In July, 1919, shortly after the present studies were begun, the writer's attention was called to a leaf spot of Kentucky bluegrass (*Poa pratensis* L.) that seemed to be generally prevalent in the fields and lawns about Madison, Wis. Although almost invariably present wherever the host was found, the spots were by no means abundant. Usually only a small proportion of the leaves were found diseased, and the majority of these bore evidence of only a single infection. Although no spores were found associated with the spots during this season, the fungus that was obtained in pure culture from the diseased tissue was so similar to other species of *Helminthosporium* in general growth characteristics that observations were resumed the following year.

The leaf spot reappeared late in May, 1920, quite as generally and sparingly as during the preceding season. On June 7, material was collected that showed, moreover, an extension of the trouble to the leaf sheaths, especially toward the base of the plant, the lowermost ones being largely involved in diffuse brown discoloration. The condition thus brought about appeared not unlike that present in wheat plants affected with the disease attributable to *Helminthosporium sativum* that has in recent years become known as "footrot." Much more severely diseased specimens (Pl. 15, A) were collected in Brooklyn, N. Y., on August 13, 1920. The foliar lesions, which are of a bluish-black color quite intense in the center and fading out gradually at the margins, here measured up to 8 mm. in length and 3 mm. in width, although usually not exceeding a half of these dimensions. Some of the leaves had withered prematurely, the withering beginning at the tip and proceeding toward the base. The bases of the lowermost leaf sheaths surrounding the "foot" or "crown" of the plant, were thoroughly permeated with a brown pigment. On microscopic examination it was found that the withered portions of the leaves, as well as the older, dead, discolored sheaths, bore in moderate profusion sporophores with spores typical of the genus *Helminthosporium*.

In addition to the localities already mentioned, the fungus has been collected at many stations in the western half of Long Island, as well as

at Bloomington, Ill.; Annapolis, Md.; Washington, D. C.; Hyde Park, Mass.; Meriden, Conn.; and Lisbon Falls, Me. It thus appears to be quite widely distributed through the northeastern and middle western sections of the country. Indeed, the possibility of a distribution nearly, if not quite, approaching in extent the range of the host, is not to be excluded; for although *Poa pratensis* is one of the most common and valuable of the grasses, both in this country and in Europe, and might thus be expected to be kept under observation by pathologists, the fungus is nevertheless very apt to escape detection. Not only are the foliar lesions caused by the parasite usually small and infrequent, but to a casual observer they may readily be mistaken, in spite of the unbroken epidermis and more intense dark discoloration, for old sori of *Puccinia poarum* Niels., almost always present in some abundance. It need hardly be mentioned that the economic loss caused by a disease ordinarily so lacking in severity is relatively insignificant; yet under certain conditions of moisture and of temperature such as would favor a multiplication of foliar lesions and accentuate the footrot symptoms, the damage may not be altogether unappreciable.

On microscopic examination, the fungus shows considerable similarity to *Helminthosporium sativum*, not only in its effect on the host, but to some extent also in regard to morphological features. The sporophores (Pl. 15, Da-g) found on leaves of *Poa pratensis*, to be sure, are appreciably greater in diameter and frequently greater in length (Pl. 15, Da) than the corresponding structure of the parasite causing spotblotch; and the tendency toward branching exhibited by them (Pl. 15, Db, e) is rarely to be found in *H. sativum*. On the other hand, complete agreement prevails with reference to coloration of the spores, the latter (Pl. 15, Ba-q) when fully mature, being uniformly dark olivaceous. In both species, too, the peripheral spore wall is relatively thick and the number of septa rarely exceeds the usual maximum of 10. With respect to spore shape, the form on Kentucky bluegrass, however, is noticeably different, its conidia being typically straight, never, as a rule, becoming distinctly curved.

The most distinctive character, however, is to be found in the germination of the spore, the germ tubes being proliferated not alone from the end segments, but indiscriminately from both intermediate and end segments regardless of position; and not infrequently every segment participates in the process. (Pl. 15, Ca, b.) This behavior would seem to suggest a measure of affinity with species having straight cylindrical spores like *H. teres* and *H. gramineum*, a suggestion borne out in a measure by the cultural characters of the fungus on ordinary media. Sporulation very rarely occurs on potato dextrose agar, although an abundance of dark aerial mycelium usually is produced. The imbedded mycelium presents an unusually distinctive aspect, for instead of consisting like that of most species of *Helminthosporium*, of a miscellaneous growth of hyphae, it is composed largely of a relatively small number of ramifying systems, all of an intense bluish black color, and bearing hundreds of branching elements.

The literature, beyond a brief abstract published by the writer (31) appears to contain no reference to any species of *Helminthosporium* parasitic on *Poa pratensis*. Karsten (74), in 1884, cited *H. flexuosum* Corda (= *Brachysporium flexuosum* [Corda] Sacc.) as occurring on the leaves of a congeneric host, *Poa stricta*. However, the obvious disparity in size and septation between the spores of the species figured by Corda

(25) and the one found parasitic on Kentucky bluegrass is such as to make it appear altogether improbable that Karsten was dealing with the form under consideration. *Napicladium gramineum* described by Peck (108) as destructive to *Poa trivialis* L., is similarly a fungus of much smaller dimensions, the 1 to 3 septate, clavate spores measuring only 10 to 12 by 30 to 60 μ . In more recent years, Baudyš (9) has reported from Bohemia, a new species of *Helminthosporium* on the living leaves of *Poa trivialis*, which he named *H. poae*. Unfortunately, the writer has not been able to secure a copy of Baudyš' paper and consequently has not been able to decide definitely as to any possible identity of *H. poae*. Baudyš, either with the species of *Napicladium* described by Peck, on the one hand, or, on the other, with the fungus attacking Kentucky bluegrass.¹⁰ As *Poa pratensis* is presumably common in Bohemia, Baudyš' failure to record his fungus as developing on this grass would seem to have considerable significance in this connection. The species parasitic on Kentucky bluegrass is accordingly described as new; and because of its widespread occurrence in meagre quantity, the name *H. vagans* is proposed.

DIAGNOSIS

Helminthosporium vagans, n. sp.

Producing well-defined, bluish-black spots 0.5 to 3 mm. wide, 1 to 8 mm. long, on the leaf blades of *Poa pratensis* L.; on the sheaths the spots less definitely circumscribed and near the base of the plant often merging into a generally diffused brownish discoloration.

Conidiophores emerging from stomata or between epidermal cells of tissues some time after death, usually singly or less frequently in pairs; typically simple although occasionally branching; dark olivaceous; usually measuring 8 to 10 μ in diameter and 50 to 280 μ in length; 1 to 10 septate, the septa occurring at intervals of 15 to 40 μ ; approximately straight up to point of attachment of first spore 40 to 150 μ from base; successive spores produced at apices of moderate or often pronounced geniculations.

Conidia dark olivaceous when fully mature; cylindrical or slightly tapering toward the hemispherical ends; measuring usually 17 to 23 μ in diameter by 25 to 130 μ in length; 1 to 10 (usually 5 to 8) septate, the septa not associated with constrictions in the peripheral wall; the latter always thick and including the dark hilum within its contour. Germinating by the production of 3 to 11 germ tubes indiscriminately from end and middle segments, a single germ tube usually being produced from several or all segments.

Habitat.—Collected on *Poa pratensis* at Madison, Wis.; Brooklyn, N. Y.; Bloomington, Ill.; Annapolis, Md.; Washington, D. C.; Hyde Park, Mass.; Meriden, Conn.; and Lisbon Falls, Me.

HELMINTHOSPORIUM RAVENELII CURTIS

Helminthosporium hoffmanni B. Mss. or *H. hoffmanni* B. & C. 1857, in Introduction to cryptogamic botany, p. 298.

Helminthosporium tonkinense Karst. & Roum. 1890, in Rev. Mycol. ann. 12, no. 46, p. 78.

Helminthosporium crustaceum P. Hennings 1902, in Hedwigia, Bd. 41, p. 147.

Although of very little economic importance, *Helminthosporium ravenelii*, owing to its conspicuousness and wide occurrence throughout many of the warmer regions of the globe, has become one of the best known members of the genus. It was described in 1848 by Curtis (26), who noted also its abundant distribution in North and South Carolina. This brief account, however, seems to have escaped the attention of mycologists generally; for when Berkeley (11) some years later figured

¹⁰ Since this text was written, Baudyš' paper has become accessible. The Bohemian fungus produces spores provided with 2 to 6 cross-walls and measuring 36 to 73 μ in length. The foliar spots occasioned by it are described as yellowish with a dark brown margin. In respect to these characteristics, the departures from the morphology of the American parasite would appear to preclude any likelihood of the two forms being identical.

the fungus in his "Introduction to Cryptogamic Botany," he designated it as *H. hoffmanni* B. and C., without any further comment beyond the words, "From specimens on *Sporobolus indicus*. Sent by Rev. M. A. Curtis." Later in a brief descriptive discussion in the "Notices of North American Fungi" Berkeley (12) cited *H. hoffmanni* B. Mss. as a synonym of *H. ravenelii*, which binomial he correctly credited to Curtis alone. Nevertheless, as the publication of the original specific diagnosis in an American journal has apparently remained relatively unknown both in this country and abroad, the name frequently has been improperly attributed to the joint authorship of Berkeley and Curtis.

The earliest collections of the fungus made by Curtis were from North and South Carolina. Material from the rest of the South Atlantic States and from the Gulf States, Georgia, Florida, Alabama, Mississippi, Louisiana, and Texas, as well as from Mexico and China, is included in numerous collections in the herbarium of the Office of Pathological Collections. Specimens of the parasite collected in Costa Rica were distributed by Sydow.¹¹ Kabát and Bubák¹² distributed material from Uruguay and Theissen¹³ material from Brazil. The fungus, moreover, has been reported from Cuba by Berkeley (12), from Bermuda by Seaver (132), from New Zealand by Kirk (78), from New South Wales by Cobb (22), and from the Philippines by Hennings (60), Baker (5), H. and P. Sydow (148), and Yates (160). There is good reason to believe that its distribution is practically coterminous with that of its host, *Sporobolus indicus* R. Whether other grasses also are subject to attack is not altogether certain, although Yates (160) records the occurrence of the fungus on the inflorescence of *Panicum auritum* in the Philippines, and *Fimbristylis* is given as the host on the covers of Theissen's Brazilian specimens. More information concerning the identity of the host material on which these records are based would be desirable. It may be stated that *Sporobolus angustus* Buckl. and *S. elongatus* R., sometimes mentioned as hosts, are listed in the Index Kewensis as synonyms of *S. indicus*.

Helminthosporium ravenelii attacks the inflorescence of *Sporobolus indicus* in our southeastern states with such regularity that, as has been observed by Curtis (26), Jennings (67), and others, it is often quite difficult to obtain a specimen of this species of grass entirely free from the fungus. Indeed, there is reason to believe that the distinctive color and texture of the diseased panicle is popularly regarded as commonplace attributes of the host, as is evidenced by the common names applied to it in the United States, namely, "black seed grass" (26) and "smut grass" (47). These terms are fairly accurately descriptive of the later stages, when the infected inflorescence has a black crusted appearance; but much less accurately descriptive of the earlier stages (Pl. 16, A) when the fungus is present as a velvety or spongy layer of a brownish olive color, that only later becomes increasingly dark.

This velvety layer, under the microscope, is seen to consist of crowded sporophores (Pl. 16, B) arising from a mat of interwoven colorless mycelial hyphae that occupy the superficial layers of the affected floral parts. Unlike the homologous structures of nearly all congeneric forms parasitic on grasses, the sporophores of *H. ravenelii* exhibit a constant

¹¹ SYDOW, H. FUNGI EXOTICA EXSICCATI. *Helminthosporium ravenelii* B. and C. No. 442. 1912.

¹² KABÁT ET BUBÁK. FUNGI IMPERFECTI EXSICCATI. No. 540. *Helminthosporium ravenelii* Curt. et Burk. 1907.

¹³ THEISSEN, F. DECADES FUNGORUM BRASILIENSIS. No. 277. 1905.

tendency toward branching. They are light fuliginous to light yellowish in color; very noticeably torulose, hence decidedly variable in diameter, this dimension ranging from 5 to 10 μ , while the length often exceeds 500 μ ; and usually septate at intervals of from 20 to 40 μ .

The spores (Pl. 16, Ca-q), borne in great abundance at the apices and geniculations of the distal portions of the fructifications, are straight or show a slight crescentic or sigmoid curve; rounded at both ends, the apical end often more broadly than the basal end, owing to a tendency toward tapering in the basal and juxtabasal segments; 12 to 19 μ in diameter by 22 to 78 μ in length; and 1 to 5 (usually 3 or 4) septate, the septa rarely associated with perceptible constrictions in the contour of the thin peripheral wall within which, at the point of attachment, the small dark hilum is readily observed. The conidia germinate readily in water, sending out a germ tube from one, or more usually from both, end cells. (Pl. 16, Da-e.)

Karsten and Roumeguère (75) have described a fungus from Tonking growing apparently on the same host (*Sporobolus tenacissimus*, the host name given, being listed as a synonym of *S. indicus* in the Index Kewensis) and corresponding to *Helminthosporium ravenelii* in all details relating to habit, color, and structure of conidiophores, as well as to color, structure, and dimensions of conidia. This form, which they designated as a new species, *H. tonkinense*, and regarded as being related to *H. ravenelii*, is undoubtedly altogether identical with the latter. Nor can there be much question that the same holds true also of *H. crustaceum* described from Java by Hennings (58) as forming dark crustaceous effuse tufts on the inflorescence of a species of *Sporobolus*. According to this botanist, *H. crustaceum* is related to *H. ravenelii* but distinct on account of its conidia. Inasmuch as the latter are characterized as—

Oblonge clavatis vel fusoidis, utrinque obtusis, rectis vel curvulis, 40-60 \times 12-16 μ , 3-5 septatis, haud constrictis, fuscis—

in all of which particulars the agreement with *H. ravenelii* is at least reasonably close, the writer is inclined to believe that Hennings's binomial should be regarded as a synonym until some evidence for the justification of a new species has been adduced.

HELMINTHOSPORIUM SATIVUM P. K. & B.

Helminthosporium acrothecioides Lindfors 1918, in Svensk Bot. Tidskr. v. 12, p. 227.
Helminthosporium gramineum of E. C. Johnson, Masee, Palm, Bassi, not Rabenhorst.
Helminthosporium inconspicuum of Peck, Atkinson, not Cooke & Ellis.
Helminthosporium Sorokinianum Sacc. 1891, in Ztschr. Pflanzenkr., Bd. 1, p. 236-239.
Helminthosporium ieres of Bakke, not Saccardo.
Helminthosporium sp. of Beckwith, Bolley, Evans, Hamblin, Hungerford, McKinney, Stakman, Stevens, Waterhouse.

Although the fungus to which it has appeared advisable to apply the binomial given by Pammel, King, and Bakke (104), probably is the species most frequently encountered by plant pathologists, it has been the subject of much confusion in the literature. This condition is largely attributable to the fact not hitherto generally recognized that it occurs on a number of graminaceous hosts, several of which, moreover, are affected by one or more congeneric parasites. As the specific characteristics of the latter have not always been clearly distinguished, and as the fungus under consideration shows a tendency toward variation in response to varied environmental conditions, occasion for erroneous identification has not been lacking.

NOMENCLATURE

In 1891, a brief anonymous account (136) appeared concerning *Helminthosporium Sorokinianum*, Sacc. (in litt), a fungus which Sorokin (135) had found occurring on the spikes of wheat and rye in the South Ussurian region in Russia. The spores were later described in Saccardo's (128, v. 10, p. 415-416) diagnosis of the species as—

acrogenis, ovato-fusoideus, majusculis, 80-100 x 30, rufobrunneis, 5-10 septatis, passim lenissime constrictis, rectis curvuliscis.

This characterization applies fairly well to the spores found occurring on wheat spikes in the United States with reference to shape and septation. The dimensions given also are not outside of the ranges in dimensions found in this country, the figures given for length corresponding closely enough, although 30 μ constitutes a maximum width (pl. 18, Fe) not attained by a large proportion of conidia. It appears quite probable, therefore, that the Russian fungus is identical with the American form. However, because the spores of the latter, when fully matured and in a living condition, are dark brown or olivaceous rather than reddish brown, the identity of the two forms can not be regarded as firmly established. Therefore, in spite of the priority of Saccardo's binomial, the writer believes it advisable to treat it as a probable synonym.

In 1909, Pammel (103) recorded the occurrence during the preceding season of a barley disease in Iowa differing from the stripe disease. A more complete account of this trouble was published in 1910 by Pammel, King, and Bakke (104), in which the casual organism was described as having fasciated fuscous brown septate conidiophores, 8 to 10 μ wide, bearing a large cylindrical dark brown spore, with 7 to 12 divisions, and measuring 15 to 20 by 105 to 130 μ . The fungus was regarded as closely related morphologically to *Helminthosporium teres*, but in the absence of comparative cultural studies was provisionally given a new specific name, *sativum*. Later, however, one of the authors, Bakke (6), presumably as a result of cultural experiments and in conformity with opinion secured from Saccardo and Ravn, definitely referred the disease to *H. teres* Sacc. Although indications are not wanting that Bakke in this later work was dealing to some extent with the latter organism, the figures as well as the text leave no room for doubt that he was in the main concerned with the same disease and the same parasite that had been discussed in the preceding Iowa publication. Inasmuch as *H. teres* and the fungus causing "late blight" of barley are not identical, representing, indeed, two quite distinct congeneric types, it would seem that Bakke was in error in repudiating *H. sativum* as an independent binomial.

In 1918, Lindfors (84) described from Sweden as *Helminthosporium acrothecioides* a fungus he had discovered on barley seed that had been germinated on filter paper. Its morphological features correspond completely with those of the American fungus developing under the warm, damp conditions obtaining in germination apparatus, when, as the writer has observed in hundreds of instances, discolored barley seeds or wheat seeds affected with "black point" are incubated on moist filter paper. The figures and the characterization of the conidia as "narrow ellipsoid to spindle-shaped, with blunt ends, 60 to 95 by 20 to 24 μ , with 7 to 9 septa, and a thick, dark olive brown episporium," apply so well to the American form that Lindfors's binomial may very safely be regarded as a synonym.

OCCURRENCE OF THE FUNGUS ON BARLEY

Of the graminicolous species of *Helminthosporium* thriving in our northern latitudes, *H. sativum* shows, perhaps, the strongest omnivorous tendency, being vigorously parasitic on a number of grasses and occurring on others apparently in a manner more nearly suggesting a saprophytic relation. Its greatest luxuriance is attained, nevertheless, on the foliage of barley, from which it originally was described. According to the records of the Plant Disease Survey, the fungus has been reported on barley in 24 states, including all of the more important barley-growing sections of the country. Güssow (48) early recorded its occurrence on the same crop in Canada.

Although the host is susceptible at any stage of development, the use of affected seed often resulting in the appearance of severe lesions in the basal portions of the young seedlings, the disease usually does not begin to show up in quantity until the plants are heading out. It is manifested by the appearance of spots varying from 0.5 to 3 mm. in width and from 2 to 15 mm. in length, usually dark brown in the center and fading gradually at the margins into the green of the surrounding tissue. (Pl. 17, B.) The lower leaf blades are first affected, the discolored areas multiplying until scores of them may be present on one foliar organ and a considerable portion of the leaf tissue is involved (pl. 17, A). As a result the leaf soon withers and dies, the discolored areas fading slightly and becoming vaguer in outline, while the parts not visibly altered in appearance take on a grayish hue. The foliar spots never become bleached in the center as those caused by *H. leersii* on *Leersia virginica*; nor exhibit a reticulate pattern, like those induced by *H. teres* on barley; nor are they surrounded by a zone of leaf tissue from which the chlorophyll has disappeared like those produced by *H. bromi* on *Bromus inermis*. At the same time the destruction of the lower leaves takes place, the disease makes progress in the younger foliage, which then succumbs in the same way, until the uppermost leaf is affected. The effect of this virtual defoliation is to hasten the ripening processes. In a season favorable for the development of the disease, the grain may be ready for harvesting perhaps two weeks earlier than when the trouble is absent. As might be expected, the yield is decreased in a measure approximately corresponding to the shortening of the growing period.

Although the foliage of barley is most severely attacked the inflorescence, as Pammel, King, and Bakke (104) pointed out, is not immune. The fungus may be found on the glumes and not infrequently on the seed. The diseased kernels usually are readily distinguished because of the dark-brown discoloration at the germ ends, a feature that has, indeed, been utilized by Atanasoff and Johnson (3) in selecting infected material for experiments on the dry-heat treatment. When such discolored kernels are placed in a germinator the fungus becomes visible usually within 24 hours as a delicate white velvety outgrowth, that soon spreads on the filter paper or other material as an effused arachnoid mycelium and produces, if the conditions are not too moist, an abundance of fructifications. A reduction in viability, usually apparent in slightly discolored seed, may become very considerable when the seed is more severely affected. After the basal sheath has been developed this organ often is attacked by the fungus and as a result takes on a yellow or light yellowish-brown discoloration. A considerable proportion of the rootlets

may be invaded in the same way, often stunting their development and softening the discolored cortical tissue. Undoubtedly, quite similar pathological processes take place when the seedlings are planted in soil. The effect of such early infection, moreover, then becomes apparent in the development of the seedling, for, in addition to the lesions on seed, sheath, and root system, conspicuous dark brown spots may occur on the first few leaves, thus giving rise to the thoroughly diseased condition described and illustrated by Atanasoff and Johnson.

It may be mentioned in this connection that a discoloration of barley seed evidently quite similar to that frequently observed in the United States was noted by a number of European writers. Zöbl (163, 164), in 1892, published some papers on "brown-pointed" (*braunspitzige*) barley, in which the discoloration is described as being most intense at the base of the seed and decreasing toward the apex. Although various fungi belonging to the genera *Sporodesmium*, *Cladosporium*, *Helminthosporium*, and *Dematium* were found associated with discolored seeds, Zöbl attributed the brown-point condition primarily to *Cladosporium herbarum*. Puchner (113), in some studies on "black-pointed" (*schwarzspitzige*) barley seed, found that these germinated abnormally, often producing plants the leaves of which bore brown spots. However, when barley seed similarly affected was treated with copper sulphate preliminary to sowing the foliar lesions failed to appear in the seedling, although during the later stages in development the foliage and inflorescence of the originally healthy plant were as subject to attack as those of a diseased specimen. Ravn (115) found a fairly close correlation existing between the prevalence of net-blotch and "brown point" (*brune Spidsers*) in the seed. Without regarding a causal relation as firmly established, he nevertheless appears to have been inclined to see in *Helminthosporium teres* the most probable cause of seed discoloration.

While the evidence adduced by Ravn would appear altogether sufficient to justify his view, as far as conditions in Denmark at the time his investigations were carried on were concerned, the fact remains that in our North Central States *H. teres* is not generally associated with black-pointed barley seeds. On the other hand, as has been mentioned before, the association of *H. sativum* with this condition appears unusually constant. For example, when discolored barley seeds from stock grown in Wisconsin are plated on agar, after proper surface sterilization, only a very small proportion of seeds will fail to give rise to mycelia and conidiophores of the parasite causing spot-blotch. Presumably *H. sativum* is of less frequent occurrence on barley in Europe than in the United States. That it is more common than the absence of references from European literature might lead one to infer is suggested, for example, by Masee's (90) account of *H. gramineum*. The ambiguity with regard to the host range of the fungus, and the longevity, color, and size of the conidia, fortunately is explained by figures of these bodies (fig. 132-6), which show beyond any doubt that this author was dealing not with the stripe fungus but with the parasite causing spot-blotch. In Lindfors' (84) description of *H. acrothecioides* the existence of a species of *Helminthosporium* on barley other than *H. gramineum* and *H. teres* eventually was recorded, but its relation to pathological lesions in the growing plants of either barley or of wheat or rye has apparently not yet been recognized.

OCCURRENCE ON WHEAT AND RYE

Helminthosporium disease of wheat affecting seedlings as well as older plants was reported, according to the files of the Plant-Disease Survey, as doing considerable damage in several seasons during the past decades, especially in North Dakota and Minnesota. In the former State, Bolley (14) found one or more species of Helminthosporium responsible in large measure for the deterioration of wheat production. Isolations made from various parts of diseased wheat plants revealed the presence, in addition to representatives of the genera *Alternaria*, *Colletotrichum*, *Fusarium*, and *Macrosporium*, of strains of Helminthosporium in the nodes and internodes of the stem, as well as on the surface and in the interior of the kernels (15). Of special interest is the account given by the same author of a type of infection designated as "brown spot" and manifested by brown discoloration of the lower portion of the wheat stems near the soil line. Such attack was found to occasion reduction in tillering, as affected stools usually consisted of only one, or more frequently, two tillers, the other tillers being represented by abortive shoots or intercepted buds. Beckwith's (10) study of the occurrence of soil fungi in North Dakota showed that strains of Helminthosporium were found occurring considerably more abundantly on the nodes and internodes of wheat in the wet season of 1909 than in the dry season of 1910.

Later, E. C. Johnson (71) published the results of experiments on certain cereals with a fungus he designated as *Helminthosporium gramineum* Rabh. Inoculation of young seedlings of wheat, barley, oats, and rye with spores from pure cultures originally isolated from the lower parts of the culms of wheat, as well as from wheat leaves and barley leaves, resulted in the prompt appearances of leaf spot on all the four graminaceous species. When wheat seeds inoculated with spores were sown, their germination was considerably reduced, and the resulting plants were stunted in comparison with uninoculated controls. Indeed, some of the inoculated seeds were attacked so promptly that they had no opportunity to germinate; in other cases, the young plants were killed before they were an inch high. The attack on the surviving seedlings was manifested by a brown discoloration at the base of the culms, usually occurring in the basal leaf sheath, and subsequently extending to the root crown, as well as by the partial brownish discoloration and reduced development of the root system. Barley and oat seed similarly treated were not perceptibly reduced in viability, although the resulting barley seedlings were somewhat retarded in growth and exhibited in smaller degree the same type of discoloration as the diseased wheat seedlings.

In spite of E. C. Johnson's statement that the strain of Helminthosporium discussed in his paper corresponded in cultural and morphological characteristics to the descriptions of Ravn (115), there are strong reasons for suspecting that his fungus was not identical with the parasite causing barley stripe. The latter, in the writer's experience, can not be made to sporulate in pure culture except in meager quantity, any profuse sporulation, such as was presumably induced in all the imperfect fungi employed by E. C. Johnson, certainly never having been observed in *H. gramineum*. Moreover, the pathological lesions produced in his experimental plants obviously bore little resemblance to those of the systemic trouble described by Ravn. On the other hand, the symptoms

correspond accurately with those noted later by Atanasoff and Johnson (3) on seedlings grown from seed infected with *H. sativum*.

In 1918, Palm (101) reported from Java the occurrence of a species of *Helminthosporium* on wheat which he designated as *Helminthosporium gramineum* ([Rabh.] Eriks.?). The fungus was found present on the glumes as well as on the perceptibly shrunken kernels, through the agency of which the author believed the infection to be transmitted. The statements relating to the long worm-shaped, usually curved, 6- to 10-septate spores measuring 65 to 110 μ in length, and 15 to 20 μ in width, and more especially the accompanying figures, indicate that the Javan fungus differs conspicuously from the parasite causing stripe but shows complete similarity to *H. sativum*, as it occurs on the same host in this country.

Considerable attention has been given during recent years to a diseased condition found prevalent on wheat in the vicinity of Granite City, Ill. Stevens (140) recognized the trouble as a typical footrot which he attributed to a species of *Helminthosporium* found constantly associated with it and producing luxuriant growth on a variety of substrata. The conidia were described as structures approaching a narrow or broadly elliptical shape measuring 24 to 122 μ , usually 80 to 90 μ , in length; containing from 0 to 13, usually 5 to 10, septa or false septa; possessing an outer thin dark wall and an inner colorless thick wall; and germinating by the production of one or two polar germ tubes. The causal relation of the fungus with the disease presumably was established, moreover, by successful inoculation of the unwounded internodes of wheat seedlings. When wheat seeds were inoculated with spores of the fungus and germinated in a seed tester, the host tissue was quickly invaded, leading to the production of brownish spots, and under favorable conditions to general rotting and death of the innermost leaves (141). Inoculation of the roots was followed by invasion and discoloration of the cortex.

McKinney (86), who also carried on studies near Granite City, Ill., similarly found a species of *Helminthosporium* present on wheat, associated with lesions often developing during the later stages of the disease. Apparently, however, he did not regard the latter primarily as a foot rot, but rather as a trouble having somewhat different symptoms which, at least during the early spring stages, was not found constantly associated either with any perceptible lesions or with any specific organisms whatever. In a later note, McKinney (87) states that all the strains of *Helminthosporium* isolated from wheat appear to be similar, if not identical, not only to one another, but also to *H. sativum* derived from barley leaves affected with spotblotch. And this similarity was found to obtain with reference to the morphology of the fungi from the two sources as well as to their pathological properties as evidenced in cross inoculation experiments.

A critical study of a *Helminthosporium* disease of wheat and rye was published recently by L. J. Stakman (138). The malady, which was unusually common in Minnesota in 1919, was manifested early in the season as a seedling blight, characterized by brown discoloration of the roots, either in extensive patches or in numerous small irregular lesions; by the presence of rust-brown streaks or blotches on the "foot" or base of the stem, later progressing to the inner sheaths; and by a general dwarfing of the plants, the leaves of which were conspicuously stunted, very narrow and pale reddish tan in color. Many of the affected plants

died in the seedling stage. Others, however, recovered and grew to maturity, although the older plants frequently suffered not only from the persisting foot lesions, but also from secondary infections. As a result of the latter, numerous dark brown spots, about 1 mm. long, appeared on leaves, nodes, neck, and glumes, and brownish streaks were found present on the internodes. The discolored areas later became paler, and developed a coating of *Helminthosporium* fructifications. On potato dextrose agar the fungus produced an abundance of spores, which were described as being straight or curved, dark blue to brown in color, 3- to 8-septate, and measuring on the average 41 by 20 μ . Cross inoculations carried out with cultures of the *Helminthosporium* species isolated from wheat and rye, indicated that the fungi from these two different hosts were as indistinguishable in respect to pathogenic properties as in respect to morphology. It is especially significant that the strains from rye infected barley, and that a form identified as *Helminthosporium sativum* produced infection on wheat.

A form of disease strikingly similar to that described by L. J. Stakman was observed on wheat by Bassi (8) during the season of 1921 near Piacenze in northern Italy. Two types of the malady, "nerume," were recognized, one affecting the tender shoots of wheat or rye in autumn, the other present the following summer on more mature plants. In the former type, growth is conspicuously stunted, the roots and nodes are involved in decay, and the leaves, besides being greatly reduced in size, assume a light reddish, olivaceous color and eventually wither and die. Characteristic lesions are found on the base of the culms either as local dark reddish streaks or as a more extensive discoloration. The roots are attacked also, the cortical tissue often being injured so severely that when the plants are pulled up the vascular elements are extracted from the cortex which remains behind. The second type of infection is manifested by the appearance on the leaves of numerous small dark brown spots, but more particularly by an attack on the nodes ("marciume dei nodi") so that the latter frequently show on their margins dark brown horizontal lines composed of spores of the fungus. Brown lesions occur on the internodes, as well as on the glumes, which in the final stages, after sporulating commences, assume a dark tinge. The kernels also often are attacked, then becoming discolored and failing to attain full development. The fungus on specimens of diseased plants sent to Padua for examination was identified as *Helminthosporium gramineum*.

In a recent paper Hamblin (49) reports the prevalence of a footrot disease of wheat due to a species of *Helminthosporium* in widely separated regions of New South Wales. The damage occasioned by the fungus in 1921 is believed to have been greater than the loss due to "take-all," varying from 2 to 3 up to 85 and 90 per cent. Apparently the symptoms of the Australian trouble are very similar to those noted in the United States and Italy. Tillering is greatly reduced, the tillers being usually not in excess of two or three. As the root system is poorly developed and affected by decay, diseased plants are easily pulled up. At and below the ground level the base of the plant shows brownish discoloration, either uniformly diffused through the culm and sheaths or present in the form of spots or streaks. The inflorescence of affected plants fails to attain normal development, some of the heads failing to set any seed, others setting seed only in a portion of the spikelets, and still others setting seed in all the spikelets, but the seeds remaining pinched and undersized. Although Hamblin gives no textual descrip-

tion of the parasite, the figures of the sporophore and conidia show an unmistakable resemblance to those of *H. sativum* developing in artificial culture or on natural substrata under moist conditions.

Another reference to the relation of an unidentified species of *Helminthosporium* to root rot of wheat is given by Raeder (114) who observed considerable damage caused by this trouble in Idaho. His description of the symptoms—stunting of the heads, shriveling of the grains, discoloration of the sheath at the base, and occasionally also of the lower nodes—certainly suggest the spotblotch fungus. Snowden's (135) report of *H. sorokinianum* on wheat in Uganda may plausibly be interpreted as referring to the same parasite.

The accounts briefly summarized in the preceding paragraphs concerning the occurrence of a species of *Helminthosporium* on wheat in association with well-defined lesions raise the questions as to whether one or several congeneric forms are concerned. The writer has examined scores of strains of *Helminthosporium* isolated from black-pointed wheat seeds (Pl. 18, Aa-Cb), from discolored portions of the stems and leaves of both young (Pl. 18, E) and more mature wheat plants, and from conidial fructifications occurring on the glumes of wheat heads (Pl. 18, D). Although the material was obtained from a considerable number of localities in the middle western section of the United States, no constant morphological differences such as distinguish the different species discussed in this paper, could be detected between the various strains. Nor was it possible to recognize any significant differences between the forms isolated from wheat and various strains of *H. sativum* isolated from barley leaves heavily affected by spot blotch. In some preliminary cross inoculation experiments undertaken by the writer, barley and wheat seedlings proved equally susceptible to attack by strains derived from the same and from the reciprocal host; and the lesions produced were indistinguishable regardless of the source of the inoculum. Such identity of morphological and physiological characteristics, altogether in harmony with the findings of L. J. Stakman (138) and of McKinney (87) have convinced the writer that for the most part a single species of *Helminthosporium*, namely, *H. sativum*, is involved in the widespread infection of wheat manifested variously by such symptoms as stunting of growth, seedling blight, basal browning, root rot, foot rot, node decay, leaf spot, stem discoloration, and black point. And as the reports of Sorokin, L. J. Stakman, and Bassi indicate, the same fungus evidently is associated with similar pathological conditions in rye.

In another connection, it is true, attention has been called to the fact that the type of injury occasioned by *Helminthosporium sativum* on the wheat plant is duplicated by the attack of several congeneric species on other hosts, as, for example, *H. vagans* on *Poa pratensis* and *H. monoceras* on *Echinochloa crus-galli*. The occurrence of one or more species of *Helminthosporium* other than *H. sativum*, associated with similar lesions is consequently not to be excluded as a possibility. Nevertheless, there seems to be little reason to believe that *H. gramineum* has ever been found parasitic on wheat in spite of the papers of E. C. Johnson, Palm, and Bassi, indicating such parasitic relation. The reports of Johnson and of Palm, as has been pointed out, appear to have been based on obviously erroneous identification of the fungus concerned. And the form of disease described by Bassi corresponds so well to the trouble investigated by L. J. Stakman that it is hardly probable that two separate species

are involved. While the Minnesota fungus was not definitely identified as *H. sativum*, its similarity to the latter fungus with regard to morphological and cultural characters is certainly very close. To be sure, L. J. Stakman states that the spores of the wheat parasite, while resembling those of *H. sativum* in shape, "contain few septations and are shorter than those described by Pammel, King, and Bakke." However, as the Minnesota fungus appears to have been studied chiefly in pure culture, where the spores of *H. sativum* ordinarily become greatly reduced in length and number of septa as compared with those developed on the host in the field, on which the original diagnosis undoubtedly was based, the difference is very readily explained.

It may not be superfluous to mention that several species of *Helminthosporium*, morphologically altogether different from *H. sativum*, have been reported as occurring on various parts of wheat and rye plants. Thus Palm (101) records the presence on the spikes of this host in Java of a relatively innocuous form with small geniculate spores which he identified as *H. geniculatum* T. & E. (152). Hennings (59) earlier described as a new species, *H. tritici*, another small-spored but apparently different fungus collected by Zimmerman in the region formerly included in German East Africa. The African form, described as being very injurious, is evidently similar in general habit to *H. ravenelii*, developing a dense crusty coating on the culms, leaves, and heads of the host. Stevens (141) makes mention of a geniculate-spored form evidently different from the one usually encountered on diseased wheat in Illinois; while L. J. Stakman records the isolation from the same host of strains of *Helminthosporium* producing smaller spores than the species generally found associated with the Minnesota disease. A species of *Helminthosporium* obviously different from *H. sativum* was described from Alabama growing apparently as a saprophyte on decaying culms of rye by Atkinson (4) under the name of *H. tuberosum*. The same author also reported *H. inconspicuum* "on living and languid leaves of *Secale cereale*," evidently in a parasitic relation. It appears at least not improbable that Atkinson, following Peck (107), applied the binomial of Cooke and Ellis not to *H. turcicum*, but to a form morphologically very similar if not altogether identical to *H. sativum*.

As has been indicated in other connections, when the inflorescence of wheat is attacked (Pl. 18, D), the kernels often are affected, resulting in dark brown, bluish brown, or nearly black discolorations involving more or less extensive and irregular patches at the germ end or extending along the ventral furrow (Pl. 18, Ba-Cb). Hungerford (64) and Waterhouse (156) noted the presence of *Helminthosporium* fructifications on wheat grains. A special type of such pathological effect in which the discoloration is relatively intense and limited to the region occupied by the embryo (Pl. 18, Aa, b) has become known as "black point." It is characteristic especially of durum wheat, having been reported by Bolley (14) in 1910 as being on the increase on this species, and more recently made the subject of investigation by Evans (38) as well as by Weniger (158) and by Henry (61). Greenhouse experiments, now in progress, the results of which will be published later, have shown that, compared to healthy seeds, badly discolored seeds show a much smaller degree of viability, and that the plants resulting from them frequently develop lesions varying in number and severity. (Pl. 18, E.) It may be mentioned that other fungi, notably one or several species of *Alternaria*, also have been found associated with discoloration of wheat grains, which, however,

while somewhat similar to the type of discoloration attributable to *H. sativum*, can usually be distinguished by its lesser intensity, being diffused brownish rather than dark brown.

Especially pertinent in this connection is Henry's (61) recent report of the isolation from black-pointed wheat kernels, of certain forms he designated as "*Helminthosporium* sp." and "*Brachysporium*," which, while of much less frequent occurrence than the spot-blotch fungus, were found to be efficient causes of black point. The writer, who was kindly permitted to examine transfers of these fungi, can only confirm the correctness of Henry's judgment in regarding the "*Helminthosporium* sp." as distinct from *H. sativum*. It appears to be different from any species figured in this paper, though, perhaps, most suggestive of *H. monoceras*. The strains designated as "*Brachysporium*" appear to represent one or several smaller-spored forms that might not improperly also have been referred to the genus *Helminthosporium*, bearing a good deal of resemblance to a species frequently observed by the writer on withered leaves of *Danthonia spicata* (L.) Beauv.

It may not be amiss to refer here to a fungus described under the name *Podosporiella verticillata* by O'Gara (98) who found it on the kernels of germinating wheat in the Salt Lake Valley, causing stunting of the resulting seedlings, and an uneven stand. The conidia of this form show a very obvious general resemblance to those of the larger species of *Helminthosporium*. The synnemata figured by O'Gara are evidently not dissimilar from the threadlike or columnar structures observable, for example, in cultures of *H. inequalis* Shear, or of *H. cyclops*. Indeed, except for the arrangement of the conidia on the sporophore, which according to O'Gara is verticillate, the fungus shows considerable similarity especially to the last named of these species.

While *Helminthosporium sativum* has not been reported as attacking maize in the field, the writer has found it of more or less frequent occurrence on the dead remains of mature plants. Cultures derived from fructifications on old culms and leaves were not observed to differ in any important detail from cultures of the spot-blotch fungus isolated from barley. In a few instances, sporophores and spores of a form similar to *H. sativum*, at least in respect to morphological characteristics, were found on dead areas of leaves of sweet corn collected on Long Island. However, as the fructifications of *H. turcicum* were also present in excessive abundance, it was not possible to draw any definite conclusions concerning the biological relations of the form under consideration. In general, its distribution on corn suggests a saprophytic existence on this host, modified, perhaps, by a capacity to establish itself on moribund foliage. It may be mentioned in this connection that while Stevens found his strains of the Illinois foot-rot organism capable of infecting corn and corn-fodder, L. J. Stakman secured negative results from the inoculation of corn plants with strains of *Helminthosporium* isolated from a node of affected wheat and from rye seed. In some preliminary infection experiments the writer applied spores of *H. sativum* from barley to corn seedlings about 5 inches high, very liberally stroking them in water suspension on the moistened leaves with a spatula, and then confined the seedlings in a saturated atmosphere for 48 hours. At the end of this time the leaves had lost their mechanical rigidity and the entire plants looked as if they had been steamed, although the controls, treated in the same way except that no inoculum was applied, were nearly normal. That much significance attaches to such injury, unlike any naturally

produced by the parasite on any host, and, indeed, unlike any injury produced under conditions obtaining in nature by any congeneric form with the exception of *H. micropus*, seems altogether improbable. The results obtained by exposing experimental plants to the rigorous treatment incident to the application of relatively large quantities of inoculum and incubation in a saturated atmosphere during long periods, should at all events be interpreted with caution. And the necessity of caution would seem especially evident in dealing with a fungus, more or less promiscuous in its parasitism, the experimental host range of which would tend to be out of all proportion to its actual range in nature.

The occurrence of *Helminthosporium sativum* on corn has brought about a measure of confusion regarding the identity of *H. turcicum*. It is interesting to note that in Peck's account (107) of *H. inconspicuum*, the spores of this fungus are described as "nearly black, septate up to 8 to 9 times;" and figured as decidedly dark, curved cylindrical, with rounded ends, attached to sporophores emerging singly from the substratum. In all details of habit and morphology the correspondence with *H. sativum* is much closer than with *H. turcicum*; and it appears probable that although Peck observed the corn disease correctly, he inadvertently based his account of the fungus not on the well characterized parasite, but on the adventitious form. Specimens deposited in the herbarium of the Office of Pathological Collections of old corn leaves from various localities in the United States, labeled "*Helminthosporium inconspicuum*," on examination, were found to bear dark olivaceous spores with non-protruding hila, not dissimilar from those of *H. sativum*, although their collapsed condition precluded the possibility of reliable identification.

OCCURRENCE OF FUNGUS ON GRASSES OTHER THAN CEREALS

Bolley (15) reported the occurrence of a species of *Helminthosporium* on quack grass collected in North Dakota and Wisconsin. As the fructifications developing on this host were held responsible in certain instances for the infection of wheat plants in the field, it is apparent that he regarded the species as identical to the parasite causing root rot and brown spot. In any case, the writer found *H. sativum* quite commonly present on quack grass in the northern tier of Middle Western States, being associated with a leaf-spot disease, affecting the foliage of plants of all ages. (Pl. 18, H.) The discolored leaf areas, although quite numerous, are decidedly smaller than those characteristic of spot blotch of barley, occurring usually in the form of linear streaks, dark chocolate brown in color, 0.3 to 0.4 mm. in width and 0.5 to 3 mm. in length. During the season of 1919 the writer collected in the vicinity of Madison, Wis., diseased green leaves as early as May 6, and as late as October 24. The injury to the host appeared to be greater than that resulting from the parasitism of *H. tritici-repentis*, although neither of the two congeneric parasites could be said to have been especially destructive. In the region about New York City, during the season of 1920, the leaf spot due to *H. sativum* was, however, relatively rare, being considerably less abundant than the blight due to *H. tritici-repentis*.

A fungus quite similar to the parasite causing "late blight" of barley was reported by Pammel, King, and Bakke (104) as occurring on *Festuca elatior* L. (= *Festuca pratensis* Hud.) in Iowa. Examination of material deposited in the herbarium of the Office of Pathological Collections only confirms the opinion of these authors concerning the similarity of the lesions to those characteristic of spotblotch of barley, and the very

probable identity of the parasite to *H. sativum*. It is interesting to note, however, that in the vicinity of New York City and Washington, D. C., during the seasons of 1920 and 1921, meadow fescue was not observed affected with the spot blotch described from Iowa, although very commonly showing the symptoms of the net blotch disease discussed elsewhere in this paper.

In addition to the graminaceous species already discussed, the literature contains references to successful infection of other species, by artificial inoculation with strains of *Helminthosporium* that, as has been pointed out, may be referred to *H. sativum*. Thus Masee (90) secured growth and abundant sporulation by transferring spores of the fungus he regarded as *H. gramineum* to leaves of *Festuca ovina*, *Briza media*, *Dactylis glomerata*, *Poa annua*, and *Arrhenatherum avenaceum* that had been cut off and incubated in a damp chamber. Stevens (141) secured infection of Sudan grass and millet as a result of inoculation with the footrot organism. E. C. Johnson (71) found that the strain of *Helminthosporium* isolated by him from the node of a wheat plant seriously attacked the foliage of young oat seedlings. L. J. Stakman (138) reports positive results from the inoculation of over a dozen new hosts with strains originally isolated from wheat and from rye. Taken altogether the results are not in complete harmony, a fact which may probably in part be explained by differences in the conditions under which the experiments were carried on. The method employed by Masee certainly would seem to make for an inordinately extensive experimental host range. On the other hand, the existence of biological races, corresponding to those of stem rust (*Puccinia graminis*) for example, is not outside the realm of possibility. Indeed, absolute agreement in regard to host interrelations between different strains of a fungus attacking so many allied graminaceous species as *H. sativum* could, perhaps, scarcely be expected.

MORPHOLOGY OF THE FUNGUS

The fructifications of *Helminthosporium sativum* make their appearance after the death of the affected tissue, emerging from the stomata or more frequently between the epidermal cells singly or in fascicles of 2 or 3. (Pl. 17, Ea-e.) According to Pammel, King, and Bakke (104), the sporophores vary from 8 to 10 μ in width, but these figures appear somewhat too high, the measurements for this dimension varying usually from 6 to 7 μ , and rarely exceeding 8 μ . The first spore is produced generally at a distance of 50 to 90 μ from the base. The scars marking the points of attachment of successive spores at well-defined geniculations occur at very variable intervals, approaching 5 μ as a minimum limit, and occasionally exceeding 60 μ . As found in nature, the sporophores rarely show more than 5 or 6 scars or more than 8 septa, the distances between the latter usually varying from 5 to 40 μ . The measurements for *H. teres* given by Bakke (6), 150 to 180 μ by 60 to 80 μ , while obviously incorrect for the width of the sporophores of the causal organism of spotblotch or "late blight" of barley, probably as a result of a typographical error, are also sufficiently in excess of the usual range in length of these structures, 110 to 150 μ , to indicate that this author was, indeed, in this instance referring to the parasite causing netblotch.

Such indication is strengthened by the portions of his description of the spores referring to their length and color, "150 to 130 μ ," and "pale

greenish gray," respectively. Plate 18, Fg, represents a 12-septate spore of *Helminthosporium sativum* that was scraped from a wheat inflorescence and found to measure 134 μ in length, which may be regarded as approximating the maximum for this dimension. The maximum width represented, for example, in the spore shown in Plate 18, Fe, is approximately 30 μ . The minimum for width of spore, as found in material occurring in nature, is about 14 μ (Pl. 17, Ca), that for length in the region of 25 μ (Pl. 18, Fc). When collected on diseased barley (Pl. 17, Ca-i) or quack grass leaves (Pl. 18, Ga-k) in midsummer, the spores are typically slightly or distinctly curved; 3 to 10 septate, widest near the middle, tapering slightly or sometimes quite considerably toward the ends which are rounded off abruptly, and show a hemispherical or hemiellipsoidal contour; and measuring usually 15 to 20 by 60 to 120 μ . On wheat heads, (Pl. 18, Fa-q), or on the bases of wheat or barley plants, apparently in response to more moist conditions, the spores are more apt to be atypical, being either straight or, if curved, curved irregularly (Pl. 18, Fd, f, j); showing unusual variability in width, which fluctuates not only with respect to different individuals but also in respect to different portions of the same spore (Pl. 18, Fi); exhibiting often marked irregularity in regard to septation, the septa occurring at unequal intervals, often at planes decidedly oblique to a plane perpendicular to the longitudinal axes of the spore (Pl. 18, Fk, n), and occasionally quite approximating a longitudinal position, thus bringing about a muriformly septate condition (Pl. 18, Ff, h, i). The same departures from the curved, long-ellipsoidal type is exhibited also by spores developed on plants in the greenhouse and perhaps to an even greater extent by those produced in pure culture on artificial media. In the latter case the diminution in size is unusually great, the spores there (Pl. 19, C, Da-c) generally not exceeding in length more than one-half the length of the typical ones to which, however, they are not markedly inferior in width. Very frequently, indeed, they become reduced to subspherical bodies, not appreciably greater in length than in diameter, often nonseptate or with a single cross wall (Pl. 19, C). A straight, short ellipsoidal shape is thus characteristic of the spores developed in the greenhouse or in artificial culture (Pl. 19, E), a shape which may be modified by irregular curvatures or distentions, or by the flattening or even incipient bifurcation of the apical end (Pl. 19, Dc).

But, however variable in shape, the spores of *Helminthosporium sativum*, when fully matured, are uniformly of a dark olivaceous color, and always exhibit a thick peripheral wall and a conspicuous hilum that is situated within the contour of the rounded basal end. As long as the peripheral wall is uninjured, germination regularly proceeds by the proliferation of two terminal germ tubes, one at the apex and the other immediately adjacent to the hilum (Pl. 17, Da, b; Pl. 18, Gc; Pl. 19, Da, b, d). Atypical spores, with the distal end flattened or bilobed, may produce three germ tubes, one arising from each of the lateral apices as well as from the proximal end. (Pl. 19, Dc.) Germ tubes apparently are never produced normally from the intermediate segments. Viability is retained for a considerable period of time, spores from material stored in the laboratory a whole year having been germinated by the writer without much difficulty.

Helminthosporium sativum is very readily cultivated on the substrata ordinarily employed in laboratories. On hard potato glucose agar containing an abundance of organic food material the aerial growth is

represented usually by a compact velvety layer of a black olivaceous color, composed entirely of short crowded sporophores. If less agar-agar is used, leaving a slight excess of free water, a fluffy, dark greenish brown aerial mycelium, interspersed often with matted masses of white mycelium, is produced. Often the vegetative growth is largely present as a firm coriaceous bluish-black crust. In older cultures masses of compacted white hyphae of secondary origin may be thrust through the layer of sporophores giving rise to an appearance suggesting contamination by another fungus. On corn-meal agar or tap-water agar, containing only small amounts of organic food material, the growth below the surface of the substratum is relatively sparse, being limited to moderately remote hyphae branching and anastomosing freely but without the production of lobulate segments. (Pl. 19.) Scattering sporophores arise at intervals as branches of these hyphae, and in the course of 4 to 6 weeks develop into long structures, intricately contorted, often bearing one or several branches, and scores of successively proliferated spores. (Pl. 19, A, B, C.) *Helminthosporium sativum* is thus readily distinguished by its macroscopic cultural characteristics from congeneric species with subhyaline spores even when occurring on the same hosts, as *H. teres* and *H. gramineum* on barley and *H. tritici-repentis* on quack grass. Cultural characters, however, are of little assistance in distinguishing it from a considerable number of forms like *H. monoceras*, that exhibit great similarity in development and in general habit of growth.

The responsiveness of *Helminthosporium sativum* to obvious differences in environmental conditions, illustrated, for example, in the results obtained by Dosedall and Christensen (30) in their study of variations in length of spores, makes it less easy to define this, as well as many other species, with as great precision as might be desired. The difficulty is further accentuated by evidence of lack of uniformity under apparently similar conditions of growth. In a recent extensive paper, Stevens (142) has called attention to morphological differences existing between strains of *Helminthosporium* isolated from wheat affected with footrot. These strains this author assigned to the "*H. sativum* group, which consists of a large number of elementary species." The mode of origin of presumably new strains as aberrant sectors in plate cultures was designated as "saltation," and found in some races to be of frequent occurrence. What the significance of such phenomena may be, and to what extent they correspond to realities in nature, constitute questions open to conjecture. In any case, the fungus under consideration can hardly be regarded as especially extraordinary. Variability of the sort represented here, is probably more nearly the rule among species of fungi than the exception. The writer is inclined to believe that the amount of morphological versatility observed in a species is often contingent in a larger measure on the possibilities its distinctive structures possess for expressing readily demonstrable differences than on the degree in which it may be lacking in genetic unity. Thus, for example, the relatively short conidia of *H. triseptatum* with a maximum of three cross walls, could never exhibit the wide fluctuations in length and septation possible in spores of species like *H. oryzae* or *H. rostratum*. This obvious limitation in the possibility of variation, may very largely account for the uniformity of the small-spored species of *Helminthosporium* as compared with the larger-spored forms, of which *H. sativum* is an example.

CONTROL

As the disease of barley and wheat due to *Helminthosporium sativum* is attributable on the one hand to primary infection of the seedling, resulting from the use of infected seed, and on the other to secondary infection of the growing plant, two lines of procedure in attempting their control are indicated. To prevent primary seedling infection, the use of none but clean seed naturally suggests itself. If affected seed stock must be used, the hot air treatment devised by Atanasoff and Johnson (3) constitutes a very effective means of obviating the primary manifestations of the disease in barley. Although these authors did not include wheat seed infected with *H. sativum* in their tests, there is good reason to believe that the hot air treatment will prevent the appearance of primary lesions in the resulting seedlings. Some preliminary trials with badly discolored wheat seed carried out in Washington indicate that treatment with certain organic mercury compounds controls seedling blight quite completely.

Although the elimination of primary infection, by bringing about a reduction of the amount of inoculum available early in the season, may well be expected to moderate subsequent infection, it is scarcely probable that injury to individual fields of barley, wheat, and rye can be prevented except by controlling the fungus on a more comprehensive scale. Such control, barring the likelihood of strictly specialized races, would appear to involve measures like the widespread use of clean or disinfected seed by all growers within the community, and the suppression of uncultivated grasses that serve as congenial hosts, as, for example, quack grass. Generally approved agricultural practices, like judicious rotation of crops, clean cultivation, and the use of manure containing diseased straw only on fields that are to be planted to immune crops—all tending toward making the inoculum of one season ineffective in reestablishing the fungus in the next—also ought to prove beneficial.

As methods of disease control contemplating the approximate elimination of a fungus as generally distributed as *Helminthosporium sativum* are necessarily rather uncertain, the possible development of resistant varieties of the various cereals affected would seem to hold forth most promise. The work of Hayes and Stakman (53) revealed pronounced differences in susceptibility to spotblotch between various varieties of barley, and showed that resistance is inherited. Thus, on crossing a rough-awned resistant type with a smooth-awned susceptible one, these authors demonstrated the possibility of obtaining a variety combining the desirable smooth-awned character of one parent with the resistance of the other. A study of commercial varieties suggested that resistant barleys of any botanical group could be produced. While in wheat and rye the organs most severely attacked are the roots and stem rather than the leaves, it is hardly possible that this fact in itself would constitute an obstacle to successful breeding work with these cereals.

HELMINTHOSPORIUM MONOCERAS, N. SP.

In September, 1920, the writer observed near Port Washington, N. Y., on Long Island, a stand of barnyard grass (*Echinochloa crus-galli* [L.] Beauv.) that appeared to be quite severely affected by a type of spotblotch. (Pl. 20, A.) The upper leaf blades, otherwise entirely green and healthy, bore dark brown or chocolate-colored spots (pl. 20, B), measuring 0.3

to 1.0 mm. in width by 1 to 3 mm. in length, without any indication of a zone of etiolated tissue, as is present on leaves of *Bromus inermis* attacked by *Helminthosporium bromi*. The lower leaves were largely withered, apparently as a result of the same pathological conditions present in the younger foliage, and exhibited an abundance of similar elliptical spots, which here, however, were somewhat larger, often attaining a width of 1.5 and a length of 5 mm. The older spots, moreover, showed less distinct outlines, having faded to a dull medium brown. On the leaf sheaths the discoloration was less intense than on the blades and extended over larger, less well-defined areas, especially near the base of the plant, the lower portions of the basal sheaths being often quite completely tinged with a diffused brown. In short, the symptoms were very similar to those previously observed on *Poa pratensis* attacked by *H. vagans*, representing a combination of foliar lesions like those caused by *H. sativum* on barley, and a footrot condition such as is caused by the latter fungus on wheat; and a cursory examination of the material might readily have led one to attribute the injury to either one or the other of these two parasitic species.

The microscope did, indeed, reveal an abundance of fructifications of *Helminthosporium* on the older withered leaf blades and dead basal sheaths of the host, which by their distribution left no doubt as to their relation to the foliar lesions observed. Somewhat to the writer's surprise the fungus, however, was markedly different in a number of details from both *H. sativum* and *H. vagans*. The dark brown sporophores (Pl. 20, Ca-Cc), which usually emerge from the stomata singly or in groups of two or three, and are only slightly greater in diameter than those of *H. sativum*, attain a height frequently more than twice as great as those of the latter species and in a corresponding measure are more remotely septate. The spores (Pl. 20, Da-n), the points of attachment of which are marked by geniculations occurring at moderately long intervals, are the most characteristic structures, however, being of a form so distinctive that they would readily be recognized in a mixture with spores of *H. sativum* or *H. vagans*, or indeed of any species discussed in the present paper. Usually widest near the middle, they taper gradually and quite uniformly toward the distal end until, at a point where the diameter scarcely exceeds one-third of the maximum diameter, they are abruptly rounded off to form the tip. The proximal portion of the spore tapers toward the base, usually somewhat more sharply, and the tapering is here prolonged uniformly until the diameter often represents less than one-sixth of the maximum diameter. A short distance above the hilum the contours usually exhibit a slight convexity. The hilum protrudes quite conspicuously, the fungus in this respect resembling *H. turcicum* and *H. rostratum*.

The conidia on being mounted in water germinate readily by two polar germ tubes, one from each end cell. (Pl. 20, Ea-c.) As has been mentioned in another connection, the spore wall is perceptibly thinner in the regions from which the germ tubes always are produced; that is, at the apex and in the narrow contracted zone adjacent to the hilum. Owing to the absence of olivaceous coloration from the modified regions, the portion of the spore near the hilum appears conspicuously subhyaline.

On the types of artificial media ordinarily employed in laboratories the fungus grows luxuriantly, though without manifesting any cultural characters which would enable one to distinguish it readily from other dark, abundantly sporulating congeneric species, as for example, *Hel-*

minthosporium sativum, *H. halodes*, or even *H. turcicum*. On media containing much organic food material, like potato glucose agar, a black velvety mat of sporophores results; on less concentrated media, like tap-water agar or cornmeal agar, growth is much less profuse and the individual fructifications are scattered sparsely over the surface. A comparison of Plate 21 with Plates 19, 23, and 25 reveals the similarity of the fungus to the other species mentioned in respect to general habit, mode of development, and relationship of conidiophore and imbedded mycelium. The conidia, which are produced in abundance (Pl. 21), although in general smaller than those developed in nature, are otherwise quite similar to the latter in shape and septation, and show very clearly the characteristic tapering of the acuminate basal portion toward the protruding hilum (Pl. 21, F).

Although observed thus far only at one station, perhaps largely because the host is not especially abundant in the region in which the writer carried on his studies, the fungus appears to be a parasite of more than moderate virulence. It would not be surprising to find it fairly common in agricultural regions where barnyard grass occurs to some extent.¹⁴ In this connection it may be mentioned that Schweinfurth and de Thuemen (1871) reported *Helminthosporium flexuosum* Corda (= *Brachysporium flexuosum* [Cda] Sacc.) on the culm and inflorescence of *Echinochloa crus-galli* in Egypt. While there is some reason to doubt that the fungi from various sources that have been referred by different writers to Corda's species are all identical with each other, such identification may safely be interpreted to indicate spores of a relatively small size, measuring approximately 8 to 16 μ in length, and divided by 2 or 3 septa. Manifestly the fungus in question is altogether different from the Egyptian form. It is apparently new to science and, owing to the characteristic shape of the proximal portion of its spores crudely suggesting that of a horn, is designated here as *Helminthosporium monoceras*.

DIAGNOSIS

Helminthosporium monoceras, n. sp.

Producing dark brown or chocolate-colored spots on leaf blades of *Echinochloa crus-galli* (L.) Beauv., at first measuring 0.3 by 1 mm., later increasing in size and eventually attaining linear dimensions five times as large. On the sheaths the spots are larger, less intensely colored, and tending to become confluent, especially toward the base of the plant, where they frequently merge into a generally diffused light brown discoloration; the foliar structures attacked dying prematurely, the withering proceeding from the tip toward the base.

Conidiophores appearing after the death of the affected tissues, thick-walled, emerging usually from stomata, singly or in groups of 2 or 3; measuring 6 to 9 μ in diameter and 120 to 325 μ in length; dark brown or olivaceous except at the extreme tip which is nearly hyaline; usually 3- to 7-septate, the septa occurring at intervals of 30 to 60 μ ; producing the first spore 120 to 200 μ from the base, its position, as well as that of subsequent spores, indicated by scars at moderate geniculations separated at intervals varying from 5 to 50 μ .

Spores yellowish when young, becoming dark olivaceous when fully matured, exactly similar in color to *Helminthosporium sativum*, *H. vagans*, and *H. rostratum*; measuring usually 15 to 22 μ in diameter and 40 to 150 μ in length; typically straight or showing a slight crescentic or sigmoid curve, yet not infrequently exhibiting more pronounced irregular or geniculate bends; widest at the middle segment except where modified by an irregular median constriction, typically tapering gradually toward the tip to one-third or one-half of its maximum width, then bluntly rounded off; tapering toward the base to approximately one-sixth of the median diameter, the contours then

¹⁴ Since this text was written the fungus has been collected on barnyard grass at Bladensburg, Md., and Takoma Park, Md., both of these stations being located in the immediate vicinity of Washington, D. C.

curving gently into the protruding hilum; 3 to 10 septate, the septa not usually associated with perceptible constrictions in the peripheral wall. The peripheral wall at maturity, thick as in *H. sativum* or *H. vagans*, except at the apex and about a subhyaline narrow zone at the proximal end immediately adjacent to the hilum, where it remains thin. Germinating by the production of two polar germ tubes, one from each of the thin-walled regions.

On artificial media, at ordinary temperatures, producing conidia smaller than those produced under natural conditions but of the same characteristic shape. Vegetative mycelium light fuliginous, 2 to 4 mm. in diameter, anastomosing abundantly by smaller subhyaline branches without the production of lobulate segments. Sporophores fuliginous, thin-walled, often exhibiting a tendency toward branching; approximately 5 μ in diameter, arising abruptly as branches from vegetative hyphae; or narrow at the point of origin and expanding more gradually; provided with septa generally at intervals of from 30 to 50 μ and proliferating spores at considerably shorter intervals than in nature, thus producing a moderately compact racemose cluster.

HABITAT.—Collected at Port Washington, N. Y., September 20, 1920, in a moderately moist situation near the sea.

HELMINTHOSPORIUM HALODES, N. SP.

During the latter part of the growing season of 1920 the writer kept under observation a stand of *Distichlis spicata* (L.) Greene growing on a salt marsh near Douglaston, N. Y., on the northern coast of Long Island. Collections of the grass made on different dates, September 10, September 26, and October 5, revealed indications of injury immediately suggesting similarity to the symptoms of spotblotch and footrot produced on other graminaceous hosts by various species of *Helminthosporium*, like *H. sativum*, *H. monoceras*, and *H. vagans*. The lesions were present on the otherwise healthy foliar parts as dark, discolored areas, with a bluish cast, not definitely circumscribed, the margins fading insensibly into the green of the surrounding tissue. (Pl. 22, A.) On the leaf blades the discolored spots were generally relatively infrequent; they were found more commonly on the sheath, especially on the upper portion immediately below the attachment of the blade. After the death of the affected tissue, the discoloration usually lost some of its intensity, the spots then appearing as rather vague blotches not readily distinguishable from similar blotches commonly found on the dead plants but attributable to other agencies.

Microscopical examination of dead affected foliar parts revealed a species of *Helminthosporium* present in meager quantity as the probable cause of the disease. Sporophores (pl. 22, Ef-g) occurring on the leaf blades were always found entirely denuded; and whatever spores could be discovered were as frequently found adhering to obviously unaffected tissues or lodged under the upper edge of the leaf sheaths as scattered on the epidermis in proximity to the sporophores. In view of the fact that the host is occasionally inundated by tidal water, an explanation for such a condition is manifestly not difficult to find. To determine whether the disease observed bore any relation to the *Helminthosporium* fructifications, freshly affected green parts were dissected out and incubated in a damp chamber. After 15 days the discolored areas were covered with a dense growth of conidiospores bearing conidia corresponding quite closely to those found in nature. Pure cultures made from spores obtained directly from the material as it was collected and from spores developed in the damp chamber further demonstrated the specific identity of the two lots of material and consequently also the parasitic nature of the fungus originally observed.

As might be expected from the similarity of pathological symptoms, the fungus shows a fairly close resemblance to *Helminthosporium sativum*.

The conidiophores, as occurring in nature (Pl. 22, Ef, g) or developed on the natural substratum in a damp chamber (Pl. 22, Ea-e), are somewhat inferior in diameter to those found on barley leaves affected with spotblotch and generally noticeably shorter. The conidia are of the same type as those of *H. sativum*. As found on material collected in the field (Pl. 22, Ba-f), however, they are usually more narrow and not as regularly crescentic, being more frequently straight or irregularly curved. In color they are usually brownish yellow instead of olivaceous. In a certain proportion of the spores, moreover, the end cells are less deeply colored and the basal and distal septa appear conspicuously darker or heavier than the intermediate cross-walls. (Pl. 22, Bd-f.) When developed in a damp chamber on diseased host material the conidia approach those of *H. sativum* in depth of coloration; but the distinction between dark intermediate segments and subhyaline or fuliginous end segments set off by conspicuously accentuated septa becomes a constant characteristic. (Pl. 22, Da-f.) And while the apical end is rounded off quite abruptly as in *H. sativum*, the proximal end shows a more perceptible tendency to taper, recalling in some instances the decidedly acuminate contour of the proximal portion of the spores of *H. monoceras*. As in the latter species, this gradual tapering is associated with a hilum that protrudes from the basal contour of the conidium.

In the species parasitic on *Distichlis spicata* the peripheral wall of the conidium varies more or less in thickness, depending apparently on the conditions under which the fructifications are developed. The darker, more mature conidia usually possess a peripheral wall which, if not as massive as in *Helminthosporium sativum*, nevertheless is of at least moderate thickness. As in *H. monoceras*, the wall is very thin at the apical end and over a narrow zone at the proximal end immediately adjacent to the hilum. Germination regularly occurs by the production of two polar germ tubes, one from each of these thin-walled regions. (Pl. 22, Ca, e, i.) In the case of immature spores and often in the brownish yellow ones found in nature the peripheral wall is thinner, frequently collapsing when the contents of the segments inclosed degenerate. Such spores may germinate by the production of lateral germ tubes from one or more of the intermediate segments as well as from the end segments (Pl. 22, Cb, c, d, f, g). This mode of germination, however, can scarcely be regarded as typical for the species.

The fungus is cultivated readily on artificial media, producing a luxuriant dark olivaceous aerial growth, consisting of a variable quantity of mycelium bearing an abundance of sporophores. When grown on tap-water agar, the fructifications (Pl. 23, A-C) resemble those developed on parts of the diseased host after incubation in a damp chamber. The spores (Pl. 23, B, D-G), which are attached at short intervals on the very irregular sporophore at wide angles and in moderately compact racemose arrangement, however, are usually perceptibly shorter. As in *Helminthosporium sativum*, the conidia frequently exhibit irregularities in shape, including flattening or bifurcation of the apical portion. (Pl. 23, D, F.)

Besides resembling in some details the different species which have already been mentioned, the fungus suggests comparison with *Helminthosporium leersii*, and perhaps more especially with *H. oryzae* and *H. rostratum*. From *H. leersii* it may be distinguished readily by the subhyaline end segments, the accentuated end septa, and the protruding hila characteristic of its spores. While *H. leersii* on artificial media

produces a greyish aerial mycelium, the growth of the parasite on *Distichlis spicata*, as has been noted previously, has a very dark if not almost black appearance. *Helminthosporium oryzae*, on the other hand, could be confused with the fungus under consideration only when cultivated on a substratum on which its spores develop dark pigment, as, for example, potato dextrose agar. The greater dimensions of the conidiophores and conidia produced by the rice parasite and the position of the hilum within the contour of the peripheral spore wall constitute, however, features by which the two species can be distinguished in spite of some similarity due to the occurrence of subhyaline end segments in both. Moreover, while the spores of *H. oryzae* tend to taper strongly toward the tip, and to a smaller extent toward the base, those of the fungus on *Distichlis spicata* show relatively slight tapering toward the abruptly rounded apex, while the proximal portion usually tapers markedly toward the base. The resemblance between the latter fungus and *H. rostratum* is attributable to similarity in color of the conidia as well as to the presence in the spores of both species, of protruding hila, and of accentuated proximal and distal septa. The parasite on *Distichlis spicata*, however, is inferior in the dimensions of both sporophores and spores and never exhibits the rostrate modification of the apical end characteristic of the conidia of *H. rostratum*. It appears not to have been described hitherto. As it is the first member of the genus, as far as the writer is aware, to be found occurring as a parasite on a host more or less frequently flooded with sea water, the specific name *halodes* is suggested.

DIAGNOSIS

Helminthosporium halodes, n. sp.

Occurring on the foliar organs of *Distichlis spicata* (L.) Greene, on which it causes a disease not usually destructive, manifested by the appearance of poorly defined bluish discolored areas especially on the leaf sheath immediately below its juncture with the blade.

Conidiophores arising from discolored spots after death of host, singly or in groups of two; measuring generally 4 to 7 μ in diameter by 60 to 150 μ in length; producing first spore usually 60 to 100 μ from base, successive spores at intervals of 5 to 15 μ at apices of geniculate irregularities; 1 to 5 septate, the length of segments highly variable, typically 15 to 30 μ .

Conidia as produced under natural conditions straight or curved; measuring 10 to 14 μ in width by 20 to 105 μ in length; 1 to 12 septate, the septa in immature spores associated with barely perceptible constrictions of the peripheral wall, in mature spores not associated with constrictions; brownish yellow, the end segments sometimes lighter in color or subhyaline, and delimited by accentuated septa; tapering slightly toward the broadly rounded apex, and more markedly toward the more narrowly rounded or somewhat acuminate basal end, which is uniformly distinguished by the protruding hilum. Mature spores germinating typically by the production of two polar germ tubes, produced at thin-walled regions at tip and immediately adjacent to hilum; germination of immature thin-walled conidia often atypical, owing to the production of additional germ tubes from one or more intermediate segments.

When cultivated on natural substratum in damp chamber, fructifications similar but capable of more extensive development; spores somewhat shorter, usually thicker, and tapering more perceptibly toward both ends; dark olivaceous, the end segments subhyaline or light fuliginous and set off by accentuated septa. On artificial media not rich in organic food material conidiophores arising as lateral branches from prostrate hyphae, bearing conidia in moderately dense racemose arrangement at geniculate irregularities occurring at short intervals; conidia as on natural substratum dark olivaceous provided with subhyaline end segments and with moderately thick peripheral wall but shorter, often being nearly ellipsoidal in shape.

HABITAT.—Collected at Douglaston, N. Y., near New York City, in September and October, 1920.

HEMINTHOSPORIUM LEUCOSTYLUM, N. SP.

In October, 1921, the writer collected specimens of *Eleusine indica* (L.) Gaertn. near Washington, D. C., some of the leaves of which were partially or wholly withered. Most frequently the tip alone was affected, but in other instances the blade was involved down to its juncture with the sheath. The dying portions of the leaf were characterized by the presence of small, irregular, poorly defined, reddish-brown spots, somewhat suggestive of the discoloration produced by *Helminthosporium avenae* on the foliage of oats.

On examining thoroughly withered portions of leaf which, like barley leaves affected with stripe, showed a pronounced tendency to split into numerous longitudinal shreds, fructifications of a fungus apparently referable to the genus *Helminthosporium* were found in moderate abundance. As these portions frequently bore also a considerable growth of undoubtedly saprophytic forms, mainly *Alternaria* spp., the spots previously mentioned were largely obliterated by miscellaneous local and diffused discolorations. It was consequently not possible to decide definitely as to the existence of any causal relation of the species of *Helminthosporium*, either to the withering observed or more particularly to the foliar lesions that appeared to be associated with it. To distinguish the fungus from the congeneric forms, *H. giganteum* and *H. cynodontis*, occurring on the same host, as well as from *H. nodulosum* B. & C., an apparently widely distributed parasite attacking the inflorescence of goose grass, it may not be superfluous to include a brief account of its morphological features.

The conidiophores (Pl. 23, Ha-e, Ia-d) exhibit a particularly striking departure of the fungus from the type that appears to be common to most graminicolous species of *Helminthosporium*. Instead of growing to a considerable length before beginning to proliferate conidia, they develop the first spore while still relatively short. Owing to this initial economy and to the moderately short intervals between successive spores, the ultimate length of the sporophore is conspicuously inferior to that of most congeneric species. Perhaps quite as remarkable is the absence of the usual deep olivaceous color from these structures, which are, generally, nearly colorless or of a light fuliginous tinge. It is interesting to note, besides, that the sporophores, like those of *H. turcicum*, appear to emerge only from the stomata, and in relatively large groups.

The conidia (Pl. 23, Ja-r), which resemble those of *Helminthosporium sativum* and many other species in being of a deep olivaceous color, in the possession of a thick peripheral wall, and in mode of germination, frequently show a pronounced tendency to taper toward the apex (Pl. 23, Jg, i). Indeed, the writer was at first inclined to refer the species to the genus *Napicladium* because of this tendency. However, as in numerous instances a subcylindrical shape is approximated (Pl. 23, Jb, p.), it appears better to refer it to the genus *Helminthosporium*, which, moreover, contains other species characterized by spores frequently tapering very perceptibly toward the apex, as, for example, *H. gramineum*. The attenuation of the peripheral wall at the places from which the germ tubes are destined to appear is very marked, being evidenced as in *H. halodes* and *H. monoceras*, for example, by small, altogether hyaline regions, one at the apex and another immediately surrounding the hilum. The germ tubes are relatively narrow, and, in elongating, more

inclined to make irregular turns and unusual angles than those of most congeneric forms. (Pl. 23, Ka-c.)

The specific name *leucostylum*, descriptive of the conidiophores of the fungus, is suggested.

DIAGNOSIS

Helminthosporium leucostylum, n. sp.

Occurring on withering or withered leaves of *Eleusine indica* (L.) Gaertn.

Conidiophores subhyaline to light fuliginous, emerging from stomata singly or in groups of 2 to 6; measuring usually 5 to 6 μ in diameter by 35 to 100 μ in length; 2 to 8 septate, the cross walls usually inserted at intervals of 10 to 30 μ ; producing the first spore 20 to 50 μ from base, and successive spores at intervals of 5 to 25 μ , the points of attachment being marked by circular scars at the apices of usually very pronounced geniculations or more rarely at the tips of short lateral branches.

Spores dark olivaceous; measuring 11 to 17 by 15 to 67 μ , typically approximately 15 by 50 μ ; 1 to 6 septate, typically 3 to 5 septate, the septa never associated with constrictions; usually narrowly ovoid, widest well below middle, near a point approximately one-third of distance from base to apex, the proximal portion exhibiting a paraboloid contour, the distal portion tapering uniformly to the narrow apex, then abruptly rounded off; more rarely and atypically subcylindrical, and, when short, ellipsoidal, ovoid or obovoid; exospore thick except at a small subhyaline spot at apex and in narrow subhyaline zone immediately surrounding the hilum which is contained within basal contour. Spore germinating by production of 2 polar germ tubes, one from each of the small hyaline regions.

HABITAT.—Collected near Washington, D. C., October 9, 1921.

During August and September, 1922, after this paper had been submitted for publication, the fungus was collected repeatedly on *Eragrostis major* in several localities in Virginia and Maryland near Washington, D. C., generally occurring together with *Helminthosporium rostratum* and, more rarely, also with *H. giganteum*. It was found to be present in abundance on the same host near Seaford, Delaware, where collections were made August 29, 1922. The relation of *H. leucostylum* to *Eragrostis major* is an obviously parasitic one, as on green and otherwise healthy leaves the fungus gives rise to dead regions that appear on the upper (adaxial) side, typically as sharply delimited medium-gray linear streaks measuring 0.3 to 0.5 mm. in width and 5 to 20 mm. or more in length. The sporophores arise on the killed areas usually in dense clusters which often are found in longitudinal alignment. Apparently they develop earlier and often in greater abundance on the upper side than on the lower side of the leaf, probably emerging from between epidermal cells as well as from the stomata. On being dried, the diseased leaves, like those of similarly affected goose grass, split readily into longitudinal shreds along the streaks representing the lesions.

The occurrence of the fungus on *Eragrostis major* suggests its comparison with *Helminthosporium hadotrichoides*, described on the same host from Delaware by Ellis and Everhart (36) in 1888. According to the diagnosis given by these authors, *H. hadotrichoides* would appear to produce conidiophores not greatly unlike those of the fungus under consideration in size and septation, but differing from them in being of a "smoky brown" color, and in having "the apex swollen so as to form a knob like the head of a pestle, 8 to 12 μ in diameter." A modification so striking and unusual could scarcely fail to arrest attention, yet was certainly never observed in any material examined by the writer. The conidia, which are rather inadequately described as "clavate-obovate, or clavate cylindrical or yellowish brown" without any mention being made either of their dimensions or septation, would seem to differ somewhat, at least in coloration, from the corresponding dark brown or dark olivaceous structures of the parasite discussed in the present account.

HELMINTHOSPORIUM TURCICUM PASSERINI

Helminthosporium inconspicuum Cooke & Ellis 1878, in *Grevillea*, v. 6, p. 88-89.

The disease of maize commonly known as "leaf blight" and less frequently as "white blast" is found in many regions of the globe in which this important cereal is cultivated. It appears to have been first observed by Passerini (105) in 1876, who noted its occurrence in Italy under the term "nebbia" and attributed it to a species of *Helminthosporium*, which he named *H. turcicum*. Two years later, Cooke and Ellis (24) described a form from New Jersey as *H. inconspicuum*, similarly thriving on maize. Although the descriptions of the American and Italian forms are not especially similar, there appears to be good reason to believe that they were based on material belonging to the same species.

In the account given by Cooke and Ellis, the American fungus is very briefly described:

Tenuissime effusum. Hyphis elongatis, septatis, nodulosis, pallidebrunneis. Sporis lanceolatis, 3-5 septatis; episporio tenui.

On *Zea mays*.

Effused, but so thinly as not to be visible to the naked eye. Spores 0.08 to 0.12 by 0.02 mm., at first with the endochrome divided, at length septate.

The parts of the statement regarding the number of septa, the visibility of the fructifications, and the alleged division of the endochrome previous to the division of the spore can scarcely be regarded as altogether correct, either for the parasite causing leaf blight or for *Helminthosporium sativum*, which, as has been pointed out in another connection, is known to occur on the organs of mature corn plants. The parts regarding the description of the sporophore, the shape and measurements of the spore, as well as the figure of the latter that accompanies the text, on the other hand, might apply about equally well to both species. Indeed the chief reason for regarding the description given by Cooke and Ellis as applying to the leaf blight fungus is not found in the single distinctive characterization—that concerning the thin episporium—but rather in the abundance of the parasite in the general region in which Ellis made his collections. In 1881, Peck (107) recorded the leaf blight disease in New York, although, as has been stated in another connection, his description of the fungus is less applicable to the parasite under consideration than to *H. sativum*. The trouble again was found in New York by Stewart (144) in 1896. In 1889 Thaxter (149) observed a serious outbreak of the disease in Connecticut, where 14 years later Clinton (21) found it again doing considerable damage. In 1903 the malady was quite destructive also in Delaware, according to the account given by C. A. Smith (133). During the same season Stone and Monahan (145) noted its abundance in Massachusetts; and Orton (99) found it very general also in eastern Pennsylvania and New Jersey. Since then it has been reported repeatedly not only from the Middle Atlantic and New England States, but from other sections as well, the records of the Plant Disease Survey indicating its presence in nearly every State east and in some of the States immediately west of the Mississippi River.

Stevenson and Rose (143) reported leaf blight of corn as occurring in Porto Rico. Robinson (122) in 1911 observed the disease in the Philippines, where it has been noted also since then by Baker (5) as well as by Reinking (117). Tryon (153) records an outbreak of the trouble in New South Wales in the season of 1886 so destructive as to attract

widespread attention; and in recent years Darnell-Smith (27) lists "leaf stripe" among the diseases affecting maize in the same Province. Yoshino (161) reported *Helminthosporium turcicum* as occurring on *Zea mays* in the Province of Higo, Japan, in 1905. According to Butler (19) the disease is fairly common in India and occurs in South Africa. The European literature concerning the disease does not appear to be extensive. Ducomet (34), in 1903, recorded its appearance under the name of "brulure" in the southwestern part of France. More recently the publication of a paper by Zhavoronkov (162) would seem to imply its distribution in Russia.

In general, leaf blight is a disease characteristic of the later stages in the development of the host. During the season of 1920, when the writer had occasion to follow its development in the sweetcorn fields of the western part of Long Island, it made its appearance toward the end of August. On plants examined on August 20, elongated straw-colored spots were present especially on the lower leaves, varying from 2 to 4 mm. in width, and from 5 to 15 mm. in length. The tissues involved in these spots were altogether dry. Usually at this stage the dry areas were delimited from the surrounding healthy parts by a brownish margin, quite conspicuous and distinct in some instances and barely distinguishable or absent in others. As the season progressed the affected areas rapidly increased in size, individual lesions frequently measuring more than 4 cm. in width and 10 cm. in length by September 16. (Pl. 24, A.) By the coalescences of the enlarging spots, extensive areas embracing often considerable portions of the leaf were found to be involved. Toward the end of September the foliage was withered to such an extent that some of the plants appeared, as some writers have suggested, as if affected by a frost.

When leaf blight appears as late in the season as in 1920, which probably was very nearly typical in regard to the development of the trouble at least for the northeastern section of the United States, the resultant economic damage is not likely to be serious. In most ordinary seasons Peck's (107) observation that *Helminthosporium inconspicuum* "seems to attack on lower leaves with vitality already impaired; not very noxious as it only hastens death of leaves by a few days or weeks," perhaps is not without a good deal of justification. Nevertheless, in other seasons, apparently as a result of weather conditions favorable to the fungus, the disease may make its appearance while the plant is still relatively young, and thus cause very considerable destruction. Thus Ducomet (34) records a severe outbreak in France in 1900 during an exceptionally wet season. According to this writer the foliar lesions appear when the plants are only 0.5 to 0.6 meters high. The destructiveness of the disease in 1903 in the States of Connecticut and Delaware apparently was associated also with its early appearance, Clinton (21) finding "many fields looking in August and September as if struck by early frost; heavy attack due to unfavorable season." In New South Wales the blight is reported (118) to appear invariably in all the late plantings of maize when the heavy autumn rains set in, particularly on low-lying situations. In the season of 1915 (118), however—

it appeared very much earlier owing to the phenomenally wet spring and early summer. Many areas were completely destroyed on account of the leaves being killed off long before the plants were half grown. Where cobbing had been well advanced the effects were not so serious.

