ZONATE EYESPOT OF GRASSES CAUSED BY HELMINTHOSPORIUM GIGANTEUM[1]

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INTRODUCTION

Helminthosporium giganteum Heald and Wolf (*6*)[2] was described in 1911 from Texas, where it was found occurring on diseased Bermuda grass (*Cynodon dactylon* L.), as the cause of lesions evidently of the eyespot type. The writer included a discussion of the fungus in a comparative account published in 1923 (*4*), in which its occurrence on goose grass (*Eleusine indica* (L.) Gaertn.) and quack grass (*Agropyron repens* (L.) Beauv.) was noted and the peculiar mode of germination characteristic of its conidia was described. In an abstract that appeared somewhat earlier (*3*) the parasite had been reported on nearly a score of additional species of grasses and an explanation offered of its method of extension as prevailing in the development of a much more destructive type of injury observed on several hosts and designated as zonate eyespot. In the present paper the degree of injury sustained by the grasses on which the fungus has hitherto been observed to occur naturally will be more fully discussed, together with certain features pertaining to the morphology and development of the parasite.

DISTRIBUTION AND SEASONAL OCCURRENCE OF PARASITE

Such fragmentary information concerning the distribution of *Helminthosporium giganteum* as it has been possible to obtain in occasional field trips undertaken for other purposes indicates that in the United States it is largely restricted to the southern and middle latitudes. Collections made by the writer at Seaford, Del., in August, 1922; at Hurlock, Md., in August, 1923; in the District of Columbia and neighboring sections of Virginia and Maryland in 1922, 1923, 1924, 1925, and 1926; and at Menfro, Mo., in August, 1924, provide clear evidence that the parasite is not limited to a strictly southern distribution. Precisely how much farther north its natural distribution extends is not known except that efforts to find the fungus in the western portion of Long Island during the seasons of 1920 and 1921, in the vicinity of Vincennes, Ind., in August, 1924, and in the vicinity of Allentown, Pa., in September, 1925, were unsuccessful, although grasses capable of serving as congenial hosts

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[2] Reference is made by number (italic) to "Literature cited," p. 492.

were present in quantity.[3] On the other hand, except apparently for mountainous and elevated regions, the parasite has been found of widespread occurrence in the Southeastern States from Virginia to Florida, while its prevalence in a number of localities in southeastern Missouri, visited in August, 1923, suggests a parallel distribution in the Mississippi Valley.

Helminthosporium giganteum shows much variability in the abundance of its occurrence from season to season. During the summer of 1922 it appeared in the vicinity of Washington, D. C., as probably the most destructive single fungous parasite affecting the Gramineae as a family, its attack on several of its hosts being of extreme severity, while on some others its attack, though less destructive, was nevertheless severe. During the seasons of 1923, 1924, 1925, and 1926 the fungus was far less prevalent and, in general, of only minor importance, although in a number of situations, as along the banks of the Chesapeake & Ohio Canal, it reappeared from year to year in nearly undiminished quantity. In addition to irregularity with respect to seasonal occurrence, it exhibits much less uniformity in local distribution than the large majority of parasitic fungi. Even in the season of 1922, when in many locations stands of Bermuda grass were all but killed as a result of the ravages of the parasite, it was not an unusual experience to find other stands of the same grass within a distance of less than 100 meters free of injury. Such pronounced inequality of distribution has been found characteristic of the fungus wherever adequate observations have been made, prevailing apparently in southeastern Missouri exactly as in Virginia and Maryland.

For such localized distribution a partial explanation may be offered. Compared to some of the more nearly ubiquitous types of foliar parasites—as, for example, *Helminthosporium sativum* P. K. & B.—*H. giganteum* produces even under favorable conditions a relatively small number of spores. These spores, as has been pointed out previously (*4, p. 676*), are the shortest lived spores of any species of Helminthosporium hitherto encountered by the writer. There is evidence, too, that they are not well adapted for extensive dispersal. The dissemination of conidia of *H. giganteum* can be studied to advantage in situations where a single isolated infected stand of a favorable host on which active sporulation is taking place is found adjacent to, or surrounded by, species of grasses allowing the production of only incipient lesions devoid of fructifications. The abundance or scarcity of sterile lesions on the uncongenial grasses in such circumstances may be regarded as a reliable index of the quantity of spores reaching any particular spot from the stand of the congenial species of grass. The numbers of such lesions fall off rapidly beyond distances of 1 to 2 meters; few are to be observed at a distance of 5 meters; only a vanishing quantity can be found at 10 meters, while none have ever been observed at a distance of 20

[3] As a pest affecting creeping bent grass in putting greens of golf courses, the fungus was found to occur during the season of 1928 in widely separated localities in the northern tier of Middle Western States. In the three localities where the writer had occasion to make observations, viz, La Fayette, Ind., Detroit, Mich., and Wooster, Ohio, natural stands of susceptible hosts (as, for example, quack grass) showed no evidence of infection with zonate eyespot. Nor were any signs of attack by *Helminthosporium giganteum* evident in the creeping bent immediately surrounding affected putting greens but not exposed to artificial watering. It appears highly probable that the success of the fungus well north of what would seem to be its natural range is contingent on the copious irrigation usual in the management of greens. As the grass is generally propagated by stolons, and since these to a large extent have been distributed from sources within the natural range of the parasite, the means by which the introduction of the latter into northern localities has been effected are sufficiently obvious.

meters. It is scarcely to be doubted that the unusual size and consequent relatively great weight of the conidia are in large part responsible for the restriction in spread. Obviously these bodies would scarcely remain suspended long in the somewhat quiet atmosphere often associated with the light, sustained precipitation that provides optimum conditions for their germination.

OVERWINTERING OF PARASITE

In the vicinity of the District of Columbia *Helminthosporium giganteum* ceases to develop vegetatively or to produce conidia with the advent of cool weather during the early part of October. The fungus appears to overwinter as dormant mycelium. At intervals during the spring of 1923, quack-grass leaves of the previous season, with well-developed lesions, were collected near Cabin John, Md., brought into the laboratory, and incubated in a moist chamber. Fresh conidia were obtained in this way until early in May, when, with the appearance of lesions on the new quack-grass foliage, the trials were discontinued. Although it was never possible to determine definitely that fresh conidia were not proliferated from the old conidiophores, most of the conidia were apparently produced on new conidiophores, and perhaps all may have had such origin.

DEVELOPMENT OF LESIONS IN RELATION TO SPECIFIC SUSCEPTIBILITY

Collectively the various grasses (pls. 1–7) found to show evidence of attack by *Helminthosporium giganteum* under natural conditions manifest the widest range in degree of susceptibility. The most general manifestation of an individual infection is the appearance on the foliage of a minute longitudinally elongated spot, the size and coloration of which vary with the host. In *Muhlenbergia schreberi* Gmel., for example, this spot first becomes visible as a sharply defined very dark speck, often not exceeding 0.05 mm. in width and 0.2 mm. in length. (Pl. 5, N–R.) Through subsequent enlargement it may attain a length of approximately 1.2 mm. and a width of 0.1 to 0.2 mm., then often revealing within these relatively minute dimensions a decolorized central region. In other hosts, where discoloration is less intense, the spots, when first recognizable, may be somewhat larger and less sharply delimited than in *M. schreberi*, and the primary lesions, before attaining definitive size, may become several times larger. The fading of the central region to yield the eyespot type of lesion generally distinctive of the disease occurs with less regularity in some hosts than in others. *Panicum dichotomoflorum* Michx., for example, as a result of frequent omission of this development, often exhibits the spot-blotch type in larger number. In timothy (*Phleum pratense* L.) the lesion is practically devoid of dark discoloration, being present as a dead region from which the normal green coloration has disappeared.

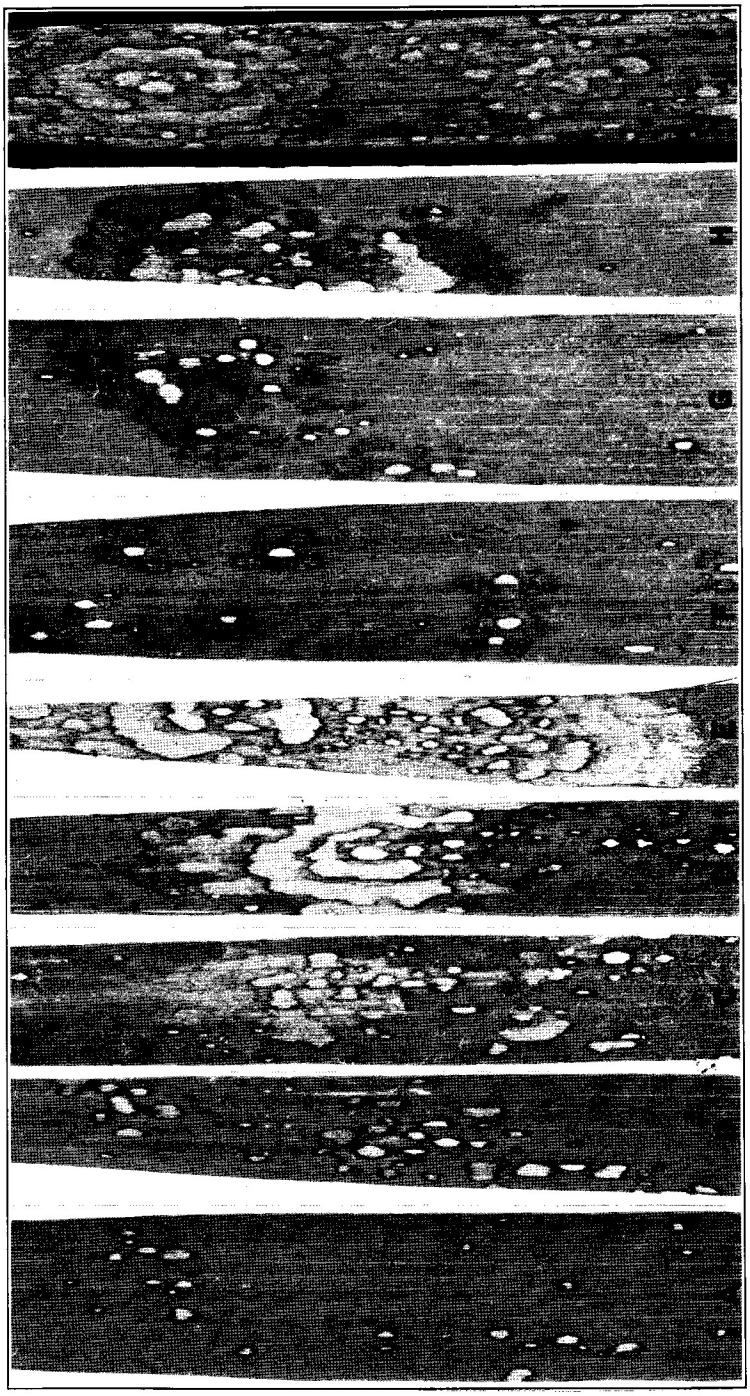
The mere occurrence of the eyespot type of lesion on a grass does not necessarily provide evidence of its suitability to serve as a host to *Helminthosporium giganteum*. In the case of many species of grasses such lesions have never been discovered except in mixed stands with more congenial hosts, on which the parasite is not only present but sporulating abundantly as well. In Virginia, Maryland, and Mis-

souri, Bermuda grass, goose grass, and quack grass appear to serve most frequently as sources of infection, most of the writer's observations on the response of other grasses having consequently been carried out when the latter occurred in immediate proximity to these widely distributed weeds, and most frequently as intimate admixtures. Under such circumstances the foliage of uncongenial hosts may bear an abundance of spots, as occurs, for example, in *Panicum clandestinum* L., or a few more remotely scattered ones may be produced, as in timothy. In any case the tissue involved never appears to give rise to fructifications of the fungus, nor can such structures ordinarily be obtained by incubation in a moist chamber. If the affected leaves are still green, the identification of the parasite may usually be accomplished, though somewhat laboriously, by isolating it from bits of tissue excised from the margins of lesions and planted on a suitable culture medium after surface sterilization followed by thorough washing with sterile water.

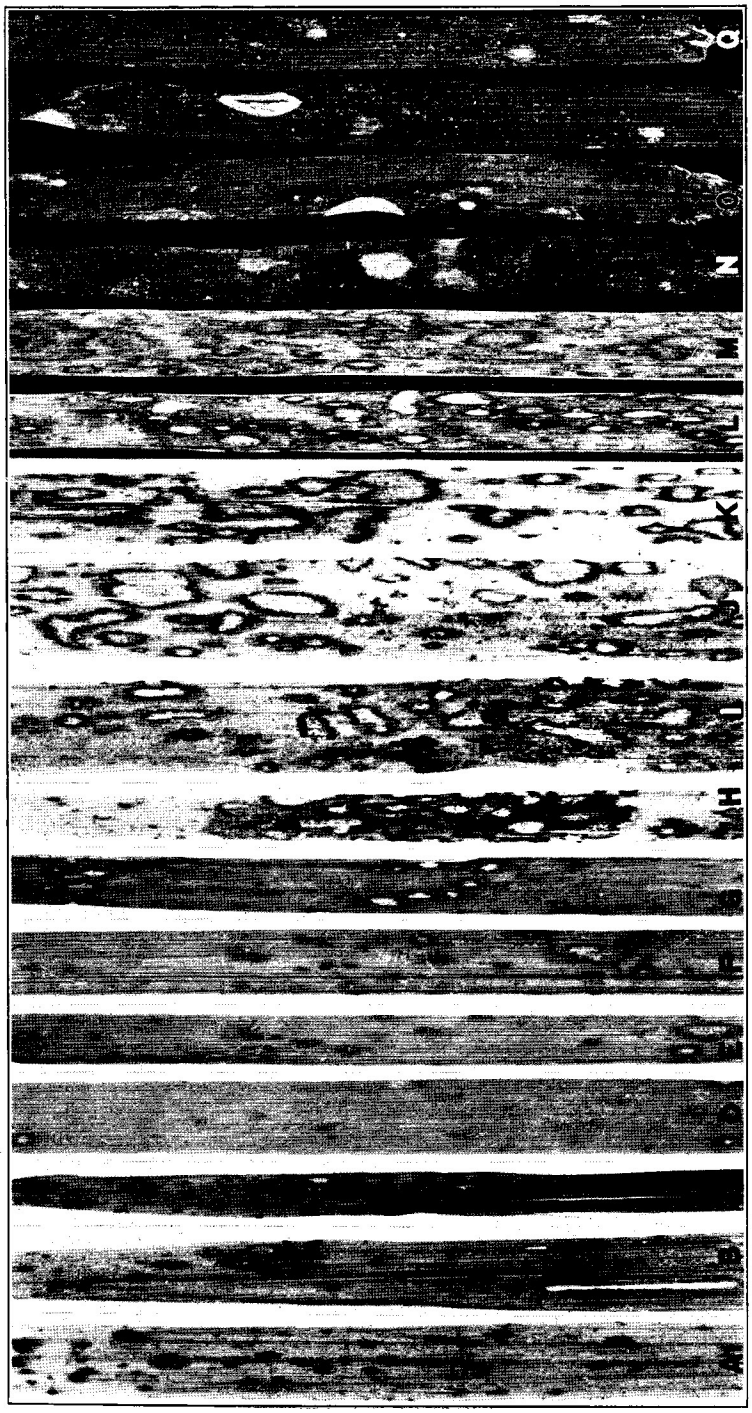
A readier and more certain method of determining the parasite under consideration as the effective causal agent is that of direct microscopic examination; for, owing to the extraordinary size of the conidia, the evacuated collapsed membranes of the individual spore usually can be discerned without the least difficulty on one surface or the other of the lesion that it produced. The examinations, it may be mentioned, revealed that very generally the greater number of infections result from spores on the upper or adaxial surface of the leaf, a fact to be attributed, perhaps, to the somewhat more effective exposure of this surface to air-borne bodies. On whatever surface the spore membranes may be found, however, they are always securely fastened to the host by the evacuated germ tubes, so that alcohol and clearing agents may be employed to improve the optical features of the material without incurring any risk of washing off the structures in question.

Most frequently the evacuated spore membranes occupy an approximately median position relative to the foliar lesion, the germ tubes from both ends having evidently been equally active in killing regions of tissue that became sufficiently extensive to coalesce into one. However, in the case of hosts in which, as in *Muhlenbergia schreberi*, the lesions are clearly delimited and very narrow, such coalescence does not always take place, particularly when the conidium is oriented in a direction transverse to that of the leaf. In such cases two distinct lesions separated by a distance not usually exceeding 0.3 mm., yet clearly evident as two to the naked eye, result from the germination of the single conidium. This condition is infrequent in fungous diseases generally, and manifestly is not readily possible with fungi having spores of more ordinary dimensions. A similar pairing is exhibited also by newly developed lesions on more favorable hosts (pl. 1, A), but owing to the enlargement and fusion of the individual spots the binary arrangement later becomes obliterated. Sometimes a spore may be more or less eccentric in position with reference to the lesion produced by it, evidently as a result of irregularities in germination due to accidents attending the process or to the previous death of some of the segments.

Among the uncongenial hosts considerable difference exists with respect to the number of lesions produced under circumstances equally favorable for infection. *Panicum dichotomoflorum* and *Muhlenbergia*



Portions of leaves of *Phalaris arundinacea* attacked by *Helminthosporium giganteum*. A–E, Series of specimens showing infection of increasing severity; F–H, Wafer-soaked zones surrounding lesions as a result of incubation in moist chamber for 16 hours; I, Leaf completely involved in extensive lesions with conspicuous zonate markings; × 2



Leaves of various grasses attacked by *Helminthosporium giganteum*. A–C, *Agropyron elongatum*, × 2; D–H, *A. intermedium*, × 2; I–M, *A. repens*, × 2; N–Q, *Agrostis stolonifera*, × 4

schreberi, when found in mixed stands with heavily infected Bermuda grass, are generally very liberally peppered with discolored spots, the lesions here being often as abundant as on the congenial hosts. On the other hand, *Panicum gattingeri* Nash, as well as timothy and Kentucky bluegrass (*Poa pratensis* L.), under the same conditions exhibit only a meager sprinkling of spots. Neither crabgrass (*Digitaria sanguinalis* (L.) Scop.) nor *Chaetochloa lutescens* (Weigel) Stuntz were ever found spotted by the fungus in the vicinity of Washington, D. C., during the five successive seasons in which observations were made. Near Kennett, Mo., however, lesions attributable to conidia of the parasite were found on both, though, to be sure, in small number. It is probable that such facts of presence or absence on a particular host may involve only casual details of distribution. On the other hand, they may point toward differences in environmental conditions, or toward possible differences in the biological constitution either of the parasite or of the grass host. In the absence of more precise information, it may be mentioned in this connection that, on the whole, the distribution of the fungus in nature does not suggest the existence of physiological varieties or races paralleling generic divisions in the Gramineae.

In the case of the more congenial hosts, the early stage in the establishment of the parasite is closely similar to the development of the small lesions just described. (Pl. 1, A, B.) The hyphae proceeding from the germinating conidium here also bring about the discoloration and death of a limited tract of tissue. On isolated eyespot lesions of such origin, fructifications of the fungus do not ordinarily arise. However, when, as in Bermuda grass, these spots become numerous and crowded, causing the leaf involved to wither somewhat generally, conidiophores appear in considerable abundance, from intervening regions as well as from the bleached areas included within the lesions.

A generally more copious production of sporophores and spores takes place on leaf tissue directly killed by the parasite as a result of a peculiar type of secondary development. This type of development is most strikingly exemplified on *Phalaris arundinacea* L. and appears to be dependent on the presence of liquid water on the surface of the leaf. When, because of heavy dews or prolonged drizzling rains, a layer of water persists 12 hours or more on infected foliage of reed canary grass, many of the eyespot lesions will be found surrounded by an enlarging water-soaked zone. (Pl. 1, F, G, H.) Microscopic examination of the surface of the leaf reveals the presence of hyphae arising near the edge of the original lesion and traversing the water-soaked zone radially to its margin, giving off branches in their course. These superficial filaments adhere very closely to the epidermis of the host, and would seem to communicate with the interior of the leaf by branches penetrating the epidermis, although the direct optical evidence for such communication is far from satisfactory. In any case, the water-soaked zone is rather accurately coextensive with the region included in the centrifugal growth of superficial hyphae. With the disappearance of the layer or film of water on the advent of drier conditions, growth of the superficial mycelium ceases and the zone of water-soaked tissue dries up, thus becoming the peripheral belt of the enlarged lesion. (Pl. 1, D.) When, as in the season of 1922, weather conditions are such as to permit repeated occurrence of the same cycle of development, many of the leaves

become entirely involved, the dead foliage, entirely covered with intricately zonate patterns, presenting a most distinctive aspect. (Pl. 1, E, I.) Irregularities in such patterns (pl. 1, D) are attributable, as might be expected, to the casual distribution of the moisture deposited, regions failing to become covered being recorded as interruptions in the zone developed during any particular moist period under consideration. The older leaves of reed canary grass usually show most extensive infection on the blade midway between base and tip. Field inspection has shown that this median portion also becomes more liberally bathed in dew, a fact due apparently to the drooping habit of the distal part and the accumulation of moisture near the keystone position on the resultant arch.

The importance of such secondary development in the biology of the parasite is considerable, as by far the larger portion of the conidiophores and conidia are produced in the extensive regions of host tissue killed thereby. The degree to which secondary development takes place on any host becomes thus a truer measure of its congeniality than the number of infections. Hosts that may well be regarded as congenial include, in addition to Bermuda grass and reed canary grass, *Agropyron repens*, *A. intermedium* Beauv., *A. elongatum* Host, *Bromus inermis* Leyss., *Eleusine indica*, *Echinochloa crusgalli* (L.) Beauv., *Elymus virginicus* L., *Lasiagrostis splendens* Kunth,[4] and *Leersia virginica* Willd. Under favorable conditions all of the grasses mentioned would seem to permit the parasite to propagate itself indefinitely. Sporulation was observed also on leaves of *Eragrostis major* Host and of *Muhlenbergia mexicana* (L.) Trin., though in such meager quantity as to render doubtful the capacity of the parasite to maintain itself on these grasses, except possibly under most favorable conditions.

ISOLATION AND ARTIFICIAL CULTIVATION OF PARASITE

The isolation of the parasite, though not excessively difficult, usually can not be accomplished with as much ease as the isolation of graminicolous species of Helminthosporium generally. Plantings made on a suitable agar medium, like maize-meal agar, with small pieces of tissue dissected from the margins of growing lesions, after surface sterilization and washings in repeated changes of sterile water, while not uniformly successful, afforded the most convenient means of securing pure cultures. The fungus, on growing out of the tissue, is recognizable by the fringe of aerial mycelium, composed of filaments of relatively large, unvarying diameter, with a distinctive branching habit, and disposed in snarls of numerous and often graceful curves. The mycelium immersed in the substratum lacks this disposition, but shows a similar degree of uniformity in diameter and a similar type of branching, with the contents generally homogeneous and moderately refringent. (Fig. 1.) Transferred to fresh media, the mycelium retains these tendencies. As growth is relatively slow, even at optimum temperatures, which seem to lie between 25° and 29° C., the snarled aerial mycelium, except at the growing margin, is usually dried out and collapsed. It then appears to the naked eye as a somewhat granular or flaky white or grayish material, sprinkled

[4] The binomial under which the plantings of this grass at the Arlington Experiment Farm were recorded and under which it was reported (5) as a host of *Helminthosporium giganteum* is retained here. Specimens kindly examined by A. S. Hitchcock were referred by him to *Stipa splendens* Trin.

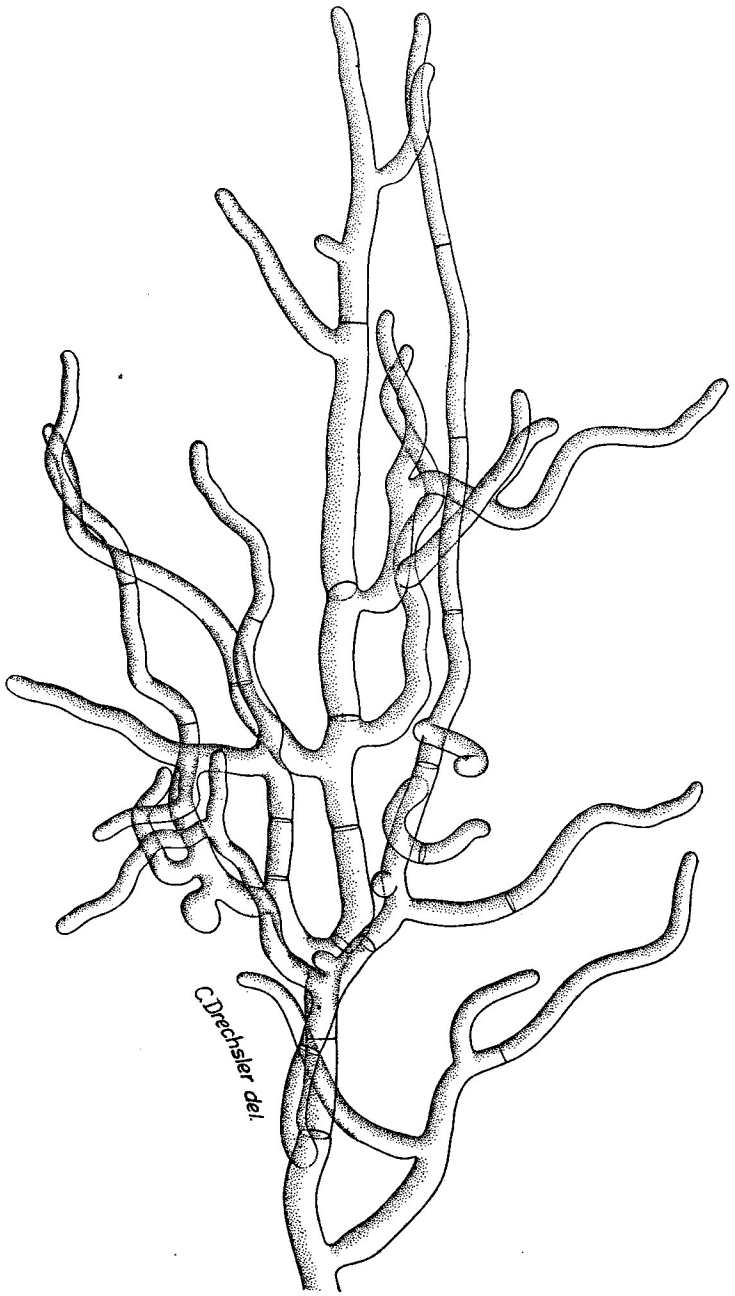


FIG. 1.—Portion of the submerged mycelium of *Helminthosporium giganteum* from the margin of growth on maize-meal agar. × 450

irregularly over the surface of the culture. (Pl. 8.) The submerged mycelium in the older portions of the culture is somewhat dark, and under the microscope appears well provided with septa, though apparently largely devoid of protoplasmic contents. A certain degree of zonation, involving both submerged and aerial mycelium, usually is evident.

Sporulation of *Helminthosporium giganteum* in culture generally is rather meager, but presents interesting features. The sporophores found scattered here and there consist of prolongations or branches of ordinary hyphae (fig. 2, D) from which they usually differ only slightly in a darker coloration and a somewhat thicker membrane. Many of the conidia are not markedly different from conidia developed under natural conditions. (Fig. 2, A–C.) Others, however, are markedly inferior in length and width. An irregular type of proliferation, evidently akin to germination, is frequent. In many instances this is expressed in the production, from the basal and apical segments where the whorl of germ tubes ordinarily arises, of two, three, or four structures that from their suggestive resemblance to conidia might be regarded as secondary conidia. (Fig. 2, C.) These may in turn become proliferous. The repetition of this process, accompanied by marked diminution in size, frequently gives rise to a ramifying system, of which the terminal elements, sometimes as little as 3.5 μ in length and 2.5 μ in diameter, are borne in short branching chains. (Fig. 3, B.) The apparatus thus produced shows marked similarities to fructifications of Hormodendron, not only in the origin of new elements by lateral and apical budding, but also in the ready disintegration of the parts. Branching systems of the same type, but without any of the larger intermediate elements resembling the conidia typical of the fungus, also are produced in some quantity directly from conidia (fig. 3, C, D) or on relatively undifferentiated mycelial branches (fig. 2, E, F; fig 3, A).

As to the possible bearing of the Hormodendronlike structures on the biology of the parasite, no information is available. So far no tendency toward proliferation other than normal germination has been observed in material collected in the field. Most of the writer's observations, however, have been made near the northern limit of the fungus, and it is not impossible that in regions of higher temperature and greater humidity the proliferous tendency may be more pronounced. In any case, regardless of its interest as a morphological detail, the Hormodendronlike development would appear to constitute a subsidiary phase resulting from a somewhat promiscuous budding process, and hence not to be compared in distinctiveness to the true conidial stage found in nature. The relationship here is comparable, perhaps, to the relationship between the widespread *Cladosporium herbarum* Link and its Hormodendron stage, which was carefully investigated by Bancroft (*1*), although the occurrence of the Hormodendron stage throughout the parasitic life of that fungus to the exclusion of the other is far from having a counterpart in the life history of *Helminthosporium giganteum*. More recently Spangler (*8*) reported the development of Hormodendron fructifications in artificial cultures of *C. fulvum* Cke. and suggested the theory that probably only one type of conidium was produced and that the two-celled bodies usually held presumptive for Cladosporium probably represent nothing but fragments of denuded conidiophores. To the extent to

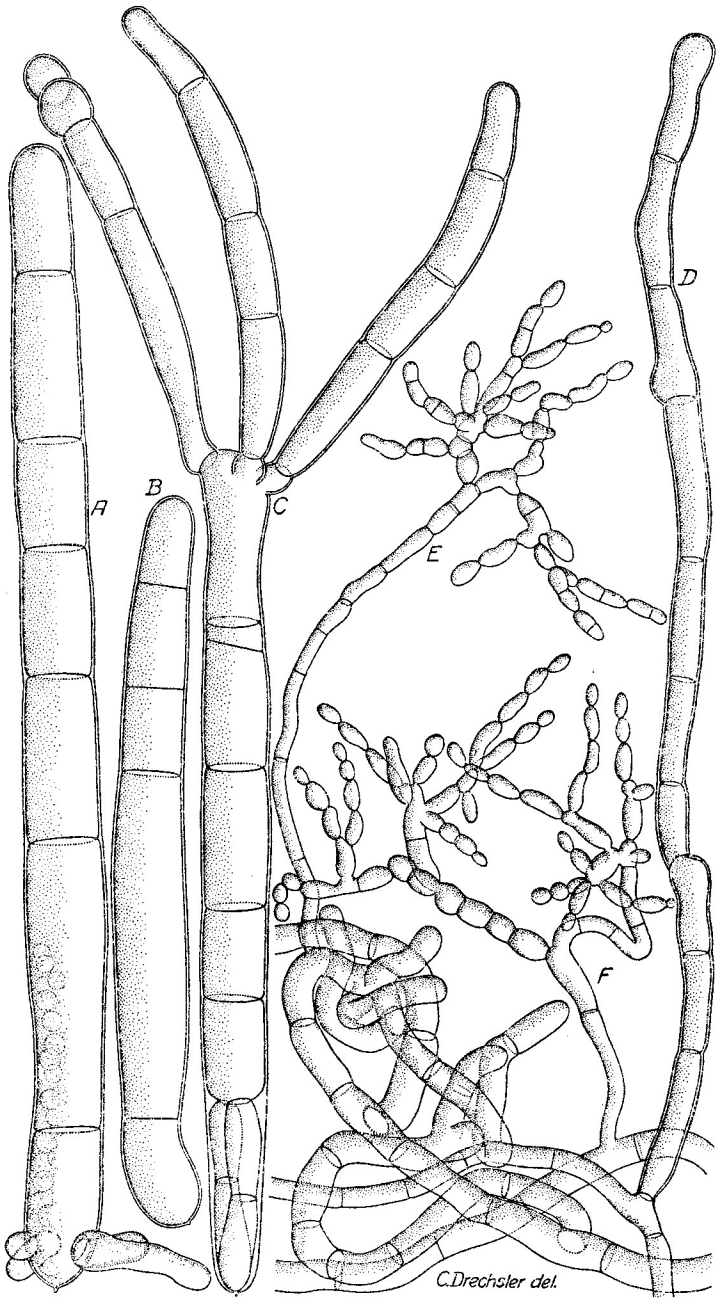


FIG. 2.—A–C, Conidia of *Helminthosporium giganteum* produced on a 20-day-old maize-meal agar culture. A, Normal germination from the basal segment, while an analogous process has given rise in C to three secondary conidia produced from the apical segment. Death of the basal segment in C has resulted in its occupation by hyphal elements arising as "Durchwachsungen" from the adjacent segment. × 450. D, Conidiophore of *H. giganteum* arising from aerial mycelium developed on maize-meal agar. × 450. E and F, Hormodendronlike fructifications of *H. giganteum* arising from aerial mycelium developed on maize-meal agar. × 450

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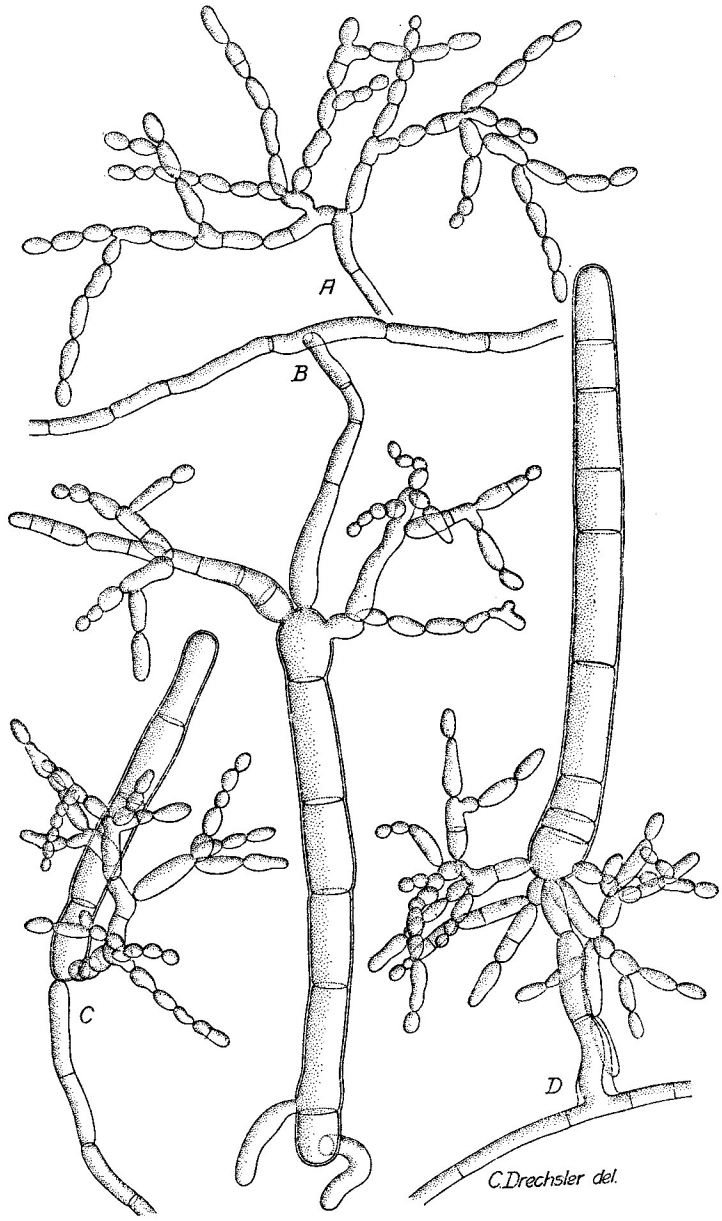


FIG. 3.—A, Hormodendronlike fructification of *Helminthosporium giganteum* arising from aerial mycelium developed on maize-meal agar. × 450. B–D, Hormodendronlike fructifications arising by proliferation from conidia of *H. giganteum* produced on maize-meal agar. × 450

which *H. giganteum* provides a parallelism, it affords little support for this view, but emphasizes rather the departures from normal morphology effected by the conditions of artificial culture. *Hormodendron hordei*, described by Bruhne (*2*) in 1894 as the cause of a leaf spot of barley (*Hordeum vulgare* L.) in Germany, is of interest in this connection as an apparently well-authenticated parasite on a graminaceous host. Although the conidia from barley leaves were always warty, they gave rise to smooth spores when cultivated artificially, and the general arrangement of parts shown in Bruhne's figure (*2, Taf. 1, fig. 4*) resembles at least superficially the proliferous condition of the parasite causing zonate eyespot. Because of the presence of septate conidia, Lindau (*7, p. 700–701*) seemed inclined to regard Bruhne's fungus as a stage of Cladosporium, even though the septate structures, as in the case of *C. fulvum*, apparently were not usually terminal, and therefore might equally well have been construed as disarticulated sporophoric segments.

TAXONOMIC RELATIONSHIPS OF PARASITE

The affinities of *Helminthosporium giganteum* remain problematical. As has been pointed out previously (*5*), the large majority of graminicolous species of Helminthosporium are referable to either one or the other of two types, one having typically straight cylindrical conidia germinating indiscriminately from the intermediate as well as from the proximal and distal segments, the other with ellipsoidal conidia germinating normally by the production of two polar germ tubes. Of the species belonging to the former type, several have been identified with ascigerous conditions referable to Pyrenophora or Pleospora, and it would seem probable that a similar affinity will be found to prevail throughout. Several species of the second type have been found connected with a perfect stage, which is represented by a peculiar type of Ophiobolus characterized by helicoid ascospores. *H. giganteum* can not apparently be assigned to either category. While the conidia it produces are cylindrical, their distinctive method of germination by the production of two whorls of three or four germ tubes, one whorl arising at a little distance from the attachment and the other at an approximately equal distance from the apex, is not indicative of any close relation to the forms connected with Pyrenophora. The general appearance of the fungus in artificial culture, its slow rate of growth, the frequent disposition of the aerial mycelium in curiously curving filaments, the Hormodendronlike structure arising from hyphae or, by secondary proliferation, from conidia, the unusually regular contours and homogeneous contents of the submerged hyphae—all these attributes taken together would seem further to set off the fungus from either of the two main categories of Helminthosporium species parasitic on grasses. Although in the production of eyespot lesions the fungus is not greatly different from certain other forms, its more extensive zonate developments presents a pathological effect of striking peculiarity.

Examination of the fungus in collections of field material from different localities and various hosts gives an impression of a high degree of morphological uniformity. The limited number of strains isolated have not revealed any differences sufficiently pronounced to predominate over the rather varied expressions of cultural characters exhibited by individual strains on the same plate culture.

The occurrence of aberrant sectors in such cultures, to which some writers attach much importance, was occasionally observed. (Pl. 8.) In no instance, however, did the variants exhibit a degree of distinctiveness sufficient to make them deserving of special taxonomic consideration.

THE HOST RANGE OF THE FUNGUS

Because of its ability to infect a large variety of hosts, and because of the wide range in degree of pathogenicity expressed, from the production of a barely discernible lesion to the almost complete destruction of the foliage of plants attacked, *Helminthosporium giganteum* might well serve as a subject for inquiry into the intimate aspects of parasitism. Owing to the difficulty of obtaining conidia of the parasite in artificial culture, however, greenhouse experimentation following the usual methods might not be easy of accomplishment. In the absence of such experimentation, field observations on mixed stands of grasses, including one or more species upon which the fungus sporulates abundantly, may not be devoid of interest. Some observations of this kind, together with descriptive data, are presented in the following paragraphs.

Agropyron repens mixed with heavily infected *Cynodon dactylon* was found severely attacked in various localities in the vicinity of the District of Columbia. Equally severe infections were observed, however, in a number of situations where no admixture of Bermuda grass was present, thus supplying proof of a degree of congeniality high enough to permit the fungus to propagate itself luxuriantly independent of other hosts. The individual lesions (pl. 2, I–M) do not generally exceed 1 mm. in width and 3 to 5 mm. in length, although sometimes the latter dimension may approximate 8 mm. They are straw colored in the center and delimited by a narrow dark-brown marginal zone. The zonate type of development usually may be observed, although the destruction of leaves more often is attributable to the abundance of moderate-sized lesions, several hundred of which not infrequently may be present on an individual foliar organ. After the death of severely infected leaves a liberal production of sporophores and spores ensues, the former arising not only from the discolored areas but also from the surrounding tissue.

The abundance of *Agropyron repens*, together with its high degree of susceptibility, seems to indicate that this grass might become the most important host of *Helminthosporium giganteum* in sections near the northern range of the parasite wherever Bermuda grass is present only in lesser quantity.

In August, 1922, at the Arlington Experiment Farm, Rosslyn, Va., *Agropyron elongatum* was found affected with *Helminthosporium giganteum*, although somewhat less severely than *A. repens*. While the infections resulting directly from germinating conidia appeared in considerable number, the lesions remained mostly of small dimensions. (Pl. 2, A.) When secondary enlargement took place and groups of lesions became confluent (pl. 2, B C), more severe effects were brought about. In the same plot another congeneric host, *A. intermedium*, revealed infection of somewhat less severity than that prevailing in quack grass, though otherwise not dissimilar. (Pl. 2, D–H.)

Agrostis stolonifera L., in September, 1922, at Arlington Experiment Farm, showed elliptical spots approximately 1 mm. in width and up to 2 or 3 mm. in length, which were readily attributed to conidia of *Helminthosporium giganteum*. The affected areas, for the most part almost white, were delimited from the healthy tissue by a very narrow, inconspicuous dark-brown margin. (Pl. 2, N–Q.) Owing, apparently, to the small size of the leaves, when a number of lesions occurred on the same blade, withering of the parts more distal in position resulted, although the entire damage caused was not excessive. No extensive zonate development was observed. As the eyespot lesions for the most part remained free from conidiophores of the parasite, it is not evident that the latter is capable of maintaining itself on creeping bent grass.[5]

Bromus inermis was found severely attacked by *Helminthosporium giganteum* at Arlington Experiment Farm during the season of 1922. The number of eyespot lesions, to be sure, was not excessive. In the absence of secondary development they generally did not attain immoderate size, those measuring more than 1 mm. in width and 2 or 3 mm. in length, including the deep-brown delimiting margins, being rather exceptional. (Pl. 3, A–D.) Secondary development, however, was relatively frequent and often extensive. (Pl. 3, D.) On the large regions of killed tissue, sporulation took place abundantly. Undoubtedly awnless brome grass may be regarded as more subject to damage than most of the several cultivated grasses included among the various hosts discussed in the present account. It may be a fortunate circumstance, therefore, that the area over which it is being grown for forage lies well north of the latitudes in which the fungus has hitherto been observed.

Chaetochloa lutescens, although often found growing in proximity to heavily infected Bermuda grass in the vicinity of the District of Columbia during the season of 1922, never exhibited any lesions due to *Helminthosporium giganteum* in any of the collections made in that general locality. That the grass is nevertheless not entirely immune from infection is evident in the occurrence of eyespot lesions in material collected near Hurlock, Md., in August, 1923, as well as in a collection made near Kennett, Mo., in August, 1924. In both cases the source of the infecting conidia was badly diseased Bermuda grass, in a stand of which the yellow foxtail grass occurred as an intimate admixture. The lesions, so few in number as almost to escape detection, were of relatively small size, not usually exceeding 1 mm. in length and 0.5 mm. in width, and of an elliptical shape, with a

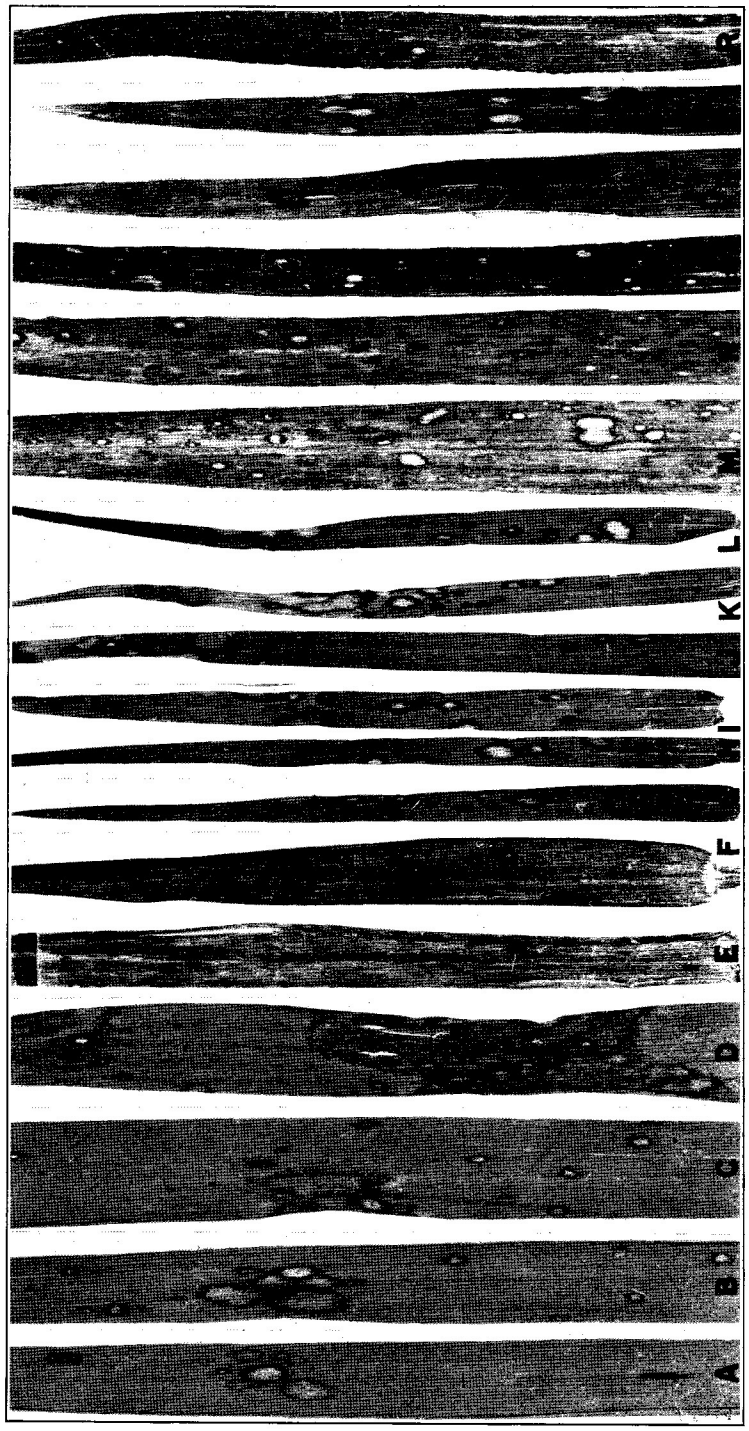
[5] Severe infection of creeping bent was noted in some of the turf plots and nursery rows at the Arlington Experiment Farm during the season of 1928, the very evident destructiveness of the parasite even in the absence of artificial watering being associated with ready centrifugal development of lesions and abundant sporulation. The position of the grass under consideration as an independent host was confirmed in a striking way by the occurrence of zonate eyespot in putting greens planted with it. This was true not only in regions generally favorable for the development of the fungus, but also, as has been mentioned in another connection, in territory not known to harbor the parasite on any host under ordinary conditions. In the vicinity of La Fayette, Ind., greens visited by the writer on Aug. 28, 1928, showed heavy infection, though perhaps owing to cooler conditions the infection then was less severe than that represented in specimens collected from the same grounds on July 20, 1928, by A. A. Hansen. Golf courses in the vicinity of Detroit, Mich., visited Sept. 1, 1928, showed the parasite active on some greens, though only in moderate or even small quantity; and a similar degree of prevalence was found also at Wooster, Ohio, visited Sept. 4, 1928. Specimens originating from near London, Ohio, from near De Kalb, Ill., from near Highland Park, Ill., and from near Minneapolis, Minn., in August and September, 1928, provide additional testimony of the efficacy and wide distribution of *Helminthosporium giganteum* as a turf parasite. It may be mentioned that not all strains of creeping bent are attacked with equal severity, some strains appearing almost completely resistant. Indeed the meager infection observed at the Arlington Experiment Farm in 1922 is to be explained by the fact that during that season only resistant types were represented in the nursery rows, whereas the destructive infection recorded for 1928 was limited to one or several very susceptible types subsequently added to the plantings.

straw-colored central portion surrounded by a brownish margin. (Pl. 3, E, F.) As might be expected, conidiophores of the parasite were never observed on any of the spots.

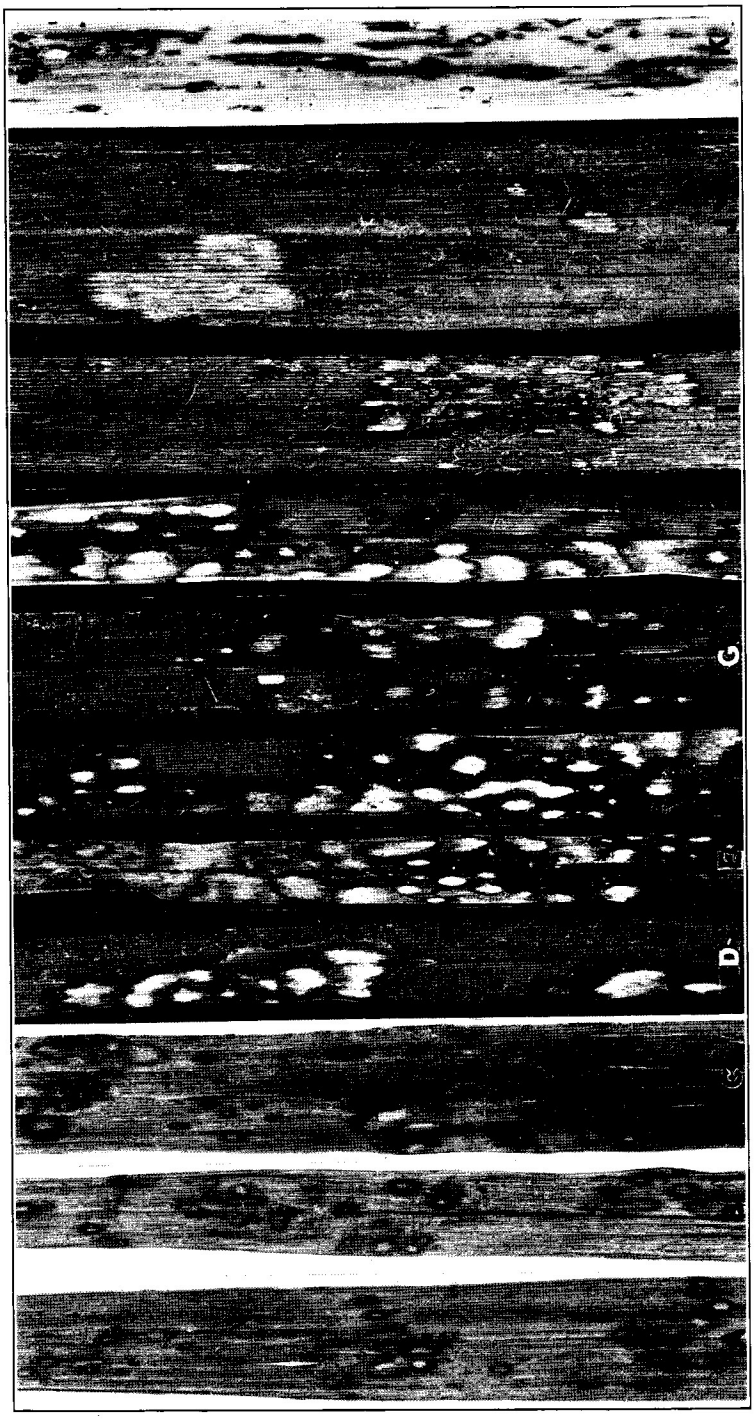
Cynodon dactylon unquestionably serves as the principal host of *Helminthosporium giganteum* in the United States. Infection by germinating conidia evidently takes place with unusual readiness, the foliage usually becoming spotted with lesions of independent origin much more abundantly than is shown in Plate 3, G–I. When conditions are favorable, the secondary type of development occurs (pl. 3, J–L) in about the same measure as in *Agropyron repens* and *A. intermedium*, and therefore perhaps somewhat less extensively than in *Phalaris arundinacea* or even in *Bromus inermis* and *Eleusine indica*. Nevertheless, because of its widespread distribution throughout at least the more favorable range of the fungus, and the readiness with which sporulation proceeds on the diseased foliage, mostly on tissue involved in the coalescence of groups of crowded individual lesions, Bermuda grass appears, on the whole, to support the parasite in as large quantity as all the other hosts taken together. The densely massed habit it frequently adopts when left undisturbed on suitable soil seems to be unusually favorable for the development of the fungus, so that the more luxuriant stands are frequently all but killed outright, the severity of such attack not being exceeded by any foliar grass disease known to the writer.

Digitaria humifusa Pers. (*Syntherisma ischaenum* Schrad. Nash), growing mixed with heavily infected Bermuda grass at Kennett, Mo., in August, 1924, bore a liberal sprinkling of lesions due to *Helminthosporium giganteum*. These lesions (pl. 3, M–O) occurred as elliptical spots rarely exceeding 2 mm. in length and 1 mm. in width, and having a straw-colored center with a reddish brown delimiting margin. The zonate type of development never was manifested. Examination of the eyespot lesions failed to reveal any conidiophores of the parasite in question. In the same location *Digitaria sanguinalis* bore eyespot lesions caused by germinating conidia of *H. giganteum*, resembling those borne on the congeneric host, but exhibiting a somewhat broader, more deeply colored border, and occurring so sparingly that their discovery entailed considerable search. The leaf shown in Plate 3, Q, was very unusual, in that nearly a dozen spots were found relatively close together, while that shown in Plate 3, R, with only two, also represents a more heavily infected condition than obtained generally. No conidiophores were found on any of the lesions on crabgrass.

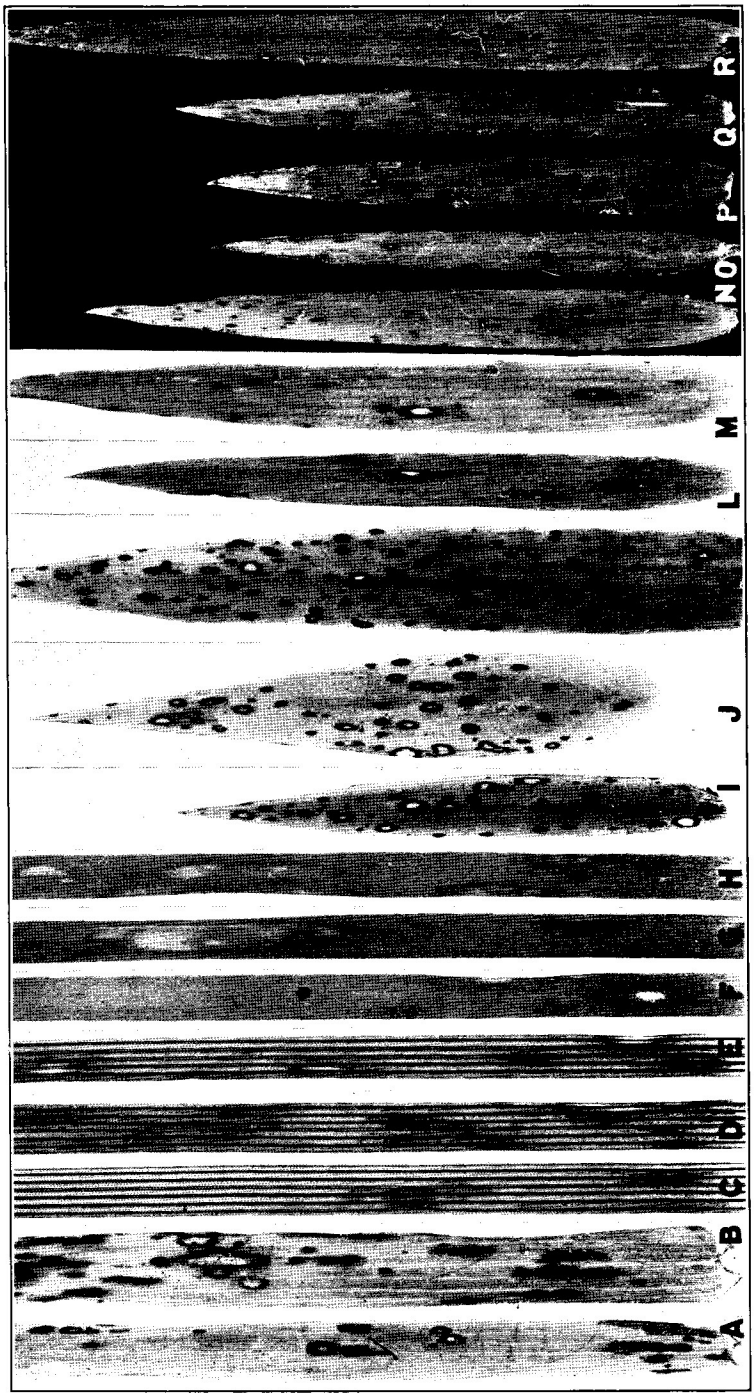
Echinochloa crusgalli was found attacked by *Helminthosporium giganteum* near Kennett, Mo., in August, 1924. It exhibited a considerable degree of susceptibility, the individual lesions being not only fairly numerous but also often showing moderately extensive secondary development. (Pl. 4, A–C.) Reddish brown coloration was somewhat conspicuous, being present on the relatively broad margins delimiting the discrete lesions, as well as in larger blotches encompassing areas killed as a result of secondary development, or resulting from coalescence of a number of separate spots. On the larger withered parts sporophores and spores were being produced in quantity. Barnyard grass would seem to show sufficient congeniality to serve as one of the more important hosts, although in the localities



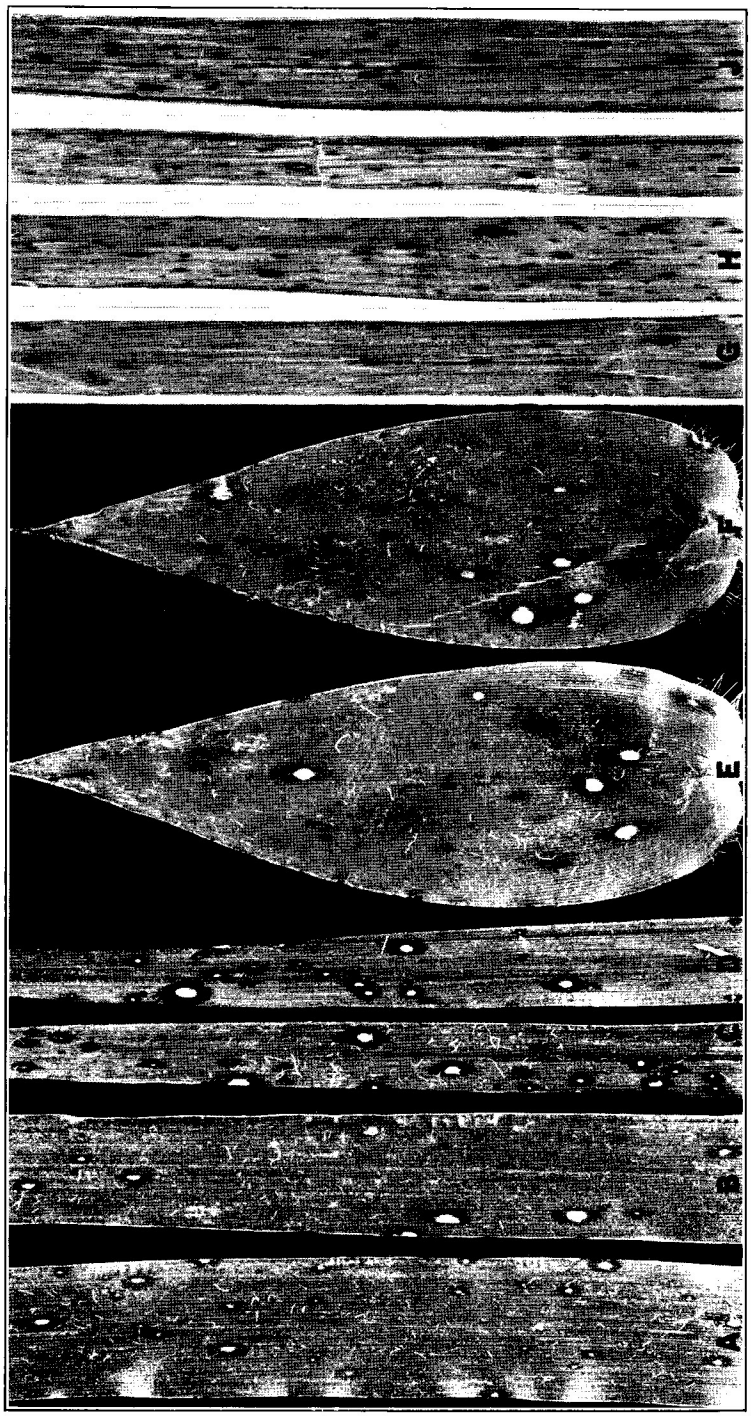
Leaves of various grasses attacked by *Helminthosporium giganteum*. A–D, *Bromus inermis*; E, F, *Chaetochloa lutescens*; G–L, *Cynodon dactylon*; M–O, *Digitaria humifusa*; P–R, *Digitaria sanguinalis*. × 2



Leaves of various grasses attacked by *Helminthosporium giganteum*. A–C, *Echinochloa crusgalli*; D–H, *Eleusine indica*; I, J, *Elymus virginicus*; K, *Eragrostis major* ×2



Leaves of various grasses attacked by *Helminthosporium giganteum*. A, B, *Eragrostis major*; C–H, *Lasiagrostis splendens*; I–K, *Leersia virginica*; L, M, *Muhlenbergia mexicana*; N–R, *M. schreberi*. × 2



Leaves of various grasses attacked by *Helminthosporium giganteum*. A–D, *Panicum anceps*; E, F, *P. clandestinum*; G–J, *P. dichotomoflorum*. × 2

in which the writer made his observations it did not occur abundantly enough to play any large part in the maintenance of the parasite.

Eleusine indica is to be included among the grasses most susceptible to *Helminthosporium giganteum*. In infected stands lesions originating from separate infections may become so numerous as to coalesce and thus lead to the withering of individual leaves, or considerable portions of a leaf may be killed directly as a result of secondary enlargement of some of the lesions. (Pl. 4, D–H.) Reddish brown coloration is present in the narrow marginal zones delimiting the individual lesions and also in less sharply localized form in markings on the larger affected parts. Sporulation under suitable conditions is abundant. Goose grass has been found more or less seriously affected wherever the parasite has been encountered. Owing to its general distribution throughout the known range of the parasite, its importance as a host of *H. giganteum* would seem second only to Bermuda grass. Like the latter, it frequently serves as the source from which other grasses in close proximity become infected.

Elymus virginicus, growing at Arlington Experiment Farm within 10 meters of diseased Bermuda grass in the season of 1922, showed a somewhat unusual condition relative to its infection by *Helminthosporium giganteum*. The individual lesions resulting directly from germinating conidia were few in number, but a large proportion of these showed extensive secondary development. (Pl. 4, I, J.) On the zonate areas of killed tissue sporophores were produced abundantly. The appearance suggested that infection of the coarse foliage by germinating conidia was attended with difficulty, but that once the parasite gained a foothold its further development centripetally took place readily. Under suitable conditions the grass would seem to be capable of serving as a congenial host.

Eragrostis major, growing in mixed stand with very heavily infected Bermuda grass near Seat Pleasant, Md., in September, 1922, exhibited meager infection by *Helminthosporium giganteum*. The large majority of lesions were of the eyespot type, elliptical in shape, from 0.2 to 0.8 mm. in width and 0.4 to 1.6 mm. in length, with a rather conspicuous deep reddish brown marginal zone surrounding a central bleached area usually of minute size. (Pl. 4, K; 5, A, B.) In a number of instances, however, secondary development had resulted in the death of more extensive portions of tissue measuring sometimes from 10 to 20 mm. in length and from 2 to 3 mm. in width, or even extending entirely across the leaf. Withering of the distal portions of certain foliar organs in some cases appeared to result from such more extensive development of the parasite, or from an unusual concentration of smaller lesions, although a certain degree of doubt as to the causal relation of the parasite was introduced because of the approaching maturity of the host. Sporophores of the fungus were found on the larger lesions and on withered parts bearing numbers of smaller spots in close proximity to one another. Such reproduction, however, was on a decidedly small scale, and it remains somewhat uncertain, therefore, whether the fungus could propagate itself successfully on stink grass alone.

Lasiagrostis splendens, growing at some distance from heavily infected reed canary grass at Arlington Experiment Farm in 1922, became severely infected with *Helminthosporium giganteum*. Individual lesions were fairly numerous, the smallest ones appearing as

uniformly dark-brown blotches. (Pl. 5, C. D.) Those of intermediate size, measuring 2 to 4 mm. in length, were generally of the simple eyespot type (pl. 5, E. F), while the more extensive morbid areas, frequently exceeding 1 cm. in length and including the entire width of the leaf, bore the zonate markings characteristic of secondary development. (Pl. 5, G, H.) On the latter type of lesion sporophores and spores of the parasite were found occurring in abundance. Because of the strong dorsiventral differentiation between the prominently veined dark-green upper surface of the foliage (pl. 5, C–E) and the smoother, lighter green under surface (pl. 5, F–H) the two aspects of the lesions appear different to a rather unusual degree. The fungus would seem capable under suitable conditions of causing more than appreciable injury to the grass and unquestionably could maintain itself thereon independent of other hosts.

Stands of *Leersia virginica*, occurring in close proximity to heavily infected Bermuda grass or quack grass at various points along the Chesapeake & Ohio Canal, have regularly become thickly peppered with numerous eyespot lesions during the five seasons in which observations were continued. While the spots usually remain relatively small, rarely exceeding 2 mm. in length and 1 mm. in width (pl. 5, I–K), they occasionally become confluent, and thus bring about the death of somewhat larger portions of leaf. Even these larger areas, however, are usually devoid of conidiophores of *Helminthosporium giganteum*, although in somewhat exceptional instances a very sparse array of such structures has been observed. That such meager sporulation, nevertheless, is not entirely without significance became evident through the discovery in September, 1922, of a pure solitary stand of white rice grass on which an infection with *H. giganteum* occurred obviously quite independent of other hosts. As this stand was situated on a large fill on which other grasses had not encroached, it was not difficult to verify the absence of external sources of infection within a radius of more than 50 meters. It is interesting to note that extensive secondary development of the fungus from relatively few lesions, rarely observed elsewhere, here accounted largely for the injury observed, which, to be sure, was inconsiderable. Sporulation on the larger tracts of leaf tissue involved in such development was only slightly more abundant than on the leaves bearing the numerous small lesions of independent origin. The grass is to be regarded, perhaps, as hardly a more congenial host than *Eragrostis major*, even though under exceptional conditions it permits autonomous propagation of the parasite.

Sometimes *Leersia virginica* can be found attacked simultaneously by both *Helminthosporium giganteum* and *H. leersii* Atk. As the older lesions caused by the latter fungus are many times larger than eyespot lesions due to the former, and never exhibit the zonate markings characteristic of the secondary development of *H. giganteum*, their identification usually entails little trouble. The smaller lesions of *H. leersii*, also, can generally be distinguished from those of *H. giganteum* because of their broader and less sharply defined marginal zone. In doubtful instances microscopic examination is necessary. Since neither fungus sporulates on any except the largest regions of affected tissue, identification of smaller spots is most conveniently

accomplished by determining the presence or absence of the evacuated spore membrane of *H. giganteum*.

Muhlenbergia mexicana, at a distance of about 5 meters from heavily infected quack grass, revealed relatively few scattering lesions of *Helminthosporium giganteum*. The larger ones were elongated elliptical in shape, measuring 2 to 3 mm. in length by 0.5 mm. in width, and showing sharp differentiation between the small central bleached portion and the narrow dark-brown delimiting zone. (Pl. 5, L, M.) Most of the lesions were of the unmodified eyespot type and quite devoid of sporophores of the parasite. Occasionally the presence of minute specklike discolorations in zonal arrangement about one of the larger lesions evidenced a somewhat meager secondary development. In certain of the largest lesions sporophores of the fungus were observed, although the total production of such structures was so small that it is to be doubted whether the fungus could persist on *Muhlenbergia mexicana* in the absence of more favorable hosts, except under very favorable conditions.

Muhlenbergia schreberi, in the same locality as *M. mexicana* but occurring in intimately mixed stand with heavily infected quack grass and goose grass, exhibited lesions of *Helminthosporium giganteum* in moderate number. These lesions were characterized by unusually small size, sharp definition of the margin from the healthy tissue and the bleaching of the center in spite of relatively minute proportions. (Pl. 5, N–R.) No extensive secondary development or evidence of sporulation ever was observed on this grass, which evidently does not permit autonomous development of the fungus. Owing to the frequent occurrence, on the more mature foliage, of numerous minute dark linear lesions somewhat resembling those due to conidia of the parasite under consideration, but associated with another fungus, spots not bleached in the center can not be identified without microscopic inspection.

Panicum anceps Michx., occurring interspersed in a stand of heavily infected quack grass during the season of 1922, exhibited eyespot lesions in moderate quantity. These lesions sometimes attained a length of 3 to 4 mm. and a width of 1.5 to 2 mm., although usually their proportions did not exceed one-half of the values mentioned. (Pl. 6, A–D.) They exhibited a bleached center on attaining a length of 1 mm., the delimiting margin being usually relatively broad and light brown in coloration, rather than dark brown. As none of the lesions were found bearing conidiophores of *Helminthosporium giganteum*, the grass can not be considered among the congenial hosts.

Panicum clandestinum, because of its habit of occupying the weedy borders of neglected fields, which, after the middle of summer in the vicinity of the District of Columbia, are often overrun with Bermuda grass, was frequently found exposed to infection from the great profusion of conidia produced by *Helminthosporium giganteum* on the latter host. The foliage then exhibited discoloration in the form of numerous dark-brown specks, or of larger nebulous blotches, or of well-defined eyespot figures, with a relatively wide, vaguely delimited marginal zone. (Pl. 6, E–F.) When the younger leaves thus affected were examined microscopically, these discolored portions could in all instances be found associated with collapsed remains of overlying conidia of the parasite. Although the larger eyespot lesions

contained bleached central areas that sometimes measured 4 mm. in length by 1.5 mm. in width, sporophores of the fungus never were observed. In spite of a relatively high degree of susceptibility to conidial infection, the grass is apparently not sufficiently congenial as a host to sustain *H. giganteum* independently.

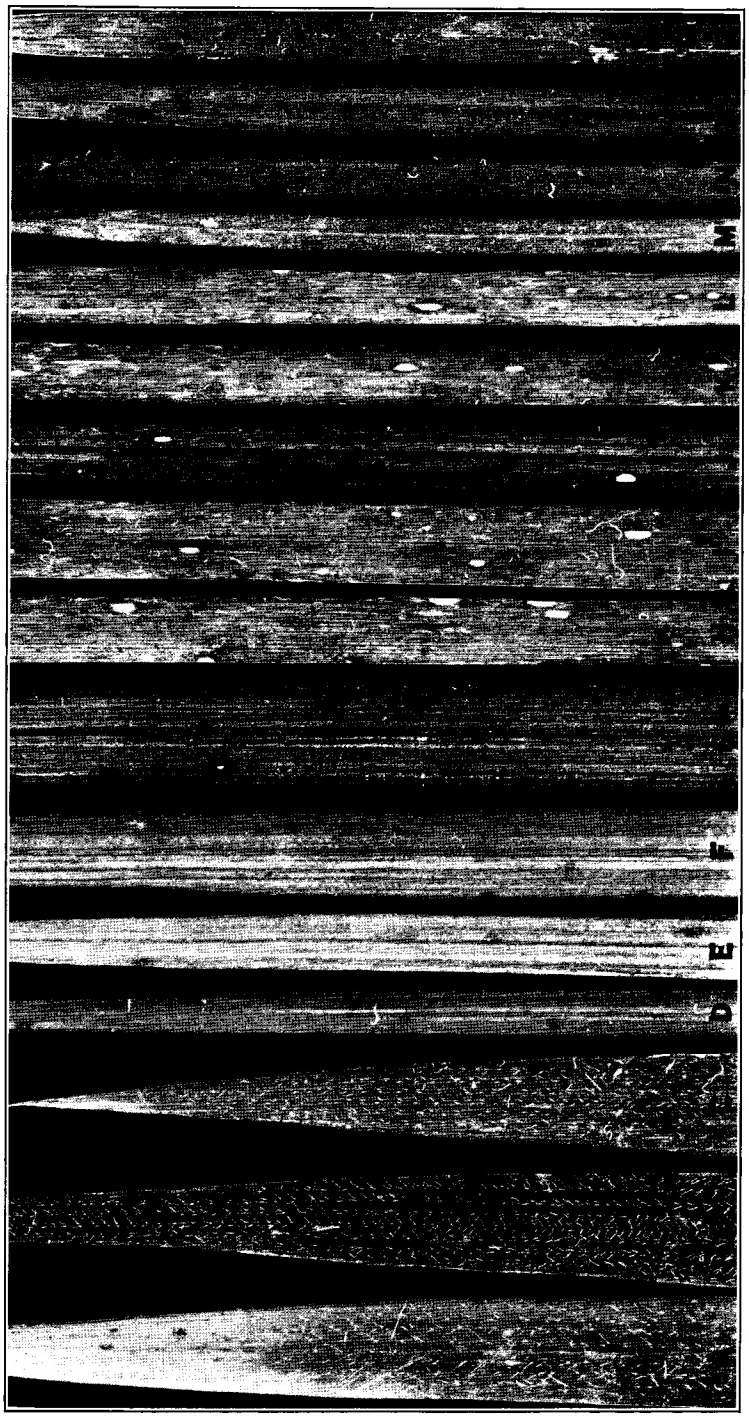
Pancium dichotomoflorum was found intermixed with infected goose grass in a number of truck fields and vegetable gardens near the District of Columbia in September, 1922. Many of the leaves thus exposed bore a varying number of lesions from infection by conidia of *Helminthosporium giganteum*. Near Kennett, Mo., where, in September, 1924, the grass occurred in mixed stand with heavily infected Bermuda grass, a considerably more abundant infection obtained. In both localities the lesions were represented by reddish-brown or dark-brown spots, rather sharply defined from the healthy tissue, somewhat linear or streaklike in outline, variable in size, often being so small as to be barely discernible, but sometimes attaining a length of 3 mm. and a width of 1 mm. (Pl. 6, G–J.) Many of the lesions were bleached in the center, but in other instances this feature was not evident. None of the material from either source revealed the presence of sporophores.

Panicum gattingeri, growing in a stand of infected quack grass at Cabin John, Md., in September, 1922, bore a meager sprinkling of eyespot lesions due to infection from conidia of *Helminthosporium giganteum*. The spots were small in size, being not more than 1 mm. long and less than half as wide, yet usually exhibiting a bleached center. (Pl. 7, A–C.) Conidiophores of the fungus never were observed. The grass is evidently considerably less susceptible to infection than any of the three congeneric species mentioned, and is to be included among the more unfavorable hosts.

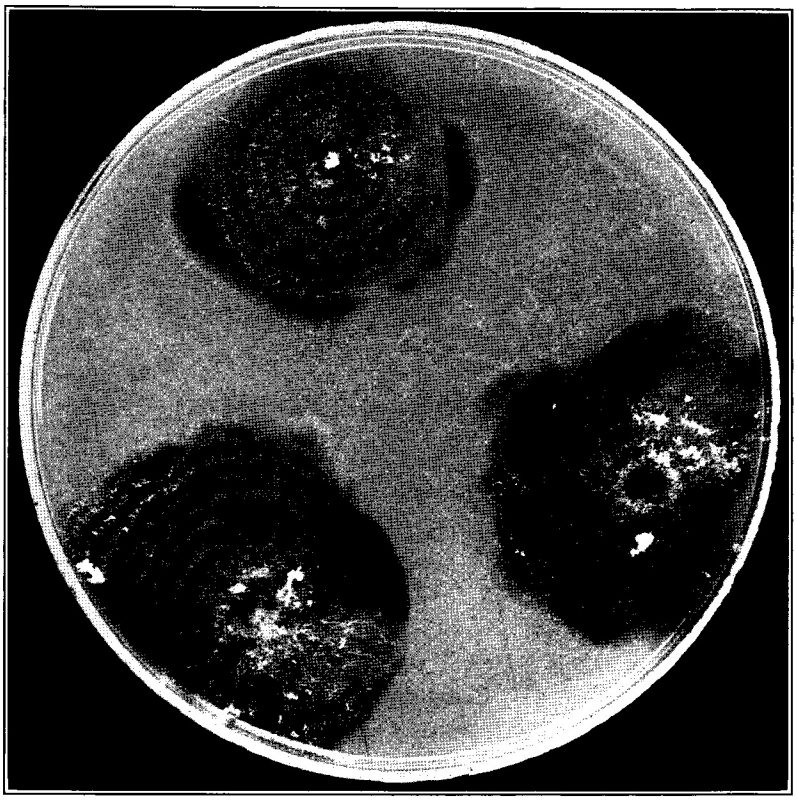
Pennisetum alopecuroides (L.) Spreng.,[6] growing at a distance of less than 1 meter from heavily infected reed canary grass at Arlington Experiment Farm in 1922, showed on some leaves scattered lesions due to infection from conidia of *Helminthosporium giganteum*. These lesions were present generally as reddish brown blotches, although a few were of the eyespot type, with the bleached center sharply defined. (Pl. 7, D–G.) None ever revealed the presence of conidiophores. In view of the quantity of inoculum to which the foliage was exposed throughout the season and the insignificance of the injury occasioned, the grass would appear to possess little susceptibility to attack by the fungus.

The extreme congeniality of *Phalaris arundinacea* as a host of *Helminthosporium giganteum* has been discussed in another connection. It must be mentioned, however, that the parasite has not been encountered on reed canary grass elsewhere than in the plots at Arlington Experiment Farm. Several wild stands observed in the vicinity of the District of Columbia never revealed any sign of infection, even during the very favorable season of 1922. As all of these stands have happened to occur in isolated situations, separated from infected grasses by wooded terrain, the absence of the fungus was not difficult to explain. Nor have infections ever been observed

[6] This host was reported previously under the binomial *Pennisetum japonicum* Trin. The change in specific name is made on the advice of Agnes Chase, who kindly examined specimens and identified them as clearly belonging to the species frequently designated as *P. compressum* R. Br. The plant is of course conspicuously different from pearl millet (*P. glaucum* (L.) R. Br.), to which it would appear the term *alopecuroides* during a long period of nomenclatorial confusion has often been erroneously applied.



Leaves of various grasses attacked by *Helminthosporium giganteum*. A–C, *Panicum gattingeri*; D–G, *Pennisetum alopecuroides*; H–L, *Phleum pratense*; M–P, *Poa pratensis*. × 2



Maize-meal agar plate culture of *Helminthosporium giganteum* 15 days after inoculation. × 1

490—2

on the ornamental form known as ribbon grass, *Phalaris arundinacea* var. *picta* L.

During several seasons *Phleum pratense*, found growing among heavily infected Bermuda grass and quack grass in a number of locations near the District of Columbia, exhibited, in meager number, lesions caused by germinating conidia of *Helminthosporium giganteum*. These lesions usually were relatively small, rarely exceeding 2 mm. in length or 1 mm. in width. (Pl. 7, H–L.) Often they consisted only of bleached portions of tissue, thus appearing as white spots, devoid of any colored margin, while in other cases a narrow brown border was recognizable. The scarcity of infection and the complete absence of conidiophores from the relatively small diseased parts denote a high degree of resistance to the parasite.

Poa pratensis, often found exposed to infection in the same situations as timothy, exhibited approximately the same low degree of suceptibility. The lesions were similarly few in number and of equally small dimensions, some, indeed, being so minute as to be barely discernible. (Pl. 7, M–P.) A conspicuous difference was represented in the dark-brown or brownish-black color of the spots on Kentucky bluegrass. The bleached center distinctive of the eyespot lesions was present only in exceptional instances, and then somewhat vaguely, most of the discoloration appearing in the form of unrelieved elongated or almost linear specks.

SUMMARY

Helminthosporium giganteum occurs generally throughout the Southern States and has been found in quantity as far north as Maryland and Missouri. In the vicinity of the District of Columbia the conidia from centers of infection do not appear to spread beyond distances of 20 meters in one season, a limitation due apparently to the large size and short period of viability of these structures, and to which may be attributed, in part at least, the frequent irregularities noticeable in the local distribution of the parasite. The fungus seems to overwinter in the form of dormant mycelium, fresh conidiophores and conidia being produced in late spring from the morbid parts of old foliage infected during the previous season.

Sporulation of the fungus occurs on the larger tracts of killed tissue, resulting either from the coalescence of numbers of individual eyespot lesions or from secondary development of such lesions. The latter type of development occurs only when the leaf surface is coated with moisture, and involves the production, centrifugally from the margin of the morbid tissue, of a prostrate mycelium that in occupying the surrounding parts brings about a water-soaked condition and later desiccation and death. As in various hosts the newly infected parts are delimited by marginal coloration, the repetition of such development brings about a characteristic zonate appearance.

Among the hosts on which sporulation was observed under natural conditions, and on which the parasite apparently could propagate itself, are to be included *Agropyron elongatum*, *A. intermedium*, *A. repens*, *Bromus inermis*, *Cynodon dactylon*, *Eleusine indica*, *Echinochloa crusgalli*, *Elymus virginicus*, *Lasiagrostis splendens*, *Leersia virginica*, and *Phalaris arundinacea*. Sporulation was observed also, though in meager quantity, on *Eragrostis major* and *Muhlenbergia mexicana*. Lesions due to infection by conidia of the parasite were

observed on *Argostis stolonifera, Chaetochloa lutescens, Digitaria humifusa, Muhlenbergia schreberi, Panicum anceps, P. clandestinum, P. dichotomoflorum, P. gattingeri, Pennisetum alopecuroides, Phleum pratense,* and *Poa pratensis* when these grasses occurred in proximity to more congenial hosts.

When grown in pure culture on artificial media the fungus develops relatively slowly. Meager and somewhat abnormal sporulation generally takes place, the conidia as well as the mycelial hyphae often giving rise to branching systems of small disarticulating elements, the whole closely resembling the fructifications usually referred to the form genus Hormodendron. This proliferous phase, and more especially the distinctive method of germination by the production of two whorls of germ tubes, one from near each end of the conidium, would seem to set the fungus apart from the two most numerous series of graminicolous forms included in the genus Helminthosporium.

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