STUDIES IN CEREAL DISEASES

X

Studies of Take-all and its Causal Organism, *Ophiobolus graminis* Sacc.

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INTRODUCTION

Take-all is a disease of various members of the grass family. It is caused primarily by a parasitic fungus, *Ophiobolus graminis* Sacc., but it develops only under appropriate environmental conditions. The disease was first recognized in Saskatchewan in 1923. Since it causes considerable damage to wheat in Western Canada, it has been made the subject of much investigation up to the present time.

The disease has been studied from various angles. Field surveys have been conducted annually since the year 1923 and these have shown the actual distribution and severity of the disease from year to year. Certain fields were inspected each season for five years in order to study the effects of crop rotation on the disease. Since 1924, experiments have been conducted in the laboratory and greenhouse during the fall and winter months. Since 1927 field plot experiments have been conducted annually at two different places in Saskatchewan.

Thus, comprehensive field surveys of actual conditions throughout the province, experiments under field conditions, and experiments under laboratory and greenhouse conditions have gone hand in hand throughout these studies. This has led to a better understanding of the problem than it would have been possible to reach by any one of these methods alone.

THE DISEASE

Common Names

Take-all is the name generally used in English-speaking countries to designate diseases of cereals caused by *O. graminis*. According to McAlpine (41) this name was applied to the disease on wheat as early as 1870 by the farmers of Australia. Other English names, which have been used to describe its later stages, are white-heads, dead-heads, and straw-blight.

Various common names, referring usually to the appearance of the affected plants or to the action of the fungus on the host, have been applied to this disease in other countries. In France, this disease, together with that caused by *Leptosphaeria herpotrichoides* de Not, is usually referred to as *piétin*, although formerly the terms *pied noir* (black foot) and *maladie du pied* (disease of the foot) also were applied to it. The Germans named the disease *Weizenhalmtöter* (wheat stem-killer) which is rather appropriate. Laar (36), in Holland, suggests the names, *Ophiobolus-Voetziekte* or *Ophiobolose*. The Boers in South Africa called it *vrotpootjie* which is the equivalent of our word, foot-rot, according to Putterill (55). The Japanese applied to it names which meant "die-back disease" and "white wilt," according to Hori (30).

Thus, while take-all may not be the most appropriate name available for this disease, it has been in use for over sixty years and is now in fairly general acceptance throughout English-speaking countries. Therefore, it seems advisable to retain it.

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Symptoms and Signs

The symptoms of the disease and the signs of the fungus on the host vary a great deal under different environmental conditions. The stage of development of the host at the time of infection also may make a difference to the resultant symptoms. The chief environmental factors affecting the symptoms appear to be soil moisture and the relative humidity of the air.

The following symptoms and signs develop under relatively moist conditions and have been regarded in the past as typical of take-all. About the time the grain is heading the plants in somewhat circular patches cease growing and become chlorotic. Stunting is usually noticeable and often very pronounced. During hot windy weather, following a rainy period, the stems and leaves of affected plants may bleach very rapidly. The roots may become so

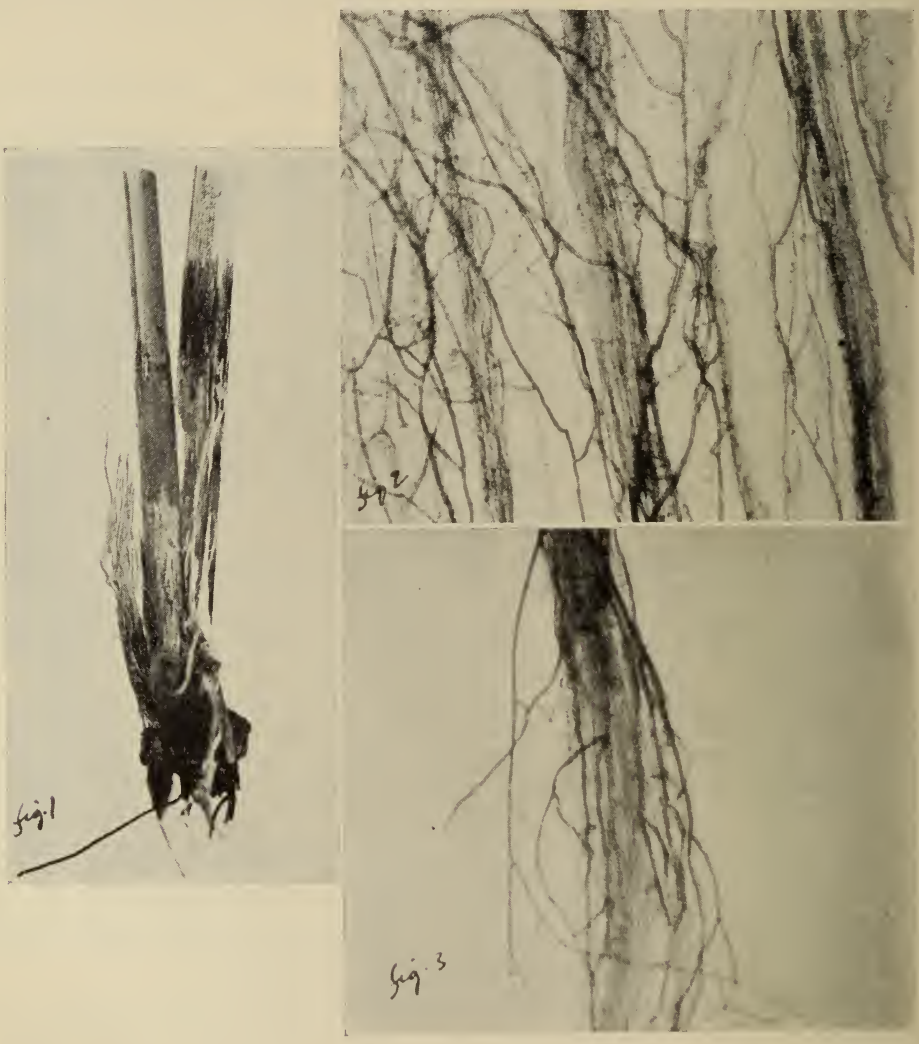


FIG. 1.—Crown and stem-base of wheat plant diseased with take-all. The sheath is partly torn away to show the black mycelial growth of *O. graminis* which developed between the sheath and the culm.
FIG. 2.—The hyphae of *O. graminis* on the inner surface of a wheat sheath.
FIG. 3.—The hyphae of *O. graminis* on a wheat rootlet.

badly decayed that they break off close to the crown of the plant if it is pulled from the ground. The crown and stem-base also are lesioned and decayed. The basal parts of the plant take on a very dark brown or black discoloration (fig. 1). A microscopic examination of the affected tissues reveals brownish, somewhat conical structures protruding from the inner surface of the walls of affected host cells. These are discussed further in the section on the histology of infection.

The signs of the fungus consist of dark brown strands of thick-walled hyphae clinging to the surface of affected parts (figs. 2 and 3), together with hyaline strands of more delicate hyphae permeating the tissues intracellularly.

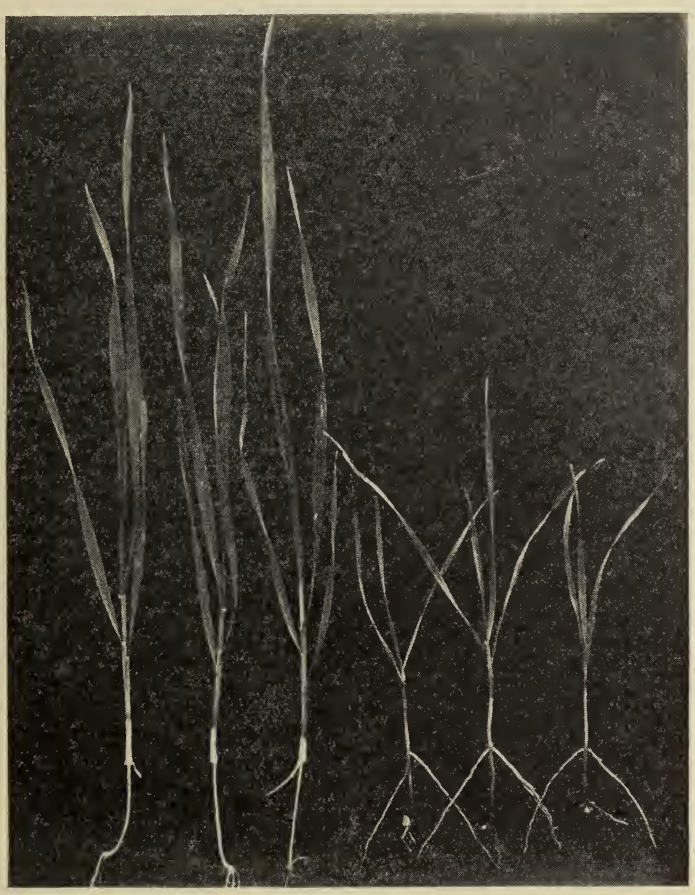


FIG. 4.—Healthy wheat seedlings (left) and diseased seedlings infected with *O. graminis* (right), showing the hastened development of the crown roots of the diseased plants.

The dark coloured external mycelium frequently forms groups of parallel hyphae or the cells of the fungus may be compacted into solid masses or plates particularly between the culm and leaf sheaths of the host. This mycelial development sometimes grows to a height of about two inches above the ground level (fig. 1). Usually the perithecia are formed between the leaf sheaths about the ground level and their beaks protrude from the outer sheath. Perithecia are not always present.

Under very dry conditions the symptoms and signs of the disease are usually much less striking and the disease is apt to be overlooked. The main symptoms under such conditions are moderate stunting, reduced tillering and blackening of certain parts of the primary root system, with occasionally some lesioning of the sub-crown internode. While this lesioning is usually darker in colour than that produced by other root-rotting organisms it may be confused with that caused by *Helminthosporium sativum* P.K. and B. or by *Fusarium* spp. The signs of the fungus under dry conditions may consist only of brown external mycelium on the surface of the primary roots and of hyaline mycelium within the tissues of the roots. This has been aptly termed "dry-weather take-all." All gradations between typical take-all and dry-weather take-all may be found. The disease sometimes appears on scattered plants rather than in patches.

Additional symptoms more evident in greenhouse infection studies than in the field are as follows: Under conditions very favourable to the fungus some of the seedlings may be killed before they have emerged from the soil; thus, pre-emergence blight may be a symptom of the disease. Ordinarily, however, the seedlings emerge and grow to a height of several inches before showing any symptoms of disease. Then the leaves, commencing with the outer one, become wilted and chlorotic due to the destruction of the primary roots and the tissues at the base of the stem. The whole base of the seedling becomes blackened and decayed in severe cases and the seedling dies. Brown conical structures occur plentifully in the affected cells. If the attack is less severe and the seedling develops crown roots it quite often recovers to a considerable extent and survives. Abnormally early development of the crown roots may occur as a result of the partial destruction of the primary root system (65) (fig. 4). In either case the signs consist of the typical brown mycelium on the exterior of the host parts and the hyaline mycelium within the host tissues. Sometimes perithecia form and sometimes they do not.

Occasionally it is difficult to tell whether a sickly plant is affected by take-all or by one of the other types of root rot. This is not at all surprising because several different root-rotting organisms may attack the plant at the same time. Moreover the lesions caused by these other organisms resemble fairly closely the lighter coloured lesions caused by *O. graminis,* although well developed take-all lesions are usually darker in colour than those produced by the other root rots which are prevalent in Saskatchewan. To diagnose a case of root rot properly, one should take into consideration the symptoms as a whole together with the signs which are present, as it is sometimes impossible to diagnose such cases of root rot by the symptoms alone.

History and Geographic Distribution

Take-all is a plant disease with a long history and its distribution is world wide. As early as 1850 agriculturists of Australia and France were noticing its effects and speculating as to its cause. It was not until several decades later, however, that the parasitic agent in its development was recognized (54).

Take-all has been discovered successively in one country after another until it is now known to occur in practically every wheat growing region of importance in the world. By the end of the nineteenth century it had been found in England (70), France (54), Germany (40), Italy (40) and Australia (41). From the beginning of the twentieth century up to the present time many articles and reports concerning this disease have appeared from different parts of Europe. They show that the disease is present in the following European countries in addition to those mentioned above; Holland (36), Denmark (22), Norway (33), Sweden (73), Bohemia (2), Switzerland (21), Portugal (5), and Russia (13). The disease was reported from Japan in 1901 (30). The first

definite reports of take-all in the United States (34), New Zealand (74), the Union of South Africa (4), and Canada (18) appeared about ten years ago. Since then it has been reported from Argentina (1) and Kenya (42).

Economic Importance

The economic importance of take-all has at times been remarkable owing to the great destruction of wheat which it has brought about in certain countries. The disease has done the greatest damage in regions where wheat has been grown on the same land year after year. Moreover, the severity of the disease varies greatly from season to season in any one region depending largely upon variations in the amount of rainfall and other meteorological factors. The disease is apt to be particularly destructive to crops on comparatively new land where the causal organism was present in the virgin sod and where wheat is being grown continually. Under conditions favourable to the disease losses of 25 to 75 per cent of the crop have not been uncommon in parts of Australia (58), the Union of South Africa (4), the United States (45) and Canada (63).

Fortunately the various factors affecting the severity of take-all seldom combine to bring about such heavy damage as that alluded to in the previous paragraph. The rotation of crops and the use of clean fallowing tends to reduce greatly the severity of the disease and in many seasons the weather conditions are unfavourable to its development so that the average losses due to it are much less than we might expect from studying the disease under conditions favourable to its development.

On the other hand it seems probable that take-all causes considerable reduction in yields under conditions where the disease is not usually recognized. Field plot work and persistent examination of field material have shown that under dry conditions the primary roots alone may be diseased and the plants prevented from developing vigorously and yielding heavily although no signs of the disease are visible above seed-level.

Take-all reduces yields indirectly by aiding vigorous weed development. When wheat plants are weakened by the fungus the weeds which are present make greater headway and offer keener competition than they do when the wheat plants are free from disease.

While the loss from take-all is undoubtedly considerable in certain years in this province the situation is not alarming. The amount of take-all appears to be decreasing gradually as the proportion of new land which is being brought under cultivation is decreasing and as crop rotation is becoming more widely practiced. The present losses could be largely avoided by an intelligent selection of crop rotations as suggested later in this bulletin under control measures.

THE CAUSAL ORGANISM

Taxonomy

Ophiobolus graminis Sacc. is one of the Pyrenomycetes. In the classification given in Engler and Prantl the genus, *Ophiobolus,* is placed in the family Pleosporaceae. Jones (31) suggested that this genus should be transferred to the Gnomoniaceae for the following reasons: he considered that true paraphyses were not present; that the asci were thickened apically and possessed a pore at their apices; and that the asci were extruded rather than projected from the ostiole at maturity.

Whether or not *O. graminis* possesses true paraphyses is still open to question. McAlpine (41) and Fitzpatrick et al (16) give technical descriptions of the fungus and in each case paraphyses are described. It is true that the structures described as paraphyses are evanescent and it is very difficult to see

them clearly in unstained water mounts. Nevertheless, these structures (fig. 5) occur regularly in the immature perithecia found in this region. They measure about 115 to 190 microns in length and about 5 to 9·5 microns in width at the base tapering to a width of about 2 or 3 microns at the tip.

The ascus appears to have a pore at the apex and this is particularly noticeable while the ascus is still immature. As Jones points out, however, the pore does not appear to be sufficiently large in diameter to permit the spores to pass through it. Apparently the spores are liberated by the dissolution of the wall of the ascus, as figured by Mangin (39).

In a recent article based on their investigations of the disease in Australia, Samuel and Garrett state that the asci of *O. graminis* are projected from the perithecium at maturity. They consider it probable that scattered infection in the wheat fields, producing the condition known as "white-heads," arises from wind-borne spores produced in take-all patches earlier in the season.

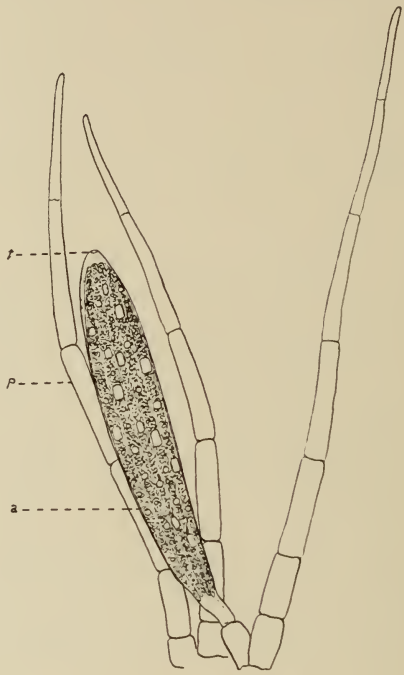


FIG. 5.—Immature ascus and evanescent paraphyses of *O. graminis*. The structure (t) at the tip of the ascus (a) looks like a pore; the paraphysis (p) which is hyaline and difficult to see in water mounts is usually longer than the ascus; it is faintly septate and tapers from the base to the tip. Paraphyses are not often found in mature perithecia.

Thus, it does not appear certain that any of the above mentioned objections to the classification of *O. graminis* in the family Pleosporaceae are valid.

Measurements given by different authors for the dimensions of ascospores of *O. graminis* vary greatly. Laar (36) gives a table containing the measurements for these structures as reported by nearly a dozen different authors. The maximum variation for spore length appearing in this table is 60 to 117·6 microns. Laar reports a range in spore length of 72·2 to 117·6 microns from material collected in Holland. McAlpine's measurements (41) are not given

in the above mentioned table. The spores which he measured varied from 70 to 112 microns in length. In Saskatchewan, over a period of years, variations from 76 to 118 microns have been noted, the average length being about 90 microns. In view of the above data the variation in spore length given in Saccardo's description of *O. graminis,* namely 70-75 microns, is considered much too narrow.

Fitzpatrick et al (16) changed the name of this species to *Ophiobolus cariceti* (B. and Br.) Saccardo. McKinney (45) has analyzed their reasons for doing so and rejects them as not entirely convincing. Without examining the type specimens of these two supposed species it is impossible to settle this question of nomenclature satisfactorily. It may be pointed out, however, that the spore lengths as reported by McAlpine (41), Laar (36) and Russell (61) agree more closely with that given in the original description of *O. cariceti,* than with that given in the original description of *O. graminis.* It seems probable that these two names are synonymous but for the present it is thought best to use the name *O. graminis* because it is so well established and the proper status of the name *O. cariceti* is not entirely clear.

Cultural Studies

In selecting a medium for carrying pure cultures of *O. graminis,* a variety of media were tested. The fungus appeared to develop best on potato dextrose agar. Table 1 gives an idea of the relative rates of growth on five of the media employed.

TABLE 1.—Comparative rate of growth of *O. graminis* on five different agar media.

Medium	Average diameter of colonies at the end of 7 days	
	1st test	2nd test
	millimeters	millimeters
Potato dextrose agar	64·0	68·5
Oatmeal agar	58·0	57·5
Czapek's agar	44·5	51·0
Beyerinck's agar	43·0	46·0
Tap-water agar	56·0	60·0

O. graminis grew well on a variety of other media such as sterilized green wheat stems, sweet clover stems, wheat kernels and ground oat-hulls. The only medium upon which mature perithecia and ascospores developed was the ground oat-hulls. Exposure of the cultures to low temperatures seemed to stimulate the production of perithecia and it seems probable that other factors also, such as light, exerted a favourable influence. Some isolation strains produced perithecia more readily than others.

A brief study was made of the rate of growth of *O. graminis* at different temperatures. The fungus was grown on potato-dextrose agar in petri dishes and the diameter of the colonies was used as a measure of the growth rate. The minimum temperature for growth appeared to be about 4° C., the optimum between 22° and 26° C. and the maximum about 33° C. These results agree closely with those reported by Davis (11).

Zonation appeared on colonies developed on potato-dextrose agar in response to sharp alternations of either temperature or light or both. Zonation did not appear on colonies produced at an even temperature in the dark.

Exposure to diffused light appeared to retard the growth of the fungus on potato-dextrose agar. Of a number of plates held at a temperature of 15° to

20° C., one group was kept in light-tight boxes while the remaining group was exposed to the light of day under the protection of a white cotton awning. At the end of seven days the darkened colonies averaged 61 millimeters in diameter while the colonies exposed to the alternating light and darkness of day and night averaged only 46 millimeters in diameter. Similar results are reported by Davis (11).

Pathogenicity Tests

Shortly after the causal organism was isolated in pure culture the pathogenicity of the fungus to wheat was demonstrated by several tests. Some of these were conducted under aseptic conditions by inoculating wheat seedlings growing on Sach's plant nutrient solution and agar in glass tubes plugged with cotton. Others were conducted in pots of sterilized soil standing in the greenhouse. In all cases small bits of agar bearing a pure culture of *O. graminis* were used as inoculum. In all of these tests the seedlings became badly diseased within a short time and a large percentage of them died within a few weeks. The results showed the fungus to be a vigorous parasite even under conditions quite favourable to the development of the host. Since the results were amply verified in the more extensive experiments dealt with later in this bulletin further details will not be given concerning these preliminary tests.

The causal organism was re-isolated from ascospores produced on seedlings inoculated with this fungus and a single-spore culture of it, designated as isolate No. 1, was used in much subsequent work.

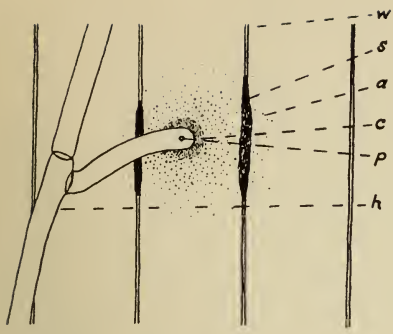
HISTOLOGY OF INFECTION

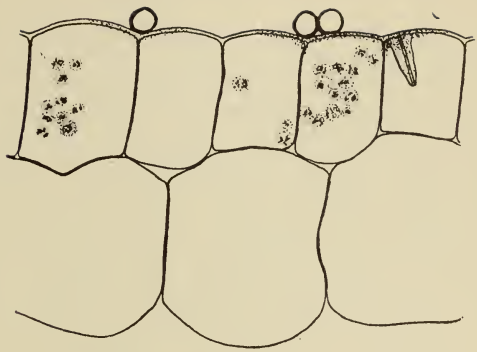
A brief study was made of the phenomena attending the penetration and disintegration of wheat tissue by *O. graminis*. A short summary (62) of this work has already been published. This phase of the study was not completed because the work of Fellows (15) and that of Robertson (59) made it unnecessary.

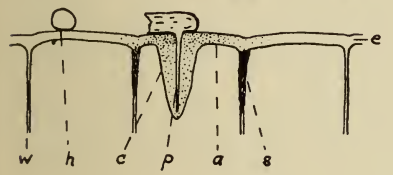
For this study young wheat seedlings were inoculated with the fungus and later either sectioned with the microtome and studied in permanent mounts or else stained while fresh and studied in temporary mounts. The permanent mounts were prepared by the paraffin method and stained with Haidenhain's iron-alum haematoxylin while the temporary mounts were stained with acid fuchsin by the lacto-phenol method.

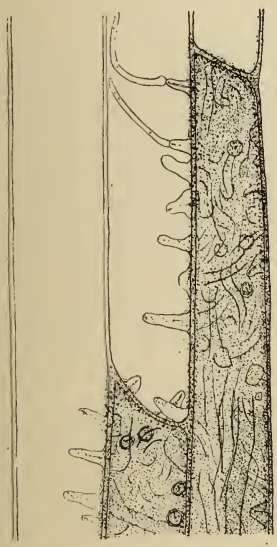
Particular attention was paid to the penetration of the epidermal cells of the coleoptile. The coleoptile is the protective sheath which surrounds the growing stem and first leaf until the tip of the latter emerges from the ground. The epidermal cells are many times as long as they are wide and their long axis is parallel to that of the stem. Their outer wall is covered with a layer of cutin and is comparatively thick so that it offers considerable protection against evaporation, parasitic fungi and other things which may be harmful to the plant tissues. The wheat coleoptile normally possesses two fibro-vascular bundles. Comparatively thin-walled parenchyma cells surround these and fill in the remainder of the space between the inner and outer epidermis of the coleoptile.

When the mycelium comes in contact with the coleoptile it spreads over the surface of the latter, branching as it goes. Numerous short blunt branches are given off and from near the tips of these, minute peg-like structures, which may be called penetration pegs, pierce the outer wall of the epidermal cells. Penetration may take place at any part of the epidermal cell without the development of distinct appressoria. Penetration appears to be largely mechanical









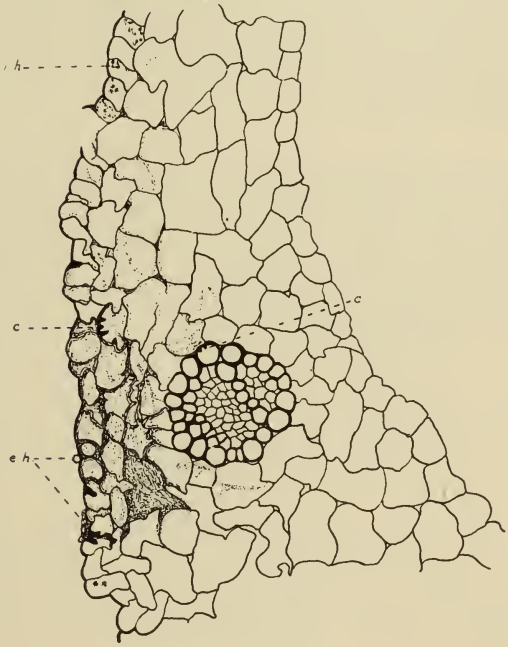


FIG. 6.—Diagrammatic representation of phenomena connected with the penetration of an epidermal cell of the coleoptile of a wheat seedling by *O. graminis*. The following things are illustrated: (w) wall between adjoining cells; (s) swellings of the wall which occur near points of penetration; (a) somewhat circular area around the point of penetration which shows a changed staining reaction; (c) callosity; (p) penetration peg; (h) external hypha; and (e) outer wall of epidermal cell.

FIG. 7.—Transverse section of epidermal cells of wheat coleoptile and both external and internal hyphae of *O. graminis*. Also a callosity in the cell on the right. Photographed from a camera lucida drawing.

FIG. 8.—Part of two epidermal cells of the coleoptile plugged with the mycelium of *O. graminis*, and callosities and invading hyphae in two adjacent cells. Photographed from a camera lucida drawing.

FIG. 9.—Transverse section of a lesion in a wheat coleoptile caused by *O. graminis*, showing external hyphae (e.h.), internal hyphae (i.h.) and callosities (c.). Photographed from a camera lucida drawing.

although the staining re-action of the host cell wall is changed around the point of penetration. Figure 6 is a diagrammatic representation of a typical case of penetration: (*w*) represents part of a cell wall separating two long epidermal cells; (*a*) represents an area of the outer epidermal wall, surrounding the point of penetration, which has stained more heavily than normal areas. The staining properties, of these more or less circular areas around the points of penetration, appear to have become altered, possibly through the action of some enzyme or toxin excreted by the fungus; (*s*) represents swelling of the cell walls which usually occurs on any walls situated near the points of penetration; (*p*) represents a minute penetration peg. As can be seen, the diameter of this is only about one-fifth of the diameter of the external hypha, (*h*); (*c*) represents the outline of a callosity seen through the outer wall of the host cell. Young (75) called these structures callosities but Fellows (15) decided that they were composed mainly of lignin and therefore called them lignitubers. Robertson (59) accepted Fellow's term but Ludtke (38) contended that these structures are formed by a membrane corresponding to the tertiary lamella in normal cells and that they are not composed of lignin. These callosities are curious, tapering, sometimes curved structures which appear to be laid down by the living host cell around the invading fungous hyphae in an attempt to shut them out. Sometimes the cell appears to succeed in this and sometimes the penetrating hypha breaks through the tip of the callosity and proceeds on into the host cell (fig. 8).

Once the mycelium has entered the epidermal cells, it often turns and grows at right angles up or down the long cells, branching as it goes. Figure 7 represents a transverse section of epidermal cells and strands of external and internal mycelium. This figure also shows a callosity. The outline of the internal mycelium is not so distinct as that of external mycelium after the latter has become aged. The diameter of the external mycelium is usually greater. The internal mycelium in living host cells is hyaline, while aged external mycelium has a relatively thick brown wall, and it appears to be empty. Sometimes when the hyphae reach the end of the cell, instead of penetrating into an adjacent cell, they turn around and grow in the opposite direction. When a group of hyphae does this the cell soon becomes more or less plugged with mycelium. Cases of such plugged cells are seen frequently among other uninfected epidermal cells, (fig. 8).

The fungus proceeds from the epidermal cells into the parenchyma cells of the cortex. The destruction of this tissue leads to the appearance of the typical dark brown lesions on the coleoptile of the host. Figure 9 shows a cross section of such a lesion. Outside of the epidermis can be seen several strands of external hyphae. Several epidermal cells on each side of the lesion show internal hyphae. Callosities are visible in several cells including one of the thick-walled cells in the sheath around the fibrovascular bundle. Thickening and discoloration of cell walls and fragments of internal mycelium appear in the parenchyma cells throughout the lesion.

The fungus appears to destroy the parenchymatous tissue much sooner than the fibrovascular tissue. This is probably the reason why, under certain conditions, the underground parts of wheat seedlings may be badly lesioned, as pointed out by McKinney and Davis (46), before the above-ground parts show any symptoms of disease. Infection appears to be limited to the underground parts of the host plant and the base of the stem for a short distance above the ground line.

GREENHOUSE AND FIELD EXPERIMENTS

Host Range Studies

THE RELATIVE SUSCEPTIBILITY OF CERTAIN WILD AND CULTIVATED GRASSES TO *O. Graminis*.—The fungus attacks a comparatively large number of plant species all of which, so far as we know, belong to the grass family. The fact that take-all was discovered in fields which had just been brought under cultivation in Saskatchewan, suggested that *O. graminis* was probably indigenous to the province and that various species of grass occurring in the native flora might be harbouring the fungus. In this province it often happens that certain native grasses which have creeping rootstocks are not completely killed when the prairie sod is broken. The most common of these species are *Agropyron smithii Rydb.*, *Bromus pumpellianus* Scribn. and *Hierochloë odorata* (L.) Wahl. These species sometimes persist for years in the cultivated fields and it has often been noted in our field inspection reports that take-all appeared to have spread from these to the wheat with which they were growing. The same is true of the imported weed, *Agropyron repens* (L.) Beauv. Accordingly it was decided that field collections of grasses from likely situations should be examined for the presence of the fungus and that pathogenicity tests should be conducted to determine the reaction of a number of these grasses to artificial inoculation with pure cultures of *O. graminis*.

Specimens of native grasses were collected for microscopic examination. Most of these were taken from take-all patches in fields of wheat but a few were taken from virgin sod. In most cases the fungus was not abundant on these specimens but both mycelium and perithecia have been found on *Hierochloë odorata* (L.) Wahl. and on *Hordeum jubatum* L. Isolate No. 4 of our collection of *Ophiobolus* cultures was isolated from a specimen of *H. jubatum* collected at Rama, Sask., in 1928 (64). The mycelium alone has been found on field collections of *Agropyron* sp. and *Bromus* spp.

Pathogenicity tests were conducted in both tubes and pots. Tubes were used for the first experiment. Three cultivated grasses, one imported weed and sixteen native grass species were tested and five tubes were sown to each species. Two of these tubes were kept as checks and the seedlings in the other three were inoculated shortly after they had commenced to grow. The tubes were kept upright in box-like racks especially designed for the purpose. The lower ends of the tubes were hidden and more or less darkened by the racks. Some of the grasses grew well under these conditions but others did not. Therefore significant results were secured from only those species which developed normally. Table 2 gives the results obtained.

TABLE 2.—Results of inoculating certain species of grass with *O. graminis*. Experiment conducted in tubes.

Species	Treatment	Germination	Height and condition in 50 days		Perithecia	Susceptibility
			inches			
Agropyron dasystachyum (Hook.) Scribn.	chk.	good	6–8	healthy	—	
	inoc.	good	4–8	dead	few	moderate
A. repens (L.) Beauv.	chk.	good	8·5	healthy	—	
	inoc.	good	7	dead	few	moderate
A. richardsonii (Trin.) Schrad.	chk.	poor	6	healthy	—	
	inoc.	poor	5	dead	few	moderate
A. tenerum Vasey	chk.	good	9	healthy	—	
	inoc.	good	8·5	dead	many	moderate
Agrostis palustris Huds.	chk.	poor	2·25	sickly	—	
	inoc.	poor	2	very sickly	—	(?)
Avena hookeri Scribn.	chk.	poor	—	no growth	—	
	inoc.	poor	—	no growth	—	(?)
Beckmannia syzigachne (Steud.) Fern.	chk.	poor	2	sickly	—	
	inoc.	poor	2	dead	—	(?)
Bromus ciliatus L.	chk.	good	5	healthy	—	
	inoc.	good	5	some dead	few	moderate
B. inermis Leyss.	chk.	good	8·5	healthy	—	
	inoc.	good	8·5	dead	few	moderate
B. porteri (Coult.) Nash	chk.	good	7	healthy	—	
	inoc.	good	6	dead	few	marked
B. pumpellianus Scribn.	chk.	good	8·5	sickly (contaminated)		
	inoc.	good	8·5	dead	none	slight
Deschampsia caespitosa (L.) Beauv.	chk.	poor	2	sickly	—	
	inoc.	poor	1·5	dead	few	slight
Elymus canadensis L.	chk.	good	8	healthy	—	
	inoc.	good	7	nearly dead	few	moderate
E. innovatus Beal.	chk.	good	7	healthy	—	
	inoc.	good	4	dead	few	marked
Festuca saximontana Rydb.	chk.	poor	1·5	sickly	—	
	inoc.	poor	1·5	dead	few	(?)
Hierochloë odorata (L.) Wahl.	chk.	poor	2	sickly	—	
	inoc.	poor	1·75	dead	—	(?)
Hordeum jubatum L.	chk.	poor	3	rather sickly	—	
	inoc.	poor	2	dead	few	(?)
Koeleria gracilis Pers.	chk.	poor	1·5	sickly	—	
	inoc.	poor	2	dead	—	(?)
Phleum pratense L.	chk.	poor	4	sickly	—	
	inoc.	poor	4	sickly	—	(?)
Poa palustris L.	chk.	poor	2	sickly	—	
	inoc.	poor	1·75	dead	—	(?)

NOTE:—The nomenclature of Rydberg's "Flora of the Prairies and Plains of Central North America" is followed in the above list of species. The seed for this experiment was very kindly furnished by W. P. Fraser, Professor of Botany at the University of Saskatchewan.

The second experiment was conducted in six-inch pots under greenhouse conditions. Twenty-four species of grass were tested. About twenty seeds per pot were sown and these were inoculated by placing bits of agar, overrun with *Ophiobolus* mycelium, in the soil with the seed.

The grasses all germinated and grew fairly well although some symptoms of infection appeared and a few seedlings died in the seedling stage. At the end of 14 weeks one-half of the plants were taken out of the pots and parts of them were examined for signs of the fungus. This helped to relieve crowding. The remaining plants were trimmed down to near the ground line and the soil in each pot was limed with 3 grams of CaO to keep the soil from becoming too acid. More inoculum was added at this stage to the soil around the base of the plants. These inoculations did not produce any immediate and marked effect. Later on, however, the plants commenced to die. Many of these were taken up and examined and in each case their roots were found to be badly decayed and perithecia were present on their stems at the ground line.

The experiment was terminated and the plants examined carefully seven months after they were sown. Although only a few of the species had been killed outright in the course of the experiment, the majority of the remaining plants bore perithecia on their stems and mycelium on their roots and lower leaf-sheaths. Table 3 gives a summary of the results of this experiment.

TABLE 3.—Results of inoculating certain species of grass with *O. graminis*. Experiment conducted in pots in the greenhouse.

Species	Seedling infection	Final condition	Mycelium on roots	Perithecia	Infection
Agropyron dasystachyum	0	sickly	plentiful	many	moderate
A. repens	0	sickly	plentiful	many	moderate
A. richardsonii	0	sickly	plentiful	many	moderate
A. smithii Rydb	1 dead	3 dead	plentiful	many	moderate
A. tenerum	1 dead	sickly	plentiful	many	moderate
Agrostis palustris	0	healthy	none	none	none
Avena hookeri	0	healthy	scarce	few	light
Beckmannia syzigachne	0	healthy	none	none	none
Bromus ciliatus	0	all dead	plentiful	many	heavy
B. inermis	0	sickly	plentiful	many	moderate
B. latiglumis (Shear) Hitchc	0	sickly	plentiful	few	moderate
B. porteri	0	mostly dead	plentiful	many	heavy
B. pumpellianus	0	fairly healthy	plentiful	many	moderate
Calamagrostis sp	0	healthy	scarce	none	light
Deschampsia caespitosa	0	healthy	scarce	few	light
Elymus canadensis	0	all dead	plentiful	many	heavy
E. innovatus	1 dead	all dead	plentiful	many	heavy
Festuca saximontana	0	healthy	none	none	none
Hierochloë odorata	1 dead	healthy	scarce	none	light
Hordeum jubatum	0	healthy	plentiful	few	moderate
Koeleria gracilis	0	healthy	none	none	none
Phleum pratense	0	healthy	none	none	none
Poa triflora	0	healthy	plentiful	few	light
Schizachne purpurascens (Torr.) Swallen	0	healthy	scarce	none	light

NOTE.—The nomenclature of Rydberg's "Flora of the Prairies and Plains of Central North America" is followed in the above list of species. The seed for this experiment was very kindly furnished by W. P. Fraser, Professor of Botany at the University of Saskatchewan.

Following the test of the native grass species one or two varieties of each of the eight sub-species of wheat were subjected to inoculation with *O. graminis*. In this test the following varieties were used: Alaska (*Triticum turgidum*), Einkorn (*T. monococcum*), Emmer (*T. dicoccum*), Acme and Kubanka (*T. durum*), Little Club (*T. compactum*), Marquis and Ruby (*T. vulgare*), Polish (*T. polonicum*), and Spelt (*T. spelta*).

Six pots of each variety were sown; three being used for checks and the seedlings in the remainder being inoculated. Six-inch flower pots were employed and the test was conducted in the greenhouse. The soil was sterilized for 3½ hours with steam under a pressure of 10 pounds per square inch. The seed was surface sterilized by dipping it in a solution of alcohol and water and then soaking it for 5 minutes in a 1:1000 solution of mercuric chloride and water following which it was rinsed in pure water. Ten seeds were sown per pot. The inoculum used was a pure culture of *O. graminis* on agar, about 1 square centimetre being used per seed and placed beside the seed when it was sown. It was planned to carry the plants through to maturity and to compare the yields of the inoculated plants with that of their respective checks but a prolonged epidemic of powdery mildew made it necessary to terminate the experiment at the end of fifteen weeks. Table 4 gives a summary of the results obtained.

TABLE 4.—Results of inoculating different species and varieties of wheat with *O. graminis*. Experiment conducted in pots.

Variety	Treatment	Germination	6 weeks		15 weeks		Average height
			Dead	Sickly	Dead	Living	
							inches
Einkorn	check	30	2	0	2	28	7
"	inoc.	28	3	8	5	23	6
Emmer	check	29	0	0	0	29	25
"	inoc.	28	2	0	2	26	24
Spelt	check	26	0	0	0	26	18
"	inoc.	27	7	9	12	15	17
Polish	check	16	0	0	0	16	25
"	inoc.	16	1	10	4	12	16
Alaska	check	23	0	3	0	23	32
"	inoc.	21	2	5	2	19	28
Acme	check	26	0	0	0	26	25
"	inoc.	29	3	6	4	25	19
Kubanka	check	29	0	0	0	29	24
"	inoc.	29	5	16	8	21	14
Little Club	check	30	0	0	0	30	15
"	inoc.	30	6	16	12	18	14
Marquis	check	27	0	0	0	27	20
"	inoc.	28	2	6	3	25	17
Ruby	check	30	0	0	0	30	23
"	inoc.	29	9	9	13	16	18

From the number of plants killed and the degree of stunting in each variety it can be seen that they were all affected to a considerable extent although Emmer, Alaska and Marquis were injured somewhat less than the others.

Two other cultivated plants, corn and flax, were subjected to inoculation with *O. graminis* under greenhouse conditions. An abundance of *Ophiobolus* mycelium was found running over the surface of the roots, when the plants were in the seedling stage, and some callosities were noticed in the epidermal cells of the roots of both species. This indicated that the fungus had attempted to penetrate the epidermal cells. However, no loss of vigour was shown by the inoculated plants of either species. Evidently these are very resistant to *O. graminis* under ordinary greenhouse conditions.

From the results of the above tests it appears that *O. graminis* (isolate No. 1) is able to infect many different species belonging to the grass family. All of these species were not equally susceptible, however, and the following, *Agrostis palustris, Avena hookeri, Beckmannia syzigachne, Calamagrostis* sp., *Deschampsia caespitosa, Festuca saximontana, Koeleria gracilis, Phleum pratense* and *Zea mays,* appeared to be practically immune. Flax, the only species outside of the grass family which was tested, also appears to be immune. On the other hand, certain native grasses, such as *Bromus ciliatus, B. porteri, Elymus canadensis* and *E. innovatus,* appeared to be almost as susceptible as *Triticum* spp. The presence of *O. graminis* on certain of the field collections of native grasses, together with the marked susceptibility of some of the species of grass commonly found in Saskatchewan, strongly support the view that the fungus is indigenous to this region. Most investigators of take-all in North America agree with this view but a few have expressed the opinion that the disease was introduced from Australia.

The above facts have a direct bearing on the development of control measures for take-all. This disease may be expected to appear in the first crops of wheat following the breaking of the prairie sod for the sod is already infested in places with the causal organism. The necessity of preventing the growth of susceptible grasses in wheat fields, where *O. graminis* is likely to exist, is quite apparent. As grasses possessing creeping rootstocks are very difficult to kill, especial pains must be taken to eradicate them, because the fungus probably

overwinters in the mycelial stage on their underground parts, and also in the perithecial stage on the crowns of such hosts. Corn and flax should prove to be of considerable value in crop rotations which are designed to control take-all, since they both appear to be quite resistant to the causal organism.

Certain other investigators have made more or less extensive investigations of the host range of *O. graminis*. Of these, Kirby's (35) deserves special attention. An extensive list of grasses together with notes on their reaction to *O. graminis* appears in his memoir. Eleven of the species listed in table 3 are not dealt with in this table. As for the remainder of those which we have tested, our results agree quite well with his except in the case of the following three species:—*Beckmannia syzigachne (erucaeformis), Bromus inermis* and *Koeleria gracilis (cristata)*. Since, as will be shown later, different isolates of *O. graminis* vary greatly in their pathogenicity to wheat it seems reasonable to suppose that that may vary somewhat in their host range.

THE RELATIVE SUSCEPTIBILITY OF OUR COMMON CEREALS TO *O. graminis*:—The next step in these investigations was to ascertain the relative susceptibility of wheat, oats, barley and rye to *O. graminis* under the conditions prevailing in this country. This question has a very important bearing on the selection of cereals for field crop rotations in districts where take-all is prevalent. This phase of the work was begun in the laboratory and supplemented by field tests.

In the case of the first test the seedlings were grown in tubes on nutrient agar. Marquis wheat, Banner oats, O.A.C. No. 21 barley, and Prolific spring rye were used as test varieties. Four tubes were sown to each species, the seedlings in one tube was kept as a check and those in the remaining tubes were inoculated with *O. graminis*. Two seeds were sown per tube. Although the seed was surface sterilized, by dipping it in 85 per cent alcohol and then soaking it in an aqueous solution of mercuric chloride, considerable contamination (mainly *Alternaria* sp.) developed from the seed coats of the oats and barley. As was the case in the pathogenicity tests described previously, *O. graminis* proved to be an aggressive parasite of wheat.

The relative susceptibility of these different cereals to *O. graminis* is shown by the following results. The inoculated wheat seedlings all died within 22 days from the time of inoculation. The barley and rye seedlings offered more resistance but all died within 40 days and 35 days respectively. The oat seedlings did not appear to be affected by *O. graminis* but the results in this case were obscured by contamination which developed from the seeds.

The next two experiments on this subject were duplicate experiments which gave similar results so they will both be considered together. They were conducted in the greenhouse in six-inch pots. The same four varieties of the cereals were used as in the previous tube experiment. In each experiment there was one check pot and two pots of inoculated seedlings of each cereal. These were sown at the rate of ten seeds per pot. To secure infection pure cultures of *O. graminis* on agar were cut into pieces about 1 x 0·5 cm. and one of these was placed against each seed as it was sown.

The following results were obtained:—The wheat was heavily attacked in the seedling stage and nearly half of the seedlings were killed; several barley and rye seedlings showed indications of infection in the seedling stage; and the oat seedlings showed none. Later on, the surviving wheat plants recovered their normal colour and most of them headed but some of them remained more or less stunted and their heads did not fill properly. The oat plants became scraggly, tillered profusely and set no seed but this behaviour seemed to be a reaction to the conditions prevailing in the greenhouse as the checks and inoculated plants behaved alike. The few barley seedlings which showed symptoms of take-all in the early stages recovered so completely that there was no difference noticeable between check and inoculated plants at maturity. Like the barley, the rye plants

which gave indications of disease in the seedling stage recovered to such an extent that the checks appeared to be in no way superior to the inoculated plants at maturity.

Further comparative tests of the relative susceptibility of the cereals were conducted under field conditions. Table 5 gives the results obtained at St. Gregor in 1927 and 1928. In these tests the cereals were sown in rows 5 feet long, spaced 8 inches apart. There were two inoculated rows and two check rows of each variety so the figures given for each in the table are the average of two rows in every case. The seed was sown by hand in rows opened up with a hoe. Infection was secured by sprinkling in a small amount of pure culture of *O. graminis,* growing on oat-hulls, with the seed as it was sown.

In the table the height is expressed in inches and it represents the average height of the row at harvest time. The figure for the percentage dead is based, for each row, on the number of seedlings which emerged so it represents the percentage which died between emergence and harvest. A comparison of the average emergence in check rows and inoculated rows showed that very little pre-emergence blight occurred.

TABLE 5.—Relative susceptibility of cereals to *O. graminis.* Experiment conducted in the field.

Cereal	Variety	Check		Inoculated		Average dead
		height	dead	height	dead	
		inches	%	inches	%	%
Wheat	Alaska	40·0	12·0	19·0	71·5	.....
"	Kubanka	40·0	2·0	16·5	83·5	.....
"	Little Club	38·5	15·5	14·0	84·5	83
"	Polish	35·5	9·5	14·5	84·5	.....
"	Reward	33·0	8·0	12·5	93·0	.....
Barley	Barks	30·5	1·5	20·0	33·0	.....
"	Can. Thorpe	37·5	1·0	24·0	33·0	.....
"	Gatami	28·5	10·0	10·5	83·5	49
"	Hannchen	32·0	6·5	20·0	35·5	.....
"	O.A.C. No. 21	33·5	6·5	21·0	61·5	.....
Rye	Ottawa Select	41·0	18·0	39·5	18·5	.....
"	Prolific	41·5	12·5	40·5	23·0	21
Oats	Banner	41·0	21·5	38·0	4·5	.....
"	Black Victor	39·5	3·0	36·5	1·0	.....
"	Gerlach	41·0	14·5	38·5	1·5	3
"	Gold Rain	41·0	9·0	38·0	1·5	.....
"	Victory	40·0	9·0	37·0	5·0	.....

It can be seen from the results of this test that these cereals react to *O. graminis* much the same in the field as they do in the greenhouse. Wheat is very susceptible, barley and rye are moderately resistant while oats are very resistant. The Gatami barley was an exception in this case, being about as badly diseased as the wheat varieties. In more recent tests, however, using Gatami barley from a different seed lot this variety has not shown any heavier infection than Hannchen and O.A.C. No. 21. While the average height of the inoculated oat rows was somewhat less in each case than that of the checks the percentage of plants which succumbed was less and no signs of disease were visible to the naked eye. This test was repeated in the field in 1928 but many of the rows of barley, oats, and rye were destroyed by ground squirrels (*Citellus franklini* (Sabine)) just previous to harvest time so that the usual data could not be secured. Judging from the notes taken in the seedling stage and from the appearance of the cereal plots just previous to their destruction, however, the results would have been very similar to those of the previous year.

In 1930 and 1931 the cereals were again tested in the field. Rod rows were sown and the yield was the main criterion of the severity of infection in these tests. Duplicate tests were run both years at Saskatoon and St. Gregor. The

rows were replicated three times so that the figures given in table 6 are the average for four pairs of rows, i.e., one inoculated and one check row in each pair. In 1931 the cereal rows at St. Gregor were damaged by ground squirrels so that yield data could not be obtained. The same is true of the oat rows at the same place in 1930. In 1930 the plots at Saskatoon were subjected to high winds and soil drifting when the grain was in the seedling stage. This resulted in an unusually high mortality in the seedling stage in the inoculated rows of barley, rye and oats and this is clearly reflected in the yields of these cereals for that year. Under the same conditions the wheat seedlings recovered more readily.

TABLE 6.—Reaction of cereals to artificial inoculation with *O. graminis* under field conditions. Rod row tests, 1930-31.

Cereal	Variety	Reduction in yield				Average reduction in yield
		Saskatoon		St. Gregor		
		1930	1931	1930	1931	
		%	%	%	%	%
Wheat	Marquis	70	37·0	50	.....	52
Barley	O.A.C. No. 21	67	22·5	38	.....	42
Rye	Prolific	46	20·5	14	.....	27
Oats	Banner	33	− 4·0	.....	.....	15

All of the above mentioned experiments and the field observations which have been made agree fairly well concerning the reaction of our common cereals to *O. graminis* in this province. It is shown that under conditions conducive to heavy infection of wheat, either in the seedling or in later stages of growth, barley becomes infected to a lesser extent, rye still less, and oats remain almost unaffected.

Judging by the literature on the subject, these cereals show about the same reaction to *O. graminis* in most parts of the world where take-all is found. It is recognized, however, that exceptions have been reported. For example, Jones (31), working in Wales, states that he secured all of the material for his cytological research from the stubble of oats infected with *O. graminis*, and that this host appears to be so severely infected, at times, that grain does not develop normally. It is also reported (3) that a sample of take-all on oats was received from Corwen, Wales, and that pathogenicity tests with the fungus isolated from it showed that it was pathogenic on wheat, oats and barley in the seedling stage. Osborn (50) reported infection of oats and the production of perithecia on this host in Australia and Ducomet (14) reported the same thing in France. Most authors are agreed, however, that oats are practically immune (35) (45) (58) (63) (68). Many reports of *O. graminis* infecting barley and rye have appeared but, with one exception (30), these hosts are considered to be less susceptible than wheat (5) (35) (41) (63) (68) (72).

Wheat Variety Tests

Different varieties of a cultivated plant sometimes show marked differences in susceptibility to certain diseases. In some cases it has been possible to secure satisfactory control of a disease by using only varieties which prove resistant to it, such as was the case with the rosette disease of wheat (44). In other cases it has been possible to cross resistant varieties, which were unsuitable in certain other characteristics, with susceptible varieties, which were otherwise suitable, to obtain a hybrid which possessed the disease resistance of the former com-

bined with the desirable cultural characteristics of the latter. With these possibilities in mind a study was made of the reactions of a wide range of wheat varieties to inoculation with pure cultures of *O. graminis.*

Technique of Pot Experiments.—The same general technique was employed in all of the pot experiments constituting a part of these variety tests. The experiments were conducted in the greenhouse. Six-inch pots were used and four pots were sown to each variety in any one test. One of these pots was used as a check and the seedlings in the other three were inoculated by scattering a weighed amount (usually 5 gm.) of ground oat-hull inoculum over the seed in each pot at seed level, before it was covered with an inch and a half of soil. The soil was a mixture of five parts of ordinary field soil to one part of pure sand. In some tests the soil was sterilized (2½ hours at 15 pounds steam pressure) and in others it was not, but each variety of wheat was tested at least once in both sterilized and unsterilized soil. The soil of this immediate vicinity is a dark brown heavy silty clay loam. An attempt was made to keep the soil in all the pots equally moist but no record of the actual degree of saturation was obtained. In the later tests the pots were shifted twice a week to reduce errors due to position as it was found that the pots at the edge of the bench lost moisture faster than those farther back. The air temperature of the greenhouse was kept as near 20° C. as was feasible but considerable variations occurred at times. Eighteen seeds were sown in each pot as the tests were terminated about the end of the seedling stage. This is about twice the number of seeds sown per pot in experiments in which the plants were to be carried through to maturity. This arrangement gave a population of approximately fifty inoculated seedlings and eighteen check seedlings of each variety in every test. The degree of stunting as compared with the checks and the number of sickly or dead seedlings were used as a measure of the severity of infection.

Wheat Variety Tests.—As wheat is more susceptible to *O. graminis* than our other cereals and as wheat is of much more economic importance to us than the others, an intensive study of the relative susceptibility of wheat varieties was made. One hundred different varieties were studied both in the greenhouse and in the field. The seed of the greater number of these was procured from the Field Husbandry Department of the University of Saskatchewan; that of twenty-five varieties was furnished by the Dominion Rust Laboratory at Winnipeg, Manitoba; while the seed of two of them, Hybride de la Paix and Teverson, was sent to us by Mr. L. Guyot of the Central Station of Phytopathology at Paris, France. These last two varieties are of particular interest because they have been reported as resistant to *piétin* in France (24). Seventy-five of the varieties were tested three times but the remaining twenty-five varieties were tested only once in the greenhouse.

The field tests were carried on for two years at both St. Gregor and Melfort. The varieties were sown in four plots of five-foot rows. The rows were spaced eight inches apart which is two inches more than the space left by seed drills in ordinary farm practice, but this made it easier to keep the weeds hoed from between the rows. One row of each variety was sown in each plot; inoculum was placed in the rows with the seed in two plots and in the other two plots no inoculum was used. Ground oat-hulls overrun with the mycelium of the fungus was used as inoculum and merely enough was scattered in with the seed to insure some of it being in close proximity to each seed. During the seedling stage notes were taken regarding the relative emergence and general appearance of the inoculated and the check seedlings. At harvest time the relative height and the percentage of dead plants in the inoculated and uninoculated rows was recorded.

Table 7 gives a summary of the results obtained in the variety tests just described. The work which it covers entailed a study of 1,000 pots and 1,200

rows of wheat. The varieties used in these experiments are listed in column 1. In columns 2, 3 and 4 is shown the percentage of seedlings of each variety, which died in the three greenhouse tests; while column 5 contains the averages of these figures. Column 6 and 7 show the percentage of dead seedlings for each variety at the end of the seedling stage in the 1928 field tests at St. Gregor and Melfort. Columns 8 and 9 show the percentage of dead plants at maturity in the 1927 and 1928 field tests at St. Gregor, and column 10 shows the average percentage for the two years.

TABLE 7.—Results of wheat variety tests in greenhouse and field experiments.

Variety	Percentage of dead plants								
	Greenhouse tests				Field tests				
					Seedling stage, 1928		Mature stage, St. Gregor		
	Test 1	Test 2	Test 3	Average	St. Gregor	Melfort	1927	1928	Average
Acme	78	76	73	76	44	42	80	80	80
Alaska	96	43	60	66	46	47	72	72	72
Arnautka	53	36	49	46	46	31	71	70	70
Aurore	63	63	55	60	70	62	75	79	77
Australian	39	23	31	31	41	50	91	62	76
Bishop	28	41	28	32	42	51	75	48	61
Brownhead	46	26	47	40	51	48	84	73	78
Brownie	75	64	69	69	52	47	78	76	77
Ceres	54	24	20	33	30	41	71	38	54
Chagot	96	87	87	90	69	58	93	73	83
Chelsea	42	31	47	40	46	57	76	59	67
Comeback	30	47	50	42	55	44	94	77	85
Dindiloa	22	24	20	22	34	44	81	55	68
Early Prolific	24	31	41	32	47	50	68	65	66
" Red Fife	26	24	22	24	39	46	70	55	62
" Triumph	59	48	57	55	46	53	79	63	71
Einkorn	69	47	64	60	54	51	85	58	71
Emmer	64	50	27	47	38	42	65	53	59
Federation	26	43	50	40	53	57	83	67	75
Florence	26	24	25	25	42	40	82	60	71
Forward	47	71	73	64	49	57	90	61	75
Garnet	76	56	76	69	61	58	84	68	76
Garton's	46	57	67	57	46	58	80	63	71
Golden	37	46	39	41	35	48	84	45	64
Huron	52	50	53	52	56	67	81	69	75
Hybride de Paix	50	56	83	63	61	49	45	72	58
Iumillo	78	95	96	90	52	54	92	69	80
Khala	71	93	81	82	46	48	86	64	75
Khapli	39	85	67	64	29	44	91	53	72
Kitchener	48	67	73	63	50	58	75	61	68
Kota	48	42	51	47	49	57	80	58	69
Kubanka	60	88	69	72	52	48	84	70	77
Little Club	31	77	89	66	61	51	85	77	81
Marquis No. 7	31	21	69	40	45	57	77	50	63
" No. 70	43	33	51	42	40	58	81	51	66
" No. 994	35	49	81	55	34	47	72	37	54
" No. 1221	33	35	55	41	35	48	79	42	60
" No. 1291	48	33	59	50	37	56	85	44	64
" No. 1293	31	27	31	30	40	55	83	53	68
" III–25–II	78	57	72	69	46	46	74	56	65
" III–25–66	54	41	42	46	57	56	90	62	76
" III–25–68	52	35	48	45	37	40	81	61	71
" No. 1207	54	9	37	33	52	51	75	62	68
" No. 1006	39	41	64	48	36	42	81	51	66
Mahmondi	80	56	71	69	62	50	78	81	79
Marouani	76	63	67	69	64	53	73	75	74
Master	80	71	87	79	59	56	91	75	83
Medeah	85	72	73	77	53	38	70	69	69
Mindum	91	62	83	79	71	54	86	84	85
Monad	81	73	83	79	61	61	86	86	86
Nabawa	22	92	94	69	64	60	82	71	76
Nodak	56	94	90	80	64	64	83	74	78
Pelissier	45	85	67	66	46	45	85	61	73
Pentad	56	89	87	77	51	41	69	64	66
Polish	84	86	82	84	68	50	85	74	79
Preston	67	69	67	68	48	59	84	59	71

TABLE 7.—Results of wheat variety tests in greenhouse and field experiments-*Concluded*

Variety	Percentage of dead plants								
	Greenhouse tests				Field tests				
					Seedling stage, 1928		Mature stage St. Gregor		
	Test 1	Test 2	Test 3	Average	St. Gregor	Melfort	1927	1928	Average
Prospector	83	85	87	85	72	54	87	82	84
Pusa	81	65	68	71	78	52	98	93	95
Quality	45	37	68	50	30	34	81	74	77
Reafern	56	45	52	51	30	31	76	62	69
Red Bobs	72	63	91	75	45	39	73	69	71
Red Fife	59	49	76	61	44	27	90	64	77
Red Russian	80	53	63	65	42	44	72	57	64
Renfrew	59	52	70	60	49	33	71	60	65
Reward	73	51	75	66	42	37	93	62	77
Riga	74	83	73	77	62	44	83	76	79
Ruby	80	82	81	81	57	50	88	75	81
Spelt	91	77	63	77	59	49	82	73	77
Supreme	89	65	71	75	47	49	92	66	79
Teverson	68	62	59	63	50	.....	53	59	56
Topaz	94	93	87	91	55	53	90	69	79
Univ. No. 222	94	74	72	80	69	57	83	75	79
Whitehead	94	61	60	72	60	40	77	73	75
White selection	78	53	57	63	52	38	80	68	74
Yandilla King	57	83	69	70	50	57	74	72	73
Alberta No. 3	31	.....	.....	.....	45	52	77	55	66
Axminster	16	.....	.....	.....	56	47	73	64	68
Blue Ribbon	16	.....	.....	.....	64	47	75	69	72
Calcutta D2B	15	.....	.....	.....	59	50	91	73	82
Crown	5	.....	.....	.....	41	39	92	59	75
Duchess	22	.....	.....	.....	65	50	91	73	82
Early Russian	0	.....	.....	.....	62	57	83	64	73
Hayne's Bluestem	5	.....	.....	.....	54	47	70	56	63
Major	5	.....	.....	.....	49	58	83	60	71
Marquillo	8	.....	.....	.....	54	47	90	62	76
Minburn	30	.....	.....	.....	59	52	67	66	66
Monad	25	.....	.....	.....	64	60	87	78	82
O.A.C. No. 85	13	.....	.....	.....	59	58	86	64	75
Pioneer	11	.....	.....	.....	47	66	74	77	75
Piper	11	.....	.....	.....	57	58	71	66	68
Power	0	.....	.....	.....	61	56	78	65	71
Prelude	13	.....	.....	.....	61	50	91	72	81
Producer	9	.....	.....	.....	64	59	85	71	78
Progress	0	.....	.....	.....	52	52	75	53	64
Reliance	7	.....	.....	.....	42	45	85	52	68
Swedish	10	.....	.....	.....	65	54	80	66	73
Tartan	9	.....	.....	.....	49	48	79	59	69
Triticum turgidum	8	.....	.....	.....	62	46	83	67	75
White Fife	17	.....	.....	.....	60	46	84	63	73
White Russian	23	.....	.....	.....	56	51	86	63	74

Slight differences appeared to exist in the relative susceptibility of the varieties and these differences seemed to be fairly consistent in the different tests. To get a mathematical measure of the significance of these differences the co-efficients of correlation between the percentage of dead seedlings of each of the first 75 varieties in the different tests was computed. The following positive correlation co-efficients were obtained: between those in column 2 and column 3, $0 \cdot 5197 \pm 0 \cdot 0568$; between those in column 2 and column 4, $0 \cdot 5213 \pm 0 \cdot 0567$; and between those in column 3 and column 4, $0 \cdot 7861 \pm 0 \cdot 0299$. The correlation between the percentage of dead seedlings for each of the 100 varieties in the field tests at St. Gregor and Melfort in 1928 (columns 6 and 7) is expressed by the following co-efficient: $+0 \cdot 5008 \pm 0 \cdot 0505$. These are comparatively significant figures and they indicate that in these tests the different varieties reacted in a fairly consistent manner to artificial inoculations with *O. graminis*. Moreover, the correlation co-efficient between the average of the three pot tests and the average of the results obtained at maturity in the 1927 and 1928 field tests

is $+0 \cdot 5659 \pm 0 \cdot 0529$, which indicates that the correlation between the results obtained in the greenhouse and those obtained in the field was fairly satisfactory.

Technique of Crock Experiments.—In order to get consistent results in experiments such as these one must have uniformity of conditions. In the pot experiments just described the factor which was hardest to control was the amount of moisture in the soil. The pots with the heaviest growth of wheat in them lost water through transpiration much faster than those with a thinner unthrifty growth. Moreover evaporation as well as transpiration appeared to be greater in pots around the edge of the bench than in pots towards the centre of the bench. Hence all subsequent work of this kind was carried on under controlled conditions as far as soil moisture was concerned. The soil was tested as it came from the bin to ascertain its moisture content and its moisture holding capacity. One-gallon glazed earthenware crocks were substituted for the six-inch pots. These were all brought to the same weight by adding pebbles to the lighter ones. An equal weight of bin soil was put in each crock and an equal weight of water was added to each. This was kept approximately constant throughout the test by placing the crocks on the scales whenever water was added and bringing them back to the original weight. Twice a week the crocks were shifted to reduce errors due to position on the bench.

While twenty-five seeds were sown per crock, as compared with eighteen per six-inch pot, the individual seedlings were given more soil as the crocks held two and a half times as much soil as the pots. Thus, crowding of the root systems was reduced.

A disease rate was computed for each crock of seedlings instead of taking the percentage of dead seedlings as a measure of the virulence of the infection. This method took into account the condition of each seedling. The disease rate was computed as follows:—

At the end of each test (4 or 5 weeks after seeding) the seedlings were dug and examined. The check seedlings were measured individually from the seed to the tip of the tallest leaf, and the approximate average of these measurements was taken as the normal height to which seedlings should have developed under the conditions of the experiment. All of the seedlings in the test were divided into different classes according to the amount of stunting which they exhibited when compared with the healthy checks and according to the lesions which they bore. Those which were slightly stunted but not lesioned and those which were noticeably lesioned but not stunted were given $\frac{1}{2}$ point each for disease. Those which were noticeably diseased and measured only from three-quarters to a little less than the average height of the checks were given a disease rate of one point each. Those which were clearly diseased and which measured between one-half and three-quarters of the height of the check were given two points apiece. Those which were badly diseased and stunted below one-half the height of the checks were given three points each. Those which failed to emerge and those which died after emerging were given four points apiece (fig. 10). Since twenty-five seeds were sown per crock and each dead or missing seedling was given four points as a disease rate, this amounted to one hundred points in all cases where all of the seedlings succumbed during the test. Therefore the disease rating is on a direct percentage basis.

This afforded a very practical and satisfactory way of summing up the condition of the seedlings at the end of any test. Stunting is one of the most striking and constant symptoms of seedling infection from *O. graminis*, hence it was made the main basis from which to compute the disease rate. Whenever possible, only good plump seed of high germinative capacity was used and thus very little of the disease rate was ordinarily due to non-germination.

Thus, in all greenhouse experiments conducted since the beginning of the year 1928, the following three improvements in technique have been practised:

(1) the soil moisture has been controlled, (2) there has been less crowding of the root systems of the seedlings, (3) a disease rate has been computed for each crock of seedlings. The following desirable results have accrued from these improvements in technique: (1) the results secured from different crocks treated alike have been more uniform; (2) the development of the seedlings has been more vigorous; (3) a truer record of the condition of the seedlings in each test has been preserved.

FIG. 10.—Wheat seedlings inoculated with *O. graminis* illustrating the different classes into which the seedlings were placed when computing the disease rate. Left to right: check, class 1, class 2, class 3 and class 4.

FURTHER WHEAT VARIETY TESTS.—Although from the results of the previous tests slight differences in varietal susceptibility appeared to exist it must be remembered that seedlings from plump, strongly viable seed are apt to resist infection of this type better than seedlings from shrunken seed which germinates less vigorously. Therefore, the question arose as to whether the consistent differences detected in the seedling stage were due to actual variations in varietal susceptibility or to variations in viability of the seed samples used. In an effort to find an answer to this question another series of tests was conducted on the following plan:—Four varieties of wheat in common use in Saskatchewan, namely Garnet, Marquis, Mindum and Reward, were employed.

Seed of these four varieties was obtained from three localities and in each case the seed had been produced at the same time in variety tests. One set of samples came from the Dominion Experimental Farm at Indian Head, Sask.; another set from the Dominion Experimental Station at Rosthern, Sask. and the remaining set from our own plots at St. Gregor, Sask. In this way it was felt that errors due to mere differences in germinative vigour of seed samples should be considerably reduced. Two tests were conductd on each sample, making six tests in all. The improved technique described above was employed in these tests. Table 8 shows the tabular notes taken on one of the six tests mentioned above. It is presented here to show an example of the data on which the disease rates in table 9 are based. The fresh weight of the seedlings was taken as they were dug but these weights were not used in computing the disease rates.

TABLE 8.—Tabular notes of variety test. Second test of seed produced at St. Gregor, Sask.

Crock No.	Variety	Treatment	Emergence	Final notes; 34 days							Disease rate	
				Green weight	Average height	Classes						
						4	3	2	1	½	Indiv.	Ave.
				grams.	inches							
1	Garnet	check.	25	10·00	11·75	2	0	0	2	6	13	
2	"	inoc.	22	2·75	4·00	18	3	4	0	0	89	
3	"	inoc.	23	3·00	4·00	20	0	3	2	0	88	88·5
4	Marquis	check	25	11·00	11·75	0	0	1	1	8	7	
5	"	inoc.	25	2·00	3·50	22	2	1	0	0	96	
6	"	inoc.	24	3·50	4·00	17	4	3	1	0	87	91·5
7	Mindum	check	22	13·50	12·50	3	1	0	1	6	19	
8	"	inoc.	21	2·50	4·00	13	12	0	0	0	88	
9	"	inoc.	18	2·50	4·00	14	10	0	1	0	87	87·5
10	Reward	check	25	11·50	11·75	0	0	0	6	6	9	
11	"	inoc.	22	2·00	3·50	23	2	0	0	0	98	
12	"	inoc.	23	2·00	3·50	20	3	2	0	0	93	95·5

Table 9 shows a summary of the disease rates of the above test and the remaining five tests of the same series. The total number of seeds of each variety sown in this series of tests was four hundred and fifty. In every test but one Mindum gave the lowest disease rate but there was so little difference in the disease rates that one would class it as quite susceptible. There is very little to choose between the disease rates of the other three varieties although the average for Reward is slightly higher than those for Marquis and Garnet. Reward gave the highest disease rate in four out of the six tests.

TABLE 9.—A comparison of the relative susceptibility of Garnet, Marquis, Mindum and Reward wheat in the seedling stage to *Ophiobolus graminis*.

Test	Source of seed	Garnet	Marquis	Mindum	Reward
First	St. Gregor	95·5	94·5	85·0	97·0
Second	"	88·5	91·5	87·5	95·5
Third	Indian Head	89·0	89·0	85·5	90·0
Fourth	"	54·0	63·5	56·5	56·0
Fifth	Rosthern	94·0	93·0	91·0	92·0
Sixth	"	50·0	49·0	46·5	56·5
	Average disease rate	78·6	80·1	75·3	81·1

Field tests of these same varieties were carried out in 1930 and 1931. The wheat was sown in rod rows eight inches apart and check rows from the same seed were sown adjacent to the inoculated rows. Four pairs of rows were sown at Saskatoon and four pairs at St. Gregor each year. The emergence was reduced considerably by the inoculation in each test but yield was used as the

main criterion of severity of infection. The yields in grams are shown in table 10 and the reductions in yields expressed in percentage of the weights of the checks are shown in columns 4, 7 and 10. The yield is the total weight of the heads from the row, in each case, expressed in grams and is not the weight of the grain alone. The weight of the heads was taken in order to save the time and energy required to thresh and clean the small samples by hand, as we had not suitable machinery for the purpose. However, to make sure that the results obtained in this manner were reliable, in 1931, one hundred rows were also threshed and cleaned by hand and the results compared. The co-efficient of correlation between the weight of the heads and the weight of the grain for the hundred rows was $+0 \cdot 9654 \pm 0 \cdot 0044$, which indicates a very high correlation. This method of harvesting probably would not be so satisfactory if the stage of maturity or the plumpness of the grain in the check rows and in the inoculated rows differed very much. In these tests, however, all of the rows matured about the same time and produced about the same quality of grain and the head-weight method of harvesting appeared to be quite dependable. As in the case of the special greenhouse tests, these four varieties showed very little difference in their susceptibility to *O. graminis* but, on the average, Reward showed a greater reduction in yield.

TABLE 10.—Results of wheat variety tests: rod-row experiments.

Variety	Saskatoon, 1930			Saskatoon, 1931			St. Gregor, 1930			Average of 3 tests
	Yield		Reduction in yield	Yield		Reduction in yield	Yield		Reduction in yield	
	inoc.	check		inoc.	check		inoc.	check		
	grams.	grams.	%	grams.	grams.	%	grams.	grams.	%	%
Garnet	57	316	.....	167	189	.....	125	364	.....	.....
"	33	434	79	245	262	20·5	198	395	54	51
"	74	308	.....	247	381	.....	.....	.....	.....	.....
"	99	211	.....	164	227	.....	185	347	.....	.....
Marquis	187	429	.....	180	259	.....	132	659	.....	.....
"	259	650	58	273	352	26·5	215	544	63	49
"	271	618	.....	356	496	.....	176	371	.....	.....
"	192	488	.....	244	334	.....	234	457	.....	.....
Mindum	237	671	.....	219	359	.....	223	739	.....	.....
"	210	677	69	336	423	19·5	263	649	60	49
"	242	902	.....	468	604	.....	303	553	.....	.....
"	214	650	.....	270	425	.....	251	662	.....	.....
Reward	59	170	.....	87	160	.....	121	434	.....	.....
"	131	277	66	119	209	47·0	216	384	74	62
"	50	308	.....	157	314	.....	221	334	.....	.....
"	90	247	.....	109	217	.....	186	385	.....	.....

Considerable discussion has appeared in the literature concerning differences in susceptibility to *O. graminis* possessed by different varieties of wheat. In most cases however, the writers are agreed that no marked differences exist in the varieties with which they have worked (9) (49). Lindau (37) states that *O. herpotrichus* attacks wheat without distinction as to varieties, but in discussing *O. graminis* he mentions reported differences in varietal susceptibility. Many have referred to slight differences in favour of certain types or groups of wheat varieties but their observations often conflict with those of other investigators. In France the late wheats as a group are considered to be more resistant to *piétin* than the early ones (20) (69) while, in Australia, Pridham (53) concluded that early-maturing, short-season wheats were less subject to take-all than late-maturing ones. Early varieties have been mentioned by others (3) (23) (74) as being more susceptible. An investigator in South Africa stated that the durum wheats were more susceptible than wheats of the vulgare group in that region (4). Kirby (35) speaks of Einkorn, Polish and Spelt as resistant varieties in his tests but their records given in table 7 show that they were moderately to highly susceptible here.

It appears from the results obtained here that certain other factors, such as the plumpness and viability of the seed are apt to have more influence on infection in the seedling stage than any genetic factors for resistance that a given variety may possess, As will be shown later, certain different strains of *O. graminis* isolated in Saskatchewan have been found to differ greatly in their pathogenicity to Marquis wheat, so that it seems quite possible that some of the discrepancies in the findings of investigators, mentioned above, may be due to the fact that they have been observing the action of different strains of *O. graminis*, as well as to the fact that they were working under different climatic conditions and testing different sets of wheat varieties. While slight differences in varietal susceptibility probably do exist between the varieties which have been tested in Saskatchewan, such differences do not appear to be sufficiently great to justify one in recommending their use as a control measure for take-all. The possibility of building up strong resistance through breeding and selection work appears to be very remote. In our tests the Marquis strains have compared very favourably with the other varieties of wheat and yet under certain conditions Marquis is killed out completely in patches in ordinary field culture.

Susceptibility of Selected Single Plant Lines of Marquis and Early Red Fife Wheat

In most of our experiments in which artificial inoculum was used it was noted that plants which survived the infection in the seedling stage usually lived to maturity and produced seed. It appeared that these plants were either more resistant than their fellows which had succumbed or else that they had escaped the infection more or less completely. In order to determine whether or not the progeny of such individuals possessed greater resistance to *O. graminis* than the average run of the variety, the seed of the most healthy-looking survivors of an experiment, designed especially for this purpose, was saved and tested with bulk seed of the same variety as a check. About one half of the progenies tested belonged to the variety, Early Red Fife, and the other half to the Marquis variety.

The majority of these tests were conducted in crocks and the seedlings were artificially inoculated. A disease rate was computed for each at the end of the seedling stage. Table 11 gives a brief summary of the results obtained.

TABLE 11.—Comparative resistance of the progenies of plants which survived artificial inoculation and of populations from bulk seed of the same varieties.

Test	Variety	Number of lines	Number of checks	Disease rates			
				Selected lines		Checks	
				Range	Average	Range	Average
1	Early Red Fife	12	6	87–96	91·5	96–99	95
2	" "	12	4	61–75	69·0	65–73	69
3	" "	8	0	74–80	77·0	.....	.....
4	Marquis	2	1	43–44	43·5	52	52
5	"	7	1	71–80	75·0	71	71
6	"	12	2	67–89	75·0	80–90	85

Except in the fourth and sixth tests, there was no suggestion that any of these lines might carry any more genetic factors for resistance to *O. graminis* than the average run of the variety to which they belonged. Unfortunately the lines giving the lower disease rates were not re-tested. It is certain, however, that none of them possessed marked resistance in the seedling stage to *O. graminis*. It appeared as though the parent plant had merely escaped heavy infection.

Longevity of the Causal Organism in Soil Kept Free of Vegetation

It is a matter of considerable importance to know how *O. graminis* remains viable during the interval of time between successive crops of susceptible host plants on the same soil. Kirby (35) states that on two different occasions the fungus lived through the summer in infested soil and produced take-all in wheat sown in the soil in the autumn. Davis (11) states that *O. graminis* will survive the winter in the mycelial and ascospore stages. Recent work by Henry (28) Moritz (49) Sanford and Broadfoot (67) and data collected at this laboratory prove that *O. graminis* is profoundly influenced by certain other soil inhabiting organisms. An attempt was made at this laboratory to find out how long *O. graminis* would survive in soil in which no host plants were allowed to grow.

Several pot experiments were conducted in which a pure culture of *O. graminis* was placed in the soil and allowed to stand for some time before wheat was sown in the pots. The object of these tests was to find out if the fungus would remain viable in uncropped soil for a period of one or more years, and attack wheat sown subsequently in this soil, and if so, whether or not the aggressiveness of the parasite would decrease rapidly with the passage of time under the conditions of the tests.

The experiment was divided into three parts, two of which were conducted in the greenhouse and the third out of doors. Two different types of soil were used in all of the tests, one half of the pots being filled with a mixture of five parts of heavy silty clay loam to one part of sand and the other half being filled with a mixture of soddy earth and well-rotted barnyard manure. In the following pages the former is referred to as soil type A and the latter as soil type B. The latter was characterized by a higher organic content. Six-inch pots were used in the greenhouse and nine-inch pots were used out of doors. All the soil was steamed for one hour at fifteen pounds pressure. While the soil in the pots in the greenhouse was "lying fallow" the pots were placed on a bench beneath a white cotton screen to protect them from most of the direct rays of the sun and they were brought up to their original weight every other week by adding water. The temperature in the greenhouse varied from about 15° C. to 25° C. while these tests were being conducted. The pots placed out of doors were sunk into the earth up to their rims and they were left exposed to the weather throughout the test and were not artificially watered. In the six-inch pots five grams of oat-hull inoculum was placed in a layer one and one-half inches below the surface of the soil in each pot. In the nine-inch pots ten grams of inoculum was used for each pot and it was distributed in three layers at depths of one, two, and three inches respectively. The seed used was surface sterilized.

In the first test, which was conducted in the greenhouse, ninety pots, forty-five of each type of soil, were used. Two-thirds of these were inoculated at the commencement of the test and the remainder served as check pots. The pots were divided into groups of six, each group containing two inoculated pots and one check pot of each type of soil. The first group was taken from under the screen and sown at the beginning of each month until the beginning of the thirteenth month, when three groups were sown. Notes on the emergence were taken at two weeks and in most cases the seedlings were dug up and examined at the end of five weeks. Those sown at the end of ten months were kept to maturity. In the case of the eighteen pots sown at the end of twelve months, however, one group was harvested at seven weeks and two groups were kept until the plants were mature.

The severity of the infection fell off rapidly after the first sowing but the fungus remained alive in certain of the pots and produced a considerable amount of disease after four months spent in the bare soil. Signs of the fungus in the form of mycelium on the roots or dark mycelial plates beneath the basal leaf sheaths were found in all groups up to that which was sown after nine months.

In the case of the pots sown after ten months and kept until the wheat was mature, there was very little evidence of disease when the seedlings were five weeks old but the infection was quite heavy at maturity. Those sown at the end of eleven months showed a few signs of *O. graminis* when the seedlings were five weeks old. In the case of the three groups sown at the end of twelve months, no symptoms of disease were noticeable when the first group was harvested at the end of seven weeks but distinct signs of *O. graminis* in the form of strands of superficial mycelium, black mycelial plates and perithecia on the sheaths of certain plants were found in the other two groups when the plants had reached maturity. The more heavily diseased plants produced only shrunken grain.

In the second test seventy-eight pots were used. The test was conducted in a manner similar to the first test except that one group was inoculated and placed under the screen at the beginning of each month for a period of one year and the whole test was sown at the same time at the end of the year. Ten seeds per pot were sown throughout the test. The plants in this test were harvested and examined at the end of seven weeks from the time that they were sown.

There was a marked decrease in the amount of infection resulting from the inoculum remaining in the soil for one month before the seed was sown but some infection was present in all of the groups. Some factors other than the time factor must have influenced the results for much more disease developed in the pots where the inoculum had lain for eleven months than in the pots where the inoculum had lain for only eight months.

It is evident from the results of these two tests that *O. graminis* is able to persist in bare soil for a period of at least one year under the conditions of the experiment and to produce more or less disease on wheat seedlings sown in the pots at the end of such a period of time.

The third test was conducted in thirty-six large pots sunk in the ground outside of the greenhouse. Inoculum was placed in the soil in twenty-four of these pots and the remainder were kept as checks. The inoculum was placed in the soil early in May in the first year of the test. Twelve pots were sown each year for three years so that the last sowing was made after the inoculum had lain in the soil for slightly over two years. Two sowings were made each year. The first sowing was made at the normal time for seeding wheat in this district but the second sowing was made relatively late. Table 12 embodies most of the data secured from this test.

During the first year the checks in the first sowing and the inoculated plants as well were attacked by a form of foot rot apparently brought on by *Fusarium* sp. This fact accounts for the heavy mortality in the check pots. However, take-all infection was heavy in the inoculated pots. The second sowing was made so late in the season that notes could not be obtained for the mature stage.

During the second season considerably more take-all developed in the early-sown group than in the late-sown group and a few perithecia formed on the diseased wheat. Many of the diseased plants bore black plates of fungous mycelium under the basal leaf sheaths.

During the third season considerable infection developed but the plants were so badly damaged late in the season by English sparrows that the usual notes could not be obtained at maturity. The infection was not so marked as in the preceding season but the sub-crown internodes of most of the plants in the inoculated pots were blackened and bore the mycelium of *O. graminis*. The sub-crown internodes of forty-nine out of fifty of the check plants were not blackened. Moreover, twenty of the check plants produced more than one stem while only seven of the inoculated plants in twice as many pots developed more than one stem.

The results of this test show that *O. graminis* was able to live for two years in uncropped soil and to produce a diseased condition in the wheat plants sown in the soil at the end of that period.

TABLE 12.—Tabulated notes of the third test concerning the longevity of *O. graminis* in soil kept free of vegetation.

Pot No.	Period in bare soil	Treatment	Soil type	Notes taken at 5 weeks				Notes taken at maturity				
				Average height	Number healthy	Number sickly	Number dead	Average height	Number healthy	Number sickly	Number dead	Percentage dead
				inches				inches				
1	Nil.....	check	A	6·0	24	0	0	22	0	14	10	42
2	.....	inoc.	"	3·0	0	19	4	6	0	0	20	100
3	.....	inoc.	"	3·5	0	25	0	8	0	6	17	68
4	.....	check	B	6·5	23	0	0	22	10	6	4	20
5	.....	inoc.	"	4·0	0	23	1	20	2	16	5	21
6	.....	inoc.	"	3·5	0	21	1	19	0	14	5	23
7	2 months.....	check	A	10·0	21	3	0	Sown too late in the season for the plants to reach maturity.				
8	.....	inoc.	"	8·0	5	16	3					
9	.....	inoc.	"	7·0	8	15	1		"	"	"	
10	.....	check	B	8·0	15	5	0		"	"	"	
11	.....	inoc.	"	9·5	13	8	1		"	"	"	
12	.....	inoc.	"	9·0	14	9	0		"	"	"	
13	12 months....	check	A	8·0	21	3	0	24	24	0	0	0
14	.....	inoc.	"	6·5	8	10	5	8	0	4	14	77
15	.....	inoc.	"	6·5	11	11	2	12	0	12	7	37
16	.....	check	B	9·0	19	0	0	25	19	0	0	0
17	.....	inoc.	"	8·0	14	10	0	18	0	16	8	33
18	.....	inoc.	"	8·0	13	8	0	18	0	17	5	23
19	13·5 months..	check	A	11·0	18	0	0	23	17	1	1	5
20	.....	inoc.	"	11·0	16	2	0	21	2	14	3	16
21	.....	inoc.	"	11·0	15	3	0	22	17	0	2	11
22	.....	check	B	12·0	18	2	0	26	18	2	0	0
23	.....	inoc.	"	11·0	13	2	0	25	4	9	2	13
24	.....	inoc.	"	11·0	13	0	0	26	12	0	1	8
25	24 months....	check	A	7·0	25	0	0	1 with blackened sub-crown internode.				
26	.....	inoc.	"	6·75	25	0	0	22	"	"	"	
27	.....	inoc.	"	6·5	25	0	0	21	"	"	"	
28	.....	check	B	7·5	23	0	0	0	"	"	"	
29	.....	inoc.	"	7·0	25	0	0	19	"	"	"	
30	.....	inoc.	"	7·0	25	0	0	16	"	"	"	
31	25 months....	check	A	.....	.....	.....	.....	0	"	"	"	
32	.....	inoc.	"	.....	.....	.....	.....	22	"	"	"	
33	.....	inoc.	"	.....	.....	.....	.....	19	"	"	"	
34	.....	check	B	.....	.....	.....	.....	0	"	"	"	
35	.....	inoc.	"	.....	.....	.....	.....	17	"	"	"	
36	.....	inoc.	"	.....	.....	.....	.....	18	"	"	"	

The results of the three experiments testify to the ability of *O. graminis* to remain alive in bare soil for long periods of time and to infect wheat sown in the soil at the conclusion of such periods. Presumably it remained throughout these periods in the mycelial stage but we are not sure of this point. Under the conditions of the experiment the fungus remained alive in bare soil for twelve months in the greenhouse and for nearly twenty-five months in pots out of doors, and at the end of these periods produced recognizable symptoms of take-all on wheat sown in the pots containing the inoculum while the checks remained free from this disease. The decrease in aggressiveness shown by the fungus was probably due partly to the exhaustion of the suitable media in the soil and partly to the interference of other soil organisms.

The Relative Pathogenicity of Different Isolates of *O. graminis*

Very few experiments have been reported in which the relative pathogenicity of different isolates of *O. graminis* have been compared. Davis (11) reported that in his experiments an isolate from New York proved somewhat more pathogenic than two others from Arkansas and Oregon respectively. Laar (36) reported pathogenicity tests of seven single-spore isolations of *O. herpotrichus* on barley and wheat. Several of these were not pathogenic to these two cereals and, of those which were pathogenic, there appeared to be two distinct physiologic forms. However, he did not discover separate physiologic forms of *O. graminis*.

At this laboratory, eight isolates of *O. graminis* have been compared with respect to their relative pathogenicity to wheat seedlings growing in the green-

house. One of these isolates (No. 31) came from Australia, two (Nos. 10 and 11) came from the United States and five (Nos. 1, 2, 3, 4 and 6) were isolated from field material collected in Saskatchewan. All of them were isolated from wheat except No. 4 which was isolated from a plant of *Hordeum jubatum* L. affected with take-all. All of the Saskatchewan strains are single spore isolations except No. 6. For the time being these are referred to as " isolates " rather than " physiologic forms."

In addition to the greenhouse tests three different isolates have been tested for several years under field conditions.

The greenhouse experiments were started in the winter of 1927-28 and the same eight isolates have been tested nearly every year since to see what changes have occurred in their relative pathogenicity. The methods used in these tests are described under " Technique of crock experiments," p. 36, except in the case of test R1 which was conducted in flower-pots. In all the other tests two crocks were devoted to each isolate and a number of crocks were added as checks. Usually each isolate was tested three times during any one season so that a total of about 150 seedlings were exposed to infection from each isolate once every year. In 1927-28 and in 1929-30 only part of the isolates were tested in any one experiment but in 1931-32 and 1932-33 all of them were tested at the same time on each occasion that the experiment was conducted. This rendered the results more nearly comparable as all of the isolates were then subjected to exactly the same environmental conditions. In addition to the above precaution, great care was taken to use inoculum on the same age, produced under identical conditions, for each test throughout this study, in so far as this was possible. Table 13 contains the tabulated notes obtained in one of these tests.

TABLE 13.—Tabulated notes of test R17 concerning the relative pathogenicity of different isolates of *O. graminis*.

Isolate number	Emergence		Final notes								
			Weight	Height	Disease classes					Disease rate	
	Total	Sickly			4	3	2	1	½	Indiv.	Average
			grams.	inches							
Check	25	0	17·25	13·0	0	0	0	0	20	10	.....
"	24	0	16·50	14·0	1	0	0	1	20	15	.....
"	25	0	16·25	13·5	0	0	0	1	16	9	11
"	25	0	16·75	14·0	0	0	0	2	20	12	.....
1	24	0	8·00	9·0	5	4	7	9	0	55	.....
1	25	0	9·00	10·0	4	3	8	8	2	50	52
2	25	2	7·00	8·0	6	6	6	7	0	61	.....
2	23	7	4·00	6·0	15	1	5	4	0	77	69
3	24	0	15·50	12·5	1	0	0	16	6	23	.....
3	24	0	15·75	12·5	1	0	0	14	8	22	22
4	20	19	3·50	5·5	13	8	3	1	0	83	.....
4	21	21	2·50	3·0	20	3	2	0	0	93	88
10	22	0	13·0	12·0	3	1	0	17	4	34	.....
10	22	0	14·0	12·0	3	2	0	14	6	35	34
11	24	0	10·50	10·5	3	1	6	13	2	41	.....
11	23	0	11·0	10·5	4	1	5	13	2	43	42
31	23	0	13·50	12·0	2	0	0	17	4	27	.....
31	23	0	14·0	12·0	2	1	0	12	8	27	27

It can be seen from the above table that the different isolates of *O. graminis* caused widely different disease rates. Also there is a fairly close agreement between the disease rates of the duplicate crocks. These two facts have stood out in practically every experiment on this phase of the work. Figure 11 illustrates the difference in pathogenicity of three different isolates in one of these tests.

FIG. 11.—Different degrees of pathogenicity to wheat seedlings exhibited by three different isolates of *O. graminis* in test R19. Left to right: check, disease rate 12; No. 1, disease rate 37; No. 2, disease rate 70; and No. 3, disease rate 21.

A summary of the disease rates obtained in three different years is shown in table 14. Isolates No. 3, 4 and 6 had not been isolated in 1927-28 so that no figures can be given for these in that season.

TABLE 14.—A summary of the disease rates obtained from eight isolates of *O. graminis* in several different years.

Test number	Year	Disease rates								
		Isolation numbers								Checks
		1	2	3	4	6	10	11	31	
R1	1927-28	48	93	...	...	...	...	...	17	14
R2	"	...	86	...	...	...	97	71	10	10
R3	"	...	90	...	...	...	98	32	51	20
R4	"	...	98	...	...	...	86	61	21	16
R5	"	54	72	...	...	...	...	...	...	13
R6	"	63	86	...	...	...	...	...	...	14
R7	1929-30	...	72	14	42	...	50	19	23	3
R8	"	50	82	10	16	...	15	...	...	8
R9	"	...	...	...	...	51	...	25	11	6
R10	"	...	...	...	...	99	48	55	18	13
R11	"	70	82	26	81	...	...	...	...	5
R12	"	61	...	...	...	98	...	54	...	8
R13	"	...	88	17	48	...	52	...	31	2
R14	1930-31	84	...	22	85	99	21	...	...	10
R15	"	51	...	12	73	84	28	...	...	12
R16	1931-32	41	69	...	85	77	42	79	...	15
R17	"	52	69	22	88	...	34	42	27	11
R18	"	25	76	23	35	90	28	28	21	16
R19	"	37	70	21	13	60	16	33	12	12
R20	1932-33	43	94	49	95	60	90	98	32	13
R21	"	31	67	28	89	30	57	76	35	15
R22	"	27	70	23	43	24	43	36	35	6
Average R14-R22		44	74	25	67	65	40	56	27	13

As may be seen from an examination of the data contained in table 14, there was considerable variation in the disease rates caused by any one isolate at different times. These variations are due in part to differences in environmental conditions and in part to more obscure causes. In test R19, all of the isolates gave disease rates falling near the lower limits of the ranges which they exhibited during the six-year period over which these tests extended. On the other hand, in test R20 most of the isolates gave high disease rates. R19 was conducted in February while R20 was conducted in December. But apart from the variations which appeared to be due to differences in environmental conditions, the pathogenicity of some of the isolates appeared to change from time to time in relation to that of the others. The behaviour of No. 10 is an outstanding example of changed pathogenicity. In 1927-28 it was one of the most aggressive isolates in the collection but since then it has been much less pathogenic. Also Nos. 1, 4, 6 and 11 have exhibited great changes in pathogenicity at different periods. No. 1 appeared to be relatively weak in 1932-33, No. 4 was weak in the experiments R8 and R19; No. 6 was strongly pathogenic for three seasons but was only slightly pathogenic by the close of the 1932-33 season; and No. 11 was weak at the beginning of the season in 1929-30. On the other hand isolate No. 2 has been consistently strongly pathogenic while strains No. 3 and 31 have been consistently only slightly pathogenic.

On the basis of their behaviour in these tests, starting with the year 1930-31, the isolates may be divided into three groups. Those causing average disease rates falling between 65 and 100 may be classed as strongly pathogenic; those causing average disease rates falling between 35 and 64 may be classed as moderately pathogenic; and those causing average disease rates falling between 10 and 34 may be classed as slightly pathogenic. Using this arbitrary scale the eight isolates would be classified as follows:—

Strongly pathogenic—(65-100) Nos. 2, 4 and 6.
Moderately " —(35- 64) Nos. 1, 10 and 11.
Slightly " —(10- 34) Nos. 3 and 31.

Relative pathogenicity tests of certain of the above isolates have been conducted under field conditions. Only three of them have been tested at any one time in the field. These tests were conducted in rod rows properly replicated and they constitute a part of the field experiments of the past three years. Mycelial cultures growing on ground oat-hulls were used to initiate the infection. An equal number of uninoculated rows served as checks. Duplicate plots were sown each year at Saskatoon and St. Gregor or Muenster. Although notes were taken showing any reductions in emergence caused by the inoculations, the reductions in yield which they caused were used as the main criteria of the relative pathogenicity of the isolates in question. Table 15 shows the results obtained in these tests.

TABLE 15.—Yield data showing the relative pathogenicity of several isolates of *O. graminis* under field conditions.

Isolate number	Average percentage reduction in yield					
	1930		1931		1932	
	Saskatoon	St. Gregor	Saskatoon	St. Gregor	Saskatoon	St. Gregor
1	37	68	53	38	2	14
2	42	32	38	62	7	32
3	3	−11	11	1	.....	.....
4	.....	.....	.....	.....	13	73

The results obtained in the field tests are not as consistent as those obtained in the greenhouse tests but No. 3 is shown to be very mild in its action in the field as well as in the greenhouse. The results given by Nos. 1 and 2 were contradictory while No. 4 appeared to be distinctly more pathogenic than the other isolates the one year that it has been tested in the field.

It appears from the results of this phase of our investigations that distinct strains of *O. graminis* differing in their pathogenicity to wheat occur in quite limited regions. Isolate Nos. 1, 2, 3 and 6 come from an area in Saskatchewan about forty by fifteen miles in extent. These isolates vary a great deal in their pathogenicity to wheat and possibly they vary in their host ranges although this remains to be seen.

The variations in pathogenicity shown to exist between different isolates have a direct bearing on the literature concerning the pathogenicity of *O. graminis*. For instance, it seems probable that Mangin (39) was dealing with a relatively weak strain in his comparative pathogenicity tests with *Leptosphaeria herpotrichoides* de Not and *O. graminis*. Also it may be that Rosen and Elliott (60) were observing the action of a comparatively weak strain when they reported that field observations indicated that infection was confined to weakened plants.

The Effect of Environmental Conditions on the Development of Take-all

Soil Moisture and Temperature.—Great differences occur in the amount of take-all reported from year to year in any given region and undoubtedly differences in precipitation and temperature determine to a great extent not only the amount of damage which the disease causes but also the type of symptoms which are exhibited. The difference in symptoms produced under relatively moist and relatively dry conditions has been described under the heading of "symptoms" but it should be emphasized that a great deal of take-all which develops under very dry conditions is not ordinarily recognized as a condition resulting from the parasitism of *O. graminis*, because the symptoms differ so much from those commonly described for take-all.

Various authors in several different countries have drawn attention to the correlation between weather conditions and the amount of take-all appearing in different years (35) (55). It is exceedingly difficult, however, to sort out the real effects of the various factors which combine to make up the sum total of the varying weather conditions. It is quite probable that any one of these factors may produce different effects upon the same disease under different conditions of the remaining factors. So that, while field observations may give us valuable leads, these need to be verified under controlled conditions. Take-all has not been very fully investigated from this aspect. McKinney (43) in 1922 reported that the greatest injury to wheat seedlings growing under controlled conditions of temperature occurred in soil held at 22° to 24° C. In 1925, however, at the conclusion of further experiments of this nature McKinney and Davis (46) reported as follows: " . . , it is evident that infection and injury are favored by moderately low temperatures (12° to 16° C.) and by fairly high soil moistures (70 to 80 per cent)." The results obtained at this laboratory are not in entire agreement with the latter conclusions.

Some years ago an investigation of the influence of soil moisture and temperature on the infection of Marquis wheat in the seedling stage by *O. graminis* was started at this laboratory. Three tests were run in temperature tanks of the Wisconsin type (32). Temperatures of approximately 12°, 16°, 20° and 24° C. were maintained in the soil at seed level. There were 8 cans in each tank and the soil in 4 of these was kept moist to 40 per cent of its water holding capacity while the soil in the others was kept at 60 per cent. Twenty-five seeds

were sown in each can and inoculum was placed in one half of the cans at seed level. The tanks were kept in a section of the greenhouse where the air temperature was held at approximately 15° C. The seedlings were examined about five weeks after they were sown. At that time the percentage of dead seedlings was the main criterion of the severity of the disease.

In table 16 the averages of the results obtained in the three tests are shown. The data are marred somewhat by the fact that the emergence in the drier soil was very poor in the second test. Moreover, in the third test the thermostat in the warmest tank failed to work on several occasions so that the temperature rose to a high degree and no data was taken, except the total emergence for the cans in this tank. Therefore, the figures in table 16 which are marked with asterisks are the average of only two tests.

TABLE 16.—The influence of soil moisture and temperature on the infection of Marquis wheat in the seedling stage by artificial inoculation with *O. graminis*.

Treatment			Notes taken at 5 weeks after seeding			
Temperature	Soil moisture	—	Emerged	Healthy	Sickly	Dead or missing
°C.	%		%	%	%	%
12	40	check	76	75	1	24
12	60	"	97	95	2	3
12	40	inoc.	87	11	36	53
12	60	"	96	0	64	36
16	40	check	78	78	0	22
16	60	"	100	98	1	1
16	40	inoc.	72	7	27	66
16	60	"	98	0	43	57
20	40	check	77	73	2	25
20	60	"	97	97	0	3
20	40	inoc.	63	5	17	78
20	60	"	95	0	18	82
24	40	check	67	58	5*	43*
24	60	"	86	86	0*	19*
24	40	inoc.	67	6*	1*	93*
24	60	"	92	0*	1*	99*

* These figures are the average of only two tests.

The principal conclusion drawn from the results of these tests was this, that *O. graminis* is a very active parasite over a fairly wide range of soil moisture and temperature conditions. Although a higher percentage of the seedlings were dead or missing from the two warmer tanks at the end of the five-week period, both the host and the fungus develop faster at these temperatures and, as the seedlings in the cooler tanks were badly diseased, it seemed possible that an equally high percentage of these seedlings would succumb to the disease by the time the host had reached the stage of development that the seedlings at the higher temperature were in at five weeks.

In order to obtain more clear-cut results it was decided to study the influence of soil moisture separately and to return to a study of the combined influence of moisture and temperature at a later date. The methods employed for the following tests are essentially those described under "technique of crock experiments" with special attention to soil moisture conditions (fig. 12). For each test the soil and sand were thoroughly mixed and the moisture content and moisture holding capacity of the mixture were determined. The computations were based on the weights obtained from duplicate cylinders in each case. The moisture holding capacity of the mixture of soil and sand varied from 47·5 per cent to 55·1 per cent in different years but it was usually very close to 50 per cent of the oven-dried weight of the soil. Equal weights of soil were added to each crock. When the seed was sown the soil was dumped out of each crock

and put back again in about five layers of equal thickness, adding approximately equal amounts of water to each layer to secure a uniform distribution of the water through the soil. Subsequently the weight of the crocks was raised to the proper level by adding water from the surface. This was done twice a week in the earlier period of the test, and every other day in the later period when transpiration had become a more important factor.

FIG. 12.—The effect of soil moisture on infection of wheat seedlings by *O. graminis*. Left to right: inoculated seedlings grown in soil 35 per cent saturated; checks in dry soil; checks in wet soil; inoculated seedlings grown in soil 65 per cent saturated. Disease rates 93, 12, 10 and 50 respectively.

To determine initially something of the effect of different soil moistures upon the seedling blight caused by *O. graminis* three tests were conducted. Each of these consisted of twelve crocks of wheat and employed moisture contents of 30, 45, 60, and 75 per cent of the moisture holding capacity of the soil. The results obtained from the third of these tests are summarized in table 17.

TABLE 17.—Effect of different soil moistures on the seedling blight of wheat caused by *O. graminis* Tabular notes of experiment M3.

Soil moisture	Treatment	Emergence		Final notes							Disease rates	
				Green weight	Average height	Disease classes					Individual	Average
		Total	Sickly			4	3	2	1	½		
%				grams.	inches							
30	check	25	0	12·5	10·0	0	0	0	0	10	5·0	.....
30	inoc.	17	17	2·5	2·5	13	11	1	0	0	87·0	.....
30	"	19	19	2·5	2·5	17	7	1	0	0	91·0	89
45	check	25	0	26·5	14·0	0	0	0	0	8	4·0	.....
45	inoc.	24	24	6·5	8·0	9	4	9	3	0	69·0	.....
45	"	24	24	5·0	7·0	6	8	10	1	0	69·0	69
60	check	25	0	34·0	14·0	0	0	0	0	14	7·0	.....
60	inoc.	23	23	7·5	8·5	7	5	8	5	0	66·0	.....
60	"	22	22	6·75	7·5	8	3	9	5	0	64·0	65
75	check	25	0	39·0	13·5	0	0	0	0	10	5·0	.....
75	inoc.	24	24	11·0	9·0	3	7	11	3	1	58·5	.....
75	"	24	24	11·5	9·0	6	5	7	6	1	59·5	59

It can be seen from the above results that the disease caused much more damage to the seedlings in the drier soil. The relative size and vigour of the normal seedlings are indicated by the green weight and the average height of the seedlings in the check crocks. In the driest soil the seedlings were considerably stunted even in the check crocks. The average height of the checks did not differ materially at the other three degrees of saturation but the green weight of the seedlings increased with increasing soil moisture, that of the seedlings from the wettest soil being about 50 per cent greater than that of the seedlings grown in soil 45 per cent saturated. The disease rate of each crock of inoculated seedlings was based upon the average height of the checks growing on soil kept at the same degree of saturation. The results of the three tests were very consistent as can be seen from table 18.

TABLE 18.—Green weight and disease rates of wheat seedlings at different soil moistures.

Moisture content	Exp. M1		Exp. M2		Exp. M3		Average disease rate
	Weight	Rate	Weight	Rate	Weight	Rate	
%	grams.		grams.		grams.		
30	3·5	90	3	75	2·5	89	85
45	5·0	75	5	53	6·0	69	66
60	5·5	67	8	45	7·0	65	59
75	8·5	51	9	43	9·0	59	51

It is evident that under the conditions prevailing in these tests differences in soil moisture had a marked effect upon the virulence of the infection, each increase in soil moisture being accompanied by a noticeable decrease in virulence (figs. 13 and 14).

Having ascertained that a relatively high percentage of moisture in the soil reduced the virulence of the disease at temperatures fluctuating between 15° C. and 25° C., similar tests were conducted at two temperature ranges controlled within fairly narrow limits. For this purpose the temperature of the air in two sections of an ordinary greenhouse was kept at approximately 15° C. and 21° C. respectively. Soil moisture was maintained for each test at two degrees of saturation, namely 40 per cent and 65 per cent, in two groups of crocks. The disease rates obtained in these tests are shown in table 19.

TABLE 19.—Disease rates obtained from the infection of wheat seedlings with *O. graminis* at two temperature ranges and two soil moistures.

Test	Temperature and soil moisture			
	15°C. (approx.)		21°C. (approx.)	
	40%	65%	40%	65%
M5	81	54	88	57
M6	75	63	97	68
M9	68	55	95	70
M13	86	60	99	70
Average	77	58	95	66

In these four tests, differences in disease rates due to differences in temperature and soil moistures were quite clear cut and consistent (fig. 15). Higher disease rates occurred in the dry soil than in the wet in both sections of the greenhouse. In the cool section the average disease rate in the dry soil was 19 points above that in the wet soil. In the warm section the difference was greater, amounting to 29 points.

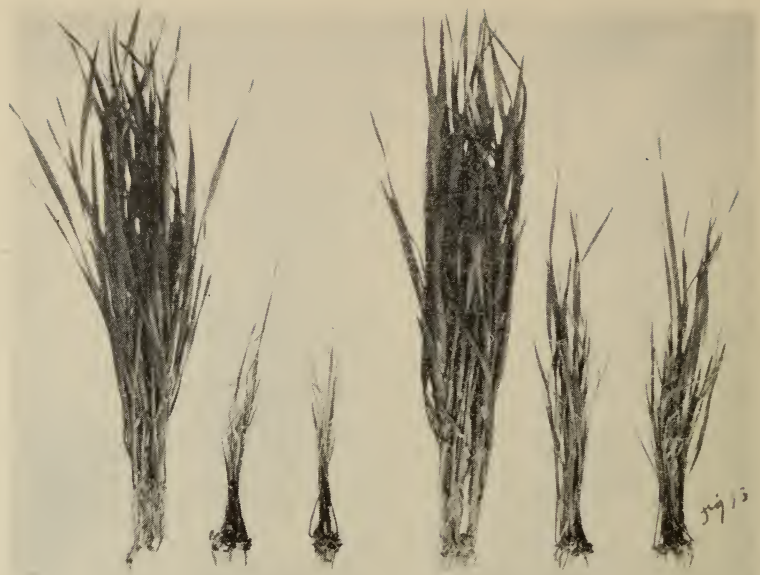


FIG. 13.—Effect of soil moisture on infection of wheat seedlings by *O. graminis*. Test M1. Left: check and inoculated seedlings from three crocks of soil 30 per cent saturated; disease rates 12, 90 and 90 respectively. Right: same from soil 45 per cent saturated; disease rates 9, 77 and 73 respectively.

FIG. 14.—Effect of soil moisture on infection of wheat seedlings by *O. graminis*. Test M1. Left: check and inoculated seedlings from three crocks of soil 60 per cent saturated; disease rates 6, 70 and 65 respectively. Right: same from soil 75 per cent saturated; disease rates 15, 58 and 45 respectively.

Higher disease rates occurred at 21° C. than 15° C. at both soil moistures. The higher temperature produced a greater difference in the dry soil (18 points) than in the wet soil (8 points). In other words an increase of 6° C. in temperature resulted in an increase of 18 points in the disease rate in dry soil and only 8 points in the wet soil.

FIG. 15.—Effect of temperature and soil moisture on infection of wheat seedlings by *O. graminis*. Left to right: check, 70°F., 65 per cent moisture, disease rate 11; inoculated, same conditions, rate 70; check 70°F., 40 per cent moisture, rate 13; inoculated, same conditions, rate 95; check, 60°F., 65 per cent moisture, rate 6; inoculated, same conditions, rate 55; check, 60°F., 40 per cent moisture, rate 9; and inoculated, same conditions, rate 68.

Next an attempt was made to discover whether the influence of moisture was exerted primarily upon the early period of infection or upon the late period of infection while the wheat was in the seedling stage. From seven to twelve days was arbitrarily taken as the early period of infection and the remaining time, that the test was in operation, was considered as the late period of infection. These periods were shorter when tests were conducted at relatively high temperatures than when they were conducted at relatively low temperatures as both host and parasite develop faster at a higher temperature. In studying this phase of the problem, the moisture content of the soil in the crocks was changed at some point of time during the course of each test in such a way that the moisture was the same for all crocks during the early period and different for eaach group during the late period or *vice versa*. Another method of separating the effect of moisture during the two periods was to harvest one half of the test at the end of the first period and the remaining half at the end of the second period and then compare the disease rates obtained from each part of the test. The results of this series of tests were fairly consistent as is shown by the data contained in table 20.

TABLE 20.—Results of experiments designed to separate the effect of soil moisture on the early and the late periods of infection by *O. graminis*.

Test	Temperature conditions	Soil moisture conditions	Disease rate	Difference in disease rate
	°C.			
M4.....	21	7 days at 50%; 26 days at35%.....	90	.....
M4.....	21	7 " 50%; 26 " 65%.....	82	8
M8.....	15	14 " 50%; 21 " 35%.....	90	.....
M8.....	15	14 " 50%; 21 " 65%.....	83	7
M10.....	15	10 " 50%; 25 " 35%.....	39	.....
M10.....	15	10 " 50%; 25 " 65%.....	46	7
M10.....	21	10 " 50%; 18 " 35%.....	75	.....
M10.....	21	10 " 50%; 18 " 65%.....	54	19
M11.....	15	14 " 40%; 14 " 50%.....	26	.....
M11.....	15	14 " 60%; 14 " 50%.....	22	4
M12.....	21	18 " 40%; 10 " 50%.....	35	.....
M12.....	21	18 " 60%; 10 " 50%.....	47	12
M16.....	15	12 " 40%; 24 " 55-45%.....	42	.....
M16.....	15	12 " 65%; 24 " 55-45%.....	33	9
M16.....	22	10 " 40%; 19 " 55-45%.....	34	.....
M16.....	22	10 " 65%; 19 " 55-45%.....	27	7
M14.....	22	10 " 40%.....	75	.....
M14.....	22	10 " 65%.....	47	28
M14.....	22	29 " 40%.....	98	.....
M14.....	22	29 " 65%.....	50	48

From the results of the above tests, in which the question was investigated from several angles, it appears that moisture exercises an appreciable effect upon the infection during both of the periods which were under investigation. The results are not as clear-cut nor are the differences in the disease rates of the different groups as great as occurred in the two series of tests summarized in tables 18 and 19. This is to be expected, however, for the differences in soil moisture did not operate for as long a period of time in these latter experiments. In two instances, the first part of M10 and M12, the disease rates for the wet and the dry soil proved to vary in the reverse manner from that which was expected. Apparently some other factors were operating which tended to reverse the usual situation. The great bulk of the data, however, shows that dry conditions favour the disease. The results of M16 constitute an exception to the usual results in respect to the effect of temperature on the disease. The light conditions were somewhat poorer in the cool section of the greenhouse owing to a thicker coating of frost on the roof, during the course of this test, and possibly that accounts for the higher disease rates occurring at the lower temperature in this case. The results of test M14 are very interesting. One half of the experiment was harvested in 10 days and a disease rate of 75 was obtained in the case of the dry soil as compared with 47 in the case of the wet soil. The other half of the experiment, which was in the same condition as the first half at the end of the 10-day period, was harvested in 29 days and the disease rates obtained were 98 and 50 respectively. It can be seen from this that the seedlings in the dry soil had continued to lose ground during the second period of the experiment while those in the wet soil had held their own.

Another question which has an important bearing on the study of moisture relations in take-all is the effect of moisture upon the development of the parasite in the soil apart from the host. In an endeavour to get some light upon this phase of the question the following experiment was planned and conducted three times.

Nine crocks were prepared in the usual manner and divided into three groups. The soil in these groups was kept at 30 per cent, 45 per cent and 60 per cent saturation, respectively, for a period of two weeks. At the beginning

of this period a certain amount of inoculum was mixed with the upper soil in two crocks of each group while the soil in the third was kept uncontaminated by *O. graminis*. At the end of the period of two weeks the crocks were all sown to wheat and the soil in all the crocks was brought to the same degree of saturation. The results obtained appear in table 21.

TABLE 21.—The effect of moisture upon the development of *O. graminis* in the soil as shown by disease ratings obtained from wheat sown after the inoculum had lain in the soil for a period of two weeks.

Test	Soil moisture; percentage of water holding capacity		Green weight	Disease rate
	Before sowing	After sowing		
			grams.	
M15.....	30% of M.H.C.....	55-45% of M.H.C.....	7·25	37
M15.....	45% "	55-45% "	5·25	53
M15.....	60% "	55-45% "	4·50	61
M17.....	30% "	55-40% "	9·00	33
M17.....	45% "	55-40% "	8·75	39
M17.....	60% "	55-40% "	9·50	34
M20.....	30% "	60-40% "	4·00	56
M20.....	45% "	60-40% "	3·25	66
M20.....	60% "	60-40% "	4·25	53

Taking the average of the results obtained in the above tests an average disease rate of 42 resulted from the inoculum lying in dry soil; an average disease rate of 53 resulted from the inoculum lying in medium moist soil; and an average disease rate of 49 resulted from the inoculum lying in wet soil for a period of two weeks before the seed was sown. This indicates that the fungus survived the two-week period in a more vigorous condition in the moderately wet and the wet soil than in the dry soil.

It appears, then, that soil moisture exerts two opposing influences upon take-all. A moderately high degree of saturation (45-60 per cent of the moisture holding capacity of the soil) of the soil is more favourable to the development of the fungus than is a low degree of saturation (30 per cent of the M.H.C.). At the same time, however, the higher degree of saturation is much more favourable to the development of the wheat seedling. Therefore when it is exposed to the attacks of *O. graminis* under moist conditions, as in tests M1, 2 and 3, the influence of the host predominates and the effect on the parasite is masked.

There are various ways in which abundant soil moisture may aid the wheat seedling in its development when exposed to the attack of the fungus. Abundant moisture is conducive to more rapid germination and growth; therefore the seedling is not exposed to infection for as long a period before it emerges and it can develop new tissues more rapidly to take the place of those injured by the parasite. During the period of germination the cells of the seedling are in a more turgid condition and probably resist infection better while in this condition. Whatever the explanation may be, it is a fact that the seedlings from the moist soil showed less lesioning and better growth at the end of the early infection period, in the foregoing experiments, than did the seedlings from the dry soil (fig. 16).

After the seedlings have developed considerable leaf area they draw moisture from the soil and transpire it comparatively rapidly. During this later period the seedlings in the drier soil are at a considerable disadvantage. They are more heavily infected and their impaired root systems cannot obtain moisture from the dry soil as well as they could from wet soil. At times, when the environmental conditions are conducive to high rates of transpiration, more wilting, with its accompanying ill effects upon the plant, occurs among the seedlings growing in dry soil. In acute cases the wilting is permanent and the seedlings die.

One other factor helps the seedlings in the more moist soil to resist the effects of the disease. It was shown when discussing the symptoms of this disease under greenhouse conditions, that moderately infected seedlings tend to develop secondary roots prematurely (fig. 4). This often enables them to secure moisture and minerals from the soil in spite of the destruction of their primary roots. A moist condition of the soil at the level at which secondary roots arise stimulates their development while a dry condition at this point inhibits it. Thus, probably there is a stronger tendency toward the early production of secondary roots when the infected seedlings are growing in moist soil than exists when they are growing in dry soil.

Fig. 16.—Effect of soil moisture on the infection of wheat seedlings by *O. graminis*. Inoculated wheat seedlings ten days after sowing. Left: germinated in soil 40 per cent saturated; right: germinated in soil 65 per cent saturated.

Then there is the fact that higher disease rates were secured in these experiments when the seedlings were grown at 21° C. than were secured when the seedlings developed at 15° C. Probably three factors are largely responsible for this result. In the first place, the rates of transpiration and evaporation are much higher at the higher temperature which means that an additional demand for water intake is being imposed on an impaired root system. Thus the seedlings would likely suffer more from wilting at the higher temperature. In the second place, it has been demonstrated (32) that low temperature favours the vigorous development of the wheat plant in the seedling stage. Other investigations (12) have shown that the cell walls of wheat seedlings vary in chemical composition at low and high temperatures and that those developed at a high temperature are more easily penetrated by *Gibberella saubinetii*. In the third place, it is known that the optimum temperature for the development of *O. graminis* is about 24° C. (11) (61). All of these factors combine to give a higher disease rate at 21° C. than at 15° C.

In view of the above results and considerations it is difficult to understand how McKinney and Davis (46) arrived at the conclusion that a temperature of 12° to 16° C. and a high degree of saturation of the soil were the conditions

most favourable for infection and injury of wheat seedlings by *O. graminis*. It is recognized, however, that their experimental methods were somewhat different from the methods used in the crock tests described above and it was decided that the question should be investigated again in temperature tanks.

Three more experiments were conducted in the temperature tanks. These were conducted in a similar manner to those described at the beginning of this section but the disease ratings were used as a measure of the severity of the disease. The temperatures maintained in the cans at seed level were approximately 12°, 17°, 22° and 27° C. The cans in each tank were divided into two groups. The soil in one group being kept 40 per cent saturated and that in the other group 65 per cent saturated. Water was added every second day. The air temperature was 15° C.

For the first test the soil was not sterilized and a severe case of browning root rot (due to *Pythium* sp.) developed in the checks in the wet soil at 27° C. It was also present in the other tanks but to a lesser extent in the cooler ones. Moreover it appears as though either the *Pythium* sp. or some other soil organisms exerted an antagonistic effect upon the *Ophiobolus* for the disease rates obtained at the higher temperatures were low as compared with the checks while at the lower temperatures the disease rates of the inoculated seedlings was fairly high. The results resemble those of McKinney and Davis (46) except that the disease rates obtained in the wet soil were not higher than those in the dry soil. The results of this experiment are shown in table 22.

TABLE 22.—The effect of soil moisture and temperature upon infection of wheat seedlings by *O. graminis* in unsterilized soil.

Temperature	Moisture	Treatment	Emergence			Final Notes							Disease rates
						Weight	Height	Classes					
			No.	Time	Sickly			4	3	2	1	½	
°C.	%			days		grams.	inches						
27	40	check	25	5	1	9·0	9·5	0	0	0	5	8	9 .....
27	40	"	25	5	0	10·0	10·0	0	0	0	0	8	4 6·5
27	40	inoc.	21	5	0	8·0	9·5	4	0	0	7	14	30 .....
27	40	"	21	5	0	9·0	9·5	4	0	0	7	14	30 30·0
27	65	check	24	5	1	9·0	9·0	3	2	2	12	6	37 .....
27	65	"	23	5	10	6·0	8·0	5	2	3	11	4	45 41·0
27	65	inoc.	24	5	1	11·5	9·5	2	0	1	11	10	26 .....
27	65	"	24	5	1	10·5	9·5	1	1	2	11	10	27 26·5
22	40	check	24	6	0	8·5	9·0	1	0	0	5	10	14 .....
22	40	"	22	6	0	8·0	8·5	3	0	0	0	12	18 16·0
22	40	inoc.	19	6	8	5·0	8·0	7	1	0	5	12	42 .....
22	40	"	24	6	1	10·0	9·5	1	0	0	6	18	19 30·5
22	65	check	23	6	0	11·0	9·5	2	0	0	4	4	14 .....
22	65	"	22	6	0	11·5	9·5	3	0	0	0	14	19 16·5
22	65	inoc.	21	6	0	9·5	9·0	4	0	2	13	6	36 .....
22	65	"	25	6	2	9·0	8·0	0	1	6	12	6	30 30·0
17	40	check	23	8	0	10·5	9·0	2	0	0	2	6	13 .....
17	40	"	25	8	0	10·5	9·0	0	0	0	1	6	4 8·5
17	40	inoc.	25	8	22	3·5	6·0	6	11	4	4	0	69 .....
17	40	"	24	8	21	4·0	6·0	5	9	5	6	0	63 66·0
17	65	check	22	8	0	11·5	10·0	3	0	0	2	8	18 ....
17	65	"	23	8	1	12·5	10·0	2	0	0	4	8	16 17·0
17	65	inoc.	20	8	18	4·5	7·0	8	6	6	5	0	67 .....
17	65	"	22	8	18	5·5	7·5	3	5	9	8	0	53 60·0
12	40	check	24	13	0	9·0	8·5	1	0	0	0	2	5 .....
12	40	"	25	13	0	9·0	9·0	0	0	0	0	2	1 3·0
12	40	inoc.	24	13	23	3·0	4·0	2	12	11	0	0	66 .....
12	40	"	24	13	20	2·5	4·0	7	13	5	0	0	77 71·5
12	65	check	23	13	1	9·0	9·0	2	0	0	0	2	9 .....
12	65	"	22	13	1	10·0	9·5	3	0	0	0	4	14 11·5
12	65	inoc.	25	13	20	3·0	4·5	6	12	6	1	0	73 .....
12	65	"	24	13	21	4·0	5·0	2	13	8	2	0	65 69·0

In order to determine what influence the organisms present in this soil were exerting on the development of the host and of the disease, a second test was conducted in which one half of the cans contained steam sterilized soil while the others contained unsterilized soil. The moisture content in all of the soil was 55 per cent of the moisture holding capacity. One half of the cans served as checks and artificial inoculum was added to the remainder. Unfortunately, taking the experiment as a whole, the inoculum was so weak that satisfactory infection did not result from it in either the sterilized or the unsterilized soil, although a light infection developed in the 12° tank. However, the organisms already present in the soil exerted a marked influence upon the development of the host seedlings as may be seen from the data concerning the uninoculated check seedlings which are presented in table 23.

TABLE 23.—The influence of soil sterilization upon the development of uninoculated wheat seedlings.

Temperature	Treatment	Emergence			Final notes								Disease rate	
		Total no.	No. days	No. sickly	Green weight	Dry weight	Average height	Classes						
								4	3	2	1	½		
°C.					grams.	grams.	inches							
27	sterilized.....	23	4	1	13·0	1·54	12·0	2	0	1	2	6	15	.....
27	"	23	4	2	12·0	1·44	11·5	2	0	3	2	8	20	17·5
27	unsterilized....	22	4	1	6·0	0·845	8·0	4	0	8	13	0	45	.....
27	"	25	4	1	6·5	0·91	8·5	1	1	10	13	0	40	42·5
22	sterilized.....	19	5	0	11·0	1·345	11·0	5	0	0	3	8	27	.....
22	"	25	5	0	15·5	1·78	11·5	0	0	1	1	6	6	16·5
22	unsterilized....	24	5	0	8·5	1·045	9·0	1	0	4	16	4	30	.....
22	"	23	5	0	8·5	1·135	9·5	2	0	2	20	0	32	31·0
17	sterilized.....	23	7	1	13·0	1·51	10·5	2	0	1	0	4	12	.....
17	"	22	7	0	13·0	1·57	10·5	3	0	0	0	6	15	13·5
17	unsterilized....	24	7	0	8·25	1·06	9·0	1	0	0	0	24	16	.....
17	"	23	7	0	9·25	1·15	9·0	2	0	0	1	22	20	18·0
12	sterilized.....	20	11	3	5·5	0·71	9·0	6	0	2	0	3	30	.....
12	"	25	11	0	7·5	0·965	9·0	0	0	0	1	6	4	17·0
12	unsterilized....	24	11	2	6·25	0·81	8·0	1	0	2	0	14	15	.....
12	"	25	11	1	6·25	0·83	8·0	0	0	1	0	20	12	13·5

The chief thing which this test revealed was the fact that there existed in this soil a parasitic organism or group of such organisms which were capable of causing a diseased condition of the seedlings. The natural infection was severe at a temperature of 27°C. and decreasingly troublesome at the lower temperatures, judging by the relative weights and disease rates of the seedlings from the sterilized and unsterilized soil. In the case of the 27°C. tank the oven-dried weight of the seedlings from the sterilized soil was nearly double that of the seedlings from the unsterilized soil, their height was greater by about one half, and their disease rate was only 17·5 compared with 42·5 from the seedlings grown in unsterilized soil. As in the previous experiment, the symptoms of browning root rot were apparent on the seedlings growing in the unsterilized soil and signs of *Pythium* sp. in the form of oospores in the tissues of the diseased rootlets were abundant. Nearly all of the seedlings in the sterilized soil appeared quite healthy, fully one-half of their disease rate being due to non-germination. The remainder of their disease rate was due, presumably, to seedborne infection. The inoculated seedlings in the 12° tank showed light but distinct symptoms of attack from *O. graminis*. The lesioning of the coleoptiles was more pronounced in the sterilized soil (fig. 17). These facts support the hypothesis that some organism or organisms were present in this soil which exerted an antagonistic action on *O. graminis* in the previous experiment and that this antagonistic action increased with increases of temperature. It is not known whether *Pythium* sp. was responsible or not but this seems probable.

Having reached the conclusion that the soil which was being used contained living organisms which interferred with the infection from *O. graminis,* a third tank test was performed similar to the first one with the exception that the soil was partially sterilized, i.e., it was given about 3 hours at 3-4 pounds steam pressure. In this case there was less interference from other soil organisms and much higher disease rates were secured from the inoculated seedlings. The results obtained in this test were more comparable with those obtained in the first three tank tests shown in table 16. They are set forth in detail in table 24.

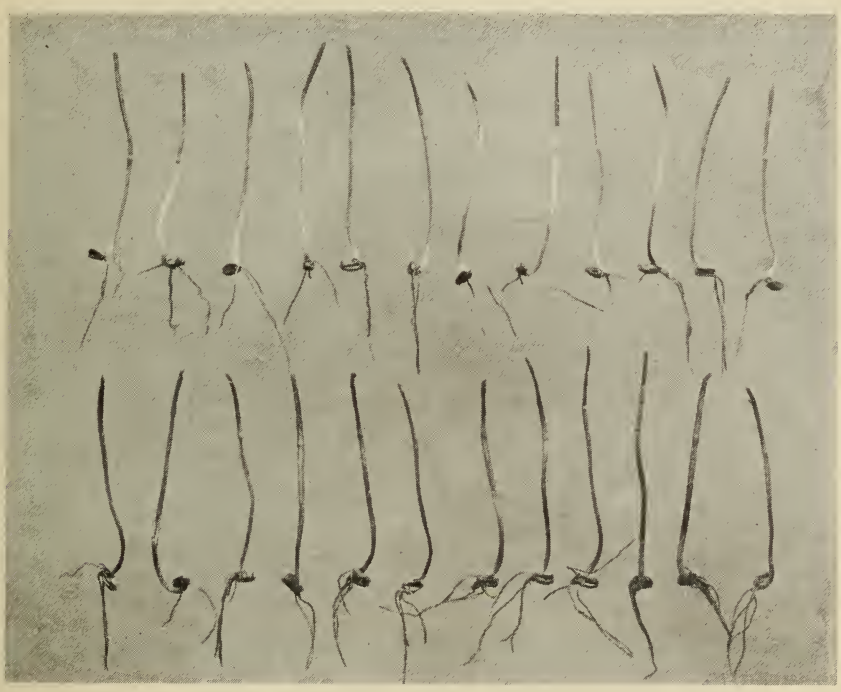


FIG. 17.—Bases of seedlings from tank experiment illustrating the antagonistic action of other soil organisms on *O. graminis.* Top row from unsterilized soil; bottom row from sterilized soil. Lesioning of the coleoptiles due to *O. graminis* was more pronounced in the sterilized soil.

As may be seen from the data presented in table 24, the disease, which showed the symptoms of typical *Ophiobolus* seedling blight, was severe in all the cans except those at 27° C. in which the soil was 65 per cent saturated, with very little difference in the disease rates of the remainder. It should be pointed out in this connection that the seedlings in the 27° C. tank were harvested on the 27th day after seeding, those in the 22° tank were harvested on the 28th day, those in the 17° tank on the 29th day and those in the 12° tank on the 32nd day. Even so, the seedlings in the coolest tank had not developed to nearly the same extent when harvested as had those in the two warmest tanks, as may be seen by their respective weights. In spite of the lower disease rates which resulted in this experiment at 27° in the wet soil, we are again forced to the conclusion derived from the previous tank experiments, namely, that *O. graminis* is severely parasitic to wheat over a fairly wide range of temperature and soil moisture.

TABLE 24.—The effect of soil moisture and temperature upon infection of wheat seedlings by *O. graminis* in partially sterilized soil.

Treatment		Emergence			Final notes								Disease rate	
Temperature	Moisture	Time	No.	Sickly	Weight		Height	Classes					Individual	Average
					Dry	Green		4	3	2	1	½		
°C.		days			grams.	grams.	inches							
27	40% check.....	5	22	0	2·842	21·2	15·0	1	0	1	0	10	11	.....
27	40% "	5	24	0	2·886	21·7	15·0	0	0	1	0	8	6	8·5
27	40% inoc.....	5	24	3	0·670	3·5	5·0	10	9	6	0	0	79	.....
27	40% "	5	25	2	0·687	3·0	5·0	11	12	1	1	0	83	81·0
27	65% check.....	5	23	1	4·823	40·6	16·0	0	0	1	1	10	8	.....
27	65% "	5	5	0	.....	data not taken; only 6 emerged							....	8·0
27	65% inoc.....	5	25	5	2·790	20·2	12·0	1	2	6	12	4	36	.....
27	65% "	5	23	3	2·520	18·3	11·0	4	4	4	13	0	49	42·5
22	40% check.....	6	25	0	2·430	19·5	14·0	0	0	0	3	8	7	.....
22	40% "	6	25	0	2·255	18·8	14·0	0	0	0	0	12	6	6·5
22	40% inoc.....	6	25	25	0·236	1·2	4·0	25	0	0	0	0	100	.....
22	40% "	6	25	25	0·258	1·2	4·0	23	2	0	0	0	98	99·0
22	65% check.....	6	25	0	4·915	48·5	17·0	0	0	0	0	8	4	.....
22	65% "	6	24	0	4·780	47·0	17·0	1	0	0	0	10	9	6·5
22	65% inoc.....	6	25	21	0·587	2·6	5·0	17	5	3	0	0	89	.....
22	65% "	6	25	22	0·300	1·3	4·5	17	8	0	0	0	92	90·5
17	40% check.....	7	25	0	2·492	21·0	14·5	0	0	0	1	2	2	.....
17	40% "	7	24	0	2·478	20·8	15·0	0	1	0	1	4	6	4·0
17	40% inoc.....	7	25	25	0·318	1·5	5·0	20	5	0	0	0	95	.....
17	40% "	7	23	23	0·280	1·3	5·0	20	5	0	0	0	95	95·0
17	65% check.....	7	24	1	3·495	32·5	13·5	1	0	0	0	6	7	.....
17	65% "	7	23	0	3·140	29·2	14·0	1	1	0	0	6	10	8·5
17	65% inoc.....	7	23	21	0·473	2·4	6·0	10	14	1	0	0	84	.....
17	65% "	7	21	18	0·418	2·0	5·0	19	4	2	0	0	92	88·0
12	40% check.....	10	25	0	1·760	13·1	13·0	0	0	0	0	10	5	.....
12	40% "	10	25	1	1·715	12·4	13·0	0	0	2	0	8	8	6·5
12	40% inoc.....	10	24	24	0·395	1·7	4·0	17	7	1	0	0	91	.....
12	40% "	10	23	23	0·370	1·7	4·0	14	10	1	0	0	88	89·5
12	65% check.....	10	25	0	2·770	22·4	14·0	0	0	0	1	4	3	.....
12	65% "	10	25	0	2·595	21·0	14·0	0	0	0	0	6	3	3·0
12	65% inoc.....	10	24	24	0·370	1·7	4·0	15	10	0	0	0	90	.....
12	65% "	10	24	23	0·435	1·9	4·0	16	8	1	0	0	90	90·0

The seedlings grown at 27° in the wet soil showed a disease rate of only 42·5 as compared with 81 from the seedlings in the dry soil. It seems probable that some soil organism which requires a moist environment and a relatively high temperature escaped the partial sterilization and exerted an antagonistic influence on the *Ophiobolus* in these cans and thus reduced the disease rate. The fact that a number of weed seeds survived the sterilization and germinated supports the view that this may have occurred. Evidently if such was the case this particular organism was not strongly pathogenic to wheat because the development of the host was exceedingly vigorous under the same conditions. Only a repetition of the test in thoroughly sterilized soil can settle this point.

Taking the results of these crock and tank experiments as a whole it is evident that the influence of temperature or moisture on take-all may vary somewhat, even under greenhouse conditions, depending upon the state of the other factors affecting the disease. For example a difference of 25 per cent in the moisture content of the soil resulted in an average difference of 19 points in the disease rate when the test was conducted in the 15° section of the greenhouse and an average difference of 29 points when the test was conducted at 21° C. in experiments M5, 6, 9 and 13. On the other hand water influences the disease through its effect on the host. It seems likely that under conditions conducive to a high rate of transpiration moderately diseased seedlings will develop much better if moisture is abundant in the soil than they will if it is scarce. On the other hand water influences the disease through its effect upon the development of soil organisms antagonistic to *O. graminis*. If such organisms

require moist conditions for vigorous development then moist conditions tend to reduce the severity of the disease in two ways, first, by increasing the vigour of the host and second, by increasing the vigour of the organisms antagonistic to *O. graminis.*

There remains to be considered the apparent disagreement between the conclusion reached, that under the conditions of our experiments low moisture contents favoured the development of take-all, and the fact that we find the disease more prevalent and destructive in wet seasons in the field in this region (63). The conditions in the two cases are very different. In the first place, the greenhouse experiments deal with the disease early in the seedling stage of the wheat while under field conditions the disease usually does not become noticeable until late in the seedling stage and it sometimes appears after the healthy plants reach the heading stage. In the second place, although the moisture is added from above in both cases it is applied with much greater regularity under the controlled conditions and the top soil is never allowed to dry out to the extent it often does in the field. Moreover the surface soil is not so "cloddy" and the subsoil is not so firm in the crocks as is the case in the field. In the third place, the infection takes place sooner and progresses more rapidly in the controlled experiments than is usual under field conditions. Various other factors such as variations in the humidity of the air, presence or absence of winds, hours and intensity of sunlight, etc., differ markedly in the two cases. Therefore, it is not surprising that the moisture relations of the disease, found to exist under the controlled conditions employed in these experiments do not apply perfectly to field conditions. These experimental conditions did not exactly duplicate natural field conditions.

The fact that take-all is not more in evidence and more destructive in comparatively dry years is probably due to the inability of the causal organism to germinate and develop abundantly in the hot dry surface soil and to bring about heavy infection under such conditions. As soon as heavy infection has taken place, however, warm dry conditions adversely affect the host. Thus the discrepancy between our findings under controlled conditions in the greenhouse and our opinions concerning the influence of moisture upon take-all in the field is more apparent than real.

From the standpoint of root rot studies there are two "critical periods" in the development of the wheat plant under field conditions. The first of these periods occurs just before the first crown roots become established. At this stage the wheat plant possesses a leaf spread of considerable extent. Under our climatic conditions the process of transpiration by the plant is apt to be proceeding at a rapid rate for a considerable part of the time. As a result of this state of affairs anything which seriously impairs the efficiency of the primary roots is liable to bring about a condition of permanent wilting. A severe infection of the primary roots or the sub-crown internode by *O. graminis* is apt to produce this condition. Hence, in take-all fields we sometimes find many shrivelled plants which have succumbed at this stage. If the plant succeeds in establishing its crown roots it may survive, in spite of the destruction of its primary root system or the cutting off of the primary roots by the destruction of the sub-crown internode.

The second " critical period " occurs as the heads of the wheat are filling. Just why this should be a critical period is not so evident. There probably occurs a sudden shift in metabolic drifts at this stage in the development of the plant. Undoubtedly, there are various factors which promote rapid transpiration at this time. The plant now possesses its maximum leaf-spread unless a large proportion of the earlier leaves have been withered by drought. The average daily temperatures of air and soil are usually at their highest at this time. At this period the plant is being drained to develop the seed and it seems probable that it cannot devote the same energy to resisting the disease;

for instance by the development of new crown roots to replace any which might be destroyed by the parasite. Therefore, if we have a very wet period at mid-summer followed by a period of high temperatures and high winds it appears that this sequence of weather conditions tends to accentuate the damage from take-all. The moist period promotes a leafy growth on the part of the plant with the retention of the older leaves in a functional condition. It probably promotes the vigorous development of the fungus at the level of the crown which is the point of origin of the crown roots and this probably leads to a heavier infection of these parts of the host. The sudden advent of a hot dry period at this juncture favours the disease. The high transpiration which ensues desiccates the sub-aerial portion of the plant and the diseased condition of the crown and crown roots prevents the plant from recouping its moisture losses by drawing fresh supplies from the soil. In take-all fields we sometimes see patches of comparatively well-developed plants which have suddenly become dead and bleached. These patches of yellow plants stand out in marked contrast to the solid green of the surrounding crop. It is probably a sequence of weather conditions such as we have just discussed which leads to this particular manifestation of the disease. The majority of wheat plants which die of take-all in the field in this region succumb during either the late seedling stage or after heading time, although a small percentage die at other stages.

One other environmental factor which appears to influence the virulence of take-all is the intensity of light and the duration of exposure. Jones, Johnson, and Dickson (32) report that wheat seedlings growing under poor light conditions at a temperature of 12° C. blighted badly when inoculated with *Gibberella saubinetii* while other seedlings growing under good light conditions showed much less blight. They suggest that any factor which caused the metabolism of the plant to be unbalanced predisposes the wheat seedling to blight. In our greenhouse experiments from year to year it has been noticed that heavier infections occur on the average during the period of poorest light conditions (November to January) than those obtained later in the winter when the light in the greenhouse is of greater intensity and duration each day. Probably this is explainable on the grounds that the seedlings develop more vigorously during late winter and early spring. The average weights of the checks supp this view. In December twenty-five check seedlings four weeks old weighed on the average about fifteen grams, green weight. Under the same conditions, except for light, they weighed about thirty grams late in the month of March. It appears that light was a "limiting factor" in the growth of the seedlings during early winter. Therefore the influence of light upon the disease may be exerted mainly through its effect upon the vigour of the host.

In these studies the chief emphasis has been laid upon the influence of soil moisture on the infection of wheat in the seedling stage but it is realized that other factors play an important part in the development of the disease and that the influence of moisture may vary with the state of the remaining environmental conditions and with the stage of development of the host. Therefore it is felt that the problem of the influence of environmental factors on the development of take-all is one which demands a great deal more study than has yet been devoted to it.

Effect of Cultural Practices on the Development of Take-all

Date of Seeding.—A study was made of the effect which the date of seeding has upon the development of take-all in the wheat crop. It was hoped that considerable infection might be avoided by sowing at a time which was unfavourable to the development of the disease. For this purpose three sow-

ings of wheat were made each season. The first was sown as soon as practicable which was about the time the farmers commenced to sow wheat during the seasons when these tests were being conducted. The second sowing was made about the middle of May when most farmers were completing or had finished their wheat seeding. The third sowing was made early in June which is several weeks later than wheat is usually sown in ordinary farm practice. An equal number of check rows and artificially inoculated rows were sown in each case. The data concerning these tests may be seen in table 25.

TABLE 25.—The effect of the date of seeding on the infection of wheat by artificial inoculation of *O. graminis*.

Year	Place	Dates sown			Reduction in emergence			Reduction in yield		
		1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd
					%	%	%	%	%	%
1928	St. Gregor.....	25/4	17/5	9/6	47·0	38	32·5	86·0	79·5	88
1929	"	6/5	16/5	29/5	.....	.....	.....	78·0	84·0	18
1929	Melfort.....	15/5	25/5	4/6	.....	.....	.....	18·0	75·0	−3
1930	St. Gregor.....	23/4	14/5	4/6	2·5	0	7·0	31·0	2·0	0
1930	Saskatoon.....	21/4	12/5	2/6	3·0	−4	4·5	16·0	−3·0	13
1931	St. Gregor.....	5/5	20/5	9/6	0·0	15	8·0	18·5	59·0	43
1931	Saskatoon.....	28/4	19/5	8/6	25·0	−3	.....	18·0	24·5	13

It might be supposed that as the spring season progressed and the air and soil became warmer that successive sowings would show either a definite increase in disease or a definite decrease according to the effect of temperature upon the disease. The data presented in table 25, however, suggests that any such simple relation which exist in the field is frequently masked by the operation of other factors. For instance there is the influence of precipitation to be considered. The amount of rain-fall which is received during this period in Saskatchewan varies greatly in different years. Other meteorological factors influencing the transpiration of the plants, and the disease indirectly through this, are total duration of sunshine, relative humidity of the air and winds. These factors also vary with different seasons. Then there is the question of the activity of soil organisms which are antagonistic to *O. graminis*. From what is already known of these (28) one would expect that the activity of these organisms would be greatest late in the spring and hence, that this would tend to reduce the amount of take-all in the late-sown crops. Therefore it is evident that the amount of take-all appearing in the infected crops from the various sowings is the resultant of a number of interacting factors and not the result of differences in temperature alone.

Owing to the uncertain state of our knowledge concerning the effect of temperature upon take-all under controlled conditions it is impossible as yet to interpret the results obtained in these tests. Therefore no recommendations can be given concerning the best time to sow wheat in soil infested with *O. graminis* until we possess more knowledge of the influence of the various factors affecting take-all under field conditions.

Depth of Seeding.—It has frequently been observed at this laboratory that deeply-sown wheat suffers more from seedling blight than does shallow-sown wheat. The results of the following experiments demonstrate that this is a fact in the case of seedlings artificially inoculated with *O. graminis*. This fact has been reported previously (64).

The first series of tests were conducted in crocks in the greenhouse. The methods followed were similar to those described previously under the heading "Technique of crock experiments." In so far as possible the only factor which

was allowed to vary between the different groups of each test was the depth at which the seed and inoculum were placed. The inoculum was put at seed level in each case.

TABLE 26.—The effect of depth of seeding on the infection of wheat seedlings by *O. graminis*.

Depth sown	Emergence		Disease rate	
	Check	Inoculated	Check	Inoculated
Inches				
1·0	24·6	24·4	4·0	60·5
2·5	24·5	24·1	7·5	69·0
4·0	24·0	21·0	12·0	84·0

The data shown in table 26 are averages of the results of three tests. There was a consistent increase in the disease rate with each increase in depth of seeding in the tests taken singly as well as when averaged. The disease rates obtained in the checks were probably due to the presence of other root-rotting fungi present in the soil. They also increased with each increase in depth of seeding. Figure 18 illustrates the appearance of check and inoculated seedlings from one of the above tests in which the infection was particularly severe.

The same question was studied, under field conditions, for two years at two different places. Four rod-rows of checks and an equal number of rows

FIG. 18.—Checks and seedlings inoculated with *O. graminis* sown at three different depths. The severity of the infection increased as the depth at which the seed was sown became greater.

of inoculated wheat were planted at a depth of two inches. A similar set of rows were planted at a depth of four inches. These rows were systematically distributed over the experimental plots.

The effect of depth of seeding on the amount of take-all resulting from artificial inoculation with *O. graminis* under field conditions may be seen from an examination of the data in table 27. The figures given for the percentage reduction in yield are based on the average yields of their checks.

TABLE 27.—The effect of depth of seeding on the infection under field conditions of wheat seedlings by *O. graminis*.

Place	Year	Depth	Emergence		Reduction in yield
			Check	Inoculated	
		inches			%
St. Gregor	1930	2	314·0	309·0	38·0
"	1930	4	287·0	270·0	62·0
Saskatoon	1930	2	311·0	313·0	70·0
"	1930	4	300·0	303·0	83·0
St. Gregor	1931	2	218·5	166·0	11·0
"	1931	4	194·0	110·0	42·0
Saskatoon	1931	2	229·0	185·0	37·0
"	1931	4	236·5	139·5	46·5

It is evident from the figures shown in this table that the inoculated wheat did not produce as high a yield in comparison with its check when sown at a depth of 4 inches as it did when sown at a depth of 2 inches. Therefore it seems that the harmful influence of deep sowing causes not only more disease in the seedling stage but also poorer yields of grain at the end of the season.

The reasons why the deeply sown seedlings should suffer more injury than the shallow sown ones are probably as follows. The deeply sown seedlings take longer to emerge and thus the growing point of the stem surrounded by the first leaves and coleoptile is exposed for a longer time to infection from the soil. Moreover the area of the plant which is exposed to infection in the soil is greater. Above all, seedlings sown at an excessive depth are apt to be weakened by the struggle to emerge from the ground and in consequence more easily fall a prey to parasitic soil fungi.

Since deep sowing predisposes the wheat to injury from take-all, one should practice shallow seeding in fields infested with *O. graminis*. It is considered good cultural practice in this region to avoid deep sowing whenever the surface soil is sufficiently moist to germinate the seed at a depth of one or two inches.

Compacting the Soil.—Different cultural methods in farm practice leave the surface soil in different conditions in respect to compactness. Some type of "packer" is regularly used by certain farmers to pack the soil after seeding. With this fact in mind several tests were conducted to ascertain the effect of packing the soil on infection from *O. graminis*. For this purpose equal amounts of soil were placed in several groups of crocks. Subsequently the soil in one group was left as loose as possible while that in the other groups was compacted to different degrees. This was accomplished by jarring the crocks and by pressing the soil down with the bottom of a glass jar. The depth of the loose soil in the crocks was about 7 inches. Therefore the bulk of the soil in those which were compacted 1 inch was reduced by one-seventh and the others in proportion. In all other particulars these tests were conducted in the same manner as were the crock experiments dealt with previously in this bulletin. A summary of the results obtained is shown in table 28.

TABLE 28.—The effect of compacting the soil upon the infection of wheat seedlings by *O. graminis*.

Experiment	Compacted	Emergence		Disease rate	
		Check	Inoculated	Check	Inoculated
	inches				
C1	0·0	23·5	19·5	9	65
C1	1·0	24·5	19·0	6	65
C1	2·0	23·0	21·0	10	67
C2	0·0	25·0	25·0	8	48
C2	0·5	23·0	25·0	2	40
C2	1·0	25·0	23·0	3	52
C2	1·5	25·0	22·0	4	50
C3	0·0	23·0	23·5	4	74
C3	0·5	24·0	24·5	5	73
C3	1·0	25·0	23·5	7	77

It is evident from the figures shown in the above table that packing the soil to the extent of one or two inches had very little effect upon the resultant disease rate under the conditions of these experiments. Nevertheless, under field conditions packing the soil after seeding may aid in controlling take-all when this operation helps to conserve moisture and leads to a more vigorous development of the crop. In the field the surface soil is frequently cloddy and filled with air spaces which interfere with the proper movement of moisture and the development of the plant's roots. Packing helps to remedy this condition.

Seed Treatment.—Experiments have been conducted in the field to determine whether or not the treatment of the seed with certain fungicidal dusts would offer any protection against infection from *O. graminis* arising from artificial inoculation. In 1927 and 1928 the tests consisted of two five-foot rows of checks and two five-foot rows of inoculated plants for each treatment, one inoculated and one check row appearing in each of two different plots. In 1930 and 1931 four rod-rows of each treatment, systematically distributed over the plots, were inoculated and four other rows, in which the seed was treated but not inoculated, were used as checks. The figures given in table 29 represent in each case the average of two rows while those in table 30 represent the average of four rows.

TABLE 29.—The effect of seed treatment on the artificial inoculation of wheat with *O. graminis*. Each figure represents the average of two five-foot rows.

Seed treatment	Plot	Emergence			Dead at maturity St. Gregor	
		St. Gregor		Melfort		
		1927	1928	1928	1927	1928
					%	%
None	check	83·0	131·5	150·5	5·5	4·5
"	inoc.	85·5	84·5	96·0	77·0	50·0
Copper carbonate	check	81·0	114·5	126·0	7·5	6·0
" "	inoc.	81·0	82·0	109·0	89·0	64·5
Dupont No. 12	check	82·0	109·0	145·0	5·5	9·0
"	inoc.	84·0	93·5	123·5	79·0	69·5
Germisan	check	91·0	.....	.....	17·5	.....
"	inoc.	72·0	.....	.....	85·0	.....
Semesan	check	.....	113·0	137·5	.....	5·0
"	inoc.	.....	96·0	119·0	.....	67·0

TABLE 30.—The effect of seed treatment on the artificial inoculation of wheat with *O. graminis*. Each figure represents the average of four rod-rows.

Seed treatment	Plot	Emergence				Reduction in yield			
		Saskatoon		St. Gregor		Saskatoon		St. Gregor	
		1930	1931	1930	1931	1930	1931	1930	1931
None	check	311	229	314	219	.....	.....	.....	.....
"	inoc.	313	185	309	166	48	23	38	6
Ceresan	check	282	241	299	226	.....	.....	.....	.....
"	inoc.	289	222	296	196	47	12	29	14
Dupont No. 12	check	292	238	302	225	.....	.....	.....	.....
"	inoc.	281	219	295	193	53	12	34	5
Semesan	check	286	239	290	236	.....	.....	.....	.....
"	inoc.	293	207	298	190	50	10	36	13

The data presented in the above tables show that the dust treatments failed to give much protection from the parasite. In 1928 and 1931 a larger proportion of the untreated seedlings failed to emerge but the condition by harvest time was no better in the treated than in the untreated inoculated rows.

Theoretically it is not to be expected that a coating of fungicidal dust on the seed would offer much protection for the roots and coleoptile of the wheat seedling after these organs had grown a short distance away from the seed. It was thought, however, that in these experiments where the fungus was placed in the row close to the seed that some beneficial effect might ensue. Apparently this did occur in 1928 and 1931 to the extent that pre-emergence blight was reduced by the treatments but the beneficial effect was not reflected in the condition of the plants at maturity, except at Saskatoon in 1931. This fact suggests that such seed treatments protect the seedlings to some extent during the early stages of germination but that they are ineffectual against subsequent infection of the roots and coleoptile from parasitic soil fungi except those situated in close proximity to the seed. Hence such seed treatments are probably of little or no value against natural infestations of *O. graminis* in the soil.

CONTROL MEASURES

In the literature on take-all, crop rotation stands out as the most practical and efficient method of controlling the disease. It has been strongly recommended by numerous writers (4) (26) (35) (45) (52) (63) (71). Where summerfallow or crops immune to take-all can be profitably alternated with wheat this practice is to be highly recommended. A number of other practices such as burning the infected stubble (6) (41) (58), changing the date of seeding (7) (20) (35), treatment of the growing crop with sulphuric acid (8) (17) (20) (55) (57) and the use of various fertilizers or soil treatments (10) (19) (25) (29) (47) (51) (60) (66) have been recommended or discussed by writers in various parts of the world.

In Saskatchewan it has been found that wheat following oats or summerfallow seldom shows more than a trace of take-all, even though the field has previously been heavily infested with *O. graminis*. In 1925, when take-all was quite prevalent in northeastern Saskatchewan, twenty-six fields were selected on private farms for systematic observation of the effect of crop rotation on the disease. No attempt was made to influence the farmer's choice of crops for these fields in the succeeding years as we wished to study the effect of the simple rotations in common use. These fields were inspected annually for five years and a record was kept of the crops sown each year and the amount of take-all appearing in each field. A summary of these records is shown in table 31.

TABLE 31.—Records showing the effect of crop rotations on take-all in Saskatchewan.

Field	Location	1925		1926		1927		1928		1929	
		Crop.	Inf.	Crop.	Inf.	Crop.	Inf.	Crop.	Inf.	Crop.	Inf.
A	St. Gregor	W	m	W	1	O	o	W	t	O	o
B	"	W	m	O	o	O	o	F	—	W	t
C	"	W	1	W	1	O	o	F	—	W	t
D	Annaheim	W	?	W	?	W	h	O	o	W	o
E	Englefeld	W	1	W	1	F	—	W	t	W	m
F	St. Gregor	W	h	W	1	F	—	W	t	O	o
G	"	W	h	O	o	F	—	W	t	W	1
						W	t	F	—	W	t
H	"	W	h	W	m	O	o	W	t	B	?
I	Muenster	W	m	F	—	W	t	B & O	o	W	t
J	Carmel	W	m	W	1	F	—	W	o	W	m
K	Annaheim	W	h	W	m	W	h	F	—	W	t
L	"	W	m	W	1	W	m	F	—	W	t
M	"	N	—	W	t	W	m	W	m	F	—
N	"	W	m	W	1	B & O	o	F	—	W	o
O	"	W	h	B & O	o	B	o	W	m	W	1
								F	—	W	o
P	Naicam	W	m	W	1	O	o	O	o	W	t
Q	Cudworth	W	h	F	—	W	t	W	1	F	—
R	St. Brieux	W	m	O	o	W	1	O	o	W	?
				W	1	W	h	B	o	B & O	?
S	Resource	W	h	B	—	W	t	W	1	B	t
T	"	W	h	O	o	O	o	O	o	O	o
U	Valparaiso	W	h	W	m	O	o	C	o	O	o
								R	?	R	?
V	Star City	W	h	O	o	F	—	W	o	W	t
W	Ethelton	W	h	G	?	N	—	W	h	W	?
X	Valparaiso	W	m	W	m	W	h	O	o	F	—
						O	o	W	t }	O	o
						F	—	W	1 }		
Y	"	W	h	O	o	W	t	O	o	F	—
										W	t
Z	Melfort	W	m	O	o	W	o	O	o	F	—

Crops:—W—Wheat; O—Oats; B—Barley; G—Brome-grass; R—Western rye grass; C—Sweet Clover; F—Summerfallow; and N—Newly broken sod.

Severity of Infection:—
o—none evident.
t—trace; several plants bearing take-all symptoms.
l—light; about 1 per cent by estimate, of plants in whole field infected.
m—moderate; 2-10 per cent, by estimate, of plants in whole field infected.
h—heavy; over 10 per cent, by estimate, of plants in whole field infected.
?—crop not inspected for take-all.

Take-all was prevalent in this region in 1925, 1927 and 1928 but it was relatively scarce in 1926 and 1929. These records support the view that take-all can be satisfactorily controlled in this region by the use of suitable crop rotations. Take field H for example; a heavy infection of take-all was present in 1925 and a moderate infection in 1926 which was a dry year; in 1927 the field was sown to oats and in 1928 it was again sown to wheat; despite the fact that take-all was prevalent that year only a trace of it was found in this field. Fields D, P, R, Y and Z also show the beneficial effect of one crop of oats. In the case of field M a trace of take-all was found in the wheat the first year after the virgin sod was ploughed; the following year a much higher percentage of the crop was diseased. This is commonly the case when new land is sown to wheat for several years in succession. Fields F, I, J, K and L illustrate the value of summerfallowing the land to reduce damage from take-all. The records from field W indicate that it is unsafe to sow wheat after breaking up brome-grass sod infested with *O. graminis.*

The effect of crop rotation on take-all was studied in many other fields for shorter periods of time and the data gathered all point to the same conclusions, namely:—*O. graminis* is present in the virgin sod; it seldom damages

the first crop of wheat on new land to any great extent, but the second and subsequent crops of wheat may be severely diseased unless the wheat crops are alternated with summer-fallow or crops of highly resistant plants; it is unsafe to sow wheat after either brome grass or western rye grass; and summer-fallow should be kept clear of all grasses which may serve as a host to the fungus.

The influence of crop rotation on take-all was also investigated on the experimental plots at St. Gregor and Melfort. The fields used for this purpose were divided into twelve plots ten feet wide with paths two feet wide between the plots. In 1927 and 1928 the whole of these fields was sown to wheat and artificially inoculated with *O. graminis* by mixing oat-hull inoculum with the seed grain and sowing it through an ordinary horse-drawn seeder. By the summer of 1928 the plots were fairly uniformly infested with *O. graminis*. In 1929 the field was sown to three plots each of wheat, barley and oats while the remaining three plots were summerfallowed. In 1930 each field was again sown wholly to wheat. Shortly before the grain was mature three samples were collected systematically along the centre of each plot, making a total of nine samples from each rotation. The heads from these samples were weighed to get an indication of the yields which were produced after one year of summerfallow, wheat, barley, and oats, respectively, following the diseased crop of 1928. Table 32 shows the yields, expressed in grams, which were obtained from these plots. It also shows the percentage which the average yields comprised of the yield following oats. The yield following oats was taken as a normal yield because little if any take-all was present in these plots and they had produced a crop every year for four years.

TABLE 32.—The influence of crop rotation on take-all. Showing the yields in grams of wheat heads from samples taken from duplicate experiments running at St. Gregor and Melfort in 1930. The percentages shown are computed by taking the average yield following oats as 100 per cent.

Sample	St. Gregor				Melfort			
	Summer-fallow 1929	Wheat 1929	Barley 1929	Oats 1929	Summer-fallow 1929	Wheat 1929	Barley 1929	Oats 1929
1	125	58	48	51	140	30	56	70
2	97	40	40	64	146	50	48	83
3	55	40	35	55	130	93	124	145
4	120	56	72	80	192	60	59	65
5	130	40	41	85	179	69	62	70
6	110	19	37	57	183	62	85	178
7	145	45	75	96	150	38	74	61
8	93	41	40	90	82	57	53	75
9	100	54	42	48	130	75	64	117
Average	108	41	47	69	148	59	69	96
Per cent	157	59	68	100	154	61	73	100

An examination of table 32 shows that there was a reduction in yield of approximately 40 per cent at both places in wheat following wheat as compared with wheat following oats. While the difference in yield may not be entirely due to the presence of take-all in the former plots it appears to be mainly due to the disease as the moisture and weed conditions were much the same in both.

Wheat after barley produced about 70 per cent of the yield produced by wheat after oats. Several German investigators have reported that in Germany foot rots of this type are especially severe in wheat following barley (23) (27) (48) but in this country wheat following wheat is more apt to be

severely damaged. This discrepancy is probably due to differences in climatic conditions and cultural practices in the two countries.

Wheat following summer-fallow produced about 155 per cent of the yield secured after oats. This was due largely to better moisture conditions, more available food supplies and fewer weeds in the former. Take-all was almost entirely absent from both.

The following practices are recommended for the control of take-all in Saskatchewan:—

(1) In districts where take-all is prevalent alternate oats with wheat for the first few years on newly broken land. Very commonly the following practice is followed:—1st year, new breaking; 2nd year, wheat; 3rd year, wheat; 4th year, wheat; and 5th year, summer-fallow. Instead of the above, the following rotation is recommended; 1st year, new breaking; 2nd year, wheat; 3rd year, oats; 4th year, wheat; and 5th year, summer-fallow.

(2) In the case of fields which have become badly infested with take-all it is recommended that these either be sown to oats or summer-fallowed the following year, as the owner may see fit, and that wheat be not sown for more than one year in succession for several years thereafter.

(3) Volunteer wheat, barley and susceptible grasses should be eradicated from infested fields so that they may not harbour the fungus during years when the fields are sown to oats or being summer-fallowed.

(4) In this province several crops such as corn, sunflowers, flax, peas, sweet clover and potatoes may be substituted for oats in a rotation designed to reduce *Ophiobolus* infestation because they appear to be quite resistant to the fungus.

Very few of the other methods suggested for the control of take-all can be recommended for this region under present conditions. Seed treatments do not appear to offer much protection from this disease. The growing of resistant varieties as a control measure is not feasible at present because we have no suitable varieties which appear to be resistant. Stubble burning as a control for take-all, while it may be effective particularly if additional straw be thrown on the diseased patches before the burning is done, has not been tested in this province. The treatment of the soil in affected patches with fungicides may give satisfactory control but this method is apt to prove expensive. Altering the date of seeding within the range of practicability in this region has not given satisfactory results. Late sowing (about the first of June) sometimes results in a reduction of take-all from artificial inoculation but this practice exposes the crop to many other dangers, particularly late summer frosts.

Therefore, like the cat in the fable, we have only one good trick to employ against this menace, but since crop rotations are effective and economically feasible our position with regard to take-all is reasonably secure.

DISCUSSION

Take-all constitutes a major problem for the grain grower in many parts of Western Canada while the land is new, particularly in wet years. When the land is subjected to crop rotation the disease tends to disappear. The investigations of the problem conducted in this province have verified these obvious facts and have helped to explain them.

It has been shown that *O. graminis* exists in the native sod as a parasite of many of the native grasses. Wheat is a very susceptible host to this fungus and naturally when the prairie sod is broken and wheat is grown on the land for several years in succession the parasite flourishes on this host and the land becomes more heavily infested with it. Under our conditions barley and rye

are less congenial hosts for this fungus and oats appear to be quite resistant to its attack. Therefore the amount of the fungus which survives from year to year in any particular field depends largely on the crops which are grown in the field. While it may prove quite unprofitable to raise wheat every year on a field because of the ravages of take-all, wheat can be sown alternately with oats or a year of fallow with very little loss from the disease. The beneficial effect of oats or summer-fallow is remarkable. It seems probable that the spores of the fungus germinate during the season and being unable to find a congenial host the new growth of *O. graminis* is crowded out by soil inhabiting organisms which are antagonistic to it. Therefore the control of take-all by this method seems to be largely biological.

The attack of the fungus on the host falls on the roots of the host in all cases and if conditions at the surface of the soil are sufficiently moist the crown and the base of the stem for an inch or two above the crown also become involved. The fungus readily penetrates the epidermal cells of the roots or coleoptile of wheat seedlings and growing intracellularly first breaks down the parenchymatous tissue of the host and later invades the fibrovascular bundles. It is probable that the invasion of the tissues by *Ophiobolus graminis* is usually followed by the invasion of *Fusarium* spp. and other soil micro-organisms as these can usually be isolated from field material infected with *O. graminis*. Plants suffering from take-all usually become stunted and wilt easily when subjected to conditions of high transpiration. Whether this is due entirely to the cutting off of the supply of soil solution or whether it is partly due to the effect of toxins is not known.

Ophiobolus graminis is very difficult to isolate from stubble or soil from infested fields unless perithecia and spores are present. For many years isolations of the fungi present in wheat stubble collected in different parts of Western Canada have been made at this laboratory and not once has *Ophiobolus* been found among these. Attempts to isolate this fungus from field material collected in take-all patches and from pots containing wheat artificially inoculated with *O. graminis* in the greenhouse by plating out bits of infected roots or stems on agar have almost invariably failed. Nevertheless this fungus grew readily from diseased parts of the host taken from seedlings infected with it in tube cultures, where no other organisms were present, when plated out by the same method. Hence the mere fact that *O. graminis* was not isolated from host parts or soil from wheat fields is by no means a conclusive proof that this particular parasite was not present in those fields.

With a comparatively dry climate such as we have in Saskatchewan rather wet years appear to offer the conditions most favourable to the production of the spores of *O. graminis* and to the infection of the host by this fungus. At the same time it appears as though the heaviest mortality occurs during periods of high transpiration. Therefore the combination of weather conditions which is apt to lead to the greatest damage from take-all is probably a moist autumn for the production of the spores and heavy rains during the early part of the following summer, to favour spore dissemination, infection and a rank development of the host followed by hot, dry, windy weather after the crop has become well infected.

It has been shown that in the case of *O. graminis* there are different strains which vary greatly in their pathogenicity to wheat. Whether the strains which are strongly pathogenic to wheat are strongly pathogenic to all other hosts of the fungus and the strains which are weakly pathogenic to wheat are weakly pathogenic to all other hosts or not remains to be seen. Moreover it has been shown that certain strains vary from time to time in their pathogenicity to wheat but why they vary thus has not been shown.

An extensive search was made among the wheat varieties obtainable in this region for resistance to take-all. Among the number were one or more

representatives of each of the commonly recognized sub-species of wheat. Unfortunately all of the varieties tested seemed to be about equally susceptible to the disease. This being the case there seems to be little possibility of breeding resistant varieties. Thus one of the most satisfactory methods of controlling plant diseases appears to be impracticable in this case. Since crop rotation is effective against the disease and since rotation of crops is strongly recommended from agronomic and economic standpoints the inability to find resistant varieties is not so serious.

It should be emphasized that take-all is only one of the types of root rot with which we are faced in this province. Besides take-all, there are the following root rots: "common root rot," due to *Helminthosporium sativum* P.K. & B. and *Fusarium* spp.; "browning root rot," due to *Pythium* spp.; and "prematurity blight," due to an unknown cause. Possibly the last named is not a root rot but the symptoms suggest that it is. In comparison with these other types take-all offers some interesting contrasts. Compared with common root rot it is not so universally distributed but is usually more destructive in fields which are heavily infested with *O. graminis*. Take-all is rarely if ever borne by the seed while common root rot frequently is. As a result, the symptoms of take-all seldom appear in the field as early in the season as those of the seedling blight due to common root rot. Take-all seldom appears in crops on summer-fallow while browning root rot is always more pronounced in summer-fallow crops. Although the symptoms of the two diseases are much the same in the late seedling stage the symptoms at subsequent stages are quite different. Whereas take-all often produces heavy mortality, browning seldom causes any actual killing of the host. Subsequent to the seedling stage the plants affected with browning frequently remain somewhat stunted, retarded in development and lacking in tillers but they usually regain their green colour and mature a reduced yield of grain of fair quality unless the frosts of late summer injure them before they ripen. The characteristic structures of their respective causal organisms serve to differentiate take-all and browning even in the seedling stage. The symptoms of prematurity blight resemble those of take-all inasmuch as the plants become bleached and the heads are empty, but the marked stunting and characteristic signs of take-all are absent in the case of prematurity blight. Just as their primary causes and symptoms differ so the control measures for the different types of root rot vary. Unfortunately crop rotation is not nearly so effective against common root rot and browning as it is against take-all.

SUMMARY

1. Take-all caused by *O. graminis* was discovered in Saskatchewan in 1923 and experimental work on it was begun immediately.
2. The symptoms of the disease and the characteristics of the causal organism have been found to agree with the descriptions of these given by investigators in other countries except that the symptoms produced under dry conditions are somewhat different.
3. Penetration of the host by *O. graminis* is described in detail.
4. Host range studies show that most of our cereals and cultivated grasses as well as many of the grass species found in the prairie sod of this region are more or less susceptible to this fungus. On the other hand oats, corn and any of the species outside of the grass family which were tested proved to be very resistant.
5. One hundred varieties of wheat belonging to eight sub-species of *Triticum* were found to be about equally susceptible to *O. graminis*.

6. The fungus remained viable in soil in pots kept free of vegetation for a period of one year in the greenhouse and two years out doors and subsequently infected wheat sown in this soil.
7. Different isolates were found to vary greatly in their ability to attack wheat. Certain ones varied considerably in their pathogenicity at different periods.
8. The effect of soil moisture and temperature upon the disease appeared to vary somewhat according to the state of other environmental conditions. On the average a relatively low soil moisture content (35-40 per cent of the moisture holding capacity of the soil) and a relatively high temperature (22°C.) were found to favour heavy infection of wheat seedlings artificially inoculated. The fungus proved to be a vigorous parasite over a fairly wide range of moisture and temperature conditions.
9. Of the cultural practices tested the only ones which were shown to have much effect on take-all were crop rotation and depth of seeding.
10. As a method of controlling the disease the use of crop rotations, in which summerfallow and crops highly resistant to *O. graminis* are alternated with wheat, is strongly recommended for this region.

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