

# INFLUENCE OF SOIL TEMPERATURE AND MOISTURE ON INFECTION OF YOUNG WHEAT PLANTS BY *OPHIOBOLUS GRAMINIS*<sup>1</sup>

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## INTRODUCTION

There are many statements in the literature regarding the influence of weather and soil drainage on the occurrence of the take-all and foot-rot diseases of wheat. In most cases, however, these reports have been based on rather casual observations which, in many instances, have been made on the foot rots in general rather than on take-all, the specific foot rot caused by *Ophiobolus graminis*. Doubtless the lack of agreement among certain workers as to the influence of temperature and moisture on the take-all disease is due largely to the fact that they have been dealing not with one disease, but with several which are very similar in appearance but caused by different parasites.

Gaillot (6)<sup>3</sup> states that in France wheat foot rot is favored by mild, moist weather, whereas Reuther (13) states that in Germany the foot disease was favored in 1913 by vernal frosts. In neither of these reports is it clear which foot rot is referred to, but it appears that these workers have in mind the foot rots as a whole. According to Lindau (10, p. 256) wet soil favors infection by *Ophiobolus graminis*, and directly in line with this Dombrovski (5) states that the proper drainage of the soil reduces losses due to this parasite.

McAlpine (11) states that opinions are most conflicting in connection with the occurrence of take-all in Australia. He states that some observers claim it to be more prevalent during wet seasons, while others say that dry seasons favor the disease. His own observations indicate that the disease occurs under all climatic conditions. Robinson (14), also working in Australia, states that a dry summer followed by a wet winter affords the most favorable conditions for the development of the disease. Sutton (16), working in western Australia, and Waters (17), working in New Zealand, claim that wet soil conditions favor take-all, whereas Hori (7), working in Japan, thinks the disease is less prevalent on poorly drained soils. In this connection, however, it should be pointed out that Hori's observations included a large number of cases of take-all on barley. It is entirely possible that the disease on this host may not react the same as on the wheat plant when placed under similar soil conditions.

In this country take-all has been observed for so short a time that little definite information is at hand concerning its development in the field under different temperature and moisture conditions. Kirby (9), working in New York, states that his observations indicate little or no difference in the amount of infection occurring on high

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<sup>2</sup> These investigations were carried on in cooperation with the Wisconsin Agricultural Experiment Station.

<sup>3</sup> Reference is made by number (italics) to "Literature cited," p. 840.

and on low ground. He states, however, that in a few fields the infection appeared to be very much heavier on the lower and wetter land. Rosen and Elliott (15), working in Arkansas, also state that the disease seems to be favored by wet soil.

One of the writers (McKinney) has observed take-all under many different field conditions, and while the disease has appeared to be more severe in low undrained portions of some fields, this has not always been the case. Obviously such apparent irregularities emphasized the necessity for studying the influence of temperature and moisture under controlled conditions, and, accordingly, a series of such experiments was planned and carried out, the results of which are presented herewith.

#### EXPERIMENTAL METHODS

All of these studies were conducted under greenhouse conditions in the soil-temperature tanks and in controlled-temperature chambers of the Wisconsin Agricultural Experiment Station, at Madison. The soil-temperature apparatus and the general methods employed in these studies were identical with those used in the studies on the *Helminthosporium* disease (12). The temperature chambers have been described by Dickson (4) and it is unnecessary to discuss them in this paper.

The soil used in these studies was a fertile loam obtained from a wood lot near Madison. Although this was virgin soil, it was infested with several grass parasites which attack wheat, and it was necessary to disinfect all of it. Usually the soil was subjected to live steam at about 1 pound pressure for four hours. In other cases it was heated for one hour at 10 to 15 pounds pressure. Both methods gave good results and produced no toxic effect on the plants. One lot of this soil contained somewhat more organic matter than the other, as indicated by their moisture-holding capacities of 67 per cent and 53 per cent, respectively.

The various soil moistures employed in any one experiment were obtained by careful weighings and moisture adjustments before putting the soil in the temperature-tank soil containers. All soil moistures were calculated on the basis of the water-holding capacity of the soil and the moisture content of the soil was maintained as nearly constant as practicable throughout the experiments. The pots were weighed each day and water was added to replace that lost.

The wheat seed used in all of the experiments was of the Goldcoin variety generally known as Junior No. 6. All seed was disinfected in a 1:1,000 solution of mercuric chloride for 10 minutes, then thoroughly washed in running water before planting.

The parasites used for inoculation were obtained from Oregon and New York. The Oregon strain was isolated by Hurley Fellows from wheat collected near Corvallis, Oreg., in 1921, by A. G. Johnson, H. P. Barss, and M. B. McKay. The New York strain was kindly supplied by R. S. Kirby. Both strains originated from single ascospores, and they maintained their pathogenicity throughout the work. The virulence of the Oregon strain seemed to become reduced toward the end of the studies, and the New York strain was used in its place. The loss of virulence of the Oregon strain may have been due to the fact that it never sporulated, and consequently all in-

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creases had to be made from mycelium. The New York strain produced ascospores rather abundantly at times and these were used for making new cultures.

The parasites were cultured in Erlenmeyer flasks, on a mixture of equal portions of barley and oats which had been thoroughly cooked and sterilized. The fungus increased rapidly on this medium, and the medium did not produce a toxic effect on the wheat plants when it was added to the soil, as was the case when cooked wheat kernels were used. Inoculations were made by adding to the sterilized soil a given weight of the barley-oat medium on which the fungus was growing. This was accomplished by first removing the upper 3 inches of soil from the containers and thoroughly mixing the inoculum with it. The inoculated soil was then returned to the pots and the seed was sown immediately. An amount of uninoculated medium equivalent to the amount added to the inoculated series was added to the controls, and they always were prepared and sown before preparing and planting the inoculated series in order to prevent accidental contamination.

The relative influences of the different temperatures and moistures were determined on the basis of the amounts of disease produced. The method used for determining the amount of disease was essentially the same as that used in the studies on the *Helminthosporium* disease of wheat (12, p. 199-200). However, owing to the fact that *Ophiobolus graminis* is a more vigorous parasite than *Helminthosporium sativum*, the wheat plants were more severely diseased in the experiments under discussion and it became necessary to classify the injuries in a different manner than was done in the previous studies referred to.

Disease manifestations were divided into three groups or types—(1) leaf and stem blight, (2) infection of tiller bases, and (3) root infection. In order that all data should represent the severity of infection as well as the number of plants infected, the various types of injury were given the numerical ratings shown in Table I. Instead of expressing the total amount of disease occurring at a given temperature as a single infection rating, the different types of injury were kept separate and the infection ratings were calculated for each independently. These calculations were made according to the method employed in the studies on the *Helminthosporium* disease previously referred to (12, p. 200).

TABLE I.—*Method of determining the numerical ratings for healthy and diseased wheat plants*

Type of injury	Class	Degree and type of injury	Numerical rating
Leaf and stem blight.....	1	None.....	0
	2	Leaves yellow.....	1
	3	Plant killed.....	2
Infection of tiller-bases.....	1	None.....	0
	2	Slight.....	1
	3	Moderate.....	2
	4	Abundant.....	3
Root infection.....	1	None.....	0
	2	Slight.....	1
	3	Moderate.....	2
	4	Abundant.....	3

## RESULTS

## HOST DEVELOPMENT

The best germination of Goldcoin wheat was obtained at soil temperatures ranging from 12° to 20° C. and at soil moistures ranging from 54.4 to 80 per cent of the moisture-holding capacity. As in the case of Harvest Queen and Marquis wheats (12), germination takes place first at the high temperatures and it is retarded at the low temperatures. During the periods of the experiments (20 to 31 days) the plants produced the greatest dry weight of the aboveground portions at temperatures ranging from 20° to 28° C. and at soil moistures ranging from 71.6 to 80 per cent. Root development seemed to be stimulated at soil temperatures ranging from 16° to 26°. All of the soil moistures employed in these experiments seemed to be about equally favorable for root development.

## DEVELOPMENT OF THE PARASITE

One of the writers (Davis) has studied the influence of temperature on the growth of the parasite in pure culture, and the results are given in another paper (1). It was found that growth took place at temperatures ranging from 4° to 33° C. The optimum temperatures for growth varied somewhat for the strains of the parasite studied. However, this variation was within the limits of 19° to 23°. The optimum for the New York strain was rather wide, growth seeming to proceed equally well anywhere between 19° and 24°, whereas the optimum temperature for the growth of the Oregon strain of the parasite seemed to be between 23° and 24°.

## DISEASE DEVELOPMENT

In no case did *Ophiobolus* infection occur in any of the plants growing in the uninoculated controls (pl. 1, A). The results obtained in all of the inoculated experiments<sup>4</sup> are tabulated in Tables II, III, IV, V, VI, and VII, and the data are shown graphically in Figures 1 to 7, inclusive. Plate 1, B illustrates the results obtained on a representative one-tenth of the plants grown in the inoculated soil in Experiment 1B.

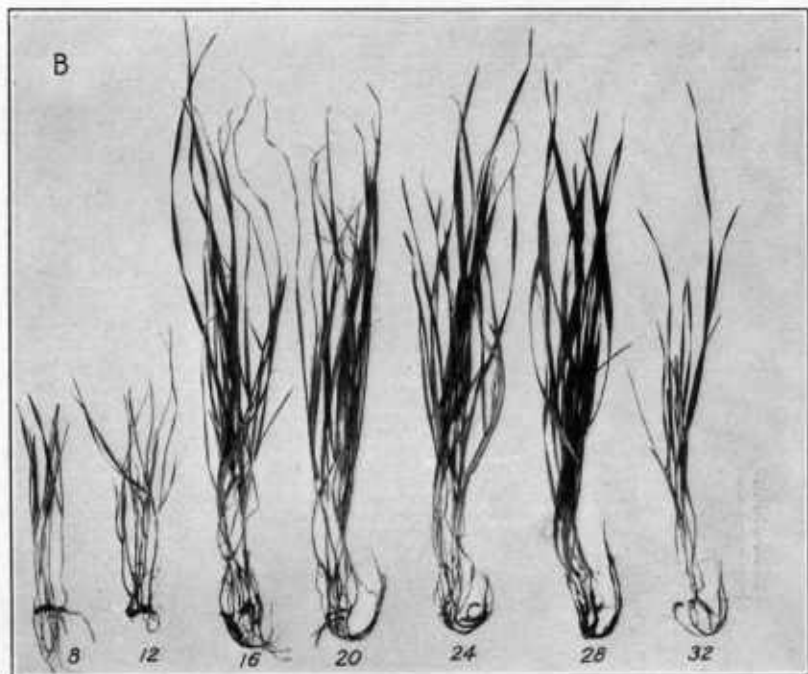
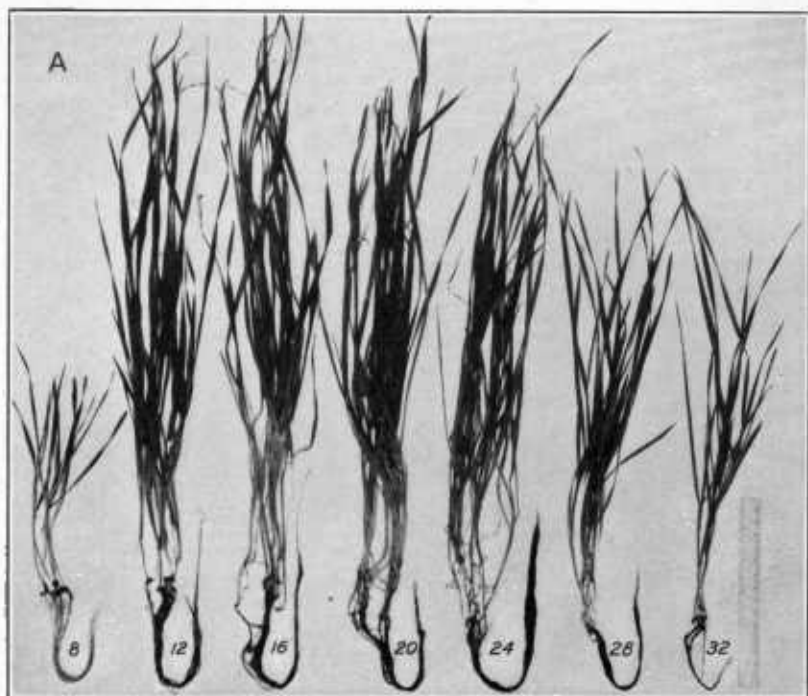
<sup>4</sup> In MCKINNEY, H. H. TAKE-ALL AND FOOT-ROT INVESTIGATIONS. U. S. Dept. Agr., Bur. Plant Indus., Cereal Courier 14: 23-25. 1922. [Mimeographed] the writers reported a preliminary experiment in which the greatest amount of injury took place in soil held at 22° to 24° C. The population of this experiment was very small and the amount of parasite used was too great for accurate results, as shown by later experiments. Owing to these circumstances and the fact that data were based entirely on top injury, these results are not considered significant and are not included among the results of the subsequent experiments.

## EXPLANATORY LEGEND FOR PLATE 1

Influence of soil temperature on the infection of Goldcoin wheat seedlings and young plants by *Ophiobolus graminis*

A.—A representative tenth of all the plants grown at the various soil temperatures in the uninoculated soil of experiment 1B. These plants were all free from infection, as was the case with all of the other uninoculated plants grown in all of the experiments

B.—A representative tenth of all the plants grown at the various soil temperatures in the inoculated soil of experiment 1B. Note the very severe infection in the plants grown at 12° C.; most of these plants died. Also note the severe root rotting on plants grown at soil temperatures below 24° C.



(For explanatory legend see p. 830)

TABLE II.—Effects of soil temperature on the infection of young Goldcoin wheat plants with *Ophiobolus graminis*

[These experiments were conducted independently of those in which soil temperature and soil moisture were varied simultaneously]

Experiment 1A <sup>a</sup>					Experiment 1B <sup>b</sup>					Summary <sup>c</sup>			
Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Leaf-blight rating	Tiller-base infection rating	Root-infection rating
8	26	0.0	0.6	33.0	8	31	1.6	13.9	25.2	8	0.8	7.2	29.1
12	26	3.2	32.0	45.5	12	29	30.4	42.5	45.9	12	19.3	37.2	45.7
16	26	3.2	28.2	43.5	16	23	17.3	42.0	42.0	16	10.2	35.1	42.7
20	32	.0	12.5	26.0	20	31	2.2	34.9	40.3	20	1.1	23.7	33.1
24	26	.0	4.5	7.7	24	28	.0	5.9	9.5	24	.0	5.2	8.6
28	26	.0	1.9	3.8	28	21	.0	7.1	3.1	28	.0	4.5	3.4
32	13	.0	3.8	.0	32	18	.0	2.8	4.6	32	.0	3.3	2.3

<sup>a</sup> Plants grown in soil having a moisture-holding capacity of 67 per cent and containing 56.1 per cent moisture; one 6-inch soil can used for each temperature; 35 seeds and 100 grams of inoculum containing the Oregon strain of the parasite used in each soil can; started Feb. 14, 1922; ended Mar. 10, 1922.

<sup>b</sup> Experiment carried on at the same time and in the same manner as experiment 1A, except that it was not ended until Mar. 17, 1922.

<sup>c</sup> Average amount of infection at each soil temperature in experiments 1A and 1B.

TABLE III.—Effects of soil temperature on the infection of young Goldcoin wheat plants with *Ophiobolus graminis*

[These results are from experiments which were a part of the soil-moisture experiments and comprise all of the data obtained in soil of relatively low-water content]

Experiment 2A <sup>a</sup>				Experiment 3A <sup>b</sup>				Experiment 4A <sup>c</sup>				Summary <sup>d</sup>						
Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Leaf-blight rating	Tiller-base infection rating	Root-infection rating
8	34	2.9	10.7	75.9	8	39	0.0	35.9	56.0	8	48	0.0	14.5	38.8	8	0.9	20.3	56.9
12	26	42.3	79.4	84.0	12	46	.0	65.2	49.0	12	46	23.8	55.8	80.0	12	22.0	66.8	71.0
16	29	24.4	78.1	69.5	16	54	16.6	69.7	68.0	16	50	28.0	78.6	81.9	16	23.0	75.4	73.1
20	24	22.9	44.4	69.5	20	53	2.8	41.5	38.0	20	50	7.0	67.3	70.6	20	10.9	51.1	59.4
24	12	.0	2.8	5.5	24	53	2.8	40.8	47.0	24	51	9.8	38.5	62.7	24	4.2	27.3	38.4
28	20	5.0	.0	.0	28	45	.0	6.6	.0	28	43	.0	10.0	16.6	28	1.6	5.5	5.5

<sup>a</sup> Plants grown in soil having a moisture-holding capacity of 67 per cent and containing 33.8 per cent moisture; one 6-inch soil can used for each temperature; 35 seeds and 100 grams of inoculum containing the Oregon strain of the parasite used in each soil can; started June 3, 1922; ended July 1, 1922.

<sup>b</sup> Plants grown in soil having a moisture-holding capacity of 53 per cent and containing 33.2 per cent moisture; one 8-inch soil can used for each temperature; 60 seeds and 400 grams of inoculum containing the Oregon strain of the parasite used in each soil can; started Feb. 21, 1923; ended Mar. 14, 1923.

<sup>c</sup> Plants grown in soil having a moisture-holding capacity of 53 per cent and containing 33.2 per cent moisture; one 8-inch soil can used for each temperature; 60 seeds and 200 grams of inoculum containing the New York strain of the parasite used in each soil can; started Mar. 31, 1923; ended Apr. 20, 1923.

<sup>d</sup> Average amount of infection at each soil temperature in experiments 2A, 3A, and 4A, having soil moistures of 33.8, 33.2 and 33.2 per cent, respectively.

TABLE IV.—Effects of soil temperature on the infection of young Goldcoin wheat plants with *Ophiobolus graminis*

[These results are from experiments which were a part of the soil moisture experiments and comprise all of the data obtained in soil of medium water content]

Experiment 2B <sup>a</sup>					Experiment 3B <sup>b</sup>				Experiment 4B <sup>c</sup>				Summary <sup>d</sup>					
Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Leaf-blight rating	Tiller-base infection rating	Root-infection rating
8	32	0.0	1.0	9.4	8	54	0.0	63.5	64.7	8	49	0.0	33.3	33.3	8	0.0	32.6	35.8
12	33	1.5	64.6	44.7	12	54	0.0	69.1	70.0	12	49	70.4	94.5	98.5	12	23.9	76.0	71.0
16	31	11.2	18.2	10.7	16	51	36.2	97.4	76.4	16	57	72.8	94.7	99.5	16	40.0	70.1	62.2
20	27	16.6	3.7	12.3	20	42	30.9	92.0	79.0	20	51	71.5	94.8	93.1	20	39.7	63.5	61.4
24	20	.0	.0	.0	24	44	28.4	78.7	70.0	24	49	60.2	93.1	89.3	24	29.5	57.3	53.1
28	17	.0	1.9	.0	28	47	2.1	26.2	37.0	28	50	.0	64.0	66.0	28	7.7	30.7	34.3
32	5	.0	.0	.0											32	.0	.0	.0

<sup>a</sup> This experiment was carried on at the same time and in the same manner as experiment 2A, except that the soil moisture was held near 54.4 per cent.

<sup>b</sup> This experiment was carried on at the same time and in the same manner as experiment 3A, except that the soil moisture was held near 55 per cent.

<sup>c</sup> This experiment was carried on at the same time and in the same manner as experiment 4A, except that the soil moisture was held near 56 per cent.

<sup>d</sup> Average amount of infection at each soil temperature in experiments 2B, 3B, and 4B having soil moistures of 54.4, 55, and 56 per cent, respectively.

TABLE V.—Effects of soil temperature on the infection of young Goldcoin wheat plants with *Ophiobolus graminis*

[These results are from experiments which were a part of the soil moisture experiments and comprise all of the data obtained in soil of relatively high water content]

Experiment 2C <sup>a</sup>					Experiment 3C <sup>b</sup>				Experiment 4C <sup>c</sup>				Summary <sup>d</sup>					
Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Number of plants	Leaf-blight rating	Tiller-base infection rating	Root-infection rating	Average soil temperature, °C.	Leaf-blight rating	Tiller-base infection rating	Root-infection rating
8	35	0.0	12.3	66.6	8	45	0.0	33.3	66.6	8	57	0.0	29.2	33.3	8	0.0	24.9	55.5
12	26	28.8	62.8	73.3	12	46	15.2	67.4	75.2	12	48	53.1	65.9	88.3	12	32.3	65.3	78.0
16	28	32.1	77.3	81.0	16	43	79.0	97.6	98.2	16	60	72.5	85.0	95.5	16	61.2	86.6	91.6
20	20	42.5	58.3	79.0	20	56	36.6	93.4	84.5	20	46	66.5	89.8	98.5	20	48.4	80.5	82.7
24	16	.0	18.7	43.7	24	37	67.5	94.5	96.4	24	48	76.0	88.2	96.5	24	47.8	67.1	78.9
28	19	.0	15.9	20.3	28	32	40.6	87.5	90.4	28	27	7.4	37.0	37.6	28	16.0	46.7	49.4
32	5	.0	6.6	20.0	32										32	.0	6.6	20.0

<sup>a</sup> This experiment was carried on at the same time and in the same manner as experiment 2A, except that the soil moisture was held near 71.6 per cent.

<sup>b</sup> This experiment was carried on at the same time and in the same manner as experiment 3A, except that the soil moisture was held near 80 per cent.

<sup>c</sup> This experiment was carried on at the same time and in the same manner as experiment 4A, except that the soil moisture was held near 80 per cent.

<sup>d</sup> Average amount of infection at each soil temperature in experiments 2C, 3C, and 4C having soil moistures of 71.6, 80, and 80 per cent, respectively.

TABLE VI.—Effects of variations in soil and air temperature on the infection of young Goldcoin wheat plants with *Ophiobolus graminis*

[The plants were grown in large chambers in which both temperature and humidity were controlled within relatively close limits. The soil was inoculated with the New York strain of the parasite, and 15 disinfected seeds were planted in each of six containers for each temperature chamber. Experiment started March 31, 1923, and ended April 27, 1923]

Temperature range, ° C.	Number of plants	Tiller-base infection rating	Root-infection rating
9.5 to 13.2.....	70	76.3	97.9
15.8 to 17.0.....	68	85.1	96.4
26.5 to 27.5.....	59	21.4	36.1

TABLE VII.—Summary of data given in Tables III, IV, and V, arranged to show the influence of soil moisture on the infection of young Goldcoin wheat plants with *Ophiobolus graminis*

Leaf blight				Tiller-base infection				Root infection			
Average soil temperature, ° C.	Low soil moisture	Medium soil moisture	High soil moisture	Average soil temperature, ° C.	Low soil moisture	Medium soil moisture	High soil moisture	Average soil temperature, ° C.	Low soil moisture	Medium soil moisture	High soil moisture
8	0.9	0.0	0.0	8	20.3	32.6	24.9	8	56.9	35.8	55.5
12	22.9	23.9	32.3	12	66.8	76.0	65.3	12	71.0	71.0	78.9
16	23.0	40.0	61.2	16	75.4	70.1	86.6	16	73.1	62.2	91.6
20	10.9	39.7	48.4	20	51.1	63.5	80.5	20	59.4	61.4	83.7
24	4.2	29.5	47.8	24	27.3	57.3	67.1	24	38.4	53.1	78.9
28	1.6	.7	16.0	28	5.5	30.7	46.7	28	5.5	34.3	49.4
32	-----	0	.0	32	-----	.0	6.6	32	-----	.0	20.0

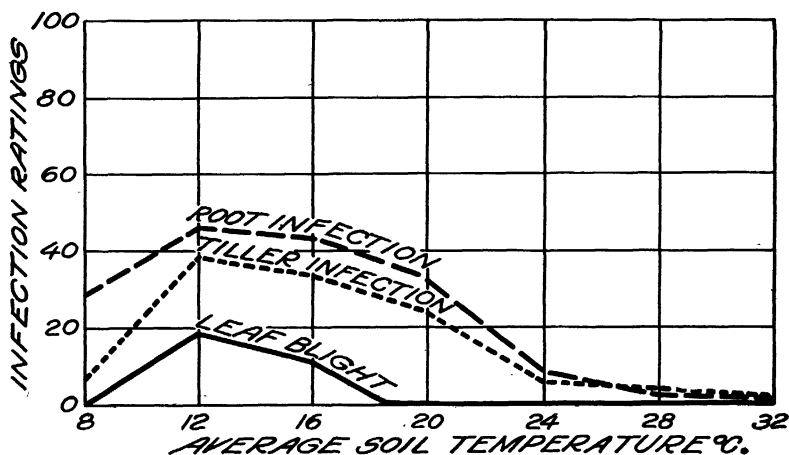


FIG. 1.—Curves showing summaries of infection ratings on the roots, tiller bases, and aboveground parts of Goldcoin wheat plants inoculated with *Ophiobolus graminis*, when grown in soil containing 56.1 per cent of moisture, and held at different temperatures, as shown in Table II



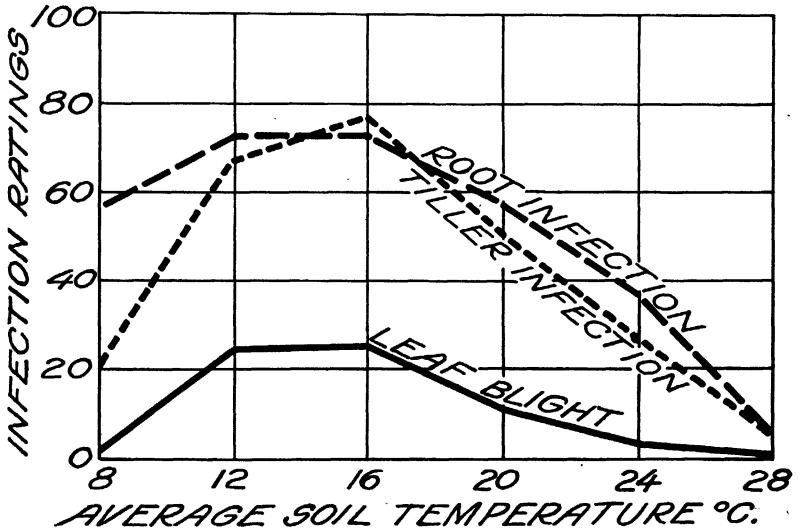


FIG. 2.—Curves showing summaries of infection ratings on the roots, tiller bases, and aboveground parts of Goldcoin wheat plants inoculated with *Ophiobolus graminis*, when grown in soil containing from 33.2 to 33.8 per cent of moisture, and held at different temperatures, as shown in Table III

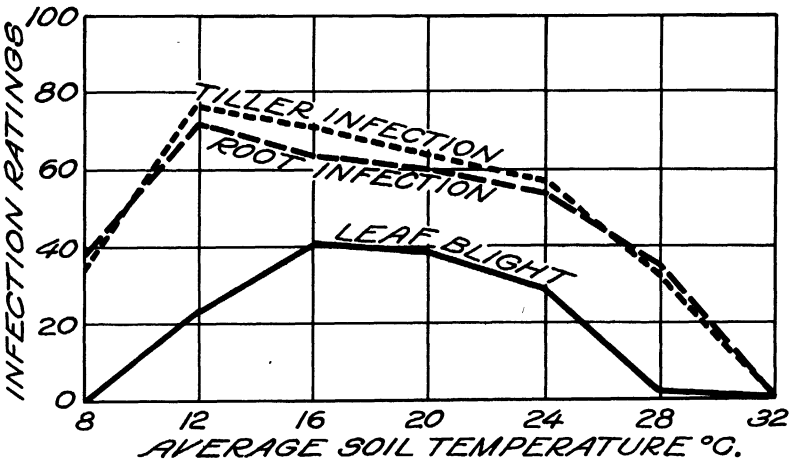


FIG. 3.—Curves showing summaries of infection ratings on the roots, tiller bases, and aboveground parts of Goldcoin wheat plants inoculated with *Ophiobolus graminis*, when grown in soil containing from 54.4 to 56 per cent of moisture, and held at different temperatures, as shown in Table IV

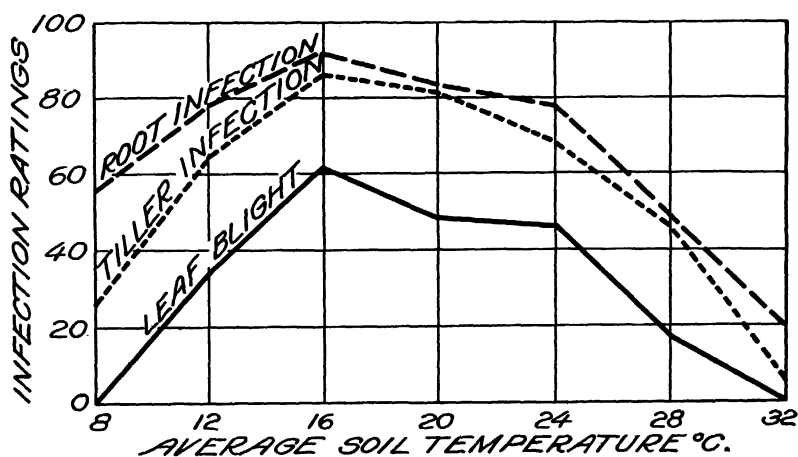


FIG. 4.—Curves showing summaries of infection ratings on the roots, tiller bases, and aboveground parts of Goldcoin wheat plants inoculated with *Ophiobolus graminis*, when grown in soil containing from 71.6 to 80 per cent of moisture, and held at different temperatures, as shown in Table V

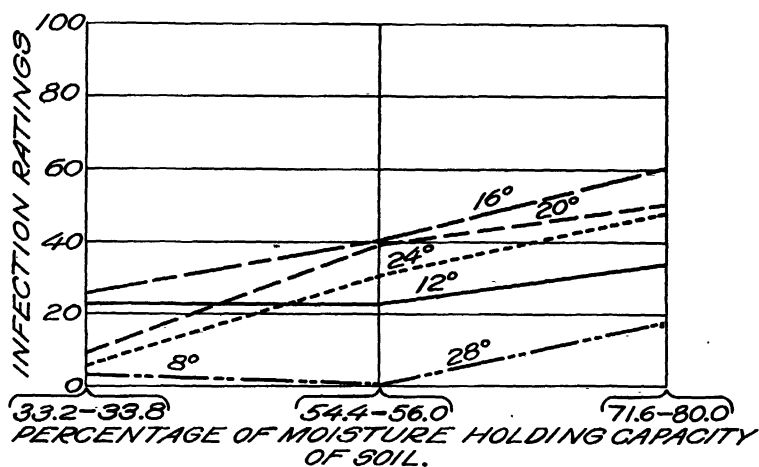


FIG. 5.—Curves showing summaries of infection ratings on the aboveground parts of Goldcoin wheat plants inoculated with *Ophiobolus graminis*, when grown at different soil moistures when soil temperature was varied simultaneously. Tabular results are given in Table VII

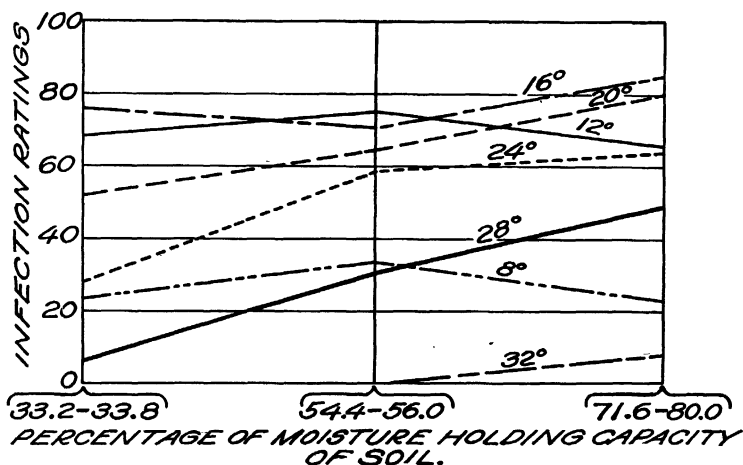


FIG. 6.—Curves showing summaries of infection ratings on the tiller bases of Goldcoin wheat plants inoculated with *Ophiobolus graminis*, when grown at different soil moistures when soil temperature was varied simultaneously. Tabular results are given in Table VII

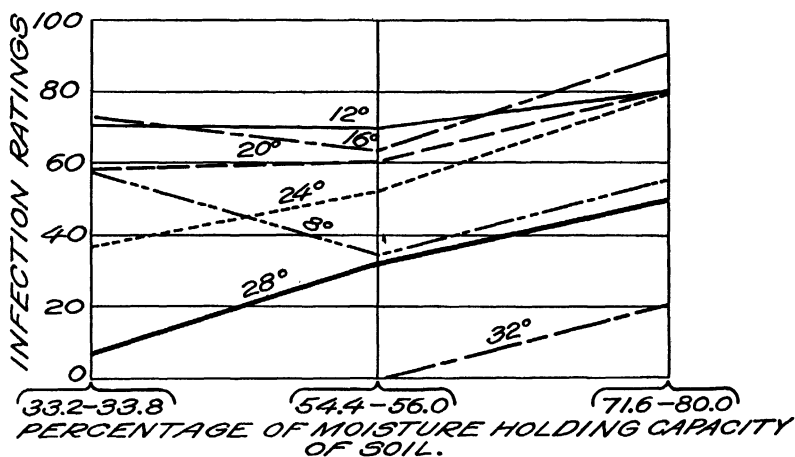


FIG. 7.—Curves showing summaries of infection ratings on the roots of Goldcoin wheat plants inoculated with *Ophiobolus graminis*, when grown at different soil moistures when soil temperature was varied simultaneously. Tabular results are given in Table VII

From the data presented, it is evident that *Ophiobolus graminis* is a vigorous root and tiller-base parasite, and also that infection is greatly influenced by soil temperature and soil moisture. Although the temperature and moisture optima shifted slightly in the several experiments, 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). In these studies it was found that *O. graminis* causes practically no injury to the very young seedlings just before emergence. The germination of seeds planted in the inoculated soils was not consistently lower than that of seeds sown in the uninoculated soil; in fact it was not uncommon to find that the germination of seed in the control soil was actually lower than that of seeds sown in the inoculated soil. It was found in these studies that infection seldom took place until the seedlings were well advanced. This was found to be the case even in the experiments in which the greatest quantities of inoculum were used. When small quantities of inoculum were used the plants showed little infection until they were well advanced beyond the seedling stage.

An examination of the summary curves in Figures 2, 3, and 4 shows that the optimum temperature for tiller-base and root injury was 12° C. in soil containing the medium amount of water, whereas 16° C. was the optimum temperature for these injuries in soils containing low and high soil moistures. Whether this shift represents an actual relationship between the joint influences of temperature and moisture or merely experimental variation is a question. The data given for the individual experiments show that the temperature optima shifted from time to time, regardless of the moisture content of the soil. This indicates that some other factors which were not so well controlled as soil temperature and soil moisture may have a decided influence on the occurrence of the disease and that the temperature optimum probably extends over a range of at least 4° to 6°. The quantity of *Ophiobolus* inoculum placed in the soil has a marked influence on the behavior of the take-all disease, as was also found in the studies on *Actinomyces scabies* (8) and *Helminthosporium sativum* (12). However, it is much more difficult to standardize the amount of inoculum of *Ophiobolus graminis* than is the case with the inoculum of the other parasites mentioned, and as the strains of *O. graminis* employed in these studies differed in their virulence it was frequently found that the quantity of inoculum used was in excess of that which would give the sharpest indications of the temperature and moisture optima.

#### DISCUSSION

Although these studies have only opened up the general subject of environmental influence on the development of the take-all disease, it is believed that the data presented represent the general influences of temperature and moisture on the infection of wheat seedlings and young wheat plants by *Ophiobolus graminis*. While it is difficult or impossible to correlate many of the field observations which have been recorded on this subject, it now appears from the experimental data herein presented that some of the seemingly contradictory reports may be in accord with the facts. As pointed out earlier, the quantity of infectious material in the soil influences the amount and severity of take-all, and this relationship doubtless is the basis for many discrepancies in field observations.

In these experiments of the writers it was found that all infected plants did not show signs of the disease on the aboveground parts. In many cases plants which appeared healthy before removal from the soil were in reality almost devoid of a root system. This condition has been noted also by one of the writers (McKinney) in several commercial wheat fields which were affected by take-all. Although data presented here show that relatively high soil moistures favor infection and injury, it is evident that these soil moistures also were favorable for the development of the host. At these soil moistures many plants sent out new roots in an attempt to replace those which had become rotted. In the present studies the writers did not subject any particular lot of plants to various temperature and moisture changes in order to determine the exact influence of hot, dry conditions following a period of cold, moist conditions or vice versa. However, on a basis of our knowledge of plant responses it is only reasonable to assume that even though cool, moist conditions do favor infection and injury, a sudden reduction in water supply and increased transpiration would produce marked leaf yellowing and killing among those apparently healthy plants which in reality have badly rotted culms and roots. One of the writers (McKinney) has noted an increase in the amount of leaf yellowing in infested fields after the beginning of a hot, dry period. Under such conditions, it might be assumed that dry, hot weather actually favors infection, but it appears that such weather only brings out the expression on the aboveground parts of injuries below ground which are favored by the opposite set of conditions. It would seem that the nonappearance, in the fall and extremely early spring, of take-all on winter wheat on infested land is probably accounted for on a basis of cool, moist conditions which favor the growth of the wheat plants although already infected. However, when the warm spring days arrive the infected plants turn yellow and finally die.

Although the optimum temperature for the development of the parasite is more limited than that for the host, it is of interest to note that the two optima appear to be very close together. On the other hand, the optimum temperature range for the disease is considerably lower than that for either the host or parasite. This relationship is exactly the reverse of that existing with the *Helminthosporium* disease of wheat, the latter disease being favored by soil temperatures which are above those favorable for the host and parasite. In a paper dealing with this latter disease, McKinney (12) suggested that the high temperature optimum for disease occurrence might be accounted for on the basis of the weakening of the host at the high, unfavorable temperatures. However, it is not possible to explain the results with *Ophiobolus graminis* on such a basis. At 12° and 16° C. the wheat plant is thrifty and robust, yet it is attacked severely by this parasite. *Ophiobolus graminis* produces severe injury at unusually low temperatures in comparison with the other wheat parasites such as *Gibberella saubinetii*, studied by Dickson (2), and *Helminthosporium sativum*, studied by the senior writer (12). It seems that the explanation of this will require the study of factors relating to both the host and the fungus and which are far more basic than the phenomena of growth rate and vigor as expressed by the ordinary methods of weight and measurement. It is believed that this also applies to the explanation of the behavior

of the Helminthosporium disease. This is supported by the results obtained by Dickson, Eckerson, and Link (3) with two hosts (corn and wheat) which possess different disease-temperature optima when attacked by *G. saubinetii*. It will be especially important to investigate these problems further, not only by the use of additional hosts and one parasite but by employing one host and several parasites which possess different disease-temperature optima. Unquestionably *H. sativum*, *O. graminis*, and the wheat plant offer opportunities in this direction.

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