U. of M.

THE UNIVERSITY OF MINNESOTA

GRADUATE SCHOOL

Report

of

Committee on Examination

This is to certify that we the undersigned, as a committee of the Graduate School, have given Julian Gilbert Leach final oral examination for the degree of Master of Science . We recommend that the degree of Master of Science be conferred upon the candidate.

Minneapolis, Minnesota

May 13 1918

C. E. Mayman

Chairman

R. T. Peterson

William S. Cooper

THE UNIVERSITY OF MINNESOTA

GRADUATE SCHOOL

Report

of

Committee on Thesis

The undersigned, acting as a Committee of the Graduate School, have read the accompanying thesis submitted by Julian Gilbert Leach for the degree of Master of Science. They approve it as a thesis meeting the requirements of the Graduate School of the University of Minnesota, and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science.

E C Stakman
Chairman

[illegible]

William S. Cooper

May 13 1918

A COMPARATIVE STUDY OF THE PARASITISM OF PUCCINIA GRAMINIS TRITICI AND PUCCINIA GRAMINIS TRITICI-COMPACTI

---o---

A thesis submitted to the graduate faculty of the University of Minnesota by Julian G. Leach in partial fulfillment of the requirements for the Degree of Master of Science. May 1, 1918.

--o--

TABLE OF CONTENTS

---o---

A COMPARATIVE STUDY OF THE PARASITISM OF PUCCINIA GRAMINIS TRITICI AND PUCCINIA GRAMINIS TRITICI-COMPACTI

INTRODUCTION

A new biologic form of Puccinia graminis Pers., was found on club wheat and grasses in the Palouse district of the Pacific Northwest in 1916, described by Stakman and Piemeisel (28, 29) and given the name, Puccinia graminis tritici-compacti. This form was later found to occur also in the southern United States (30). The exact geographic distribution is as yet unknown. In the South it is only known to occur in Alabama, Louisiana and south-eastern Texas; in the Pacific Northwest, only in the Palouse district and in Oregon. It has never been found in the Great Plains area nor in the upper Mississippi Valley. No P. graminis tritici has yet been found west of the Rocky Mountains nor in the southern states where P. graminis tritici-compacti has been found.

P. graminis tritici-compacti resembles P. graminis tritici more than it does any other biologic form. It has been shown to differ morphologically from P. graminis tritici in the size and shape of urediniospores (29, 31). Those of P. graminis tritici are elliptic to ovate while those of P. graminis tritici-compacti are ovate to ellipsoid and slightly shorter than those of P. graminis tritici. Parasitically they have been shown to differ

chiefly in their action on a few varieties of Triticum vulgare Vill. (30). Such varieties as Haynes bluestem, Minn. 169, Marquis, C.I. 3641 and Kubanka, C.I. 4063, all hard spring wheats, are highly resistant to P. graminis tritici-compacti but very susceptible to P. graminis tritici.

The discovery of this form may be of great economic importance. It may explain to a large extent the diverse opinions as to the relative rust resistance of various varieties of wheat in different sections of the country. Since the wheats commonly grown in the spring wheat area are resistant to this new biologic form it appears to eliminate the theory held by many that epiphytotics of stem rust in the North are the result of spores blown up from the far South each spring.

An apparent correlation was noticed between the "hardness" of wheat varieties and their resistance to P. graminis tritici-compacti (30). The significance of this is readily seen when we note that in the regions where this biologic form is known to occur there are grown the so-called "soft" wheats, while the "hard" wheats are grown in the regions where it has not been found. If this should prove to be a true correlation, it would indicate strongly that this biologic form is the result of an adaptation of the fungus to the soft wheats.

It has been shown that relative softness or hardness of wheats are to a large extent determined by climatic factors (14,18). If there proves to be a definite relation between the hardness of a wheat and its resistance to this form, it is possible that the resistance also may be modified by climatic influences. This

question has an important bearing in breeding rust-resistant varieties.

This apparent correlation is also very suggestive as to the probable basis for biologic specialization among the rusts and for rust resistance in wheats.

From what has been said it is evident that it is of great economic as well as scientific importance to know definitely the degree of stability, the infection capabilities, and other important characteristics of the biologic form, P. graminis tritici-compacti.

OBJECTS OF THE INVESTIGATION

Stated briefly the objects of the work recorded in this thesis were:

(1) To determine further the constancy of the biologic form, P. graminis tritici-compacti.

(2) To determine the comparative infection capabilities of P. graminis tritici and P. graminis tritici-compacti especially on varieties of wheat.

(3) To find more varieties, differing in degree of resistance to the two biologic forms, which might be of value as differential hosts.

(4) To determine in so far as possible the influence of climatic factors on the susceptibility of wheat varieties commonly resistant to P. graminis tritici-compacti.

(5) To investigate further the apparent correlation between the hardness of the common wheats and their resistance to P. graminis tritici-compacti in the hope of throwing some light on the question of the basis for biologic specialization and rust resistance.

MATERIALS AND METHODS

The work obviously involved the use of many varieties of wheat. These were obtained from several widely separated sections of the country, i.e., Minnesota, Kansas, Texas, Louisiana, Alabama, Virginia and Washington.[1] The Minnesota varieties were pure line selections made in the Section of Plant Breeding, Division of Agronomy and Farm Management, University of Minnesota. Some of the remaining varieties also were pure line selections; others were not. Inoculation results indicated a relatively large percentage of mixed seed in several instances.

A strain of P. graminis tritici-compacti, which was collected near Brundige, Alabama, in May 1917 and cultivated in the Plant Pathology greenhouse of the University of Minnesota since that date, was used throughout the experiments.

The strain of P. graminis tritici used had been collected at the University Farm, St. Paul, Minnesota in the spring of 1916. Previous to its use in these experiments it had been cultivated on wheat for twenty-five generations.

The methods employed were essentially the same as those described by Stakman and Piemeisel (29). The seedlings were grown in four inch clay pots and thinned to ten plants in each pot previous to inoculation. The first leaf of each plant was inoculated when from three to seven days old. The leaves were thoroughly

---

1. For supplying the above varieties thanks are due to Mr. H.K.Hayes of the Minnesota Experiment Station, Mr. L. E. Melchers, Kansas State Agricultural College, Mr. A. H. Ledigh, Texas Agricultural Experiment Station, Mr. C. W. Edgerton, Louisiana Agricultural Experiment Station and Mr. E. F. Gains, State College, Washington.

wetted by rubbing them several times between moistened thumb and forefinger. Fresh urediniospores were then placed upon the upper surface of the leaves with a moist, flat inoculating needle. After inoculation the pots were put into shallow pans of water and covered with a bell jar for forty-eight hours. They were then removed and placed on the greenhouse benches. The plants were trimmed as often as necessary to leave only the one inoculated leaf. A high percentage of successful infection was secured in this way.

Due to the close similarity of the two forms of rust used, every precaution was taken to prevent accidental infection. The two forms were kept in different sections of the greenhouse and in so far as was practicable only one form was worked with the same day. In fact the majority of the inoculations with P. graminis tritici-compacti were completed before any work was done with the other form.

The rusts were tested at frequent intervals by inoculating varieties of known resistance or susceptibility and at no time during the work was there any indication that contamination had occurred. The strain of P. graminis tritici-compacti was grown on club wheat as a normal host and used for comparison throughout the work. Haynes bluestem, Minn. 169, was used as the normal host for P. graminis tritici.

As a criterion for judging the relative resistance of a variety the character of infection was used in all cases. No consideration was given to the number of uredinia as this is determined to a large extent by environmental conditions during the period of infection and is not necessarily an index to the resistance of the host. The number of uredinia may vary with the amount of inoculum, the relative percentage of viable spores used, and the

moisture conditions during the first forty-eight hours after inoculation. Marshall Ward (35), Stakman (26) and others have shown, and anyone who has worked with rusts will agree, that true resistance is an intracellular phenomenon and must be judged, except in cases of complete immunity, by the nature of the injury caused by the developing mycelium after infection has taken place.

The early development of telia and the production of purple pigment on inoculated plants have been mentioned as indications of resistance of oat varieties to crown rust, (Puccinia lolii avenae McAlpine)(23). These factors could not be depended upon in this work, for telia often develop very early on many of the most susceptible varieties, and the production of purple pigment was a constant and characteristic reaction of other very susceptible ones.

RESULTS OF VARIETY TESTS

Table 1 gives the results of inoculations on 72 varieties of wheat with the two biologic forms of rust. Each variety is listed under the name by which it was received. The state number is given wherever it is known and the varieties from each state are grouped together. The spring wheats are listed first, the hard winter wheats next, followed by the soft winter varieties. In the third column each variety is classified according to its relative "hardness". In making this classification the system described by Hayes, Bailey, Arny, and Olson (13) was followed. C., represents "corneous", S.C., "sub-corneous", S., "starchy", and S.S., "sub-starchy". The inoculation results are given in the form of a fraction, the denominator indicating the number of plants inoculated and the numerator the number which developed uredinia. The character of infection is always indicated.

Table 1 - Results of inoculations with Puccinia graminis tritici-compacti and Puccinia graminis tritici on varieties of wheat

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
1.	Durum (Speltz Marz) Minn. 337	Spring	C.	Division of Agronomy & Farm Management, Univ. of Minn.	0/39	4	Numerous minute sharp dead areas	0/10	1	Heavily flecked
2.	Durum (Mindum) Minn. 470	do.	C.	do.	1/20	2	do. One leaf with a few minute uredinia	0/10	1	do.
3.	Royalton Minn. 1037	do.	S.C.	do.	26/26	3	Small uredinia with well defined hypersensitive areas	8/9	1	Heavy, normal infection
4.	Poultofka Minn. 1164	do.	S.C.	do.	17/18	2	Heavy, normal infection	10/10	1	do.
5.	Bearded Bluestem Minn. 146 x Preston Minn. 168	do.	S.S.	do.	19/19	2	Small uredinia; little or no hypersensitiveness	9/9	1	do.
6.	Marquis Minn. 1239	do.	S.C.	do.	3/28	3	Highly resistant, minute uredinia; sharp flecks and distinct dead areas	7/8		do.

Table 1 - Continued

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
7.	Turkey Winter Minn. 578 x Fife Spring Minn. 165	Spring	S.C.	Division of Agronomy & Farm Management, Univ. of Minn.	1/20	2	Highly resistant, minute uredinia; sharp flecks and distinct dead areas	10/10	1	Heavy, normal infection
8.	Turkey Winter Minn. 529 x Fife Spring, Minn. 165	do.	S.S.	do.	5/20	2	do.	9/10	1	do.
9.	Barletta, Minn. 1178 C.I. 3297	do.	S.S.	do.	21/152	15	Very highly resistant, extremely small uredinia, characteristic minute dead areas	45/47	5	do.
10.	Turkey (Cosgrove) Minn. 529	Winter	S.C.	do.	17/30	3	Uredinia small, distinctly hypersensitive	10/10	1	do.
11.	Turkey Minn. 829	do.	S.C.	do.	15/20	2	Uredinia medium in size, slightly subnormal			
12.	Odessa Minn. 558			do.	19/19	2	Heavy, normal infection	8/8	1	do.

Table 1 - Continued

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
13.	Turkey Minn. 829 x Odessa Minn. 642	Winter	S.C.	Division of Agronomy & Farm Management, Univ. of Minn.	18/19	2	Uredinia small, little or no hypersensitiveness	9/19	1	Heavy, normal infection
14.	Turkey Minn. 829 x Odessa Minn. 558(a)	do.	S.C.	do.	15/20	2	Uredinia small with hypersensitive areas well defined	9/10	1	do.
15.	Turkey Minn. 829 x Odessa Minn. 558(b)	do.	S.C.	do.	29/29	3	Uredinia medium in size; slightly subnormal	9/9	1	do.
16.	Odessa Minn. 642 x Turkey Minn. 829	do.	S.S.	do.	14/14	2	Small to medium uredinia; moderately hypersensitive	10/10	1	do.
17.	Turkey Minn. 829 x Odessa Minn. 558(c)	do.	S.C.	do.	17/19	2	Uredinia small with hypersensitive areas well defined	13/17	2	do.
18.	Odessa Minn. 558 x Turkey Minn. 829	do.	C.	do.	18/20	2	Uredinia medium in size; slightly subnormal	7/9	1	do.

Table 1 - Continued

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
19.	Minn. 552 x Turkey Minn. 839	Winter	C.	Division of Agronomy & Farm Management, Univ. of Minn.	17/18	2	Small uredinia with hypersensitive areas well defined	8/8	1	Heavy, normal infection
20.	S. P. I. 32766	do.	S.	do.	17/19	2	Heavy, normal infection	6/9	1	do.
21.	Harvest King Minn. 643	do.	S.	do.	20/20	2	do.	9/10	1	do.
22.	Malakof Minn. 918	do.	S.C.	do.	19/21	2	do.	9/9	1	do.
23.	Big Frame Minn. 1481	do.	S.C.	do.	17/19	2	do.	7/9	1	do.
24.	Jones Longberry Minn. 1478	do.	S.C.	do.	17/19	2	do.	10/10	1	do.
25.	Turkey N.K. & Co. Minn. 1488	do.		do.	19/21	2	do.			
26.	Crimean P 765	do.	S.C.	Kansas State Agricultural College	5/9	1	Extremely minute uredinia; other leaves heavily flecked	10/10	1	do.

Table 1 - Continued

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
27.	Crimean Kan. 1627	Winter	C.	Kansas State Agricultural College	15/17	2	Variable; mostly small uredinia & hypersensitive. A few normal infections	10/10	1	Heavy, normal infection
28.	Defiance Kan. 373	do.	S.C.	do.	15/16	2	do.	9/9	1	Moderate infection, slightly subnormal. No definite hypersensitive areas
29.	Defiance Kan. 2123	do.	S.C.	do.	18/20	2	Medium to minute uredinia; sharp hypersensitive areas. Variable	10/10	1	Good infection though slightly subnormal. No hypersensitive areas
30.	Defiance Kan. 2123	do.	S.C.	do.	17/17	2	Variable; small uredinia with sharp hypersensitive areas to normal infection	8/9	1	Heavy, normal infection
31.	Alberta Red Kan. 2048	do.	C.	do.	15/17	2	Extremely minute uredinia; other leaves heavily flecked	10/10	1	do.
32.	Alberta Red Kan. 2106	do.	S.C.	do.	19/19	2	Uredinia medium in size; sharp hypersensitive areas; variable	10/10	1	do.

Table 1 - Continued

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
33.	Red Winter Kan 2132	Winter	S.S.	Kansas State Agricultural College	14/17	2	Variable; medium to minute uredinia with sharp hypersensitive areas	10/10	1	Good infection though slightly subnormal
34.	Red Winter Kan. 2101	do.	S.C.	do.	12/16	2	Variable; minute uredinia with hypersensitive areas to normal infection	11/12	1	Heavy normal infection
35.	Red Winter Kan. 2102	do.	S.C.	do.	13/17	2	do.	10/10	1	do.
36.	Red Winter Kan. 196	do.	S.C.	do.	4/9	1	Minute uredinia; other leaves heavily flecked. Sharp hypersensitive areas	9/9	1	do.
37.	Turkey Kan. 2026	do.	C.	do.	7/17	2	Minute uredinia and large dead areas	9/10	1	do.
38.	Turkey Kan. 570	do.	S.C.	do.	9/9	1	do.	10/10	1	do.
39.	Turkey Kan. 2098	do.	C.	do.	14/18	2	Variable; medium to minute uredinia with sharp hypersensitive areas	7/8	1	Moderate infection, slightly subnormal

Table 1 - Continued

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
40.	Turkey Kan. 3039	Winter	S.C.	Kansas State Agricultural College	9/10	1	Variable; normal infection to minute uredinia with sharp hypersensitive areas	10/10	1	Good infection, slightly subnormal
41.	Turkey Kan. 3039	do.	S.C.	do.	11/15	2	Minute uredinia, distinct hypersensitive areas	7/8	1	Heavy, normal infection
42.	Turkey P 1083	do.	S.C.	do.	19/19	2	Variable; minute uredinia with distinct hypersensitive areas to normal infection	9/10	1	do.
43.	Belaglina P 750	do.	S.C.	do.	9/18	2	Minute uredinia, distinct hypersensitive areas	10/10	1	do.
44.	Bearded Fife Kan. 3094	do.		do.	25/37	4	Minute uredinia, distinct hypersensitive areas	8/9	1	Good infection, slightly subnormal. No hypersensitiveness
45.	Champanka Kan. 1183	do.	S.C.	do.	17/18	2	Variable; uredinia medium in size, distinctly hypersensitive	10/10	1	Heavy, normal infection
46.	Kharkoff Kan. 3001	do.	S.C.	do.	14/17	2	Small uredinia, distinctly hypersensitive. Variable	7/9	1	do.

Table 1 - Continued

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
47.	Kanred P 762	Winter	S.C.	Kansas State Agricultural College	17/18	2	Minute to medium uredinia, distinct hypersensitive areas	0/10	1	Dead areas at tips of leaves
48.	P 1066	do.	S.C.	do.	18/30	3	do.	0/10	1	do.
49.	P 1068	do.	S.C.	do.	18/37	4	do.	0/10	1	do.
50.	Romanella P 1036	do.	C.	do.	15/17	2	Variable; normal infection to minute uredinia with sharp hypersensitive areas	10/10	1	Heavy, hormal infection
51.	Iowa Red Winter P 706	do.	S.C.	do.	17/18	2	Variable. Good infection; uredinia medium in size, slightly hypersensitive	10/10	1	do.
52.	Pesterloden Kan. 1635	do.	S.C.	do.	11/17	2	Variable; normal infection to minute uredinia; sharp hypersensitive areas, numerous flecks	8/10	1	do.
53.	Hungarian Kan. 2194	do.	S.C.	do.	7/9	1	Good infection; slightly subnormal	10/10	1	do.

Table 1 - Continued

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
54.	P 2141	Winter	C.	Kansas State Agricultural College	11/14	2	Minute uredinia; distinct hypersensitive areas	10/10	1	Heavy, normal infection
55.	Kan.(Is)1644	do.	C.	do.	14/18	2	do.	10/10	1	do.
56.	Kharkof T.S. 1500	do.	S.C.	Texas Substation No.6, Denton, Tex.	21/27	3	Small uredinia, distinctly hypersensitive	10/10	1	do.
57.	Kharkof T.S. 583	do.	S.S.	do.	26/30.	3	do.	10/10	1	do.
58.	Turkey T.S. 1497	do.	S.S.	do.	7/17	2	Variable; very hypersensitive to normal infection	9/10	1	Medium to large uredinia, slightly subnormal
59.	Crimean T.S. 1499	do.	S.C.	do.	27/31	3	Minute to medium uredinia, distinctly hypersensitive	3/50	5	Normal infection on three plants. Other plants developed no uredinia; no flecks
60.	Bartgrosskomegir T.S. 1504	do.	S.	do.	16/16	2	Heavy, normal infection	10/10	1	Heavy, normal infection
61.	Ferguson's Mediterranean	do.	S.	do.	18/24	3	Variable; very hypersensitive to normal infection	9/10	1	do.
62.	Mediterranean	do.	S.	do.	30/30	3	Good infection, slightly subnormal	9/9	1	do.

Table 1 - Continued

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
63.	T.S. 709	Winter	S.	Texas Substation No.6, Temple, Tex.	15/17	2	Heavy, normal infection	10/10	1	Heavy, normal infection
64.	Forester's Bluestem Mediterranean	do.	S.	do.	16/19	2	Small uredinia, distinctly hypersensitive	10/10	1	do.
65.	Farmer's Mediterranean	do.	S.	do.	23/29	3	do.	10/10	1	do.
66.	T.S. 2399	do.	S.	do.	9/10	1	Heavy, normal infection	7/9	1	do.
67.	Red May	do.	S.	Louisiana Agricultural Experiment Station, Baton Rouge, La.	10/10	1	do.	10/10	1	do.
68.	Fulcaster	do.	S.	do.	10/10	1	do.	10/10	1	do.
69.	Purple Straw	do.	S.	do.	18/20	2	do.	8/9	1	do.
70.	Golden	do.	S.	do.	9/10	1	do.	9/9	1	do.

Table 1 - Continued

No.	Variety	Type	Relative Hardness	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
					Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
71.	Alabama Bluestem	Winter	S.	Alabama Agricultural Experiment Station, Auburn, Ala.	20/20	3	Heavy, normal infection	10/10	1	Heavy, normal infection
72.	Coppei (Club wheat)	?	S.S.	Washington Agricultural Experiment Station, Pullman, Wash.	20/20	2	do.	20/20	2	do.

Of the spring wheats tested, Mindum and Speltz Marz, both durums, and Royalton, Marquis and Barletta, showed a high degree of resistance to P. graminis tritici-compacti (Plates I, II and III). The Turkey Winter x Fife Spring hybrids were also very resistant, while the Bluestem x Preston hybrid was only slightly so. Poultofka was very susceptible. All of these spring varieties with the exception of Mindum and Spletz Marz were highly susceptible to P. graminis tritici.

The hard winter varieties showed varying degrees of resistance to P. graminis tritici-compacti. The majority of them however were very resistant, especially those of the Turkey or Crimean group. The six Turkey x Odessa hybrids were moderately resistant, the type of infection in most cases resembling the more resistant parent. In two cases, Nos. 14 and 17, the hybrids showed greater resistance than the resistant parent. Only a few varieties showed any resistance to P. graminis tritici, three of which were, however highly resistant. These were the Kansas varieties, (Kanred) P 762, P 1066 and P 1068. They developed no uredinia when inoculated with P. graminis tritici but were only semi-resistant to P. graminis tritici-compacti, developing minute to medium uredinia. These varieties have been previously reported by Melchers and Parker as resistant to "stem rust" (19, p.79). Concerning greenhouse tests of these varieties it was stated, "Among 150 varieties inoculated in the seedling stage and at heading time all were found susceptible except the three mentioned. On these, no uredinia were formed either on seedlings or on older plants." Under field conditions, however, it is stated that from 5% to 35% infection was recorded. It would be of interest to know whether this difference in resist-

ance was due to better conditions for rust development in the field or to a different form of rust from the one used in the greenhouse.[2]

Nearly all of the soft winter wheats from Texas, Louisiana and Alabama were susceptible to both forms of rust. The varieties of Mediterranean wheat from Texas showed a fair degree of resistance to P. graminis tritici-compacti. Carleton (4, p.161) mentions this group of wheats as being "fairly resistant to rust." This resistance is perhaps one of the reasons why these varieties have found favor in this section.

The variety listed as T. S. 1499 which was highly resistant to P. graminis tritici and semi-resistant to P. graminis tritici-compacti was found upon inquiry to be the same as the Kansas variety, Crimean, P 762, having been introduced into Texas in 1914.

THE CONSTANCY OF THE BIOLOGIC FORMS

The difference in infection capabilities of the two biologic forms was remarkably constant throughout all the tests. Of the 72 varieties inoculated, 52 showed various degrees of resistance to P. graminis tritici-compacti, while only 13 varieties gave indications of resistance to P. graminis tritici. Inconsistencies occurred in only a few varieties and these could undoubtedly be attributed to mixed seed. It will be noticed that those varieties which are resistant to P. graminis tritici are also resistant to P. graminis tritici-compacti but not always to the same degree. Several

---

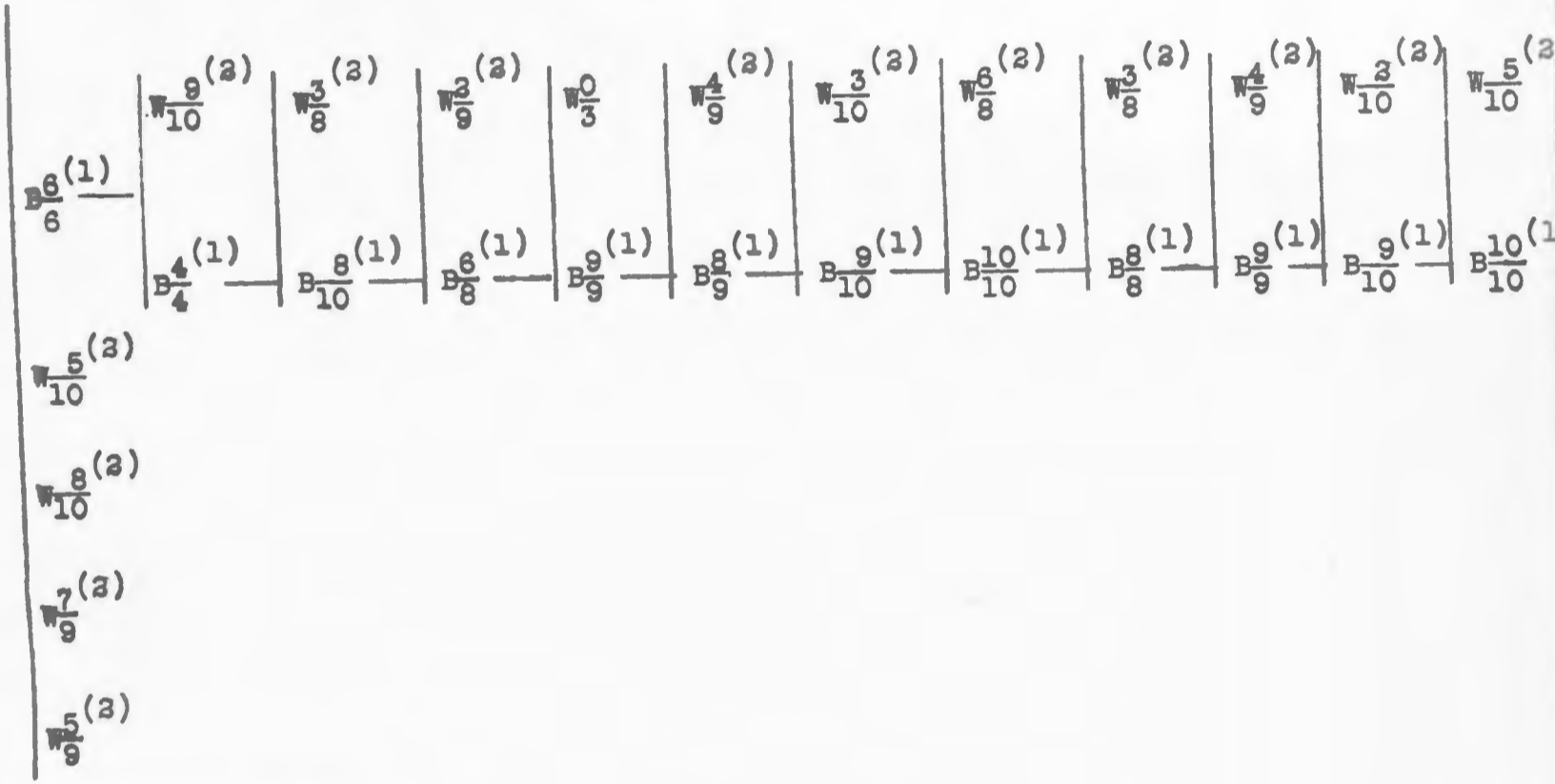
2. Since the completion of this work a new strain of P. graminis to which these varieties are very susceptible has been found by the Minnesota Station.

varieties, however, which are highly resistant to P. graminis tritici-compacti are susceptible to P. graminis tritici. (Plates I and III.) In all cases, those varieties which show normal susceptibility to P. graminis tritici-compacti are also very susceptible to P. graminis tritici. Only two varieties, Mindum and Speltz Marz, both durum wheats, were found to be highly resistant to both forms of rust. These facts would indicate that the two biologic forms are distinct and constant, P. graminis tritici-compacti being a more highly specialized form with a narrower host range.

Although it appears to have been proven conclusively that one biologic form of P. graminis cannot be changed to any great extent by the use of bridging hosts or other methods (31), on account of the very slight differences between these two forms, it was thought advisable to make an attempt to break down these differences by means of host influences. There are two methods by which, theoretically this change could be brought about, (a) by the use of "bridging hosts" and (b) by the constant association of the rust with an uncongenial host.

To test the first of these methods P. graminis tritici-compacti was grown for a number of consecutive generations on barley which is a common host for the two forms. From each generation on barley, transfers were made to Haynes bluestem, Minn. 169 which is resistant to P. graminis tritici-compacti. Diagram 1 shows the results of this experiment. After growing for eleven generations on barley the rust did not infect Haynes bluestem any more vigorously than it had at the beginning of the experiment.

Diagram 1. Result of bridging experiment with Puccinia graminis tritici-compacti



B - Barley, Manchuria, Minn. 105
W - Wheat, Haynes bluestem Minn. 169
CW - Club wheat, Brown Gloria

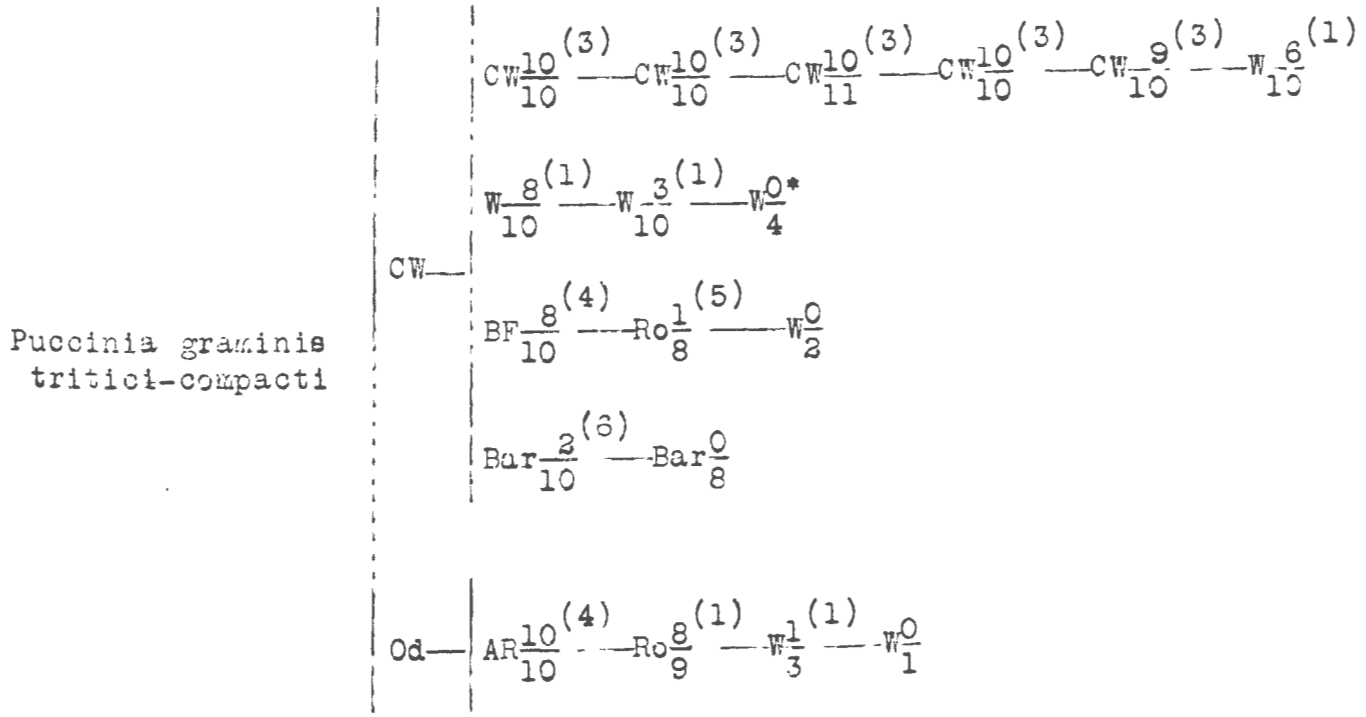
(1) Normal infection.
(2) Extremely hypersensitive, minute uredinia and numerous flecks.

To determine the effect of constant association of the rust with an uncongenial host attempts were made to propagate P. graminis tritici-compacti continually on a single resistant variety or successively on several resistant varieties.

Diagram 2 gives the results of these attempts. In all cases the rust instead of increasing in vigor appeared to become weaker a and for this reason, together with the decreasing amount of inoculum ran out entirely after a few generations.

These results furnish additional evidence that the two biologic forms are constant and well fixed, and that P. graminis tritici-compacti is not a mere variant strain of P. graminis tritici.

Diagram 3. Results of successive transfers of Puccinia graminis tritici-compacti to resistant hosts



W.....Haynes bluestem, Minn. 169
BF....Bearded Fife, Kan. 2094
Od....Odessa, Minn. 558
AR....Alberta Red, Kan. 2106
Ro....Royalton, Minn. 1037
Bar...Barletta, Minn. 1178
CW....Club wheat, "Brown Gloria"

(1) Extremely hypersensitive; minute uredinia and numerous flecks.
(2) Medium to minute uredinia; sharp hypersensitive areas.
(3) Heavy, normal infection.
(4) Medium uredinia; sharp hypersensitive areas.
(5) Extremely minute uredinia; numerous small sharp dead areas.
(6) Extremely minute uredinia; numerous small sharp dead areas; one leaf with several fairly large uredinia.

* This experiment was repeated several times with the same results.

THE INFLUENCE OF CLIMATIC FACTORS ON RUST-RESISTANCE

By referring to Table 1 it can be seen that a classification of the varieties according to geographic source classifies them also with remarkable accuracy in regard to susceptibility and resistance to P. graminis tritici-compacti. There is also a decided correlation between the hardness and softness of the wheat and its resistance and susceptibility to this form. There are, however, a few exceptions to the rule. Again, the spring wheats as a class are more resistant to P. graminis tritici-compacti than the winter wheats. In general it can be said that, with a few exceptions, the hard spring wheats are resistant to P. graminis tritici-compacti, while the soft winter wheats are susceptible. (Plate II.) The hard winter varieties show varying degrees of resistance and susceptibility.

The possible influence of climatic factors on susceptibility and resistance to P. graminis tritici-compacti has been mentioned. It is important to know whether a resistant hard wheat from the North will become susceptibile when grown in the south, or conversely, if a soft susceptible variety will become resistant when grown in the North. If there is a true relation between hardness and resistance such a result could be expected.

Sufficient data for drawing final conclusions on this point could not be obtained in the short time covered by this work. Perhaps the only method by which this question can be answered satisfactorily is to interchange the desired varieties between the North and South and keep them under observation for a number of years. Such an experiment has been begun by the Minnesota Experi-

Barletta wheat was either a resistant one, unwittingly selected, or that it had become resistant as a result of being grown in Minnesota as a spring wheat, and susceptible as a result of being grown in Virginia as a winter wheat.

In the hope of determining what had taken place, seed of all the previous crops of the strains of Barletta grown at the Minnesota Station was obtained. Twenty-six seed of the original introduction were also available. Unfortunately only one of these latter seed germinated. The one plant, however, as well as all those resulting from the seed of each of the succeeding years were found to be highly resistant (Plate IV, fig. 2). These results, given in Table 2, show that this variety was resistant at the time of introduction and that it had not acquired the resistance as a direct result of climatic influences. More work must be done, however, before definite conclusions can be drawn.

Table 2 - Results of inoculations with Puccinia graminis tritici-compacti and Puccinia graminis tritici on different strains of Barletta wheat

No.	Variety and Strain	Type	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
				Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
1.	Barletta C.I. 3297 1912 seed*	?	Province of Buenos Aires, Argentina*	0/1	1	Extremely minute dead areas			
2.	Barletta C.I. 3297 Minn. 1178 1914 seed	Spring	Division of Agronomy & Farm Management, Univ. of Minn.	0/30	3	do.	10/10	1	Heavy, normal infection
3.	Barletta C.I. 3297 Minn. 1178 1915 seed	do.	do.	0/30	3	do.	10/10	1	do.
4.	Barletta C.I. 3297 Minn. 1178 1916 seed	do.	do.	0/30	3	do.	10/10	1	do.
5.	Barletta C.I. 3297 Minn. 1178 1917 seed	do.	do.	21/153	15	A few extremely minute uredinia, numerous minute dead areas	45/47	5	do.

* Twenty-six of the original seed which were sent to the Minnesota Agricultural Experiment Station in 1913. Only one seed germinated.

Table 2 - Continued

No.	Variety and Strain	Type	Source of Seed	Puccinia graminis tritici-compacti			Puccinia graminis tritici		
				Result	No. of Trials	Character of Infection	Result	No. of Trials	Character of Infection
6.	Barletta C.I. 3296 Rod row 982	Winter	Arlington, Va.	30/30	3	Heavy, normal infection	20/20	2	Heavy, normal infection
7.	Barletta C.I. 3300 Rod row 985	do.	do.	29/29	3	do.	20/20	2	do.
8.	Barletta C.I. 3300 Rod row 985	do.	do.	31/31	3	do.	19/19	2	do.

THE IMPORTANCE OF BIOLOGIC FORMS IN THE WORK OF BREEDING VARIETIES OF WHEAT RESISTANT TO STEM RUST

The use of rust-resistant varieties of wheat has long been recognized as one of the best methods of preventing damage by rust. In obtaining such varieties two general methods have been followed, namely, that of determining the relative resistance of the already existing varieties, and the production of new varieties by hybridization. Several existing varieties have been shown to be more or less resistant, but this quality of resistance has not often been found in combination with other desirable qualities. Considerable work has been done in recent years in crossing these resistant varieties with more desirable types with the aim of securing a resistant variety of good quality.

Heretofore plant breeders in this line of work have considered resistance to stem rust of wheat as a single character. This, as we can readily see from the above results, is not a safe procedure, for a variety may be highly resistant to one of these biologic forms and very susceptible to the other. Resistance is specific for each form of rust and therefore more than one character has to be dealt with. The complexity of the problem is of course greatly increased with the addition of each new character.

It is obvious also that the plant breeder must know with how many and with which biologic forms he is dealing in his variety tests. He must not only know which forms are present in the field nursery, but if his work is to be complete he must make greenhouse tests of his varieties with pure cultures of each of the biologic forms.

From the viewpoint of the plant breeder it is also extremely important to determine the exact limits of the geographic distribution of each of these biologic forms. A knowledge of all existing forms (see footnote 2), the infection capabilities, and the geographic distribution of each is essential to efficiency in breeding rust-resistant varieties of wheat.

RUST-RESISTANCE AND BIOLOGIC SPECIALIZATION

Disease resistance in plants has long been a question of much interest. In recent years, however, it has become a problem of extreme importance. The use of disease resistant varieties offer in many cases the only apparent method for disease prevention. The production of such varieties is becoming one of the most important problems of the plant breeder and plant pathologist. At present comparatively little is known of the fundamental causes of disease resistance. It is, however, very evident that a thorough knowledge of the factors controlling resistance is necessary for the maximum efficiency in breeding disease resistant varieties.

A considerable amount of experimental work has been done to determine these factors and a review of the literature on the subject shows that the phenomenon is a variable one and may differ widely with the various types of host and parasite. Stakman (25) has given a relatively complete review of the literature pertaining to this subject; therefore only the most important papers will be mentioned here.

Valleau (33, p.391), working with the brown-rot of plums, correlates resistance with "(a) a thick skin; (b) the production of

parenchymatous plugs which fill the stomatal cavity; (c) the production of corky walls in the lining cells of the stomatal cavity; and (d) firmness of fruit after ripening."

Kinney (15), working with the same fungus also correlates resistance with the texture of the skin.

Jones (14) showed that some varieties of potatoes are more resistant than others to certain potato diseases, and attributes the variation to chemical as well as morphological characters of the host.

Massee (22) and others have attributed much importance to the influences of chemotaxis.

Fulton (10), however, working with several species of fungi failed to find evidence of any definite chemotropic sensibility to nutrient substances or other chemical compounds in solution.

Cook and Taubenhaus (6) consider that tannin and other associated substances are important factors in resistance.

Tisdale (32) describes the penetration of wilt-resistant flax plants by Fusarium lini and attributes the failure of further development of the fungus to three possible factors, "(a) The permanent chemical composition of the resistant plant may be of such nature as to be injurious to the fungus. (b) The protoplasm of the resistant plant may be more highly sensitive than that of the susceptible plant, thus reacting more readily in the production of those phenomena which cause wilt resistance. (c) The stimulation to new cell divisions and the laying down of cork walls which seem to serve as a barrier to further invasion by the already weakened hyphae."

These few citations serve to substantiate the above statement that disease resistance is a variable phenomenon and differs with the host and parasite involved.

More work of this nature has been done with rusts of cereal crops than with any other plant disease, yet no satisfactory explanation for rust resistance has so far been offered.

Anderson (1) states that the flinty, hard varieties of wheat are more resistant to rust due to their high silica content.

Comes (8), working with wheat rust, concludes from observation and analyses that the biochemical factor which enables plants to resist parasitic fungi is the acidity of the cell sap.

Cobb (5) attempted to explain resistance of wheat to rust as due entirely to morphological characters of the host, such as small stomata, thick epidermis, waxy coating, etc.

Ward (35), however, working with the brown rust of bromes, proved conclusively that resistance was independent of any morphological characters of the host.

Biffen (2) also concludes that morphological characters of the host have no relation to the resistance of wheat to P. glumarum.

Bolley (3, p.182) holds that the phenomenon is a physiological, rather than a morphological one, and states that, "The facts point quite clearly to the probable influence of chemical agencies, perhaps toxins, arising from the direct existence of fungus attacks upon the host."

Stakman (26) has shown that when a resistant host is inoculated with certain biologic forms of Puccinia graminis a limited number of cells near the point of infection are killed and the fungus fails to develop normally. In normal infection of a sus-

ceptible host, however, the fungus grows vigorously without serious injury to the host cells. This injury of the cells of a resistant host was termed hypersensitiveness. The degree of hypersensitiveness was observed to vary in direct proportion to the degree of resistance of the host.

Freeman (11, p.115) calls attention to the difference between disease escaping, disease enduring, disease resisting and immune varieties, and states that, "The exact nature of the cytologic forces which make possible or impossible a parasitic reaction are only partially understood.....The possible role of enzymes in such inter reactions is suggestive and recent activity in the study of enzymes from the standpoint of the biologist and chemist bids fair to throw much needed light on cell activities."

The work of Marshall Ward who first carefully investigated the intimate relations between host and rust parasite and who perhaps has done more work on this problem than anyone else, is of outstanding importance and is worthy of careful review.

After proving that the morphological characters of the host had no influence upon true resistance Ward (34) began a careful histological study of the phenomena involved in the infection of resistant bromes by Puccinia dispersa. He showed that the germ tube gained entrance through the stomata in a normal manner, but instead of developing normally it either killed a few cells and then disintegrated, or grew very slowly and never produced pustules. In normal infection he pointed out that no immediate injury to the host cells was noticeable and that a fine adjustment between host and parasite, resembling a state of symbiosis, was the result. A wide range in degree of resistance was found and he noted that

the resistance varied inversely with the ability of the fungus to enter into this symbiotic relation with the host cells. He (36, p.151) explains this action as follows. "All evidence points to the existence in the cells of the fungus of enzymes or toxins, or both, and in the cells of the host plant anti-toxins or similar substances, as a decisive factor in infection or immunity, although I have as yet failed to isolate any such bodies."

Ward's histological work has been verified by Marryat (21) with Puccinia glumarum and semi-immune host plants, by Gibson (12) with Uredo chrysanthemi and many hosts widely separated taxonomically, and by Stakman (26, 27) with several biologic forms of Puccinia graminis and hosts both partially and highly resistant.

Marryat (21, p.137) in discussing her results concludes, "We are therefore forced to fall back upon the theory that immunity to disease is due in these cases to the production of certain toxins and anti-toxins by host or parasite or both, which are naturally destructive. Gibson (12) concludes that when a germ tube enters any but the proper host a struggle ensues, resulting in the death of the parasite and a few cells of the host. The nearer the plant to the proper host taxonomically the longer will be the struggle. Stakman (26, 27) obtained similar results with the biologic forms of P. graminis and calls attention to the fact that "the relations between plant and parasite in partially resistant and almost totally immune plants are different in degree only."

In further work on the problem Ward (35, p.272), in attempting to detect the presence of toxins or anti-toxins, germinated urediniospores in leaf extracts of congenial and uncongenial hosts. Concerning this experiment he states, "All attempts of this kind

were in vain, however, since vigorous spores germinate equally well in extracts of the leaves of their own host-species and of their antagonistic host-species.....The positive results do show, however, that the failure of spores from B. mollis to develop pustules on B. sterilis, for instance, is not due to mere exudation of some antagonistic soluble extract,--the antagonism must be due to something far more subtle than a mere soluble poison oozing from the cells."

This work has been verified by the writer, but since it is possible that toxins or anti-toxins may be formed as a direct result of fungus invasion as suggested by Bolley (3) it was thought advisable to make an effort to detect the presence of such substances in the immediate region of rust infection. Accordingly the following experiment was carried out.

Three varieties of wheat showing varying degrees of resistance were selected, viz., (a) Barletta, Minn. 1178, highly resistant to P. graminis tritici-compacti, (b) bluestem, Minn. 169, semi-resistant to P. graminis tritici-compacti, (c) Brown Gloria (club wheat), very susceptible to P. graminis tritici-compacti. All three varieties are very susceptible to P. graminis tritici. Ten plants of each of the above hosts were inoculated with the two forms of rust. Ten plants of each variety were left uninoculated as checks. After twelve days the plants inoculated with P. graminis tritici were all developing large, normal uredinia, but of those inoculated with P. graminis tritici-compacti only the club wheat was showing normal infection. On the bluestem Minn. 169 there were a few minute uredinia and numerous distinct flecks, while on Barletta there was no indication of the development of

uredinia, merely a few extremely minute dead areas.

Late in the afternoon of the twelfth day after inoculation, these infected areas and also an equal area of the uninfected plants were carefully trimmed out, put in separate test tubes, placed out over night and allowed to freeze. The temperature was well below zero, (Fahrenheit). Early the following morning each sample was thoroughly ground in a mortar with the addition of one c.c. of distilled water. This liquid extract was then filtered under pressure and from each sample hanging-drop plantings were made with urediniospores of each of the two rusts. These plantings were made in duplicate and check plantings of each rust was made in distilled water.

The germination of the spores was watched at frequent intervals for twenty-four hours after planting and notes taken on each set. Germination was complete in the entire series after about seven hours. After this time the germ tubes ceased to grow, became vacuolated, somewhat twisted and a few showed signs of disintegration. This deterioration of the germ tubes was general for all members of the series and no appreciable differences in this respect could be detected between the individual plantings. The notes were tabulated and a study of the table showed that, although there was considerable variation in the percentage of germination and in length of germ tubes, there was no correlation with the resistance of the host from which the extract was made.

This experiment gives no evidence that there is a toxic substance secreted by a resistant host in response to rust infection.

Ward, being unable to demonstrate the presence of toxins and anti-toxins in resistant hosts to uphold his hypothesis, continued his investigations further, approaching the question from a slightly different viewpoint. He states the problem as follows (36, p.139). ".....The evidence suggested some such assumption as the following. The fungus when growing on a species of Bromus A, may refuse to infect another species B, either because B secretes some body of the nature of an enzyme or anti-toxin which effectually keeps the mycelium of the fungus at bay, or because the fungus habituated to the peculiar nutritive or other conditions afforded it by the host plant A, cannot immediately adapt itself to the very different conditions offered by the species B. Although the attempts to isolate any such anti-toxins failed and experiments of a preliminary character to test the effect of differences of nutrition yielded nothing of a positive nature, I showed in a discussion of the factors concerned that some subtle relations between host and parasite must be assumed to account for the curious facts of immunity and predisposition on the part of the former and capacity and incapacity for infection on the part of the latter, in each case in various degrees according to the species of host offered for infection or on which the fungus had hitherto been reared.....If the varying infective power of the fungus towards different species of host plant is solely from the 'nutritive conditions' afforded it by the host-plant it has been growing upon, two cases are possible--(1) these 'nutritive conditions' may be simply the expression of the power of the tissues to yield certain food-substances to the parasite in the proper proportions and in sufficient quantity, or they may

imply some more subtle relations between the mycelium of the fungus and the living contents of the host cells. For instance it may be not sufficient that the food substances suitable to the fungus should exist in the cells of the host, but that they must be there in a certain superabundance or be presented in a certain manner and so on; or it may be that the fungus must be vigorous up to a certain standard before it can obtain a hold on such food and so on."

Working under these assumptions he performed numerous experiments to test the effect of mineral starvation on resistance and susceptibility. From these experiments he concludes (36, p.145) that, "Lack of minerals in no way secured immunity from infection though seedlings deficient in phosphorus or in nitrogen tended to show retardation of infection." Failing to find any satisfactory evidence from this work, he again falls back upon his toxin and anti-toxin hypothesis.

Similar results on the effect of mineral elements on susceptibility and resistance to P. graminis have also been reported by Stakman (26).

Finally Ward (37, p.38), in his last published work on this problem describes the development of hyphae of P. glumarum in a resistant wheat as follows. "In short these hyphae show evident signs of degeneration in all respects, and we conclude, from comparison with experimentally starved hyphae, that they are undergoing death-changes owing to one of two events, viz., they are either starving from the want of food supplies or they are being poisoned."

Concerning the nature of the "experimentally starved

hyphae," which were obtained by keeping previously infected leaves in a carbon dioxide free atmosphere, he remarks (37, p.41). "The phenomena--starvation of hyphae in a nest of dead cells, or the corrosion of cells beneath the spores sown on a leaf--are similar in all these cases to what occurs on the so-called immune plants we have dealt with."

This comparison, however significant it may have appeared to Ward, was not sufficient to cause him to discard his previous hypothesis which he restates in this paper (34, p.21) as follows. "In other words, infection, and resistance to infection, depend on the power of the Fungus-protoplasm to overcome the resistance of the cells of the host by means of enzymes or toxins; and reciprocally, on that of the protoplasm of the cells of the host to form anti-bodies which destroy such enzymes or toxins, or to excrete chemotactic substances which repel or attract the Fungus-protoplasm."

This hypothesis in the light of our present knowledge of biologic specialization and from observations made during the course of this work, is very unsatisfactory.

It is unsatisfactory, first, because no one has yet been able to demonstrate the existence of either toxins or anti-toxins in the plant cells or fungus. Ward admitted that he was unable to detect any such substance in the leaf extract of resistant hosts and the writer has verified this and has also been unable to detect any substance toxic to germinating spores in extracts from leaves of uncongenial hosts in the immediate region of infection.

In the second place, these toxins or anti-toxins, if they should exist, would necessarily have to be specific for each form

of rust, else we could not account for such phenomena as we find with the biologic forms described in this paper where a given host is highly resistant to one form and very susceptible to another.

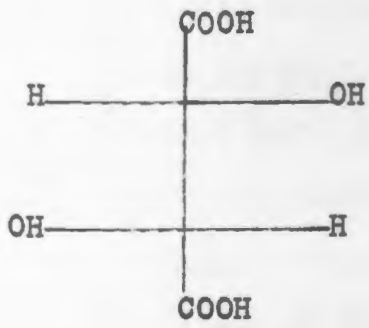
Moreover, since it has been shown that the phenomenon of resistance is the same in hosts partially resistant and in those highly resistant (27, 21) we must assume that these toxins or antitoxins are present in all plants, even those widely separated taxonomically from the type host of the rust. We would have to assume that all plants possess this peculiar substance except those few species which are susceptible to the rust.

Our inability to account for specific toxins in all these cases and our present knowledge of biologic specialization in rusts, together with facts observed in the prsent work, strongly indicate that rust resistance is not a phenomenon involving toxins and antitoxins but, viewed in the light of recent researches in stereochemistry and enzyme activity, is rather one of specific food relations, i.e., a specificity of food requirements on part of the fungus and a specificity of food production on part of the host.

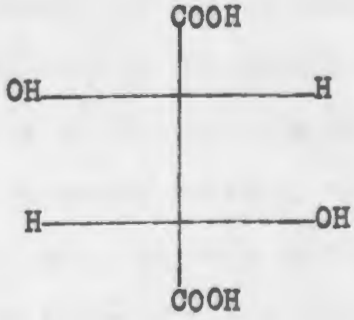
This hypothesis involves two assumptions. First, that each biologic form of rust has a specific food requirement and, second, that the products of cell metabolism are specific for each species and variety of host plant.

As evidence in behalf of the first assumption several examples of known specificity of food requirements among fungi may be mentioned. The classical example of the specificity of the action of Penicillium glaucum in relation to dextro-, levo-, and racemic-tartaric acids first demonstrated by Pasteur in 1861 is well known. Dextro- and levo-tartaric acids differ only slightly

in molecular configuration, having the following structural formulae:



Dextro-tartaric acid.



Levo-tartaric acid.

These formulae, it will be noticed, differ only in the relative arrangement of their component units, one being the mirror image of the other.

Racemic-tartaric acid consists of a mixture of these two acids in equimolecular proportions. If a dilute solution of racemic-tartaric acid is exposed to the action of Penicillium glaucum, the acid is split, the dextro form being consumed while the levo form remains in solution.

Later workers have shown numerous instances where the dextro forms of glucose, mannose, galactose and fructose are consumed by various kinds of micro-organisms while the levo forms are not affected. When Penicillium glaucum acts upon mandelic acid (racemic), however, the levo form is consumed and not the dextro. On the other hand, when the same solution is acted upon by Saccharomyces ellipsoideus the dextro form but not the levo form is consumed.

This selectivity and specificity shown by many species of fungi is to a large extent explained on a basis of enzyme action the specificity of which is too well known to discuss here.

Dox (9) who has made a careful study of the enzymes of Penicillium and Aspergillus calls attention to the marked chemical and physiological differences in strains of Penicillium answering the same morphological description. Numerous cases of specificity are described and in regard to the constancy of this action he concludes that, "There is no evidence that enzymes not normally found by the organism in demonstrable quantities can be developed by special methods of nutrition."

Schellenberg (24) also describes two strains of Penicillium glaucum which are morphologically similar but show marked specificity for different hemicelluloses. Several other fungi are also described showing a corresponding specificity of action on hemicellulose.

Many similar examples involving slight differences in molecular configuration could be mentioned, all of which point to a specific relationship between these differences and the protoplasmic structure and nutritive mechanism of the organisms.

It is interesting to note in this connection the recent work of Knudson (6) in which he shows that galactose and mannose are toxic to certain green plants, while glucose, sucrose and other sugars are readily assimilated.

Just what the specific food requirements of the biologic forms of stem rust under discussion are, is of course not known and perhaps will never be known until we understand better the intimate metabolism of the plant cell or until we succeed in

growing rusts on artificial synthetic media. Whatever they may be, from our general knowledge of obligate parasitism we are justified in assuming that they are more specific than those of facultative parasites or saprophytic fungi.

That the required food is an intermediate product of cell metabolism and is a carbohydrate, or some substance closely related to the carbohydrates, is strongly indicated by the fact that the rusts will not develop on a host deprived of its carbohydrate food supply, while mineral starvation has no appreciable influence on their development. This was shown by Ward (37) for P. glumarum and by Mains, (20) for P. sorghi and P. coronata, whose work has been verified in part by the writer with the biologic forms of P. graminis.

As evidence to justify the second assumption it is only necessary to refer to the work of Reichert (25) on, "The differentiation and specificity of starches in relation to genera, species, etc." In this work Reichert proves conclusively that starches exist in plants in different stereoisomeric forms that are specifically modified in relation to varieties, species and genera. In his own words, "The history of starch from the moment of the utilization of carbon dioxide and water to form an aldehyde, through the various steps of synthesis of monosaccharoses, disaccharoses, and polysaccharoses to the ultimate appearance of starch, and the reversal of these steps when the starch is consumed as food, is upon logical grounds conceived to be one of continuous and consecutive enzyme action. The enzymes synthesize starch and its precursors and no other substances, because they can build up only such chemical structures as have configuration complement-

ary to themselves, each tending naturally to build those forms which have the closest configuration; and likewise each analyzes only such substances as have the same stereochemic relationship. If, as stated, protoplasm uses only such organic substances as have a complementary stereochemic form, it follows as a corollary that starch has a corresponding configuration, and that if starch has such a conformable structure so must have the enzymes that produce it. In other words every enzyme formed by any given protoplasm is specifically produced to carry out operations which are directly or indirectly essential to the existence of protoplasm itself and must ipso facto bear a stereochemic relationship to its mother substance; therefore, protoplasm, enzyme, and product have in common the same fundamental stereochemic peculiarities. In fact as the results of these researches go to show, every synthetic organic substance produced by any given protoplasm through the agency of its enzymes has a configuration in agreement with that of the protoplasm. If, as must be admitted, corresponding kinds of protoplasm in different organisms differ, the corresponding synthetic metabolites will differ, and conversely if the latter differ so must the former. Hemoglobins which are corresponding substances have been shown to differ in specific relationship to genera and species; and the same extraordinary phenomenon has been brought to light in respect to starches."

In this work the starches of over three hundred species of plants were studied and abundant evidence is presented to justify the above statement. It is of importance to note in this connection that Reichert (25, p.376) on the basis of starch peculiarities has divided the type hosts of the biologic forms of

Puccinia graminis into two distinct groups corresponding with the classification of the biologic forms on the basis of parasitism by Stakman and Piemeisel (29, p.492) and on morphological characters by Stakman, Piemeisel and Levine (31).

In addition to these two assumptions it is necessary to explain the injurious effect of the invading fungus on the cells of resistant plants. This is explained by the well known fact that fungi on being starved secrete an excess of enzymes. Is it not logical to assume that it is these enzymes, secreted by the fungus only when it fails to find abundant, readily available food which are injurious to the plant cells? A parallel case is that described by Cooley (7) in which Sclerotinia cinerea secreted a cellulose hydrolyzing enzyme when grown on filter paper with no other nutrient supplied but when small quantities of peach juice or other soluble carbohydrates such as glucose was added no cellulose hydrolysis occurred.

With this evidence for the justification for the above assumptions the following hypothesis is offered to explain the facts of resistance as observed in this work and in that of previous workers:

Each biologic form of rust has its specific food requirements, conforming with the molecular configuration of its protoplasm. This food, which is in turn specific in relation to the protoplasm which produces it, is found only in a limited number of host species. When a given biologic form of rust invades a plant which does not contain this specific food the fungus consequently dies of starvation and in this process of starvation secretes an enzyme which is injurious to the plant cells with which it comes into contact.

This hypothesis would seem to explain the observed facts better than any previously offered. It does not require the assumption of the universal presence of specific toxins and antitoxins, the existence of which we have no evidence, not even in resistant hosts in the immediate region of infection. On the other hand there is abundant evidence to justify the assumption of specific food relations between host and parasite.

This hypothesis is offered to explain not only the facts of resistance but also those of biologic specialization, two probably identical phenomena. A study of the behavior of the biologic forms described in this paper shows clearly that no distinction can be made between the two phenomena on a basis of causal factors.

SUMMARY

1. Puccinia graminis tritici-compacti is a distinct and constant biologic form which cannot be changed easily by host influences.

2. The infection capabilities of the two forms studied on 72 varieties of wheat show that: (1) P. graminis tritici-compacti has a narrower host range than does P. graminis tritici, (2) as a rule the hard spring wheats are resistant to P. graminis tritici compacti, while the soft winter wheats are susceptible, (3) the hard winter wheats show varying degrees of resistance to P. graminis tritici-compacti, and (4) neither of these groups of wheats as a class are resistant to P. graminis tritici.

3. Barletta Minn. 1178, Marquis Minn. 1239, Royalton Minn.1037 and Haynes bluestem Minn. 169 are highly resistant to P. graminis tritici-compacti, but very susceptible to P. graminis tritici.

The three Kansas varieties, P 762, P 1066 and P 1068 are highly resistant to P. graminis tritici but only semi-resistant to P. graminis tritici-compacti. These seven varieties are valuable as a means of differentiating the two biologic forms.

4. Sufficient data are not available for drawing conclusions on the influence of climatic factors on rust resistance. Observations on certain varieties indicate, however, that climatic influences have little or no direct effect on resistance or susceptibility to P. graminis tritici-compacti.

5. A thorough knowledge of all the existing biologic forms of P. graminis, including the infection capabilities and exact geographic distribution of each, is extremely important in breeding varieties of wheat resistant to stem rust.

6. The following hypothesis is offered to explain the phenomena of rust resistance and biologic specialization in rusts: "Each biologic form of rust has its specific food requirements, conforming with the molecular configuration of its protoplasm. This food which is in turn specific in relation to the protoplasm which produces it, is found only in a limited number of host species. When a given biologic form of rust invades a plant which does not contain this specific food the fungus consequently dies of starvation and in this process of starvation secretes an enzyme which is injurious to the plant cells with which it comes into contact."

LITERATURE CITED

1. Anderson, H.C.S. Rust on wheat experiments and their object. Agri. Gaz. New South Wales, 1: 1. 1890.

2. Biffen, R.A. Studies in the inheritance of disease resistance. Jour. Agr. Sci., 2: 109-128. 1907.

   Studies in the inheritance of disease resistance. II. Jour. Agr. Sci., 4: 421-429. 1913.

3. Bolley, H.L. Observations regarding the constancy of mutants and questions regarding the origin of disease resistance in plants. Am. Nat., 42: 171-183. 1908.

4. Carleton, M.A. The small grains. The Macmillan Co. 1916.

5. Cobb, N.A. Contributions to an economic knowledge of the Australian rusts. Agr. Gaz. New South Wales, 3: 55. 1890.

   Contributions to an economic knowledge of the Australian rusts. Agr. Gaz. New South Wales, 3: 181-213. 1893.

6. Cook, M.T., and Taubenhaus, J.J. The relation of parasitic fungi to the contents of the cells of the host plant. I. The toxicity of tannin. Del. Coll. Agr. Exp. Sta. Bul. 91: 1911.

   The relation of parasitic fungi to the contents of

the cells of the host plants. II. The toxicity of vegetable acids and oxidizing enzyme. Del. Coll. Agr. Exp. Sta. Bul. 98. 1913.

7. Cooley, J.S. A study of the physiological relations of Sclerotinia cinerea (Bon.) Schröeter. Ann. Mo. Bot. Garden, 1: 291-326. 1914.

8. Comes, Orazio. Della resistenza dei frumenti alle ruggini stato attuale della questione e provvedimenti. Att. R. Ist. Incoraggimento Napolis, 6.9. 421-441. 1913. (Abstract) Internat. Inst. Agri (Rome) 4: 117-119. 1913.

9. Dox, Arthur Wayland. The intracellular enzymes of Penicillium and Aspergillus. U.S. Dept. Agr. Bur. An. Ind. Bul. 120. 1910.

10. Fulton, Harry R. Chemotropism of fungi. Bot. Gaz., 41: 81-107. 1907.

11. Freeman, E. M. Resistance and immunity in plant diseases. Phytopath. 1: 109-115. 1911.

12. Gibson, Miss C.M. Notes on infection experiments with various Uredineae. New Phytol., 3: 184-191. 1904.

13. Hayes, H.K., Bailey, C.H., Arney, A.C., and Olson, P.J. The color classification of wheat. Jour. Amer. Soc. Agron., 9: 1917.

14. Jones, L.R. Disease resistance of potatoes. U.S. Dept.

Agr. Bur. Plant Ind. Bul. 87. 1905.

15. Kinney, L.F. The plum rot and its effect on plum culture in Rhode Island, R.I. Agr. Exp. Sta. 9 Ann. Rept. 191-192. 1896.

16. Knudson, Lewis. The toxicity of galactose and mannose for green plants and the antagonistic action of other sugars towards these. Am. Jour. Bot., 4: 430-437. 1917.

17. Le Clerc, J.A., and Leavitt, Sherman. Tri-local experiments on the influence of environment on the composition of wheat. U.S. Dept. Agr. Bur. Chem. Bul. 138. 1910.

18. _____ and Yoder, P.A. Environmental influences on the physical and chemical characteristics of wheat. Jour. Agr. Research. 1: 375-391. 1914.

19. Melchers, Leo E., and Parker, John H. Three varieties of hard red winter wheat resistant to stem rust. (Abstract) Phytopath., 8: 79. 1918.

20. Mains, E.B. The relation of some rusts to the physiology of their hosts. Am. Jour. Bot., 4: 179-220. 1917.

21. Marryat, Dorothea C.E. Notes on the infection and histology of two wheats immune to the attacks of Puccinia glumarum, yellow rust. (With plate II). Jour. Agr. Sci., 2: 127-137. 1907.

28. Massee, George. On the origin of parasitism in fungi. Phil. Trans. Roy. Soc. London, B. 197: 7. 1904.

33. Parker, John H. Greenhouse experiments on the rust resistance of oat varieties. U.S. Dept. Agr. Bul. 629. 1918.

34. Schellenberg, H.C. Untersuchungen uber das Verhalten einiger Pilze gegen Hemizellulosen. Flora, 98: 257-308. 1908.

35. Reichert, Edward Tyson. The differentiation and specificity of starches in relation to genera, species, etc. Carnegie Inst. Wash. Publ. 173. 1913.

36. Stakman, E.C. A study in cereal rusts: physiological races. Minn. Agr. Exp. Sta. Bul. 138, 56 p. 9 pl. Bibliography p. 50-54. 1914.

37. _____ Relation between Puccinia graminis and plants highly resistant to its attack. Jour. Agr. Research 4: 193-200. 1915.

38. _____ and Piemeisel, F.J. A new strain of Puccinia graminis. (Abstract) Phytopath. 7, p. 73. 1917.

39. _____ _____ Biologic forms of Puccinia graminis on cereals and grasses. Jour. Agr. Research, 10: 429-495. 1917.

30. _____ and Hoerner, G.R. Puccinia graminis tritici-compacti in southern United States. (Abstract) Phytopath., 8: 77. 1918.

31. _____, Piemeisel, F.J., and Levine, M. N. Studies on the plasticity of biologic forms of Puccinia graminis. Manuscript not yet published.

32. Tisdale, W.H. Flaxwilt: A study of the nature and inheritance of wilt resistance. Jour. Agr. Research, 11: 537-605. 1917.

33. Valleau, W.D. Varietal resistance of plums to brown-rot. Jour. Agr. Research, 5: 365-395. 1915.

34. Ward, H. Marshall. The bromes and their rust fungus, Puccinia dispersa. Ann. Botany, 15: 560-562. 1901.

35. _____ On the relations between host and parasite in the bromes and their brown rust, Puccinia dispersa Erikss. Ann. Botany, 16: 233-315. 1902.

36. _____ Experiments on the effect of mineral starvation on the parasitism of the uredine fungus, Puccinia dispersa, on species of Bromus. Proc. Roy. Soc. London, 71: 138. 1902.

37. _____ Recent researches on the parasitism of fungi. Ann. Botany, 19: 1-50. 1905.

PLATE I

(A) *P. graminis tritici-compacti* and (B) *P. graminis tritici* on 1. Club Wheat (Brown Gloria), 2. barley (Manchuria Minn. 105), 3. Haynes bluestem Minn. 169, 4. Royalton Minn. 1037, 5. Marquis Minn. 1239, and 6. Barletta Minn. 1178.

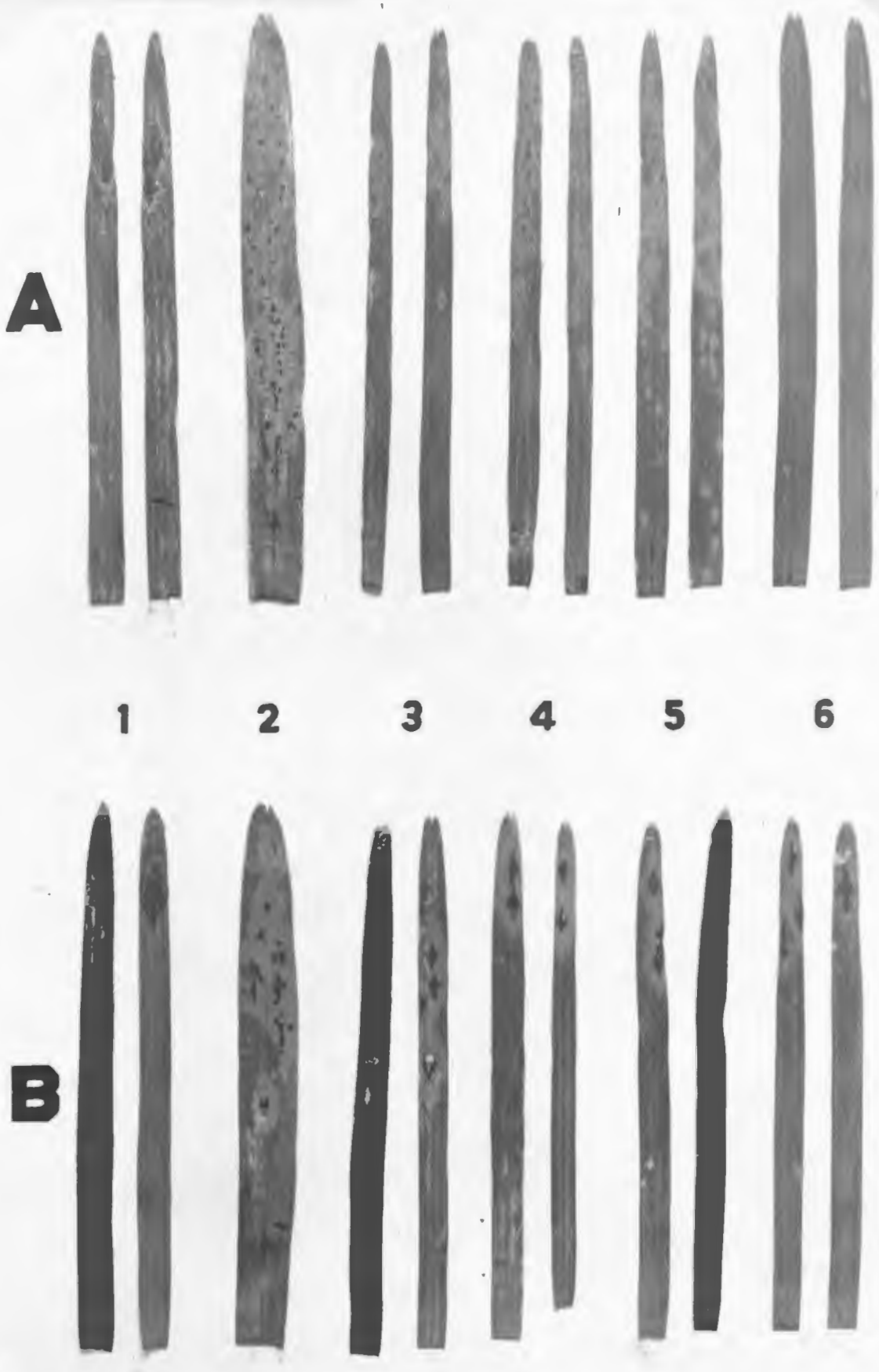
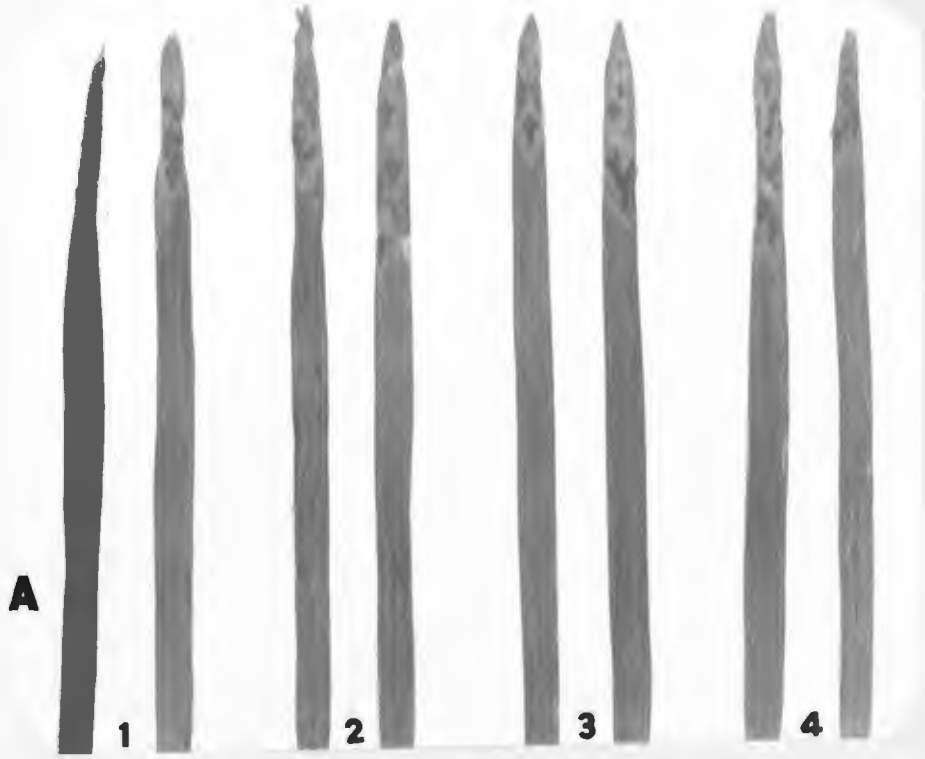

A
1
2
3
4
5
6
B

PLATE II

P. graminis tritici-compacti on (A) varieties of soft winter wheat, 1. Fulcaster, 2. Purple Straw, 3. Red May, 4. Golden, and (B) varieties of hard spring wheat, 1. Marquis, 2. Royalton, 3. Mindum (durum), 4. Speltz Marz (durum).


A
1
2
3
4

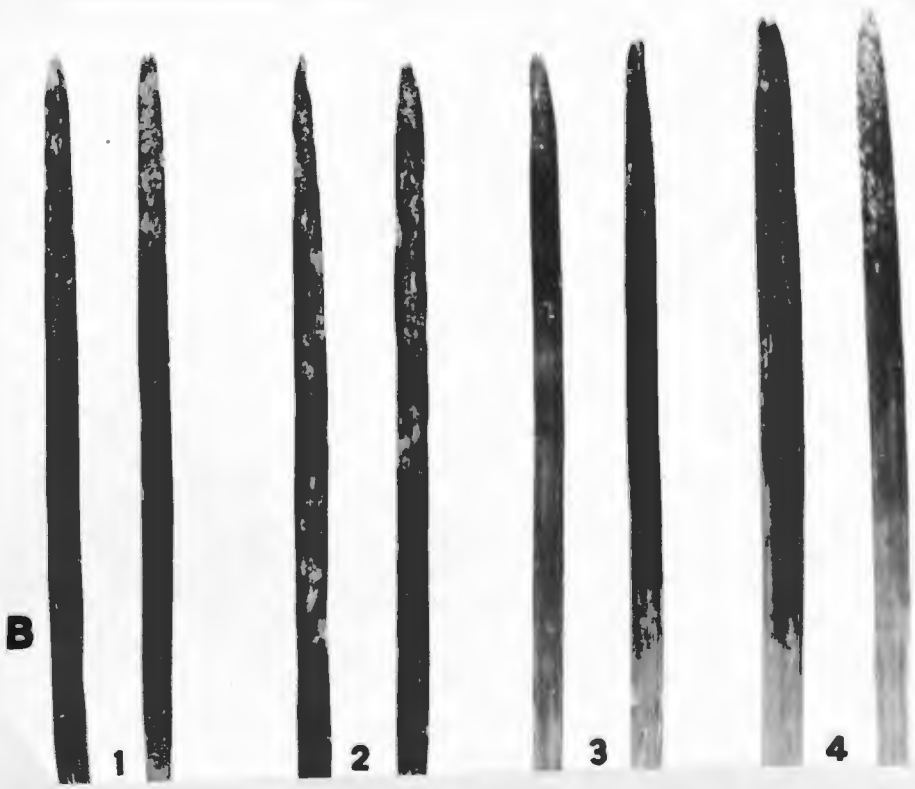

B
1
2
3
4

PLATE III

Fig. 1. (A) *P. graminis tritici-compacti*, and
(B) *P. graminis tritici* on Barletta Minn. 1178.

Fig. 2. (A) *P. graminis tritici-compacti*, and
(B) *P. graminis tritici* on Marquis Minn. 1239.

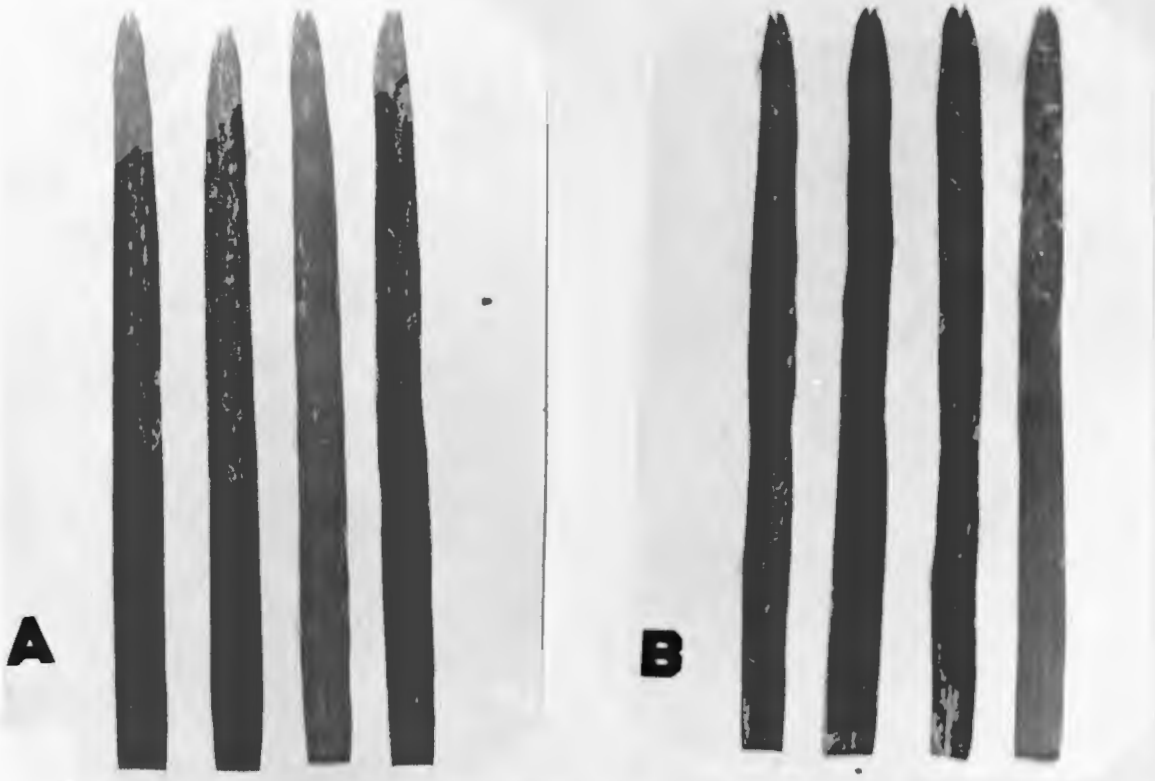


Fig. 1.

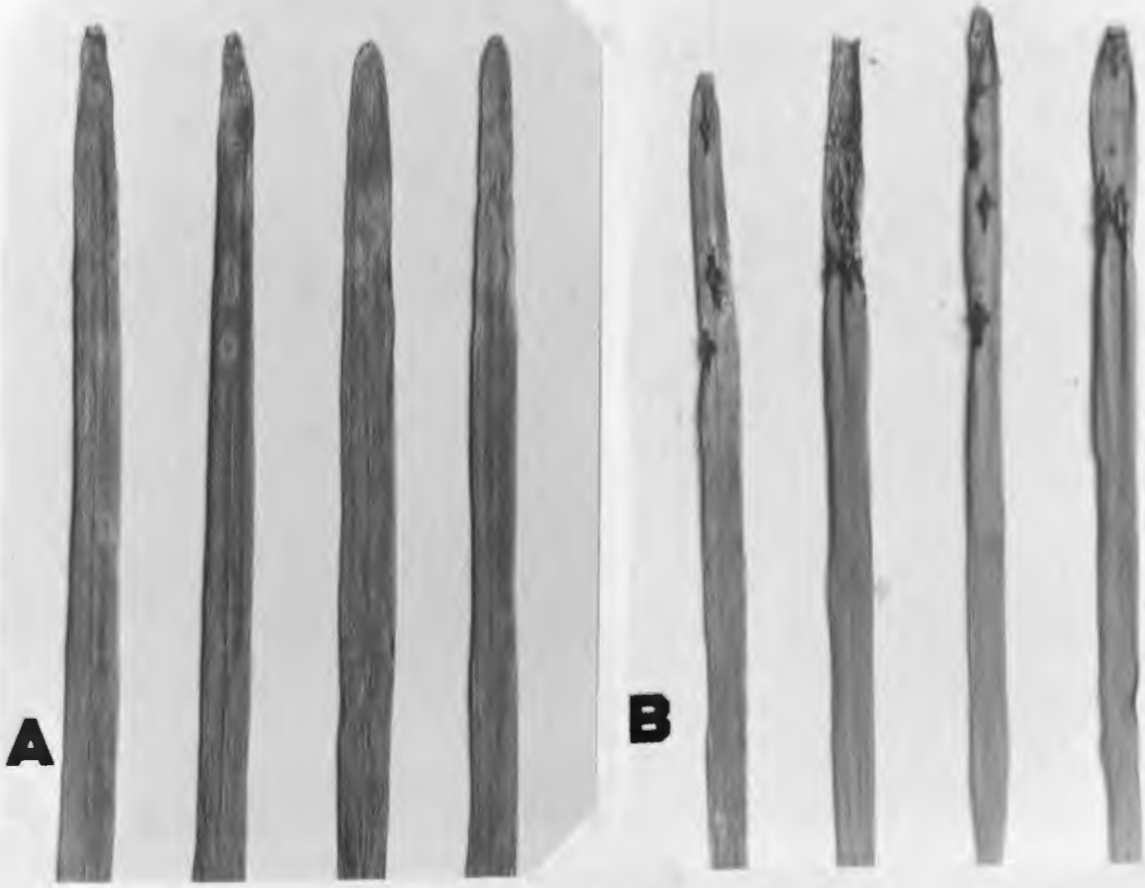


Fig. 2.

PLATE IV

Fig. 1. *P. graminis tritici-compacti* on three strains of Barletta wheat from Arlington, Va. All very susceptible. Fig. 2. *P. graminis tritici-compacti* on Barletta, Minn. 1178 from (A) from seed grown in Buenos Aires, Argintina, 1913, B, C, D and E, from seed grown at the Minn. Exp. Station in 1914, 1915, 1916 and 1917 respectively. All highly resistant.

Fig. 1.

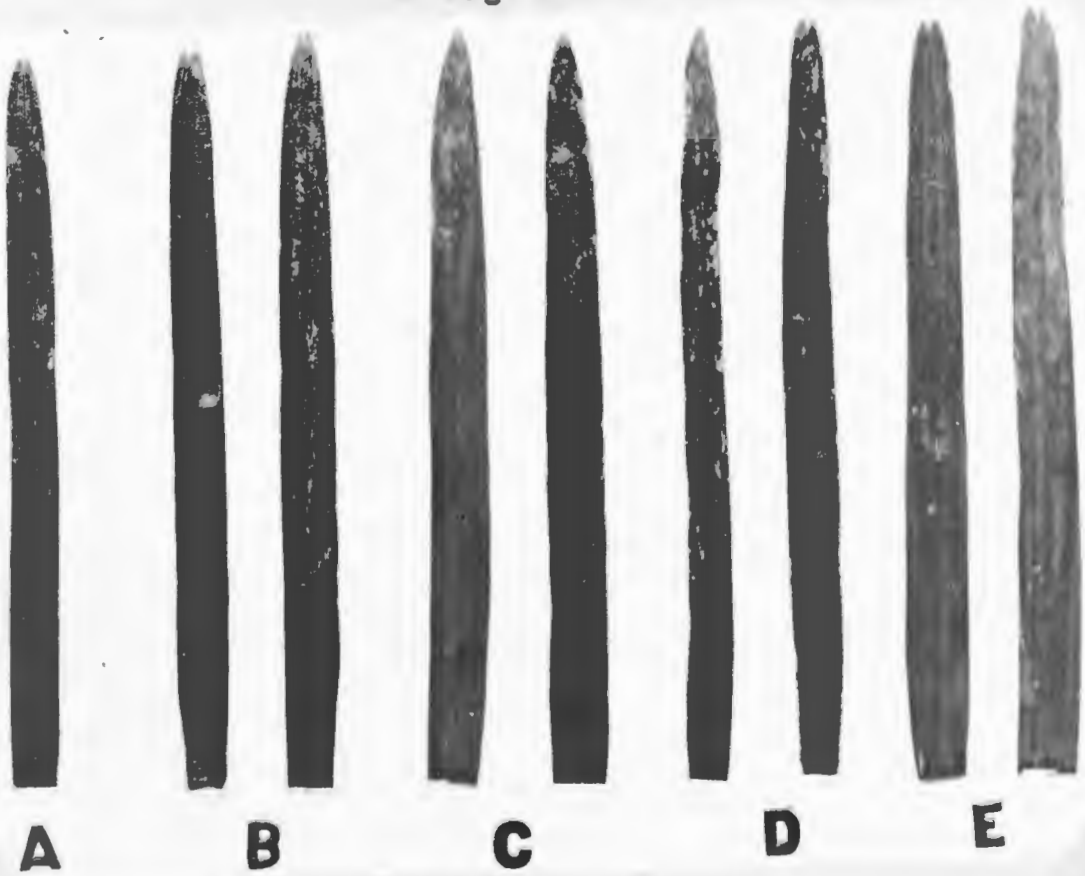


Fig. 2.