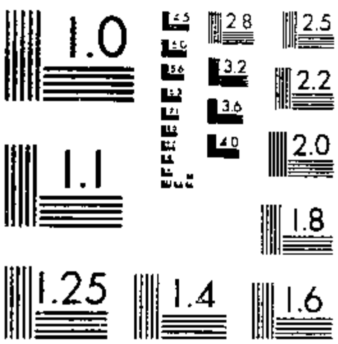
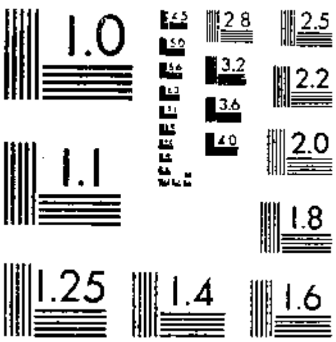
TB 313 (1932) USDA TECHNICAL BULLETINS UPDATA
STUDIES ON PHYSIOLOGIC SPECIALIZATION IN PUCCINIA TRITICINA
JOHNSTON, C.O.; MAINS, E.B. 1 OF 1

START





MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A

TECHNICAL BULLETIN No. 313 — MAY, 1932

UNITED STATES DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

STUDIES ON PHYSIOLOGIC SPECIALIZATION IN PUCCINIA TRITICINA[1]

By C. O. JOHNSTON, *Associate Pathologist, Division of Cereal Crops and Diseases, Bureau of Plant Industry*, and E. B. MAINS, *Professor of Botany, University of Michigan, formerly Agent, Division of Cereal Crops and Diseases, Bureau of Plant Industry*[2]

CONTENTS

INTRODUCTION

The problem of physiologic specialization in parasitic fungi continues to be one of vital interest to plant pathologists and plant breeders everywhere. Although the urge to discover new physiologic forms merely to increase the number in any particular species is rapidly diminishing, it is impossible to escape the practical necessity of continually searching for, describing, and cataloguing new forms. Modern plant breeding rightfully demands this knowledge as an invaluable aid in the production of improved disease-resistant varieties of crop plants.

Although Mains and Jackson (*10*)[3] described 12 physiologic forms of the leaf rust of wheat, *Puccinia triticina* Eriks., in 1926, it was realized at the time that these comprised only a few of the forms present in the United States, and that the number would require extension from time to time. Since 1926 studies on physiologic specialization have been conducted concurrently at the Purdue University (Indiana) and the Kansas agricultural experiment stations. The data obtained on the occurrence of new physiologic forms are presented in this bulletin, together with a revision and coordination of the data on physiologic forms of *P. triticina* as presented by various writers.

[1] The investigations here reported were conducted by the Division of Cereal Crops and Diseases, Bureau of Plant Industry, in cooperation with the Department of Botany and Plant Pathology of the Kansas Agricultural Experiment Station and the Department of Botany of the Purdue University (Indiana) Agricultural Experiment Station.

[2] The writers gratefully acknowledge many helpful suggestions received from M. N. Levine and H. B. Humphrey during the course of the studies here reported.

[3] Italic numbers in parentheses refer to Literature Cited, p. 21.

108557°—32——1

HISTORY

In 1926 Mains and Jackson (*10*) proved the existence of 12 physiologic forms of *Puccinia triticina* through the use of 11 varieties of common wheat as differential hosts. Two years later Scheibe (*13*) described 3 new forms from collections made in central Europe and designated them as forms 13, 14, and 15. He also stated that form 11 was the only one described by Mains and Jackson from North American material found by him in central Europe. In this paper Scheibe unwittingly has introduced an error into the literature on physiologic forms of *P. triticina*. Seed of the differential varieties was furnished him by Mains, but since the publication of his data in 1926 (*10, p. 101*) Mains had discarded Turkey 47 from the list. This was done because the reaction of Turkey 47 to the 12 described forms was the same as that of Malakof (C. I.[4] No. 4898) and because Turkey 47 had a tendency to cross very readily with other varieties in the field. Therefore, seed of Turkey 47 was not sent to Scheibe when he requested seed of the 11 standard varieties. A supply of Michigan Amber 29–1–1–1 was sent him at that time, however, as a very susceptible variety upon which to grow stock cultures. Mains had found Michigan Amber very satisfactory for that purpose because it had proved susceptible to nearly all of the known physiologic forms. Scheibe, however, apparently considered Michigan Amber as a substitute for Turkey 47 and therefore as having the same reactions to forms 1 to 12, inclusive, as Turkey 47. In his paper (*13, p. 593*) he has assigned the reactions of Turkey 47 in Mains and Jackson's data to Michigan Amber 29–1–1–1 for all of the first 12 forms except form 11, for which he gives the reactions he obtained with European rust collections. Michigan Amber 29–1–1–1 has not been shown by published data to have differential reaction to physiologic forms of *P. triticina* and should be eliminated from the list of differential varieties.

Waterhouse (*17*) noted the occurrence of two forms of leaf rust of wheat in Australia in 1929. These forms were interesting in that they had identical reactions on the 11 standard varieties used by Mains and Jackson. However, when the Australian variety Thew was added to the list it was found that there were really two forms, to one of which Thew was resistant, while to the other it was susceptible. Although Waterhouse thus described two new physiologic forms, he did not give them definite numbers, merely designating them as "Aust. 1" and "Aust. 2."

In May, 1930, another paper by Scheibe (*14*) increased the number of known physiologic forms of *Puccinia triticina* to 23. Forms 16 to 23, inclusive, were described from collections made in Germany, Latvia, Estonia, Poland, Bulgaria, and Hungary in 1928 and 1929. Scheibe's studies indicated that in Europe there are two main groups of physiologic forms, a west-European group composed of 5 forms and an east-European group of 7 forms. He points out that the west-European group is composed of forms that are relatively "nonaggressive" on the 11 standard varieties, while the eastern group is composed of "aggressive" forms to which many of the standard varieties are highly susceptible.

[4] C. I. indicates accession number of the Division of Cereal Crops and Diseases, formerly Office of Cereal Investigations.

Aside from the researches of Mains and Jackson in the United States and those of Scheibe in Germany, data on physiologic forms of *Puccinia triticina* are very meager. The two forms described by Waterhouse already have been mentioned. Wellensiek (*18*) studied several collections of leaf rust from different parts of the Netherlands and found three forms —11, 14, and 15—all of which had been found by Scheibe in Germany. Dodoff (*4*) has described a new form resulting from experiments conducted in Bulgaria. Unfortunately, however, he has followed Scheibe's error in considering Michigan Amber a differential variety. Another physiologic form, form 25, has recently been discovered and described in Europe by Tscholakow (*16*). In the United States Johnston (*8*) described an aberrant physiologic form in 1930, and that constitutes the only form described in this country since 1926.

MATERIALS AND METHODS

DIFFERENTIAL OR STANDARD VARIETIES

The varieties used in these studies as differential hosts for the identification of physiologic forms were the same as those originally used by Mains and Jackson (*10*) with the exception of Turkey 47, Norka (C. I. No. 4377), and "unnamed" (C. I. No. 3747), which have been dropped from the list. The unnamed spring varieties were described by C. E. Leighty in the paper by Mains and Jackson (*10*), but no names were given them. Since the varieties are in use in various parts of the world and it is often confusing to refer to several different varieties under the general term "unnamed," it was deemed advisable to name them. The following names, therefore, have been adopted and used in these studies:

Unnamed, C. I. No. 3747=Similis, C. I. No. 3747.
Unnamed, C. I. No. 3756=Carina, C. I. No. 3756.
Unnamed, C. I. No. 3778=Brevit, C. I. No. 3778.
Unnamed, C. I. No. 3779=Loros, C. I. No. 3779.

Although descriptions of these varieties have been given by Mains and Jackson, several distinctive characteristics of some of them are useful in detecting mixtures in the greenhouse or field. Webster (C. I. No. 3780) and Similis (C. I. 3747) are essentially identical in agronomic characters and reaction to physiologic forms of leaf rust. Both are characterized by very weak straw and are inclined to lodge in nursery sowings. Both have long, lax, bearded, somewhat speltoid spikes with extremely long beaks and light-brown glumes. Because of its similarity to Webster in reaction to all known physiologic forms, Similis was dropped from the list of varieties used in the studies herein reported.

Carina develops somewhat stiffer straw in field sowings than either Webster or Similis. It is characterized by white chaff with a distinct keel carried to the base of the glume, and beaks that frequently are as long as the awns, especially under greenhouse conditions.

Brevit is easily distinguished from all of the other spring varieties by its short beak. It also has somewhat stiffer straw than either Webster or Similis, but is inclined to lodge at the time of maturity.

Loros has long beaks, which, in the greenhouse, frequently are as long as the awns. Under field conditions it stands a little better than Webster, Similis, Carina, and Brevit and is inclined to have darker brown glumes. In the seedling stage, in the greenhouse, this variety often shows a serious physiologic weakness of the leaf tissues of the first seedling leaf (prophyllum) that often makes it extremely difficult to get satisfactory rust readings. This weakness usually is manifested by a somewhat water-soaked appearance of the tissues, even before inoculation. After removal from the moist chamber such areas dry up very rapidly, giving that part of the leaf a scalded appearance. (Fig. 1.) This frequently happens despite the most careful handling. The tissues apparently are very delicate and sensitive to sudden changes in environmental conditions, as well as to even very slight pressure such as occurs in the case of hand inoculations. The scalded areas often embrace the entire area on which spores have been sown, which naturally results in no visible infection. Sometimes the injury begins at the tip of the leaf and covers most of the leaf area. More frequently, however, the injury occurs as large scalded areas near the center of the leaf, leaving areas of normal green tissue at the tip and base.

FIGURE 1.—Seedlings of Loros wheat (C. I. No. 3779), showing typical scalding of leaves after removal from the moist chamber

Norka probably possesses the stiffest straw of the spring sorts used in past experiments as differential varieties. It also has a much denser spike and smaller kernels than any of the spring varieties discussed above. Norka was dropped from the list of differential varieties used in the experiments reported in this bulletin because all preceding investigations had shown it to have reactions the same as those of Malakof to all known physiologic forms.

The four winter-wheat varieties used as differentials, viz, Malakof (C. I. No. 4898), Mediterranean (C. I. No. 5332), Hussar (C. I. No. 4843), and Democrat (C. I. No. 3384), are fully described by Clark, Martin, and Ball (2).

It has been very difficult to keep pure seed of differential varieties in sufficient quantities for detailed physiologic form testing and to supply other investigators with seed. Considerable natural crossing has occurred in some varieties, and there has been some mechanical mixture owing to threshing and handling of seed in quantities. All of the varieties have been repeatedly pure-lined and tested. From these only the best lines have been retained for use in the United States and sent to investigators abroad. In the writers' experiments several plants of each variety were inoculated with each rust culture and occasional off-type plants were easily identified by their differences in plant characters or reaction to rust. Such plants were recognized as mixtures and discarded from the experiment without further consideration.

METHODS OF STUDY

All the original data presented in this bulletin were secured from experiments conducted with seedling plants in the greenhouses at Manhattan, Kans., and La Fayette, Ind., in the winter and very early spring of the period from 1926 to 1930, inclusive. Rust collections were made in the field at various points in the United States, usually in spring and summer. Uredinial material on green leaves usually was collected. The leaves were dried and stored in glassine envelopes in the refrigerator until needed for greenhouse testing. When ready for use the spores were scraped from the leaf with a small moistened spatulate instrument and either spread directly on moistened leaves or placed in a drop of water on a glass slide, from which they were then transferred to the leaves. Transfers from field collections usually were made to the first seedling leaves of some susceptible variety of wheat such as Turkey or Michigan Amber. The film of water causes the spores to cling readily to the leaf surface when the spatula, covered with moistened spores, is rubbed over the leaf. The lower surface of the leaf seemed to be a little better than the upper surface for this purpose.

The inoculated seedlings were then placed in small moist chambers, the bottoms of which were covered with sphagnum moss that had been thoroughly wet down just before the seedlings were placed upon it. In the earlier experiments the tops of the moist chambers contained a pane of glass to admit light, but this was later found to be unnecessary, and in most experiments the seedlings were in absolute darkness during the infection period. At Manhattan small galvanized-iron cylinders were used for moist chambers, and after the plants were in place several thicknesses of newspaper were placed over the top and thoroughly wet with tap water. A pane of greenhouse glass or a layer of board was placed upon this. The paper cover was wet down twice daily by sprinkling with tap water. This was found to give the required relative humidity inside the moist chambers, and excellent infections resulted, although light was excluded. In the earlier experiments at Manhattan great difficulty was experienced in getting satisfactory infections with any regularity.

Apparently this was due to the very dry atmosphere and the difficulty of maintaining a high humidity in the moist chambers. Spores of *Puccinia triticina* must be in contact with condensed moisture for satisfactory germination. Under proper moist-chamber conditions the leaves should be covered with dew.

Most investigators have followed the practice of keeping plants in the moist chamber 48 hours. There are serious objections to this method because the seedlings often are spindling and etiolated when removed and the tissues are very delicate and tend to scald easily. In the writers' experiments it soon became apparent that, if optimum conditions for infection were provided, perfectly satisfactory infections were obtained in 24 hours in the moist chambers. This not only speeded up the work greatly, but the seedlings came out of the chambers in sturdier condition and were less likely to scald. The seedlings usually were removed from the moist chambers to the greenhouse benches late in the evening when there was no sun on the greenhouse glass to cause scalding.

The stock culture thus established was then transferred to 10-day to 12-day-old seedlings of the differential varieties that had been grown in a separate compartment of the greenhouse where there were no cultures of rust. Occasionally time can be saved by transferring spores directly from the material collected in the field to a set of differential varieties. However, very frequently a field collection either fails to germinate or germinates very poorly, and the whole set of differentials is then lost. When the stock-culture method was used the individual cultures were placed in separate compartments and several tests frequently were made from the original stock. Transfers from stock cultures to differential varieties were made by hand in the same manner as described for the establishment of a stock culture. Rust readings on differential varieties were made when infection was fully developed, which usually varied from about 14 days after inoculation in midwinter to 10 days or less in late spring. During the period of very short days and low light intensity the incubation period often was remarkably long.

If the first test showed a rust collection to be a mixture of physiologic forms, single-spore or single-uredinium transfers were made to seedlings growing under lantern globes with a thin layer of cotton over the top to exclude stray spores. If two or three varieties showed both flecks and uredinia, or had uredinia of different types on the same leaf, pure-culture transfers to plants grown under lantern globes were made from each type. Because of the greater ease of handling and of securing a greater number of successful transfers, a large portion of pure-line cultures came from single-pustule transfers. Well-isolated pustules were selected in making them. The spores were carefully collected on a moistened spatula and transferred to seedlings under lantern globes. Such cultures usually proved to be pure, but if there still was an indication of mixture the process was repeated until pure cultures were obtained. Once a pure-line culture was established, its purity could be maintained indefinitely by transferring it to fresh seedlings under lantern globes.

As already stated, the writers' experiments were conducted only with seedling plants in the greenhouse in the winter and early spring.

All the foregoing conditions are important, as has been demonstrated by various investigators. Johnston and Melchers (*9*) demonstrated that several varieties of wheat reacted differently to leaf rust at different stages of growth. Data secured in these studies clearly show that some of the differential varieties are susceptible as seedlings but resistant at heading time. This change in reaction usually begins on the second, third, or fourth leaf, so that readings made on leaves other than the primary leaf may not be reliable.

It is now a well-known fact that environmental conditions often have a marked effect on the type of reaction exhibited by a variety. Mains and Jackson (*10*) noted that Hussar (C. I. No. 4843) often was highly resistant to a form of leaf rust during the fall and winter and only moderately or slightly resistant to the same form in the late spring. Waterhouse (*17*) found that Thew, Hope, Iumillo, Hussar (C. I. No. 4843–2), and Carina (C. I. No. 3756–4) were susceptible to certain forms of leaf rust in the summer and resistant in winter tests. In studies made during the winter and summer he noted also very marked differences in the behavior of certain differential varieties to forms of *Puccinia graminis tritici* and *P. graminis avenae*. The same was true of a collection of *P. simplex* (*anomala*) on certain varieties of barley. Johnson (*7*), working with stem rust of wheat in Canada, found that increases in temperature tended to change the type of infection of certain physiologic forms on some differential varieties. Gordon (*5*) found the same to be true of the reaction of Joanette oats to forms 1, 3, 4, and 5 of *P. graminis avenae*. Peturson (*12*), working with physiologic forms of *P. coronata avenae*, concludes that several of the differential varieties reacted very differently to several of the forms, depending on the temperature at which the plants were held after inoculation.

Care also must be taken not to confuse effects produced by other causes with those produced by rust infection. Doak (*3*) has shown that the wilting of inoculated plants for a short time will bring about death of infected cells. Susceptible varieties may be made to appear highly resistant, moderately resistant, or of indeterminate reaction, depending on the point in the incubation period when wilting occurred and also on the amount of wilted tissue.

These researches suggest explanations for some of the conflicting results obtained at different times and by different investigators. They also point out the necessity for conducting experiments of this nature under environmental conditions as similar as possible.

INFECTION TYPES AND REACTION CLASSES

Most investigators recognize three main classes of reaction of host varieties to rust, viz, resistant, susceptible, and indeterminate. It also is generally recognized that resistance is expressed by three distinct types of infection, and susceptibility by two such types, although they also may be considered as five types of susceptibility. These can be said to show a gradual gradation from the highest type of resistance to complete susceptibility. (Fig. 2.) These types of infection therefore have been designated by the Arabic numerals 0, 1, 2, 3, and 4, 0 representing the greatest resistance and 4 the highest susceptibility. These types are adequately described for leaf rust by

Mains and Jackson (*10*), and their classification has been adopted in these studies.

Although the heterogeneous type of infection described by Stakman and Levine (*15*) as "type X" was occasionally encountered by Mains and Jackson, it was not described by them nor used in their table of reactions. It was observed and recorded by Scheibe in Germany and Waterhouse in Australia in their studies on leaf rust of wheat. Scheibe used the reaction as distinguishing characteristics of forms 22 and 23, and Waterhouse noted that under certain conditions several of the differential varieties exhibited an "intermediate type X" reaction to the two Australian forms. Stakman and Levine define the heterogeneous X type as follows:

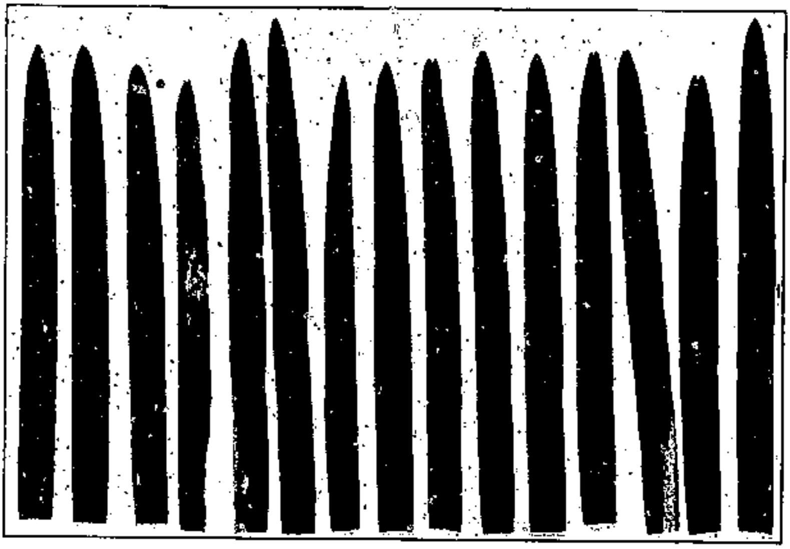


FIGURE 2.—Types of infection produced by *Puccinia triticina* on varieties of wheat. From left to right the types are 0, 0, 0, 1−, 1, 2−, 2, 2+, 3, 3+, 4, X, X, X, and mixed. The latter is a mixture of two forms on the same leaf

> Uredinia very variable, apparently including all types and degrees of infection on the same blade; no mechanical separation possible; on reinoculation small uredinia may produce large ones, and vice versa. Infection ill defined.

This is essentially the conception that most investigators have had of the X-type infection. This type of infection very frequently is encountered in F_1 hybrids and heterozygous segregates in later generations, when resistant and susceptible varieties have been crossed. In such a case it is considered an "intermediate" type of reaction. The use of the term "intermediate" would be very useful in certain respects. For example, it was frequently observed in the course of the writers' studies that a certain variety would give a type 2 or 2+ reaction at one time and at a later reading would give a type 3 reaction to the same rust form. In reality, the variety had a reaction varying from moderate resistance to moderate susceptibility, which could readily be considered intermediate. Varieties having a reaction of 2–3 can not be placed in either resistant or susceptible categories, since they actually are intermediate between these two in reaction. They therefore should be classed as intermediate or variable. The term "variable" is used in this bulletin to designate different reactions of the same variety to the same form at different readings, and the term "indeterminate" to designate the occurrence of type X infection.

There has been one marked difference in the method of presenting data for use in the identification of physiologic forms of the various races of stem rust and for leaf rust of wheat. Stakman and Levine (*15*), Newton (*11*), Bailey (*1*), Waterhouse (*17*), and others have recently used mean infection types alone with modifying symbols for recording slight fluctuations in the reaction of a variety to a form of rust. Mains and Jackson (*10*), Scheibe (*13, 14*), and Dodoff (*4*) have always used the observed range in types of infection instead of means. Each method has several points in its favor. Infection means require less space in tabulation, are more easily recorded, and probably give greater uniformity to cereal-rust literature. Ranges of infection are very useful in that they indicate precisely the limits observed for the recorded form on each variety. They also probably are more readily understood by persons not closely conversant with rust literature who may have occasion to use such data. The data presented in this bulletin therefore are presented in terms of ranges wherever such readings were obtained. It should be borne in mind that where a reaction of 2–3 is indicated other investigators may constantly obtain reactions of type 2 or type 3 for the same form on the same variety. In such cases the data in Table 1 and in the key are applicable even though no variability had been shown.

TABLE 1.—*Reaction of differential varieties of Triticum vulgare*[1] *to physiologic forms of Puccinia triticina*

Physiologic form	Type of infection on wheat variety—								Described by—
	Malakof	Carina	Brevit	Webster	Loros	Mediterranean	Husser	Democrat	
1	0	0	0	0	0	1	1	0	Mains and Jackson.
2	0–1	0–1	0–1	0	0–1	4	3–4	4	Do.
3	0–1	0–2	2–2+	0–2	2–4	3–4	0–1	4	Do.
4	0–1	4	4	1	3–4	3–4	2–2+	1–2	Do.
5	4	0	0–1	0–1	0–1	4	0–2+	4	Do.
6	4	2	4	1–2	3	3–4	3	3–4	Do.
7	4	1–2	1	4	1	4	1	4	Do.
8	4	1	4	4	4	3–4	1	1	Do.
9	4	1–2	1–2	4	4	0–1	1–2+	0–1	Do.
10	4	4	4	4	4	1–2	1–2	1–2	Do.
11	0	2+	3–4	1–2	3–4	1–2	0–2	0–2	Do.
12	0	4	4	1	4	4	4	4	Do.
13	4	4	2–	4	4	0	4	0	Scheibe.
14	0	2–	4	1	4	0	4	0	Do.
15	0	0	0–1	0	0–1	4	0–1	4	Do.
16	0	0	0	0	0	0	2	0	Do.
17	4	0	0	0	0	0	4	0	Do.
18	0	4	2	4	4	0	4	0	Do.
19	4	4	2	4	4	0	1	0	Do.
20	4	4	4	4	4	0	4	0	Do.
21	4	4	2	4	4	4	4	4	Do.
22	X	4	4	1–2	4	0–1	0–1	0–1	Do.
23	X	4	2	4	4	0	4	0	Do.
24	4	3–4	1–2	4	4	0–2	4	X	Dodoff.
25	0	2	4	0	2	4	0	4	Tscholakow.
26	0	4	4	0	4	0	4	0	Waterhouse.
27	3–4	2	1–2	3–4	3	2	2–3	2–3	Johnston.

[1] According to the rules of botanical nomenclature the name of this species is *Triticum aestivum*, but as *T. vulgare* is in general use among agronomists, the writers give preference to that form.

TABLE 1.—*Reaction of differential varieties of Triticum vulgare to physiologic forms of Puccinia triticina*—Continued

Physiologic form	Type of infection on wheat variety—								Described by—
	Malakof	Carina	Brevit	Webster	Loros	Mediterranean	Hussar	Democrat	
28	4	1+	1+	2+	3	4	3	4	Johnston and Mains.
29	4	2-3	2-3	2-3	4	1-2+	3	1	Do.
30	4	2-3	2-3	3	3-4	4	1-2+	4	Do.
31	4	2	1-2	4	4	1-2	3-4	1-2	Do.
32	0	2	X	1-2	3-4	4	1-2	4	Do.
33	0	1	2+	0-1+	4	2+	1	4	Do.
34	0	0	0	0-1	1	4	X	4	Do.
35	4	2+	2+	4	4	4	1	4	Do.
36	2-3	0	0-2	0	0-2	2+	1-2	2+	Do.
37	3-4	2+	2	0-2	3-4	2+	2	2+	Do.
38	0	2-2+	1-2	0-1	3-4	2+	1-2	2+	Do.
39	3-4	2-3	2-3	0-1	4	3-4	0-1	3-4	Do.
40	4	4	2	0	3-4	4	4	2-3	Do.
41	4	2-3	2	4	4	2	2	3-4	Do.
42	4	2-3	3	4	4	3-4	4	4	Do.
43	4	3	3	1-2	4	1	2	1-2	Do.
44	0	2	2	0-2	4	X	0-1	4	Do.
45	0	3-4	2+	4	4	3-4	2	3-4	Do.
46	0-1	2-3	2	0-1	4	2	1-2	3-4	Do.
47	4	3	2	4	0	2	0	2	Do.
48	4	3-4	2	4	4	2-3	2	0	Do.
49	4	3	3	2	3-4	0	4	0	Do.
50	4	2	4	2−	3	0	2	0	Do.
51	0	1	3	1	3	2	3	3	Schaal, Stakman, and Levine.
52	4	0	1	0	1	4	3	4	Do.
53	0	1	2	1	1	0	3	0	Do.

EXPERIMENTAL RESULTS

COORDINATION OF PUBLISHED AND NEW DATA DEALING WITH PHYSIOLOGIC SPECIALIZATION IN PUCCINIA TRITICINA

In order to bring the data on physiologic forms of *Puccinia triticina* into closer harmony, the data on physiologic forms of leaf rust, as reported by Mains and Jackson, Scheibe, Dodoff, Waterhouse, and Johnston are presented in Table 1. The data on 26 additional physiologic forms are also included in this table. It will be noted that three varieties used by other investigators are not included in this table, viz, Norka, Similis, and Michigan Amber. Norka and Similis, as previously stated, are omitted because their reactions to all known physiologic forms are almost identical with those of Malakof and Webster, respectively. Michigan Amber has been omitted because it has shown no differential reaction to any of the known forms. Scheibe found it susceptible to all of the forms found by him in central Europe, and Mains and Jackson used it as a susceptible host for their stock cultures. Since there is also an error in the reactions of the variety to the first 12 physiologic forms as given by Scheibe (*13*), it seems desirable to eliminate it from the list of differential hosts and the reaction record.

With this misunderstanding corrected, there remains the difficulty of distinguishing between physiologic forms 1 and 16. In the key presented on page 11 they are separated only by the slight differences in reaction of Hussar. The reaction of this variety to form 1 is type 1, and to form 16, type 2. There is some question as to the validity of differences as small as this, especially with Hussar, and it is likely that form 16 is actually form 1. For the sake of maintaining the form numbers used by Scheibe, form 16 is included in the data herein presented; but it is felt that it is the same as form 1.

In the designation of forms in Table 1 the numbers of the forms described by Mains and Jackson and by Scheibe have been retained. Although Waterhouse (*17*) had described two forms before Scheibe's (*14*) paper of 1930 appeared, he assigned no numbers to them except "Aust. 1" and "Aust. 2." However, in so far as the standard varieties are concerned, these two forms constitute only a single form. Waterhouse found it necessary to add Thew to the list of varieties to separate the two forms. Dodoff (*4*) also apparently was unaware of the work of Waterhouse and described a form he encountered in Bulgaria as form 24. Tscholakow also has described a new form to which No. 25 has been given. It therefore becomes necessary to place Waterhouse's data immediately after Tscholakow's in Table 1 and to assign No. 26 to his physiologic form. No. 27 was assigned to the aberrant physiologic form described by Johnston (*8*). Forms 28 to 53, inclusive, are forms here described for the first time. Of these, forms 28 to 35, inclusive, were found by E. B. Mains in his experiments at La Fayette, Ind., forms 36 to 50, inclusive, were found by C. O. Johnston in experiments conducted at Manhattan, Kans., and forms 51, 52, and 53 are forms encountered by Schaal, Stakman, and Levine [5] in experiments at St. Paul, Minn.

While every effort was made to simplify the key for identification of forms and to retain its dichotomy, it has been necessary to make use of characters other than the directly opposite resistance and susceptibility. The introduction of the indeterminate and variable types into the data made this a necessity, but it is believed that the usefulness of the key has not been impaired. When the key and the table of reactions are used together, as they must be for accuracy, it is relatively easy to ascertain the physiologic form or forms of a rust collection.

Analytical key for the identification of physiologic forms of Puccinia triticina, determined on the basis of their parasitic behavior on differential varieties of Triticum vulgare

Form No.

- Malakof resistant—
  - Carina resistant—
    - Brevit resistant—
      - Loros resistant—
        - Mediterranean resistant—
          - Hussar resistant—
            - Hussar type 1 ---- 1
            - Hussar type 2 ---- 16
          - Hussar susceptible ---- 53
        - Mediterranean susceptible—
          - Hussar resistant ---- 15
          - Hussar indeterminate (X) ---- 34
          - Hussar susceptible ---- 2
      - Loros variable ---- 3
      - Loros susceptible—
        - Mediterranean resistant—
          - Democrat resistant ---- 38
          - Democrat susceptible ---- 33
        - Mediterranean indeterminate (X) ---- 44
    - Brevit indeterminate (X) ---- 32
    - Brevit susceptible—
      - Hussar resistant—
        - Democrat resistant ---- 11
        - Democrat susceptible ---- 25

[5] Unpublished data.

- Malakof resistant—Continued.
  - Carina resistant—Continued.
    - Brevit susceptible—Continued.
      - Hussar susceptible— (Form No.)
        - Democrat resistant 14
        - Democrat susceptible 51
  - Carina variable 46
  - Carina susceptible—
    - Brevit resistant—
      - Mediterranean resistant 18
      - Mediterranean susceptible 45
    - Brevit susceptible—
      - Hussar resistant 4
      - Hussar susceptible—
        - Democrat resistant 26
        - Democrat susceptible 12
- Malakof variable 36
- Malakof indeterminate (X)—
  - Brevit resistant 23
  - Brevit susceptible 22
- Malakof susceptible—
  - Carina resistant—
    - Brevit resistant—
      - Webster resistant—
        - Loros resistant—
          - Mediterranean resistant 17
          - Mediterranean susceptible—
            - Hussar resistant 5
            - Hussar susceptible 52
        - Loros susceptible—
          - Mediterranean resistant 37
          - Mediterranean susceptible 28
      - Webster susceptible—
        - Loros resistant 7
        - Loros susceptible—
          - Mediterranean resistant—
            - Hussar resistant 9
            - Hussar variable 27
            - Hussar susceptible 31
          - Mediterranean susceptible 35
    - Brevit susceptible—
      - Webster resistant—
        - Mediterranean resistant 50
        - Mediterranean susceptible 6
      - Webster susceptible 8
  - Carina variable—
    - Brevit resistant 41
    - Brevit variable—
      - Webster resistant 39
      - Webster variable 29
      - Webster susceptible 30
    - Brevit susceptible 42
  - Carina susceptible—
    - Brevit resistant—
      - Webster resistant 40
      - Webster susceptible—
        - Loros resistant 47
        - Loros susceptible—
          - Mediterranean resistant—
            - Hussar resistant 19
            - Hussar susceptible—
              - Democrat resistant 13
              - Democrat indeterminate (X) 24
          - Mediterranean variable 48
          - Mediterranean susceptible 21

Malakof susceptible—Continued.
 Carina susceptible—Continued.
  Brevit susceptible—
   Webster resistant— Form No.
    Hussar resistant 43
    Hussar susceptible 49
   Webster susceptible—
    Hussar resistant 10
    Hussar susceptible 20

RELATIONSHIP AND VARIATIONS OF PHYSIOLOGIC FORMS

Stakman and Levine (*15*), in the case of stem rust, and Mains and Jackson (*10*), in the case of leaf rust, recognized that the addition of proper differential varieties might make possible the separation of cultures that had previously been considered a single form. Waterhouse (*17*) found that the variety Thew divided form 26 into two forms under certain conditions. Scheibe (*14*) has also pointed out that certain physiologic forms are really closely related members of composite groups. As far as the 11 standard varieties were concerned, they appeared to be a single form but could be differentiated by the reaction of other varieties. The writers' experiments also have frequently indicated that the addition of other varieties to the list of differentials might divide described forms into two or more forms. New forms were not described on such a basis, however.

Many instances of the manifestation of the same phenomenon, in a slightly different way, have also been encountered. It frequently has been observed that two or more forms differ from each other only in the reaction of a single variety. If this difference is high resistance opposed to high susceptibility, it probably is real and constant. If, however, it is between resistance and intermediacy, or susceptibility and intermediacy, there is some doubt as to the actuality of the difference. Johnson (7) has shown that the heterogeneous type can be changed by variations in temperature, and Waterhouse (*17*) observed that the X-type reaction was very common in cultures of *Puccinia triticina* on the standard varieties in the greenhouse at certain periods of the year. All the cultures of the writers were grown on differential varieties for several uredinial generations but usually over a relatively short period of time. Table 2 shows some comparisons of closely related forms that differ only in a few respects, principally by a difference in the reaction of a single variety.

TABLE 2.—*Comparison of several physiologic forms of Puccinia triticina that differ from one another only slightly*

Physiologic form	Number of uredinial generations tested	Type of infection on wheat variety—							
		Malakof	Carina	Brevit	Webster	Loros	Mediterranean	Hussar	Democrat
3	8	0–1	0–2	2–2+	0–2	2–4	3–4	0–1	4
15	8	0	0	0–1	0	0–1	4	0–1	4
34	7	0	0	0	0–1	1	4	X	4
37	8	0	1	2+	0–1	4	2+	1	4
44	8	0	2	2	0–2	4	X	0–1	4

In the comparison of forms 3, 15, and 34 it will be noted that the main difference between them is in the variable reaction of Loros in the case of form 3 and the indeterminate reaction of Hussar in the case of form 34. The point is still more striking when forms 33 and 44 are compared. In this case Mediterranean exhibits a 2+ reaction to form 33 and an indeterminate reaction to form 44. Only a slight fluctuation in environmental conditions might be necessary to cause such a slight difference, although the reaction of Mediterranean to each form seemed to be rather constant during the period they were under study and the infection type in each given case might have been quite typical for the variety.

Another condition also has been encountered in these experiments that indicates that some physiologic forms, at least, are really groups of forms. In the course of the writers' studies they have frequently purified, and carried for several generations, cultures that could be run down to described forms in the key but really differed constantly from those forms. Four such cases are shown in Table 3 where certain cultures are compared with described physiologic forms.

TABLE 3.—*Comparison of certain physiologic forms of Puccinia triticina with cultures that apparently are closely related*

Form and culture Nos.	Number of trials	Type of infection on wheat variety—							
		Malakof	Carina	Brevit	Webster	Loros	Mediterranean	Hussar	Democrat
Type form 9		4	1–2	1–2	4	4	0–1	1–2+	0–1
J–170	7	3–4	2	2	3–4	3–4	2+	2	2+
Type form 16		0	0	0	0	0	0	2	0
J–186	6	0–1	0–1	1–2	0–1	1–2	2+	2	2+
Type form 31		4	2	1–2	4	4	1–2	3–4	1–2
J–166–1–9–1	8	4	2	2	4	4	0	4	0
Type form 37		3–4	2+	2	0–2	3–4	2+	2	2+
J–586–A–1	7	4	2	2+	0	4	0–1	2	0–1
J–39–1–1–1	7	3–4	2	2	2	4	0–1	2	0–1

While none of the variant types was tested over more than a single greenhouse season, the readings secured on them at various times during that season constantly indicated that they differed slightly from the forms to which they apparently were related. In the case of culture J–170, Mediterranean and Democrat were constantly much less resistant than to form 9, to which the key indicated it belonged. Culture J–186 showed much the same relationship to form 16, although the difference between the two was still more striking. In culture J–166–1–9–1 the situation is reversed, however, and Mediterranean and Democrat have a more resistant reaction than to form 31. It is much the same with regard to the difference between cultures J–586–A–1 and J–39–1–1–1 and form 37. Here, however, there are also slight differences between the three cultures in their behavior on Webster.

Although many physiologic forms have been very constant in their behavior on differential varieties, certain forms have proved to be variable. The variations apparently are of two main types, viz, those caused by changes in environmental conditions and those due to small but inherent differences between components of a group of allied strains. Those variations due to environment are fluctuating and the differences indicated by them are only apparent. The differences between group components, on the other hand, are constant and real. It seems, therefore, that certain physiologic forms at least can not be considered as basic units or genetic entities, as some investigators have assumed. They apparently are groups of forms that probably could be further divided. Two methods of attaining further separations present themselves; (1) to make finer distinctions on the basis of types of infection, and (2) to increase the number of differential varieties. The latter would seem to be the more desirable of the two methods if further division of physiologic forms of *Puccinia triticina* proves to be necessary. From a purely mycological standpoint there seems to be good reason for describing as many physiologic forms as possible and for making the finest possible divisions. From a practical standpoint, however, there is considerable doubt about the necessity for finer divisions than are possible with the present group of differential varieties. Increases in the number of varieties mean increases in the time, labor, space, and expense required for physiologic-form determinations. It is admitted that many forms probably could be further divided by increasing the number of varieties, but it should be pointed out that plenty of varieties and hybrids have been found to have resistance to the physiologic forms as they now exist. The economic necessity for finer divisions therefore does not seem to be great.

Scheibe (*14*) gives the reactions of 3 cultures of form 13 and 6 collections of form 11 when used to inoculate 11 standard varieties and 17 other varieties of wheat that his experiments had proved also had differential reaction. His data (*14, Table 7*) show that, although the cultures are all typically forms 13 and 11 as far as the 11 standard varieties are concerned, the individual collections actually differ when the host range is extended. He therefore raises the question as to whether 11 standard varieties are enough to differentiate sufficiently the possible physiologic forms of *Puccinia triticina*. The writers have frequently encountered varieties of wheat having differential reaction to leaf rust, but for the sake of uniformity and facility these varieties have not been added to the list of differential varieties.

DISTRIBUTION AND PREVALENCE OF PHYSIOLOGIC FORMS OF PUCCINIA TRITICINA IN THE UNITED STATES AND CANADA

The matter of the distribution and prevalence of physiologic forms of pathogenic organisms is one of considerable interest. Mains and Jackson (*10*), prior to 1926, found that forms to which Malakof (C. I. No. 4898) was resistant were more abundant in the eastern and southern parts of the United States, while those forms to which Malakof was susceptible were more prevalent in the Central West. Scheibe (*14*) found that the most aggressive physiologic forms were most abundant in eastern Germany and eastern Europe, while the less aggressive forms were more common to western Germany and western Europe.

In the writers' experiments since 1926 the conclusion of Mains and Jackson that physiologic forms of rust are neither fixed nor limited in their distribution has been amply verified. The forms that have been isolated during this period in the greenhouse experiments at La Fayette, Ind., and Manhattan, Kans., and the States and Provinces in the United States and Canada in which the rust collections were made are listed as follows:

Form 1.—Washington, Idaho, Montana, Kansas, Georgia.
Form 2.—Colorado, Kansas.
Form 3.—Georgia, Tennessee, North Carolina, Virginia, Ohio, Indiana, Kansas, Oklahoma, Minnesota, North Dakota, Washington, Idaho, Nova Scotia.
Form 5.—Mississippi, Georgia, North Carolina, Virginia, Maryland, Tennessee, New York, Ohio, Indiana, Kansas, Oklahoma, Texas, Montana, Washington.
Form 6.—Georgia, Tennessee, Indiana, Ohio, Texas.
Form 9.—Georgia, North Carolina, Maryland, Texas, Oklahoma, Kansas, Missouri, Nebraska, Iowa, South Dakota, North Dakota, Minnesota, Colorado, Montana, Oregon, Washington, Ontario, Quebec.
Form 10.—Indiana, Missouri, Colorado, Montana.
Form 11.—Washington, Idaho, Oregon, Texas, Kansas.
Form 15.—Iowa, North Dakota.
Form 20.—Kansas, Texas.
Form 27.—Texas.
Form 28.—Georgia, Virginia, Tennessee, Indiana, Wisconsin.
Form 29.—Tennessee, Virginia, Indiana, Ohio, Kansas, Missouri.
Form 30.—Georgia, North Carolina, Virginia, Tennessee, Ohio, Indiana, Illinois, Wisconsin, Oklahoma, Kansas, New York, Ontario, Quebec, Nova Scotia.
Form 31.—Kansas, Ohio, Georgia.
Form 32.—Virginia, Tennessee, Ohio, Wisconsin, North Dakota, Idaho, Oregon, British Columbia.
Form 33.—Georgia, North Carolina, Tennessee, Texas, Kansas, Nebraska, South Dakota, North Dakota.
Form 34.—Georgia, Tennessee, Ohio, Indiana, Washington.
Form 35.—Tennessee, Kansas.
Form 36.—Kansas, Texas.
Form 37.—Kansas, Iowa, North Dakota.
Form 38.—Oklahoma, Kansas.
Form 39.—Kansas.
Form 40.—Kansas, Oklahoma.
Form 41.—Texas, Kansas.
Form 42.—Texas, Oklahoma, Kansas.
Form 43.—Kansas.
Form 44.—North Dakota, Iowa.
Form 45.—Missouri, Kansas.
Form 46.—Kansas.
Form 47.—Oklahoma, Texas, Kansas.
Form 48.—Oklahoma, Kansas.
Form 49.—Oklahoma, Kansas.
Form 50.—Minnesota.
Form 51.—Texas.
Form 52.—Minnesota.
Form 53.—Georgia.

Several of the forms originally described by Mains and Jackson have a very wide distribution. Forms 3, 5, and 9 have been found in nearly all parts of the United States from which rust collections have been received. However, form 9 has not been encountered so frequently in the Ohio Valley and in the Southeastern States as it has in the Mississippi Valley and in the Great Plains. Forms 3 and 5 are more frequently isolated from southeastern and eastern collections than is form 9. Eight of the 12 forms described by Mains and Jackson have been reisolated since the publication of their results in 1926. Form 1, which is very similar to, if not identical with, form 16 of Scheibe, seems principally to be a form of northwestern distribution. It has been encountered once in collections from

Georgia and once in those from Kansas. Form 2 was isolated only infrequently and from a relatively small area in Kansas and Colorado. Forms 6, 10, and 11 also seem to be relatively unimportant, judging from their distribution and prevalence. Of the forms described by Scheibe in Europe, only forms 11, 15, and 20 were encountered in the writers' studies. Form 15 has appeared rather frequently in recent years in collections of leaf rust from North Dakota and Iowa, but form 20 has been encountered only twice, once in collections made in Texas and once in those from Kansas.

Some of the forms described for the first time in this bulletin have been under investigation long enough to indicate a rather wide distribution. Others have been studied a much shorter time and their distribution and prevalence are imperfectly known. Forms 34 to 52, inclusive, have been encountered only in the Mississippi Valley and the eastern Plains States from Texas and Tennessee northward. That should not be considered the full extent of their distribution, however. They were isolated from rust collections made in that area and studied in the greenhouse at Manhattan. Collections made outside of that area during the same years were not studied at Manhattan.

The data suggest that physiologic forms 3, 5, 9, and 30 are the most abundant forms in the United States, but they do not picture the situation for any particular area for any definite period of time. The situation for the Mississippi Valley and the Great Plains area during the seasons of 1928 and 1929 is indicated by the data presented in Table 4.

TABLE 4.—*Distribution of physiologic forms of Puccinia triticina in the Great Plains area as indicated by isolations from field collections made in 1928 and 1929*

Year and State	Collections tested	Collections containing—		Physiologic forms isolated and number of times (shown in brackets) each was encountered
		Mixture of forms	Individual form	
1928	*Number*	*Number*	*Number*	
Kansas	40	23	17	9 [33], 37 [6], 36 [4], 5 [2], 38 [2], 1 [1], 3 [1], 11 [1], 20 [1], 39 [1].
Oklahoma	4	1	3	9 [4], 37 [1].
Texas	5	1	4	9 [3], 11 [1], 27 [1], 36 [1].
Nebraska	1		1	9 [1].
Iowa	2		2	9 [2].
North Dakota	2		2	9 [2].
Total	54	25	29	9 [45], 37 [7], 36 [5], 5 [2], 11 [2], 38 [2], 1 [1], 3 [1], 20 [1], 27 [1], 39 [1].
1929				
Kansas	46	18	28	9 [32], 13 [9], 5 [1], 2 [3], 3 [5], 29 [1], 30 [1], 31 [1], 35 [1], 40 [1], 41 [1], 42 [1].
Oklahoma	10	7	3	9 [6], 13 [2], 5 [1], 3 [1].
Texas	37	25	12	9 [7], 13 [6], 3 [2], 5 [1], 6 [1], 20 [1], 33 [1], 42 [5].
Nebraska	4	2	2	9 [4], 13 [1], 33 [1].
Iowa	1	1	0	9 [1], 15 [1].
Missouri	2	2	0	9 [1], 10 [1], 29 [1].
Colorado	1	1	0	2 [1].
Montana	1	1	0	9 [1], 13 [1].
North Dakota	3	2	1	9 [3], 13 [1], 3 [1], 32 [1], 33 [1].
South Dakota	5	1	4	9 [5], 33 [1].
Total	110	60	50	9 [60], 13 [20], 3 [9], 33 [4], 5 [3], 2 [4], 6 [1], 10 [1], 15 [1], 20 [1], 30 [1], 32 [1], 35 [1], 40 [1], 41 [1], 42 [6], 29 [2], 31 [1].

It must be admitted at the outset that these data are fragmentary, at best, especially as regards the whole leaf-rust population of the area. It is obvious that, even with hundreds of rust collections from evenly distributed points over an area, only a scant representation of the physiologic-form flora is obtained. The collections from which the data in Table 4 were derived were not made at evenly distributed points, nor in equal numbers in the various States. They therefore indicate only general trends in form distribution. They do indicate rather strongly, however, that form 9 is the most prevalent and widely distributed form in the area. This has consistently been the case in studies conducted at Manhattan, Kans., since 1926. Of the 54 collections of rust studied in 1928, slightly more than half were composed of only a single form. In such cases form 9 was the form most frequently encountered. Although somewhat more than half of the cultures studied in 1929 proved to be a mixture of forms, physiologic form 9 was again the dominant form. This is well illustrated in the analysis of the data recorded in 1929. Of the 50 cultures that consisted of a single form, 34 were of physiologic form 9. While 60 of the cultures proved to be a mixture of forms, it was possible to identify the forms composing the mixture in only 34 instances. Of these, 31 were composed of 2 forms; 2 of 3 forms; and only 1 of 4 forms. Of the 31 containing 2 forms, form 9 was one of the constituents in 23 cases. Of the cultures containing 3 and 4 forms each, form 9 was a constituent in each case.

The reason for the dominance of physiologic form 9 in the western Plains area is not definitely known, but it can not be doubted that it is particularly well adapted. In most of the cases where field collections of leaf rust have proved to be mixtures of two or more physiologic forms, form 9 usually has comprised the largest part of the mixtures.

It has been noted consistently that physiologic form 9 is the one that most frequently overwinters in Kansas, Oklahoma, and Texas. Collections made during the late fall, winter, and early spring at points in these States have usually been pure form 9. This point is well illustrated in Table 5 by data on the physiologic-form content of collections of leaf rust made at Manhattan during the seasons of 1927–28 and 1930–31, and at Denton, Tex., in the spring of 1928.

TABLE 5.—*Physiologic forms of Puccinia triticina collected at Manhattan, Kans., and Denton, Tex., during different months of 1927, 1928, 1930, and 1931*

Place	Date of collection	Physiologic forms isolated	Place	Date of collection	Physiologic forms isolated
Manhattan, Kans.	June 11, 1927	9, 3, 11, 37, 29.	Manhattan, Kans.	June 30, 1930	9, 13, 19, 3.
	Nov. 25, 1927	9, 29.		Oct. 23, 1930	9, 19, 13, 15.
	Nov. 30, 1927	9.		Nov. 14, 1930	9, 19.
	Dec. 20, 1927	9.		Dec. 26, 1930	9.
	Jan. 6, 1928	9.		Jan. 5, 1931	9.
	May 15, 1928	9, 13.		Feb. 24, 1931	9.
	June 15, 1928	9, 3, 13, 15.		Mar. 6, 1931	9.
Denton, Tex.	Feb. 13, 1928	9.		Apr. 13, 1931	9.
	Mar. 18, 1928	9.		May 20, 1931	9, 5, 13.
	Apr. 10, 1928	9.			
	May 22, 1928	9, 3, 2, 13.			

These data show that at Manhattan the number of physiologic forms may be numerous in summer and early fall, but that physiologic form 9 is the one most generally encountered in late fall and winter. Although no data are available on forms present at Denton in the fall and winter months of 1927–28, form 9 was the only form present in collections made in the early spring of 1928. At both stations the number of forms did not increase to any appreciable extent until about the time of maximum infection at each station.

Whether the data presented above mean that physiologic form 9 is able to overwinter in greater abundance than other forms in the southern Great Plains can not be said with certainty. It can be stated, however, that in experiments covering the period of 1926 to 1931, inclusive, it has been the form usually encountered late in the fall and early in the spring, as well as the form present in greatest abundance during the spring rust season. It has therefore been considered the dominant form in the southern Plains area. Other forms are found, to be sure, but usually after leaf-rust infection is fairly well advanced, and then in relatively small amounts as compared with form 9.

The situation in the Ohio Valley and in the southeastern United States seems to be much different in that no one form appears to be dominant year after year. It is true that forms 3 and 5 are isolated more frequently than any others over a period of several years, but not with the frequency with which form 9 has been found in the Great Plains. A larger number of forms are isolated in the eastern area in any particular season than in the Great Plains area. The reason for this is not clear. If a susceptible species of the aecial host of *Puccinia triticina* occurred in the Eastern and Southern States, the explanation might be said to lie in the hybridization of forms. Jackson and Mains (*6*), however, failed to find any native leaf-rust-susceptible species of Thalictrum. Scheibe (*14*) states that Eremejeva, in Russia, succeeded in obtaining positive infection in 16 species and varieties of Thalictrum, but that *T. minus* and *T. flavum* showed the most decided susceptibility. He also states that Bondarzew has pointed out that these are the species that occur in Russia and become the most severely rusted. Scheibe then ventures the opinion that here there is good circumstantial evidence of the rôle of certain species of Thalictrum in the genesis of new physiologic forms. It may also explain why he found a larger number of physiologic forms in eastern than in western Europe. In the United States, however, the native species of Thalictrum, as far as they have been tested, are resistant to *P. triticina*, and yet there are often many physiologic forms present in a single season. This is especially true of the eastern part of the United States. It seems, therefore, that some factor or factors other than the presence of the aecial host must be sought to explain the distribution and abundance of physiologic forms of leaf rust of wheat in this country.

GENERAL DISCUSSION

Although only 26 physiologic forms of *Puccinia triticina* new to North America are described in this bulletin, many more probably could have been described if finer divisions had been attempted.

Throughout the studies herein reported evidence indicating that some forms could be subdivided was frequently encountered. This seemingly could have been done on the basis of constant differences in infection types produced by different cultures on the same variety. Although infection types have been constantly recorded in data on physiologic forms of cereal rusts, the separation of forms and the construction of keys have been based almost entirely on reaction classes. There seems little doubt that separations could also be made on the basis of infection types, but such data would be much more difficult to use, and errors due to the effect of environment would be more frequent. There seems to be little need for finer distinctions, but it should be kept in mind that they could be obtained. If such necessity arose, reliable results could be obtained only under carefully controlled conditions that could be duplicated by other investigators.

The occurrence within physiologic forms of strains that differ slightly but constantly from one another is not admitted by all investigators. Some feel that these are merely variations, apparently constant for a time but fluctuating if the form be cultured often enough. In such cases it is assumed that the variation is caused by changes in environment. While the writers have had only a few forms in continuous cultures for more than a year, they have tested many forms as frequently as possible during a greenhouse season. This in itself subjected the cultures to considerable change in environment, since the temperature, humidity, length of day, and quality of light vary rather widely during this period. When certain cultures were found to react constantly and to be slightly different from described forms, it seemed reasonable to regard them as members of group forms.

Further evidence that certain physiologic forms are really groups of forms is encountered when they are tested with a larger number of varieties. The matter of increasing the number of differential varieties, thus making it possible to split some of the physiologic forms into two or more forms, probably merits careful consideration. It remains only to determine whether the need is urgent enough and the return sufficient to compensate for the vastly increased amount of time, labor, space, and expense that would be involved were such a course pursued. It is also well to consider how far such a process is likely to be carried. With the thousands of varieties of wheat there would seem to be many thousands of possibilities, and it is likely that a structure so unwieldy as to be practically useless would result. In the United States one of the most frequent uses of physiologic-form determination is in connection with programs of breeding wheats for resistance. There has been no difficulty in finding varieties with resistance to physiologic forms as they now are known. If these forms actually are composites of several forms it is clear that resistance to them is inherited as a unit. It therefore becomes possible to breed for resistance to several forms by a single operation instead of the several operations that would be required if parental varieties were resistant only to finer divisions of the present physiologic forms. In breeding for resistance to leaf rust in the southern Great Plains the senior writer has constantly obtained the greatest field resistance in crosses involving resistance to several physiologic forms. Therefore, it would seem reasonable to retain the present differential varieties as basic standards, recognizing that others may be added for special purposes, or when it seems advisable to make finer distinctions than now seem necessary.

SUMMARY

All the data on physiologic forms of *Puccinia triticina* are brought together and a key and a table of infection types for 53 physiologic forms are presented.

Thirty-nine physiologic forms, occurring in North America, are described.

The "unnamed" differential varieties of wheat, C. I. Nos. 3756, 3778, 3779, and 3747, are named Carina, Brevit, Loros, and Similis, respectively.

Similis and Norka have been dropped from the list of differential varieties because of their similarity in rust reaction to Webster and Malakof, respectively. It also is pointed out that Michigan Amber does not belong in the group of differential varieties.

Data are presented showing that certain physiologic forms are variable in their expression, and that some forms apparently are closely related members within integral groups that might be separated by the addition to the list of proper differential varieties of wheat.

Distribution and prevalence of physiologic forms in the United States are, as far as known, independent of the occurrence of species of Thalictrum. Physiologic form 9 has proved to be more prevalent and abundant in the southern Great Plains than other forms. In the eastern half of the United States forms 3 and 5 are more frequently encountered than is form 9.

Some evidence is presented indicating that physiologic form 9 is particularly well adapted to conditions in the Great Plains. It is the form most frequently collected in late fall, winter, and early spring.

LITERATURE CITED

(1) BAILEY, D. L.
1925. PHYSIOLOGIC SPECIALIZATION IN PUCCINIA GRAMINIS AVENAE ERIKSS. AND HENN. Minn. Agr. Expt. Sta. Tech. Bul. 35, 33 p., illus.

(2) CLARK, J. A., MARTIN, J. H., and BALL, C. R.
1922. CLASSIFICATION OF AMERICAN WHEAT VARIETIES. U. S. Dept. Agr. Bul. 1074, 238 p., illus.

(3) DOAK, K. D.
1930. NECROTIC EFFECT PRODUCED BY WILTING OF SUSCEPTIBLE VARIETIES OF WHEAT INFECTED WITH LEAF RUST. (Abstract) Phytopathology 20: 120–121.

(4) DODOFF, D. N.
1931. PHYSIOLOGIC FORMS IN THE LEAFRUST OF WHEAT (PUCCINIA TRITICINA ERIKSS.) IN BULGARIA. Zemledelska Misal v. 2, no. 2, [In Bulgarian, with English summary.]

(5) GORDON, W. L.
1930. EFFECT OF TEMPERATURE ON HOST REACTIONS TO PHYSIOLOGIC FORMS OF PUCCINIA GRAMINIS AVENAE ERIKSS. AND HENN. Sci. Agr. 11: 95–103, illus.

(6) JACKSON, H. S., and MAINS, E. B.
1921. AECIAL STAGE OF THE ORANGE LEAF RUST OF WHEAT, PUCCINIA TRITICINA ERIKS. Jour. Agr. Research 22: 151–172, illus.

(7) JOHNSON, T.
1931. STUDIES ON CEREAL DISEASES. VI. A STUDY OF THE EFFECT OF ENVIRONMENTAL FACTORS ON THE VARIABILITY OF PHYSIOLOGIC FORMS OF PUCCINIA GRAMINIS TRITICI ERIKSS. AND HENN. PART I. STUDIES ON THE EFFECTS OF ENVIRONMENTAL FACTORS ON THE UREDINIAL DEVELOPMENT OF CERTAIN PHYSIOLOGIC FORMS OF PUCCINIA GRAMINIS TRITICI. Canada Dept. Agr. Bul. 140 (n. s.).
(8) JOHNSTON, C. O.
1930. AN ABERRANT PHYSIOLOGIC FORM OF PUCCINIA TRITICINA ERIKSS. Phytopathology 20: 609–620, illus.
(9) ——— and MELCHERS, L. E.
1929. GREENHOUSE STUDIES ON THE RELATION OF AGE OF WHEAT PLANTS TO INFECTION BY PUCCINIA TRITICINA. Jour. Agr. Research 38: 147–157, illus.
(10) MAINS, E. B., and JACKSON, H. S.
1926. PHYSIOLOGIC SPECIALIZATION IN THE LEAF RUST OF WHEAT, PUCCINIA TRITICINA ERIKSS. Phytopathology 16: [89]–120, illus.
(11) NEWTON, M.
1922. STUDIES IN WHEAT STEM RUST (PUCCINIA GRAMINIS TRITICI). PART I. BIOLOGIC FORMS OF WHEAT STEM RUST (PUCCINIA GRAMINIS TRITICI) IN WESTERN CANADA. Roy. Soc. Canada, Proc. and Trans. (3) 16: 153–197, illus.
(12) PETURSON, B.
1930. EFFECT OF TEMPERATURE ON HOST REACTIONS TO PHYSIOLOGIC FORMS OF PUCCINIA CORONATA AVENAE. Sci. Agr. 11: 104–110.
(13) SCHEIBE, A.
1928. STUDIEN ZUM WEIZENBRAUNROST, PUCCINIA TRITICINA ERIKSS. I. METHODEN UND ERGEBNISSE BEI DER BESTIMMUNG SEINER PHYSIOLOGISCHEN FORMEN (BIOTYPEN). Arb. Biol. Reichsanst. Land u. Forstw. 16: [575]–608, illus.
(14) ———
1930. STUDIEN ZUM WEIZENBRAUNROST PUCCINIA TRITICINA ERIKSS. III. ÜBER DIE GEOGRAPHISCHE VERBREITUNG DER EINZELNEN PHYSIOLOGISCHEN FORMEN UND FORMENKREISE IN DEUTSCHLAND UND IN SIENEN ANGRENZENDEN GEBIETEN. Arb. Biol. Reichsanst. Land u. Forstw. 18: 55–82, illus.
(15) STAKMAN, E. C., and LEVINE, M. N.
1922. THE DETERMINATION OF BIOLOGIC FORMS OF PUCCINIA GRAMINIS ON TRITICUM SPP. Minn. Agr. Expt. Sta. Tech. Bul. 8, 10 p., illus.
(16) TSCHOLAKOW, J. W.
1931. EIN BEITRAG ZUR PHYSIOLOGISCHEN SPECIALISIERUNG DES WEIZENBRAUNROSTES, PUCCINIA TRITICINA ERIKSS. Arb. Biol. Reichsanst. Land u. Forstw. 19: 407–411.
(17) WATERHOUSE, W. L.
1929. AUSTRALIAN RUST STUDIES, I. Linn. Soc. N. S. Wales, Proc. 54: [615]–680, illus.
(18) WELLENSIEK, S. J.
1930. ORIËNTEEREND ONDEZOEK OMTRENT PHYSIOLOGIESE SPECIALISATIE VAN PUCCINIA TRITICINA ERIKS. IN NEDERLAND. (ORIENTATION ABOUT PHYSIOLOGIC SPECIALIZATION OF PUCCINIA TRITICINA ERIKS. IN THE NETHERLANDS.) Tijdschr. Plantenziekten 36: 1–10, illus.

ORGANIZATION OF THE UNITED STATES DEPARTMENT OF AGRICULTURE WHEN THIS PUBLICATION WAS LAST PRINTED

Secretary of Agriculture	ARTHUR M. HYDE.
Assistant Secretary	R. W. DUNLAP.
Director of Scientific Work	A. F. WOODS.
Director of Regulatory Work	WALTER G. CAMPBELL.
Director of Extension Work	C. W. WARBURTON.
Director of Personnel and Business Administration.	W. W. STOCKBERGER.
Director of Information	M. S. EISENHOWER.
Solicitor	E. L. MARSHALL.
Weather Bureau	CHARLES F. MARVIN, *Chief.*
Bureau of Animal Industry	JOHN R. MOHLER, *Chief.*
Bureau of Dairy Industry	O. E. REED, *Chief.*
Bureau of Plant Industry	WILLIAM A. TAYLOR, *Chief.*
Forest Service	R. Y. STUART, *Chief.*
Bureau of Chemistry and Soils	H. G. KNIGHT, *Chief.*
Bureau of Entomology	C. L. MARLATT, *Chief.*
Bureau of Biological Survey	PAUL G. REDINGTON, *Chief.*
Bureau of Public Roads	THOMAS H. MACDONALD, *Chief.*
Bureau of Agricultural Engineering	S. H. MCCRORY, *Chief.*
Bureau of Agricultural Economics	NILS A. OLSEN, *Chief.*
Bureau of Home Economics	LOUISE STANLEY, *Chief.*
Plant Quarantine and Control Administration	LEE A. STRONG, *Chief.*
Grain Futures Administration	J. W. T. DUVEL, *Chief.*
Food and Drug Administration	WALTER G. CAMPBELL, *Director of Regulatory Work, in Charge.*
Office of Experiment Stations	JAMES T. JARDINE, *Chief.*
Office of Cooperative Extension Work	C. B. SMITH, *Chief.*
Library	CLARIBEL R. BARNETT, *Librarian.*

This bulletin is a contribution from

Bureau of Plant Industry	WILLIAM A. TAYLOR, *Chief.*
Division of Cereal Crops and Diseases.	M. A. MCCALL, *Principal Agronomist, in Charge.*

U. S. GOVERNMENT PRINTING OFFICE: 1932

For sale by the Superintendent of Documents, Washington, D. C.

END