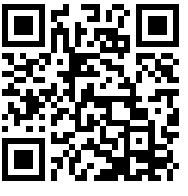

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PHYSIOLOGIC SPECIALIZATION IN PUCCINIA CORONATA AVENAE[1]

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The Bureau of Plant Industry in cooperation with the Iowa Agricultural Experiment Station

CONTENTS

INTRODUCTION

The existence of physiologic forms of *Puccinia coronata avenae* (Corda) Eriks. and Henn., as in other of the cereal rusts, has been reported by Hoerner (*18*),[3] Popp (*30*), Parson (*28*), Murphy (*24*), Frenzel (*15*), and Peturson (*29*). In this bulletin are presented (1) a standardized numerical designation for the physiologic forms of *P. coronata avenae* reported to date in North America; (2) something of the nature of these forms and their relationship to their gramineous and alternate hosts; (3) data showing the prevalence and geographic distribution of the forms in the years from 1927 to 1932, inclusive; (4) the reaction of oat varieties to natural and artificial inoculation; and (5) the gramineous-host range of six forms.

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[2] The writer expresses his appreciation to the following, all of the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U.S. Department of Agriculture: H. B. Humphrey, principal pathologist, under whose direction these investigations were conducted; T. R. Stanton, senior agronomist, for furnishing seed of the new and foreign varieties studied; and M. N. Levine, pathologist, for invaluable assistance in the preparation of the manuscript; also to B. Peturson, assistant pathologist, of the Dominion Rust Research Laboratory, Winnipeg, Canada, for furnishing data and assistance necessary for the adoption of a standardized numerical designation for the physiologic forms of crown rust; I. E. Melhus, head of the department of botany and plant pathology, and S. M. Dietz, associate professor of botany, both of the Iowa State College, for assistance and helpful suggestions; and to many who kindly sent collections of rust from the United States, Canada, and Mexico.

[3] Italic numbers in parentheses refer to Literature Cited, p.47.

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HISTORY

Hoerner (*18*) first reported the presence of physiologic specialization within *Puccinia coronata avenae*. He distinguished four physiologic forms on the basis of the reaction of two oat varieties, Ruakura ((Iowa no. 73) C.I.[4] 2025), and Green Russian ((Iowa no. 96) C.I. 2890), as follows: Form 1, infects both varieties normally; form 2, infects both varieties weakly; form 3, infects Ruakura weakly and Green Russian normally; and form 4, infects Ruakura normally and Green Russian weakly.

Popp (*30*) identified 22 cultures of *P. coronata avenae* collected from five Provinces of Canada. Using Green Russian, Sterisel ((Sterilis selection) C.I. 2891), and White Russian (Minn. no. 539) as differential oat varieties, he distinguished four physiologic forms as follows: Form 1, infects Sterisel weakly, White Russian normally, and Green Russian normally; form 2, infects all three varieties weakly; form 3, infects Sterisel normally, White Russian weakly, and Green Russian weakly; and form 4, infects all varieties more or less normally.

Parson (*28*) obtained 15 collections of *P. coronata avenae* from the United States and Canada. Using four oat varieties as differential hosts, he distinguished five physiologic forms:

Ruakura (C.I. 2025) resistant:
Avena sterilis nigra resistant ..... form 3
Avena sterilis nigra susceptible:
Red Rustproof (C.I. 1815) resistant ..... form 5
Red Rustproof (C.I. 1815) susceptible ..... form 4
Ruakura (C.I. 2025) susceptible:
Green Mountain (C.I. 1892) resistant ..... form 2
Green Mountain (C.I. 1892) susceptible ..... form 1

Parson determined the reaction of 27 varieties, selections, and species of oats to each of his forms and found none resistant to more than three of them. He noted that certain forms tended to produce teliospores soon after urediospores appeared, whereas other forms produced teliospores much later or not at all. He found no correlation between resistance and early teliospore formation.

The writer (*24*) obtained 45 collections of *Puccinia coronata avenae*, of which 32 were from *Avena* and 13 from *Rhamnus*. An equal number of cultures isolated from these collections were tested individually on pure-line selections of 33 varieties and species of oats. Eight of these, acting as differential hosts, disclosed the following nine physiologic forms:

Belar (C.I. 2760) resistant:
Red Rustproof (C.I. 1079) resistant:
College Algerians (C.I. 2052) resistant ..... form 3
College Algerians (C.I. 2052) susceptible ..... form 8
Red Rustproof (C.I. 1079) susceptible:
Cowra (C.I. 2761) resistant ..... form 9
Cowra (C.I. 2761) susceptible ..... form 7
Belar (C.I. 2760) susceptible:
Iowa no. 69 (C.I. 2463) resistant:
Avena strigosa (C.I. 1782) resistant:
Anthony (C.I. 2143) resistant ..... form 4
Anthony (C.I. 2143) susceptible ..... form 2
Avena strigosa (C.I. 1782) susceptible ..... form 1
Iowa no. 69 (C.I. 2463) susceptible:
Hawkeye ((Iowa no. 102) C.I. 2464) resistant ..... form 6
Hawkeye ((Iowa no. 102) C.I. 2464) susceptible ..... form 5

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

The 13 aecial collections from five species of *Rhamnus* were identified as follows: Four from *R. cathartica* L. were form 3; six from *R. lanceolata* Pursh., were form 5; one each from *R. tinctoria* Waldst. and Kit., *R. montana* Rosten., and *R. infectoria* L. were forms 7, 8, and 9, respectively.

Peturson (*29*) studied the effect of temperature on host reactions to physiologic forms of *Puccinia coronata avenae*. The effect of temperature on the development of four physiologic forms on six differential host varieties was determined. Green Mountain (C.I. 1892), White Tartar (C.I. 551), and Green Russian were resistant to his form 7 at a constant temperature of 57° and 70° F. and susceptible at 77° F., whereas Red Rustproof (C.I. 1039), Sterisel (Sterilis selection), and Ruakura were uniformly susceptible at these temperatures. The reactions of the same varieties to Peturson's forms 1, 3, and 4 were not affected by changes in temperature, except that Red Rustproof was resistant to form 4 at 57° F. and susceptible at 70° and 77° F. Peturson emphasizes the importance of maintaining a uniform temperature while identifying forms of *P. coronata avenae*.

Frenzel (*15*) studied 55 cultures of *Puccinia coronata avenae* (*P. coronifera* f. sp. *avenae* Kleb.) isolated from 27 collections collected throughout Germany in 1928 and 1929. He isolated 33 physiologic forms among these collections by the differential reaction of nine oat varieties. Four of these, Ruakura, Red Rustproof (C.I. 1815), Green Mountain, and *Avena sterilis* var. *nigra* (C.I. 840–49) had previously been used by American investigators as differential hosts. Frenzel considered a difference of 0-type reaction contrasted with a 1-type as sufficient to differentiate physiologic forms. He observed a heterogeneous or X-type reaction on Green Mountain and *A. sterilis* var. *nigra* to certain forms. Single-spore isolation from the resistant-type and susceptible-type pustules within those heterogeneous types failed to segregate forms that would produce homogeneous types on the particular variety involved. There was no apparent regularity in the geographic distribution of the 33 forms. Only 2 of the 20 isolated from the 1928 collections were reisolated from those collected in 1929.

Frenzel observed a marked difference in the rapidity of teliospore formation on certain varieties with certain physiologic forms. He considered this difference sufficiently important to warrant its possible use in differentiating physiologic forms. He determined the reaction of 198 varieties of oats to 8 of his forms and found that, with few exceptions, all were completely susceptible. He also determined the reaction of 19 species of grasses to 13 forms and found very slight evidence of physiologic specialization in relation to the species tested.

MATERIALS AND METHODS

Leaves infected with *Puccinia coronata avenae* were collected from naturally inoculated oat plants and from *Rhamnus* naturally and artificially inoculated in 1927 to 1932, inclusive. Because of their short germination period, aecial collections were immediately transferred to oat plants and the resulting uredial stage was continued, or the infected leaves were stored in the refrigerator. All cultures were maintained on the variety Iomine (C.I. 2827) in 1927 and 1928. This variety, however, showed some resistance to certain forms, and

Markton (C.I. 2053) was substituted for it in 1929, 1930, 1931, and 1932.

Single-uredium cultures were isolated by inoculating Markton or Iomine plants sparsely with spores from a particular collection. About 6 or 7 days after inoculation, before any uredia had opened, a plant bearing a single uredium was selected. It was then placed under a covered lamp chimney and the urediospores were allowed to mature. Because of the possibility of the presence of more than one physiologic form in a collection, two single-uredial isolations were usually made from each collection. Each culture sprang originally from a single uredium.

Seedling plants usually were inoculated between 4 and 6 p.m. The first leaf of each was drawn gently between the moistened forefinger and thumb; then the entire plant was moistened with a constant-pressure sprayer. The plants were then moved to the stock-culture room where each plant was inoculated with the desired culture by applying with a flat needle a small amount of crown-rust urediospores to the moistened surface of the first leaf. The plants were again sprayed, placed in a moist chamber, and kept there about 14 hours. In order that the plants might not dry too quickly or otherwise become injured, the chambers were opened at about 8 a.m. and the plant retained in the open chamber until about 4 p.m.

Where infection types were to be determined, the plants were placed in muslin compartments like those described by Melhus, Dietz, and Willey (*23*), and those used for stock cultures were held under lamp chimneys. The tops of the chimneys were covered with a thin layer of cotton held between two pieces of cheesecloth, and this was fastened with a rubber band. Each lamp chimney would cover the contents of a 3-inch flowerpot. The pots were supplied with water by subirrigation.

Glass chambers lined with muslin and packed with sphagnum moss and tanks made of sheet metal with a false bottom and glass top were satisfactory moist chambers.

Special precautions were taken throughout these investigations to prevent contamination. All plants were sown, grown, and prepared for inoculating in a separate greenhouse where there were no infected plants. By spraying the walls, roof, and hot steam pipes of the room used for inoculating with a fine spray of water just before inoculation, it was found, by use of check plants, that contaminating spores were effectively removed from the air. This humid atmosphere also seemed to inhibit the spread of spores while inoculation was in progress. Before preparing plants for inoculation and with each change in culture, the hands and arms were thoroughly washed with soap and water. The flat needle used for applying the urediospores was sterilized by heating.

SELECTION OF DIFFERENTIAL OAT VARIETIES

It is obviously desirable that all investigators of physiologic specialization in crown rust should use a uniform method of numbering the physiologic forms identified. This necessitates the adoption of a uniform and standard set of differential hosts.

In order to give a standard designation to each physiologic form reported to date in North America, it was necessary to include in the standard set of differential hosts certain of the differential varieties used by earlier investigators. After considerable preliminary work,

during which approximately 300 varieties were inoculated with 10 different cultures (representing 6 physiologic forms) of crown rust, 33 potential differential hosts were selected. These 33 varieties were inoculated with a total of 245 different cultures, representing 13 physiologic forms. The number of differentials employed in identifying forms was then reduced to the minimum. Thus, 11 varieties were selected as standard differential hosts for the identification of physiologic forms of *Puccinia coronata avenae*. The name, C.I. no., and previous designation of each variety, and the names of the investigators who have previously used these varieties as differential hosts for identifying physiologic forms of crown rust are presented in table 1.

TABLE 1.—*Standard differential oat varieties used to identify physiologic forms of Puccinia coronata avenae*

Variety	C.I. no.	Previous designation	Investigators
Ruakura [1]	2025	Iowa no. 73	Hoerner (*18*), Parson (*28*), Peturson (*29*), Frenzel (*15*).
Green Russian [2]	2890	Iowa no. 96	Hoerner (*18*), Popp (*30*), Peturson (*29*).
Hawkeye	2464	Iowa no. 102	Murphy (*24*).
Anthony	2143		Do.
Sunrise	982		Not previously reported.
Green Mountain	1892		Parson (*28*), Peturson (*29*), Frenzel (*15*).
White Tartar	551		Peturson (*29*).
Red Rustproof	1815		Parson (*28*), Peturson (*29*), Frenzel (*15*).
Sterisel	2891	Sterilis selection	Popp (*30*), Parson (*28*), Peturson (*29*).
Belar	2760		Murphy (*24*).
Glabrota	2630		Not previously reported.

[1] The Ruakura Rustproof variety used by Popp (*30*) may have been Ruakura (C.I. 2025). Ruakura Rustproof was not tested by the writer.

[2] B. Peturson, of the Dominion Rust Research Laboratory, Winnipeg, Canada, informed the writer in a letter dated Aug. 25, 1931, that the Green Russian used by Parson (*28*) did not react to certain of his physiologic forms as did Green Russian ((Iowa no. 96) C.I. 2890). The writer was unable to obtain seed of the Green Russian used by Parson.

Prior to the adoption of these 11 standard differential hosts all cultures were identified by the differential reaction of 33 oat varieties, within which group were included the 8 reported as differentials by the writer (*24*), and all except Sterisel and Glabrota of the standard differential varieties mentioned. Seed of these 33 varieties was obtained from S. M. Dietz and L. C. Burnett, of the Iowa Agricultural Experiment Station, and from T. R. Stanton, of the Division of Cereal Crops and Diseases, Bureau of Plant Industry. In April 1930 seed of Ruakura, Green Russian, Sterisel, Green Mountain, Red Rustproof (C.I. 1815), and White Tartar was received from B. Peturson, of the Dominion Rust Research Laboratory. This seed was of the same origin as that used by Hoerner (*18*), Popp (*30*), Parson (*28*), and Peturson (*29*). Because of its origin, the seed of the varieties obtained from Peturson was used as the source for the corresponding standard differential hosts. The reaction to physiologic forms 1 to 8, inclusive, and 10, 13, and 20 to 28, inclusive, of each of the varieties secured from Peturson and of the corresponding varieties already in use was determined and found to be similar.

Ten or more seedlings of each differential variety were inoculated in the first-leaf stage with each culture of crown rust studied. The first 7 of the 11 standard differential hosts gave a heterozygous reaction to one or more cultures of crown rust. When a variety appeared heterozygous for reaction to a particular culture a larger number of

plants was inoculated and the predominating reaction was recorded. Continuous selection of seed from these predominating types has apparently purified each variety to the extent that heterozygosity is of little concern. Pure-line selections from each variety have been tested with all forms except 10, 17, and 18. These strains are now being increased as a source for homozygous standard differential varieties [5] for the identification of physiologic forms of crown rust.

INFECTION TYPES OF CROWN RUST

In recording the reaction of different oat varieties to crown rust, it was necessary to adopt a series of rust manifestations which would describe the classes of host reactions observed. The infection types of crown rust observed were similar to those described by Stakman, Levine, and Bailey (*32*) for *Puccinia graminis avenae* Eriks. and Henn. and are here described as follows:

Host reaction	*Symbol and infection type*
Immune	I, No macroscopic evidence of infection.
Nearly immune	0, No uredia formed; necrotic areas or chlorotic flecks present.
Highly resistant	1, Uredia few, small, always in necrotic areas; also more or less necrotic areas produced without the development of uredia.
Moderately resistant	2, Uredia fairly abundant, small to midsized, always in necrotic or very chlorotic areas; necrotic areas seldom without uredia.
Mesothetic	M, Apparently a combination of two or more extreme types in varying proportions.
Moderately susceptible	3, Uredia abundant, midsized, and surrounded by chlorotic areas; necrotic areas entirely absent.
Completely susceptible	4, Uredia abundant, large; no necrosis or chlorosis immediately surrounding the uredia.

The reaction of all plants to crown rust was recorded on the tenth day following inoculation and checked on the fourteenth day. From date of inoculation to that of recording, the plants were kept at approximately 70° F. and ordinarily within the range of 65° to 75°, and with light and moisture conditions as near as practicable to the optimum for growth of the oat plants.

The infection type of crown rust on a specific pure line of oats inoculated with a specific physiologic form apparently would be very constant if temperature, light, atmospheric humidity, soil moisture, and nutrition were uniform and constant. Under the conditions of this investigation these factors could be only partly controlled. Physiologic forms were not identified in the summer or whenever the

[5] Morphological descriptions of the strains selected as standard differential hosts are not presented because different strains of a particular variety may be morphologically identical but react differently to one or more of the physiologic forms described. The varieties, with the exception of Hawkeye and Anthony, to which the strains selected as standard differential hosts belong have been described elsewhere. Archer (*2*) describes Ruakura; Etheridge (*13*), Green Russian, Green Mountain, White Tartar, Red Rustproof, and Sterilis selection (very similar to Sterisel); Callaghan (*4*), Belar and Sunrise; and Marquand (*22*), *Avena strigosa glabrescens* (Schreb.) Marquand (Glabrota). Hawkeye originated as a selection from a Richland (C.I. 787)×Green Russian (C.I. 2890) cross by S. M. Dietz, of the Iowa Agricultural Experiment Station. It is an awnless, midseason, yellow oat with no outstanding differentiating character and more or less intermediate between the parent varieties. The origin and description of Richland have been reported by Burnett, Stanton, and Warburton (*3*) and Stanton, Griffee, and Etheridge (*34*). Anthony was developed by the Minnesota Agricultural Experiment Station as a selection from a Victory ×White Tartar cross. It is a midseason, white oat with erect, equilateral panicles and occasional nontwisted to slightly twisted, subgeniculate awns. Anthony is similar to the Victory type described by Marquand (*22*).

outside temperature was too high to allow a constant greenhouse temperature of approximately 70° F. Artificial light was used in the winter and during cloudy weather, in order that the light might be more nearly uniform.

With these precautions, however, a fluctuation within an infection type was sometimes observed, especially on certain varieties when inoculated with certain physiologic forms. A variation occasionally occurred when the temperature was kept constantly within the range of 68 to 72° F. and when light, soil moisture, and atmospheric humidity conditions were apparently constant, although not controlled. The most common variances were 0–1, 3–4, and vice versa. Variations from 1–2 also were infrequently observed. On certain differential varieties, when inoculated with certain physiologic forms, an M-type of infection will be produced when maintained at a temperature of 65° to 75°, while at 55° to 65° there will be produced a 0–1 type, and at 75° to 85° a 3–4 type will develop. A variation from a low to a high infection type, or vice versa, was observed only when there were great differences in temperature during the period between inoculation and the appearance of the mature uredia, and then there was always an intermediate temperature range at which an M-type would appear and remain constant. Within the temperature range in which a particular M-type appears there is no apparent evidence to indicate that it is any less constant than any other type that is influenced by temperature changes. All of the M-types studied were variable when subjected to sufficiently great temperature changes, although only a comparatively small proportion of the other infection types are apparently significantly influenced by changes in temperature or other environmental factors.

In the present investigation, a difference of at least two infection types was considered necessary to establish a new form, that is, a type 0 contrasted with a type 2, 3, 4, or M; a type 1 contrasted with a type 3, 4, or M; or a type 2 contrasted with a type 4. It was unusual when the reaction of a differential variety to a particular physiologic form varied more than two types under the normal greenhouse conditions maintained during this investigation.

FIELD TESTS OF OAT VARIETIES

A knowledge of the field reaction of varieties studied under greenhouse conditions is very desirable. From 1928 to 1931, inclusive, uniform crown-rust nurseries were grown, at one time or another, at 12 different locations in the central and southern portions of the United States. Additional varieties were grown at Ames, Iowa, in 1929 to 1932, inclusive, and at Manhattan, Kans., in 1929 and 1930. The location of the uniform crown-rust nurseries, the number of oat varieties included annually, and the names of the cooperators at each of the experiment stations where the nurseries were grown are given in table 2.

The percentages of crown-rust infection were determined according to the scale illustrated by Durrell and Parker (*12*). In addition to the differences in percentage of infection, marked differences in infection types were observed. These types are often difficult to determine because usually uredia occur in different stages of development. There are also differences in maturity of the host plants and mesothetic reactions, due possibly to the presence of more than one form.

An attempt was made to obtain the rust estimates at the time of maximum crown-rust infection; for obvious reasons, however, this could not always be accomplished. Numerical equivalents were arbitrarily assigned the 10 infection types recorded under field conditions, in order that infection coefficients might be calculated. The infection types recorded under field conditions and their numerical equivalents are as follows: 0, 0.1; 0–1, 0.2; 1, 0.3; 1–2, 0.4; 2, 0.5; M, 0.6; 2–3, 0.7; 3, 0.8; 3–4, 0.9; 4, 1.0. The coefficient of infection was then calculated by multiplying the numerical equivalent by the percentage of infection.

TABLE 2.—*Location of uniform crown-rust nurseries, number of varieties grown each of the years 1928–31, and names of cooperators at the cooperating experiment stations*

Location	Varieties grown in—				Cooperators
	1928	1929	1930	1931	
	Number	*Number*	*Number*	*Number*	
Ames, Iowa	88	100	100	50	L. C. Burnett.
Knoxville, Tenn	88	100	100	50	S. H. Essary.
Clemson College, S.C	----	----	100	50	W. W. Rogers.
Experiment, Ga	88	100	100	50	R. P. Bledsoe.
Tifton, Ga	88	100	----	----	W. J. Davis.
Gainesville, Fla	----	----	----	30	A. H. Eddins.
State College, Miss	88	100	100	----	L. E. Miles.
Calhoun, La	----	----	----	30	John P. Gray.
Denton, Tex	88	100	100	50	P. B. Dunkle.
Stillwater, Okla	88	100	100	50	J. C. Ireland, C. B. Cross.
Fayetteville, Ark	----	----	----	50	C. K. McClelland.
Manhattan, Kans	----	100	100	50	C. O. Johnston, J. H. Parker.

IDENTIFICATION OF PHYSIOLOGIC FORMS

Hoerner (*18*), Popp (*30*), Parson (*28*), Peturson (*29*), and the writer (*24*) have, among themselves, more or less independently identified and described 15 separate physiologic forms of *Puccinia coronata avenae* occurring in North America. Each investigator, except Hoerner, employed one or more differential varieties not used by his predecessors and omitted one or more they did use. Also, each identified two or more physiologic forms not identified by his predecessors. Because each worker used a somewhat different set of differentials it is difficult to compare certain of the forms he describes. Two collections apparently representing the same physiologic form may be identified as two distinct forms when new differential varieties are employed. Many of the later forms are doubtless those that were present and probably collected by previous investigators but were not recognized as distinct forms because they lacked the differential varieties necessary to identify them. For this reason a comparison of the yearly geographic distribution of the physiologic forms reported by these various investigators would be of limited value.

An attempt has been made to adopt a standardized numeration for the 15 forms reported as occurring in North America. Hoerner's forms 1, 2, 3, and 4 (*18*) were considered the basis for this standardized numeration because of their priority. Popp (*30*) next described four forms. His forms 2 and 1 were apparently the same as Hoerner's 2 and 3, respectively, while his 3 and 4 were apparently distinct from any 2 of Hoerner's 4 forms and are, for that reason, assigned the standard key numbers 5 and 6, respectively. Likewise, standard numbers have been assigned the physiologic forms described by Parson (*28*)

and Peturson (*29*). Apparently 10 distinct forms had been identified in North America prior to this investigation. These and 5 additional forms reported by the writer in a preliminary publication (*24*) have been arranged chronologically and assigned standard numbers 1 to 15, inclusive (table 3). The first culture of crown rust that produced the infections reported for one of these standard forms was considered typical of that particular form. Two or more forms might be, and often were, isolated that produced the same infection for a particular form as a given form reported by these earlier investigators on the differential hosts they employed. In such instances the first form isolated was considered typical of the one previously reported, while additional forms were assigned standard key numbers above 15 in accordance with their parasitism on the added differential varieties. Fortunately, cultures representing forms 1 to 10, inclusive, were isolated in this investigation, and the reaction of all the standard differential varieties to each form was obtained.

TABLE 3.—*Host reactions to physiologic forms of Puccinia coronata avenae on differential varieties of Avena spp., expressed in means of types of rust infection*

Designation of physiologic forms						Reaction of differential hosts										
As recorded in literature					Standardized numeration	Avena sativa					A. sativa orientalis		A. byzantina			A. strigosa
						1	2	3	4	5	6	7	8	9	10	11
Hoerner (*12*)	Popp (*20*)	Parson (*26*)	Peturson (*29*)[1]	Murphy (*24*)		Ruakura	Green Russian	Hawkeye	Anthony	Sunrise	Green Mountain	White Tartar	Red Rustproof	Sterisel	Belar	Glabrota
1	----	1	1	5	1	4	4	4	4	4	4	4	4	4	3	0
2	2	----	6	----	2	1	0	4	0	0	0	0	0	1	0	0
3	1	3	3	3	3	0	4	4	4	0	4	4	0	0	0	0
4	----	----	7	----	4	3	1	4	0	4	M	1	4	4	4	0
----	3	----	----	----	5	0	1	4	0	4	0	0	4	3	4	0
----	4	4	4	----	6	0	4	4	4	4	4	4	4	4	4	0
----	----	2	----	1	7	4	4	0	0	4	0	0	4	4	4	0
----	----	5	----	----	8	1	3	4	4	0	4	4	1	3	2	0
----	----	----	2	----	9	1	2	3	3	2	3	3	1	1	2	0
----	----	----	5	2	10	4	4	4	4	1	1	1	4	4	4	----
----	----	----	----	4	11	4	4	0	0	2	0	4	4	4	4	4
----	----	----	----	6	12	4	4	0	4	3	4	0	4	3	3	0
----	----	----	----	7	13	4	4	4	4	2	4	4	4	0	0	3
----	----	----	----	8	14	1	4	4	4	1	4	4	4	0	0	0
----	----	----	----	9	15	0	4	4	4	4	4	4	4	4	1	0
----	----	----	----	----	16	1	4	0	0	0	1	4	0	0	0	4
----	----	----	----	----	17	0	4	4	0	4	1	4	4	----	4	0
----	----	----	----	----	18	0	4	0	0	0	0	4	0	----	0	0
----	----	----	----	----	19	0	4	4	1	1	1	4	1	0	1	0
----	----	----	----	----	20	4	4	4	0	4	0	0	4	4	4	0
----	----	----	----	----	21	0	0	4	4	0	4	4	4	4	4	0
----	----	----	----	----	22	0	4	4	0	4	0	0	4	4	4	0
----	----	----	----	----	23	4	4	4	4	0	4	4	0	4	2	0
----	----	----	----	----	24	0	4	4	4	0	4	4	0	0	0	4
----	----	----	----	----	25	4	4	4	0	4	4	0	4	4	4	0
----	----	----	----	----	26	4	4	4	0	4	0	4	4	4	4	0
----	----	----	----	----	27	4	4	4	0	4	4	0	4	0	4	0
----	----	----	----	----	28	4	0	4	1	0	4	4	0	3	3	0
----	----	----	----	----	29	0	2	0	0	0	0	0	2	2	0	0
----	----	----	----	----	30	4	4	4	3	4	4	4	4	3	4	3
----	----	----	----	----	31	3	3	3	M	3	3	M	4	4	4	0
----	----	----	----	----	32	4	M	4	M	M	M	M	3	2	M	0
----	----	----	----	----	33	4	0	3	3	4	3	3	4	3	M	I

[1] Peturson's reactions for his forms 1, 6, 3, 2, and 5 were obtained from him directly through correspondence dated Apr. 15, 1930.

From 1927 to 1932, inclusive, 533 cultures of *Puccinia coronata avenae* were collected in the United States, Canada, and Mexico. Among these, 33 physiologic forms were identified by the specific reaction of 11 differential oat varieties. The mean infection type induced on each of the standard differential varieties by each of the 33 forms and the designation recorded in literature for each form previously reported by American investigators are presented in table 3. The reactions of Glabrota (C. I. 2630) to form 10 and of Sterisel to forms 17 and 18 are not known, because these forms have not been isolated since these varieties became available.

The reactions recorded in table 3 were determined on the first leaf of seedling plants. The second leaf infrequently showed a reaction class indicative of considerably more susceptibility than that on the first leaf of the same plant. For identification purposes the first leaf was the most sensitive and convenient, therefore only its reaction was used for differentiating physiologic forms. Each reaction represents an average for all the cultures identified as that particular form. These reactions may be grouped into three classes: *Resistant*, *mesothetic*, and *susceptible*. Then the 11 standard differential varieties can be arranged in a trichotomous key for the identification of the 33 physiologic forms.

Analytical key for the determination of physiologic forms of *Puccinia coronata avenae* determined on the basis of their parasitic behavior on differential varieties within the genus *Avena*.

Variety and behavior	*Physiologic form*
Ruakura resistant:	
Green Russian resistant:	
Hawkeye resistant	29
Hawkeye susceptible:	
Anthony resistant:	
Sunrise resistant	2
Sunrise susceptible	5
Anthony susceptible:	
Red Rustproof resistant	9
Red Rustproof susceptible	21
Green Russian susceptible:	
Hawkeye resistant:	
Glabrota resistant	18
Glabrota susceptible	16
Hawkeye susceptible:	
Anthony resistant:	
Sunrise resistant	19
Sunrise susceptible:	
White Tartar resistant	22
White Tartar susceptible	17
Anthony susceptible:	
Sunrise resistant:	
Red Rustproof resistant:	
Sterisel resistant:	
Glabrota resistant	3
Glabrota susceptible	24
Sterisel susceptible	8
Red Rustproof susceptible	14
Sunrise susceptible:	
Belar resistant	15
Belar susceptible	6
Ruakura susceptible:	
Green Russian resistant:	
Anthony resistant:	
Sunrise resistant	28
Sunrise susceptible	4
Anthony susceptible	33

Variety and behavior	*Physiologic form*
Ruakura susceptible—Continued.	
Green Russian mesothetic	32
Green Russian susceptible:	
Hawkeye resistant:	
Anthony resistant:	
Sunrise resistant	11
Sunrise susceptible	7
Anthony susceptible	12
Hawkeye susceptible:	
Anthony resistant:	
Green Mountain resistant:	
White Tartar resistant	20
White Tartar susceptible	26
Green Mountain suceptible:	
Sterisel resistant	27
Sterisel susceptible	25
Anthony mesothetic	31
Anthony susceptible:	
Sunrise resistant:	
Green Mountain resistant	10
Green Mountain susceptible:	
Red Rustproof resistant	23
Red Rustproof susceptible	13
Sunrise susceptible:	
Glabrota resistant	1
Glabrota susceptible	30

Peturson (*29*) has reported that the reaction of Green Mountain, White Tartar, Green Russian, Red Rustproof, Sterisel, and Ruakura to standard forms 1 and 3 was not influenced by temperature, but that the reaction of all these varieties, except Sterisel and Ruakura, to forms 4 and 6 was affected to some extent by temperature. He suggested 70° F. as best adapted to the identification of physiologic forms and probably most easily maintained by the average investigator.

The effect of temperature on the reaction of certain varieties to certain forms was noted early in this investigation. The reactions recorded in table 3 were determined on plants held at approximately 70° F., i.e., within the range 65°–75°. At a temperature of 85° certain forms could not be distinguished from each other, while at 55° forms could be differentiated that were indistinguishable at 70°.

In January 1933 the writer had available four greenhouse rooms in which the temperatures were automatically controlled. The mean temperature in these four rooms was 55°, 65°, 75°, and 85° F., with an allowed range for each of 50°–60°, 60°–70°, 70°–80°, and 80°–90°, respectively. The infection type produced on the differential varieties and on Victoria, Bond, and Markton infected with forms 1 and 7 when exposed to these temperatures from the time of inoculation until uredia first appeared is shown in table 4. The reaction of the varieties infected with form 1 varied only slightly. M types were produced on Hawkeye and Anthony at 55°, otherwise the reactions were not significantly affected. There was, however, an evident tendency toward a more susceptible reaction at the higher temperatures, and vice versa.

The effect of temperature on the reaction of the varieties to form 7 was striking. At 85° F. this form could not accurately be distinguished from form 1. Green Russian, Hawkeye, Anthony, Sunrise, Green Mountain, and White Tartar were resistant to form 7 at 55° but susceptible at 85°. M-types were produced on all these varieties, with the exception of White Tartar, at a temperature between which

they produced resistant and susceptible reactions. An M type would probably be produced on White Tartar at some temperature between 75° and 85°. Red Rustproof, Sterisel, and Belar were very susceptible to "scalding" at 80° or above, thereby making accurate determination of infection types very difficult, and often impossible to determine. At 55° uredia appeared 3 to 4 days later than at 70° or above.

TABLE 4.—*Infection type produced on 14 oat varieties infected with forms 1 and 7 at 55°, 65°, 75°, and 85° F.*

Varieties tested		Infection type with physiologic form—							
Name	C.I. no.	1				7			
		55°	65°	75°	85°	55°	65°	75°	85°
Ruakura	2025	3	3+	4	4+	3	3+	4	4+
Green Russian	2890	3−	3+	4	4	1	M	3+	4+
Hawkeye	2464	M	3+	4	4	0	1	M	3+
Anthony	2143	M	3−	3+	4	0	1	M	3
Sunrise	982	3+	3+	3+	4	2	M	3+	4
Green Mountain	1892	3	3	3+	4	0	0	M	3+
White Tartar	551	3+	3+	4	4	0	0	1	3
Red Rustproof	1815	3+	3+	4	4	3	3+	4	4+
Sterisel	2891	3+	3+	4	4	3	3+	4	4
Belar	2760	3	3+	3+	4	3	3+	4	4
Glabrota	2630	I	I	0	0	I	I	0	0
Victoria	2401	0	0	1−	1	I	0	0	0
Bond	2733	I	I	0	0	I	I	0	0
Markton	2053	3+	3+	4	4	3+	4	4	4+

NATURE OF PHYSIOLOGIC FORMS IDENTIFIED

The 33 physiologic forms identified differed greatly in versatility[6] and pathogenicity,[7] although groups of somewhat similar forms may be discerned. By assigning numbers 1 to 11, respectively, to the standard differential varieties in table 3, a descriptive formula may be given each form by writing the numbers representing the varieties resistant to it. These formulas, arranged in the order of versatility and pathogenicity, are presented in table 5. They are more convenient and accurate for use in identifying forms than is the analytical key previously described.

Physiologic forms 30 and 1 are the most aggressive and virulent forms identified. Bond, Victoria (C.I. 2401), and Victoria (Scasso) (C.I. 2764) are the only varieties resistant to form 30. Form 1 is slightly less aggressive than form 30 in that it is unable to induce a susceptible reaction in Glabrota. This form, however, is apparently of much greater economic importance because of its prevalence and wide distribution, as will be shown later. The seedling reaction to form 1 has been determined for approximately 300 varieties and selections, and only 4 varieties—Glabrota, Bond, and the 2 Victorias—were resistant to it.

[6] "Versatility" applies to the number of oat varieties that a form is capable of infecting readily. Where the number is comparatively large the form is referred to as "aggressive", and where the number is relatively small the form is referred to as "restricted."

[7] "Pathogenicity" refers to the relative vigor of rust attack as expressed by the infection type. A form inducing a susceptible reaction in a given variety is described as "virulent", while one causing a resistant reaction or that is incapable of producing any evidence of infection is "nonvirulent."

TABLE 5.—*Descriptive formulas for the physiologic forms of Puccinia coronata avenae*

Physiologic form no.	Numerical formula [1]	Physiologic form no.	Numerical formula [1]
30		27	4, 7, 9, 11.
1	11.	4	2, 4, 7, 11 (6).
33	2 (10).	8	1, 5, 8, 10, 11.
31	11 (4, 7).	14	1, 5, 9, 10, 11.
6	1, 11.	7	3, 4, 6, 7, 11.
32	9, 11 (2, 4, 5, 6, 7, 10).	22	1, 4, 5, 7, 11.
10 [2]	5, 6, 7.	24	1, 5, 8, 9, 10.
13	5, 9, 10.	28	2, 4, 5, 8, 11.
15	1, 10, 11.	5	1, 2, 4, 6, 7, 11.
25	4, 7, 11.	3	1, 5, 8, 9, 10, 11.
26	4, 6, 11.	9	1, 2, 5, 8, 9, 10, 11.
12	3, 7, 11.	19	1, 4, 5, 6, 8, 9, 10, 11.
11	3, 4, 5, 6.	16	1, 3, 4, 5, 6, 8, 9, 10.
23	5, 8, 10, 11.	18 [3]	1, 3, 4, 5, 6, 8, 10, 11.
17 [3]	1, 4, 6, 11.	2	1, 2, 4, 5, 6, 7, 8, 9, 10, 11.
21	1, 2, 5, 11.	29	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11.
20	4, 6, 7, 11.		

[1] Numbers in this column refer to the standard differential varieties as they are numbered in table 3. The varieties represented by the numbers included in a particular physiologic form formula are resistant to that form, except those indicated by numbers within parentheses, which represent varieties that produce a mesothetic reaction.
[2] Reaction of Glabrota to form 10 is unknown.
[3] Reaction of Sterisel to forms 17 and 18 is unknown.

Form 29 is in direct contrast to form 30 in that all of the standard differential varieties are resistant to the one and susceptible to the other. The remaining 30 forms are fairly evenly distributed between these two extremes.

Mesothetic or M types of infection were produced by forms 4, 31, 32, and 33. These appeared constant under the conditions of this experiment, but a lower or higher temperature range probably would affect them, as previously stated.

Apparently there is slight correlation between versatility and pathogenicity. A very aggressive form is often completely nonvirulent on certain varieties, whereas a very restricted form will attack these same or other varieties with great virulence. Glabrota, for example, is extremely resistant to the very aggressive form 1 and completely susceptible to the restricted form 16.

Raines (*31*) probably was the first to note that cultures of crown rust may vary in their ability to produce telia. A culture collected in the vicinity of New York City produced teliospores only moderately, whereas one from Ames, Iowa, grown at the same time, under similar conditions, and on the same host material, produced teliospores abundantly. By selection, Raines secured 36 cultures 20 of which produced no teliospores under greenhouse conditions, and 35 cultures 30 of which produced more than 50 percent of telia.

Parson (*28*) noted that certain of his physiologic forms consistently produced teliospores about 3 weeks after inoculation, while others were never observed to produce teliospores. He did not agree with the opinion of Parker (*27*) that early production of teliospores was definitely correlated with the resistance of the host plant. He suggested instead that early formation of teliospores is possibly characteristic of restricted, "narrowly specialized" forms.

Frenzel (*15*) observed his forms 2, 9, 10, 11, 17, and 20 for teliospore production. He found that forms 2 and 10 consistently produced teliospores earlier and more abundantly than the remaining four forms. Forms 9 and 11 produced teliospores later and less abundantly,

whereas in forms 17 and 20 no teliospores developed until 38 days following inoculation. Frenzel found that teliospores appeared first on resistant plants. Forms having a strong tendency toward teliospore production, such as 2 and 10, would form teliospores on susceptible plants a few days later than on resistant ones, although forms with a slight tendency toward teliospore production, such as 9 and 11, formed teliospores only on certain resistant plants.

Differences in rate of teliospore formation between certain forms were noted at the beginning of the present investigation. Observations of different cultures representing the same physiolgic form were not always consistent, however. On April 26, 1929, 13 cultures were collected from artificially inoculated *Rhamnus* leaves. These cultures were purified by repeated single-uredium isolations and identified in December 1929. On the basis of the reaction of 33 varieties (including all of the standard differentials except Sterisel), each of these 13 cultures behaved like physiologic form 18. Seedling plants of the varieties were inoculated December 6, 1929, while in the two-leaf stage, and were maintained under the same environmental conditions at 68° to 72° F. On December 16, eight of the cultures had produced telia on Red Rustproof (C.I. 1079), Red Rustproof (C.I. 1805), Cowra, Iowa No. 69, and Magistral (C.I. 2460). These five varieties showed a type 1 infection with each of the 13 cultures, whereas the remaining 18 resistant varieties showed a type 0. On December 20 these same 8 cultures had produced some telia on each of the 10 susceptible varieties, but the remaining 5 cultures had not then produced telia on any of the 33 varieties. Two of the five remaining cultures began to produce telia on certain of the five resistant varieties mentioned above on December 27, and on December 30 all five varieties were bearing some telia. It was not until January 2, 1930, that telia began to appear on the susceptible varieties inoculated with these same 2 cultures, and they had not appeared on all the susceptible varieties until January 8. On January 10, 35 days after inoculation, telia had not appeared on any of the 33 varieties inoculated with the remaining 3 cultures. This same experiment was repeated twice during the spring of 1930 with very similar results.

Apparently physiologic form 18 could be divided into 3 subforms: (1) A form producing telia rapidly and represented by 8 of the 13 cultures; (2) a form producing telia slowly and represented by 2 cultures; and (3) another form apparently not producing telia on seedling plants and represented by 3 cultures. The cultures representing subform 1 frequently produced telia without any evidence of uredial development.

On the basis of observations made, 10, 14, 21, 28, and 35 days following inoculation of seedling plants of the differential varieties, the 33 physiologic forms described in table 3 may be similarly classified, as follows: Group 1—2, 3, 5, 8, 9, 16, 18, 19, 22, 23, 24, 28, 29; group 2—2, 3, 4, 5, 7, 8, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 27, 32; and group 3—1, 6, 12, 18, 25, 26, 30, 31, 32, 33.

Six of the 33 forms (2, 3, 5, 8, 16, and 19) were represented by cultures in groups 1 and 2, two forms (12 and 32) were represented by cultures in groups 2 and 3, and form 18 was represented in groups 1, 2, and 3.

On the basis of parasitic reaction on the differential varieties and rapidity of telia production, 43 physiologic forms could be differen-

tiated among the 533 cultures studied. Acceptance of rate of telial production as a differentiating character for identifying physiologic forms would, however, entail much additional time and labor without apparently adding much to our knowledge of the pathogenicity and versatility of the form included. Hence, it seems preferable to omit rate of telial production as a character on which to identify physiologic forms and to employ it for differentiation of subforms. Whenever practicable, the rate of telial production of all cultures identified should be observed, especially so when a new physiologic form is present.

There is apparent a positive correlation between rapidity of telial production and restricted forms. A comparison of the above classification with the physiologic-form formulas previously presented will show that most of the forms exhibiting early telia production are, in general, the more restricted ones. Obviously the reaction of 11 standard differential varieties is not a wholly dependable criterion as to whether a physiologic form is aggressive or restricted. The reaction of 33 differential varieties to 13 forms and 266 varieties to 6 of these same forms has not, however, materially affected this ranking.

A discussion of the relation between type of infection and rapidity of telial production is presented under the heading "Reaction of Oat Varieties."

PHYSIOLOGIC FORMS COLLECTED FROM RHAMNUS

Sixty-five collections of crown rust were obtained from naturally and artificially inoculated *Rhamnus* species in 1928, 1929, and 1930. An equal number of cultures isolated from these collections were identified and found to represent 14 physiologic forms. The distribution of the forms obtained from *Rhamnus* according to the species from which they were collected is given in table 6.

TABLE 6.—*Physiologic forms identified and number of cultures collected from different species of Rhamnus in 1928, 1929, and 1930*

Collected from—	Cultures identified as physiologic form—														Total isolations	
	1	2	3	4	5	6	8	13	14	15	16	18	19	23	Cultures	Forms
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
R. cathartica	----	----	13	1	----	----	1	----	----	----	----	----	----	----	15	3
R. chlorophora	----	----	----	----	----	----	----	----	----	----	----	----	1	----	1	1
R. infectoria	3	1	4	----	1	----	1	----	1	1	----	10	2	1	25	10
R. lanceolata	9	----	----	----	----	----	----	----	----	----	----	----	----	----	9	1
R. montana	----	----	----	----	----	----	----	----	1	----	----	3	2	----	6	3
R. spp. (from Peiping, China)	----	----	----	----	----	1	----	----	----	----	----	----	----	----	1	1
R. spp. (from Siberia)	----	----	----	----	----	----	----	----	----	1	----	----	----	----	1	1
R. tinctoria	----	3	1	----	----	----	1	1	----	----	1	----	----	----	7	5
Total	12	4	18	1	1	1	3	1	2	2	1	13	5	1	65	14

Eight cultures, identified as form 3, collected from *Rhamnus cathartica*, and 6, identified as form 1, collected from *R. lanceolata*, were from naturally inoculated plants growing under field conditions. The remaining 51 cultures were collected from artificially inoculated plants growing under greenhouse conditions.

Forms 14, 15, and 18 were collected only from artificially inoculated *Rhamnus*, and forms 6, 8, 13, 19, and 23 either from artificially inoculated *Rhamnus* or from oat plants growing near naturally inoculated

Rhamnus. In the light of the investigations conducted by Dietz (*10*), Craigie (*5, 6, 7, 8, 9*), Hanna (*17*), Newton, Johnson, and Brown (*26*), Stakman, Levine, and Cotter (*33*), Allen (*1*), Waterhouse (*36*), and others, it seems probable that certain of these forms, particularly those of rare occurrence, may have arisen by hybridization or segregation.

On September 23, 1928, some nearly mature volunteer plants of Hawkeye oats were collected at Ames, Iowa. They were heavily infected with crown rust, both in the telial and uredial stages. Nine different single-uredium cultures were identified. Six of these proved to be physiologic form 1 and three physiologic form 3. Early in March 1929 the telial material of this same collection was used to inoculate plants of *Rhamnus infectoria* and *R. montana*. Abundant infection was secured on both. A total of 16 unopened aecial cups, 13 from *R. infectoria* and 3 from *R. montana*, were carefully picked with sterilized forceps. The aeciospores from each were used to inoculate Markton oat plants, and the progeny of the single-uredium isolations were identified in the usual manner. Thirteen cultures obtained from the same number of aecial cups from *R. infectoria* were identified as follows: 9 were form 18; 2 were form 1; 1 was form 3; and 1 was form 19. The 3 cultures from *R. montana* were identified as form 18.

Form 1 does not produce teliospores readily on growing plants, but telia have been observed on maturing adult plants, especially when held under somewhat adverse environmental conditions. It is probable, therefore, that teliospores representing both forms 1 and 3 were present in the collection. One or both forms are apparently heterozygous, and either parental form might have reappeared on *R. infectoria* as a progeny of the original forms or as segregates resulting from hybridization. Forms 18 and 19 apparently originated by hybridization between forms 1 and 3, or as segregates from one or both forms. The fact that teliospores were collected from a pure-line selection of Hawkeye (C.I. 2464), which is highly resistant to form 18, is further evidence that this form was not present in the original collection.

In the spring of 1929 teliospores of forms 2 and 7 were produced under greenhouse conditions and allowed to mature at a temperature of 60° to 65° F. Leaves bearing these teliospores were collected, dried, and then stored over the winter in burlap bags hanging outside the greenhouse. In March 1930 an attempt was made to inoculate *Rhamnus alnifolia* L'Hér., *R. caroliniana* Walt., *R. cathartica*, *R. chlorophora* Dipp., *R. davurica* Pall, *R. frangula* L., *R. infectoria*, *R. koraiensis* Schneid., *R. lanceolata*, *R. purshiana* DC., *R. smithii* Greene, *R. tinctoria*, *R. utilis* Decaisne, and unidentified *Rhamnus* species from Peiping, China, and Siberia. Apparently the teliospores of form 7 did not germinate; at least, there was no evidence of infection on any of the species inoculated with this form. The absence of infection resulting from the inoculation with form 7 frustrated an attempt to hybridize the two forms by mixing their pycnial exudates.

All the species inoculated with form 2, except *Rhamnus caroliniana*, *R. frangula*, and *R. davurica*, showed some sign of infection. Necrotic areas were produced on *R. chlorophora*, *R. purshiana*, *R. utilis*, and the *Rhamnus* species from China and Siberia. Normal spermogonia with no aecia were produced on *R. alnifolia*, *R. lanceolata*, and *R. smithii*. Normal spermogonia and aecia were produced on *R. cathartica*, *R.*

infectoria, and *R. tinctoria*. The infection on all species, except *R. infectoria* and *R. tinctoria*, was slight. For this reason the apparently immune species *R. caroliniana*, *R. frangula*, and *R. davurica* might have escaped infection. This, however, seems improbable because there were 5 individual plants of *R. davurica*, 3 of *R. caroliniana*, and 2 of *R. frangula*. It is possible that normal aecia would have developed on *R. alnifolia*, *R. lanceolata*, and *R. smithii* had the nectar of the spermogonia been mixed. Unfortunately, this was not done. The infected *Rhamnus* plants were kept separate in muslin compartments but were not protected from greenhouse insects and air currents.

A total of 14 unopened aecia, 5 each from *Rhamnus infectoria* and *R. tinctoria* and 4 from *R. cathartica*, were collected and aeciospores from each of these used to inoculate Markton plants. The 14 cultures were stored in the uredial stage until the following winter. Single-uredium cultures were then isolated from each culture and identified in the usual manner. The 5 from *R. infectoria* were identified as forms 2, 3, 8, 14, and 23, each culture representing a different form. The 5 cultures from *R. tinctoria* were found to represent 3 forms, 3 being form 2 and 1 each forms 3 and 8. Two of the cultures from *R. cathartica* were identified as form 3 and one each as forms 4 and 8. Among cultures from the 14 cups resulting from inoculation with physiologic form 2, 6 physiologic forms were identified. Forms 2 and 3 were each found in 4 aecial cups, form 8 in 3, and forms 4, 14, and 23 each in 1 aecial cup. Physiologic form 2 evidently is heterozygous.

Additional single-uredium isolations from cultures originating from single aecial cups disclosed the fact that a single aecial cup apparently contains only one form.

These data from naturally and artificially inoculated *Rhamnus* also indicate that certain *Rhamnus* species may have a differential reaction; that is, certain species tend to harbor specific forms, while others harbor many forms. The numbers are too small, however, to support definite conclusions.

PREVALENCE AND GEOGRAPHIC DISTRIBUTION OF PHYSIOLOGIC FORMS

The prevalence and geographic distribution of physiologic forms of crown rust are of considerable interest, especially to the plant breeder. In the period from 1927 to 1932, inclusive, 533 cultures collected from 35 States and Provinces in the United States, Mexico, and Canada have been identified and studied. Although this is a comparatively short period and the number of cultures is small, these facts should be indicative of the prevalence and distribution of the forms present during that time.

SURVEY OF 1927

Six physiologic forms were identified among 10 single-uredium cultures, isolated from an equal number of collections obtained in 1927.[8] The distribution of these forms among 7 States in the United States and 1 Province in Canada is shown in table 7. The collections were all from naturally inoculated oats growing under field conditions. One collection from Ste. Anne de la Pocatière, Quebec, was obtained

[8] Nine of the collections secured in 1927 were furnished by L. D. Leach, now junior plant pathologist, University of California, who made a preliminary study of physiologic specialization and identified three physiologic forms. Unpublished data.

from Victory oats growing near infected *Rhamnus cathartica*. Five cultures were identified as form 7. This form was apparently prevalent throughout Iowa, Missouri, Kansas, and Oklahoma in 1927. Form 3 probably was disseminated from the infected *R. cathartica* bushes near which it was collected in Quebec. Form 1 was collected by the writer in October from volunteer oats near Mason City, Iowa. Owing to the limited number of cultures identified little significance can be given to the distribution and prevalence of the forms identified in 1927.

TABLE 7.—*Distribution of physiologic forms of Puccinia coronata avenae in the United States and Canada in 1927*

Region and State or Province	Collections of physiologic form—						Total isolations	
	1	3	7	10	11	12	Cultures	Forms
Southern Great Plains:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Texas						1	1	1
Oklahoma			1				1	1
Kansas			2				2	1
South-central region:								
Missouri			1				1	1
North-central region:								
Iowa	1		1				2	2
Illinois					1		1	1
Northern Great Plains:								
North Dakota				1			1	1
Canada:								
Quebec		1					1	1
Total	1	1	5	1	1	1	10	6

SURVEY OF 1928

Form 1 was by far the most widespread and prevalent form in 1928 (table 8). It was the predominating form in the southern Great Plains and in the south-central, north-central, and southeastern regions of the United States. Form 1 was not represented in cultures from the northeastern region or Canada. Four of the cultures representing form 1 were collected from naturally inoculated *Rhamnus lanceolata* in Iowa. Three cultures of form 3—two from Iowa and one from Nebraska—were from naturally inoculated *R. cathartica*. Form 3 was also collected from naturally infected oat plants in Iowa, Ohio, Ontario, and West Virginia, but in each instance *R. cathartica* was reported as growing nearby. Just why form 7, the most prevalent in 1927, should appear only in southern California and western Texas is uncertain. Forms 13, 14, and 15 were new ones collected only from artificially inoculated *R. tinctoria*, *R. montana*, and *R. infectoria*, respectively.

TABLE 8.—*Distribution of physiologic forms of Puccinia coronata avenae in the United States and Canada in 1928*

Region and State or Province	Collections of physiologic form—						Total isolations	
	1	3	7	13	14	15	Cultures	Forms
Western States:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
California	2		3				5	2
Oregon	1						1	1
Southern Great Plains:								
Texas	4		2				6	2
Oklahoma	1						1	1
South-central region:								
Missouri	1						1	1
Mississippi	4						4	1
Southeastern region:								
Florida	1						1	1
Georgia	4						4	1
Tennessee	1						1	1
West Virginia		1					1	1
North-central region:								
Iowa	10	3		1	1	1	16	5
Northern Great Plains:								
Nebraska		1					1	1
North Dakota	1						1	1
Northeastern region:								
Ohio		1					1	1
Canada:								
Ontario		1					1	1
Total	30	7	5	1	1	1	45	6

SURVEY OF 1929

Physiologic forms 7 and 1 were without doubt the most prevalent forms in 1929 (table 9). Form 7 was represented in 76 cultures collected in 14 States and form 1 in 48 from 13 States. These forms were apparently the predominating ones in all regions from which collections were obtained except the northern Great Plains. Seven of the cultures from Iowa, representing form 1, were collected from *Rhamnus;* 4 from *R. lanceolata;* and 3 from *R. infectoria.* One of the cultures from *R. lanceolata* was from a naturally inoculated plant; the remaining 6 were from artificially inoculated plants. Eleven of the twenty cultures from Iowa, identified as form 3, were collected from *Rhamnus;* 5 from naturally inoculated *R. cathartica;* and 3 each from *R. cathartica* and *R. infectoria,* artificially inoculated. The remaining 17 cultures, representing form 3, were collected in localities where *R. cathartica* is prevalent. Two cultures from Iowa, representing forms 16 and 19, were collected from artificially inoculated *R. tinctoria* and *R. infectoria,* respectively. All of the cultures identified as form 18 were collected from artificially inoculated *Rhamnus:* 10 from *R. infectoria* and 3 from *R. montana.*

TABLE 9.—*Distribution of physiologic forms of Puccinia coronata avenae in the United States in 1929*

Region and State or Province	Collections of physiologic form—								Total isolations	
	1	3	7	12	16	17	18	19	Cultures	Forms
Western States:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Oregon	1		3						4	2
Southern Great Plains:										
Texas	3		3						6	2
Oklahoma	5		1						6	2
Kansas	5		15			1			21	3
South-central region:										
Missouri		1	3			2			6	3
Mississippi	5		4						9	2
Southeastern region:										
Florida	5		4						9	2
Georgia	2		7						9	2
Alabama	2								2	1
Tennessee	6		6						12	2
Virginia	2		4						6	2
West Virginia	1	3	3		7	2			16	5
North-central region:										
Iowa	10	20	19	2	7	3	13	2	76	8
Minnesota	1		3						4	2
Northern Great Plains:										
South Dakota			1						1	1
North Dakota		4							4	1
Total	48	28	76	2	14	8	13	2	191	8

SURVEY OF 1930

Twenty-one forms were identified among 112 cultures collected in 1930 from 17 States in the United States and 3 Provinces in Canada (table 10). Fifteen of these were forms not previously isolated by the writer. The discovery of so many forms previously unknown probably was partly due to the extensive area from which collections were obtained. Cultures were procured from Florida, Maine, Quebec, Ontario, Manitoba, Oregon, Texas, and many intervening States. Also, as previously stated, a number of new forms apparently resulted from hybridization or segregation on artificially inoculated *Rhamnus* species.

TABLE 10.—*Distribution of physiologic forms of Puccinia coronata avenae in the United States and Canada in 1930*

Region and State or Province	Collections of physiologic form—											
	1	2	3	4	5	6	7	8	13	14	15	19
Western States:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Oregon	2			2								
Southern Great Plains:												
Texas	2			1								
Oklahoma	2			1	1							
Kansas	2						2					
South-central region:												
Mississippi		1										
Southeastern region:												
Florida	4											
Georgia	8											
Tennessee							2					
West Virginia	2		1						1			
North-central region:												
Iowa	2	4	4	2	1	3		3		1	1	4
Illinois												
Wisconsin												2
Minnesota												
Northern Great Plains:												
North Dakota												
Northeastern region:												
New Jersey												
New York		2										
Maine		2										
Canada:												
Manitoba		2	2			1						
Ontario		2										
Quebec			1					2				
Total	24	13	8	6	2	4	4	5	1	1	1	6

Region and State or Province	Collections of physiologic form—									Total isolations	
	20	21	22	23	24	25	26	27	28	Cultures	Forms
Western States:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Oregon			2							6	3
Southern Great Plains:											
Texas										3	2
Oklahoma	3									7	4
Kansas										4	2
South-central region:											
Mississippi								1		2	2
Southeastern region:											
Florida										4	1
Georgia										8	1
Tennessee				2			2			6	3
West Virginia										4	3
North-central region:											
Iowa	2			1		4				32	13
Illinois									2	2	1
Wisconsin			2							4	2
Minnesota					2	1				3	2
Northern Great Plains:											
North Dakota									3	3	1
Northeastern region:											
New Jersey				2						2	1
New York										2	1
Maine										2	1
Canada:											
Manitoba	2	1			2		2			12	7
Ontario										2	1
Quebec				1						4	3
Total	7	1	4	6	4	5	4	1	5	112	21

Form 1 was the most widely distributed and prevalent of all in 1930. It was, however, apparently limited almost entirely to the region where it may hibernate on fall-sown or volunteer oats. Two cultures from Iowa were identified as form 1. One of these was collected from naturally inoculated *Rhamnus lanceolata* and the other from oats growing near these infected bushes. Apparently form 1 spread northward but little, neither was it widely disseminated from *Rhamnus*. The next most prevalent and widely distributed was form 2, a form standing in direct contrast to form 1 insofar as virulence and aggressiveness are concerned. Except for one culture from Mississippi, it was collected only in the Northern States and Canada.

Form 2 was no doubt dependent upon *Rhamnus* for dissemination in that year. Four of the cultures from Iowa, representing form 2, were from artificially inoculated *Rhamnus;* one was from *R. infectoria* and three were from *R. tinctoria*. Forms 20, 22, 23, and 26 were limited in prevalence but widespread in distribution. Two forms, 14 and 15, were collected only from artificially inoculated *Rhamnus* and, as previously stated, probably originated as a result of hybridization or segregation.

Forms 3, 6, 8, 19, 21, 24, 25, and 28 were collected only in the spring-sown-oat region, whereas forms 4, 5, 7, 13, and 28 were most prevalent in the winter-oat States. Form 7, the most prevalent in 1929, was apparently very limited in distribution in 1930, being collected only in Kansas and Tennessee, where it was prevalent in 1929.

Four cultures of form 3 from Iowa were collected from artificially inoculated *Rhamnus*, two from *R. cathartica* and one each from *R. infectoria* and *R. tinctoria*. A single culture of each of forms 4, 5, 6, 14, 15, and 23, from Iowa, were collected from artificially inoculated *R. cathartica*, *R. infectoria*, *R.* spp. (from Peiping), *R. infectoria*, *R.* spp. (from Siberia), and *R. infectoria*, respectively. Three cultures of form 8, from Iowa, were collected from artificially inoculated *R. cathartica*, *R. infectoria*, and *R. tinctoria*. Four cultures from Iowa, representing form 19, were obtained from artificially inoculated *Rhamnus*, one each from *R. chlorophora* and *R. infectoria*, and two from *R. montana*.

SURVEY OF 1931

Five forms, not previously identified by the writer, were isolated from 127 cultures collected from 16 States in the United States and Mexico and 3 Provinces in Canada in 1931. In addition to these, 11 forms previously isolated were recovered, making a total of 16 forms identified among the 1931 collections (table 11). Form 1 was again the most prevalent, although form 7 was equal in distribution. Both forms were limited in occurrence mainly to the region of winter-oat production. Forms 4, 11, 16, 20, 24, 25, and 30 were limited to the spring-sown-oat area, while forms 2, 6, and 29 were found only in the Northern States and Quebec. Form 30, the most aggressive and virulent form so far identified, was represented by one culture from Florida.

TABLE 11.—*Distribution of physiologic forms of Puccinia coronata avenae in the United States, Mexico, and Canada in 1931*

Region and State or Province	Number of collections of physiologic form—																Number of total isolations	
	1	2	3	4	6	7	9	11	16	20	24	25	29	30	31	32	Cultures	Forms
Western States:																		
California	1									2		2					5	3
Oregon				2		2									1		5	3
Mexico:																		
Coahuila						2											2	1
Guanajuato						1											1	1
Querétaro	1			1		1											3	3
Southern Great Plains:																		
Texas	17					1	1			3					1		23	5
Oklahoma				1		4											5	2
Kansas	6					2									1		9	3
South-central region:																		
Louisiana	1		1			3				3							8	4
Arkansas	1														1		2	2
Missouri	3															2	5	2
Southeastern region:																		
Florida	9							1	1		3			1		1	16	6
Georgia	5			1		3			3								12	4
Tennessee				1									1				2	2
North-central region: Iowa	9					1	4						1				15	4
Northern Great Plains: North Dakota			2		1												3	2
Northeastern region: New York													5				5	1
Canada:																		
Manitoba															2		2	1
Quebec		1											1			2	4	3
Total	53	1	3	6	1	20	5	1	4	8	3	2	8	1	6	5	127	16

SURVEY OF 1932

Nine forms were isolated from 48 cultures collected from 16 States in the United States and 1 Province in Canada in a preliminary study of the collections obtained in 1932 (table 12). All except form 33 had been collected in previous years. Forms 1 and 7 continued to be the most widely distributed. Form 16, prevalent in Georgia and Florida in 1931, was the next most widely distributed. None of the cultures was collected from *Rhamnus*, although one culture from Iowa, representing form 3, was collected from oats growing near infected *Rhamnus cathartica*.

Form 33 is important because it is the only one known to be capable of producing a susceptible reaction on Bond. The history of form 33 indicates that it probably originated as a mutant in a culture representing form 1. A single-uredium culture, isolated from a collection obtained at Temple, Tex., in June 1932, was identified in November as form 1. The culture was then transferred to another greenhouse and increased for use in a study of inheritance of resistance to form 1. Successive generations of the cultures were used to inoculate hybrid plants of which Bond was one parent. The Bond parent was used as a check and consistently produced a nearly immune reaction until late in January 1933 when a single large uredium was observed on one Bond plant. This uredium was increased and the resulting culture identified as form 33. Additional single-uredium cultures from the same original collection were all identified as either form 1 or 7. Bond has consistently produced a susceptible reaction to form 33, although Green Russian (C.I. 2890), Glabrota, and the two Victoria varieties have been immune or nearly immune.

TABLE 12.—*Distribution of physiologic forms of Puccinia coronata avenae in the United States and Canada in 1932*

Region and State or Province	Collections of physiologic form—									Total isolations	
	1	3	4	6	7	16	25	29	33	Culture	Forms
Western States:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No*	*No.*	*No.*	*No.*	*No.*
Oregon					2					2	1
Southern Great Plains:											
Texas	2				1					3	2
Kansas	1				1		1			3	3
South-central region:											
Louisiana	1									1	1
Arkansas	1			1		1				3	3
Southeastern region:											
Florida	1			1						2	2
Georgia	2					1				3	2
Tennessee	2				2	1				5	3
North-central region:											
Iowa	3	1	1	3	1				1	10	6
Illinois	1				1	1				3	3
Indiana					1					1	1
Wisconsin								1		1	1
Michigan	1				2					3	2
Northern Great Plains:											
North Dakota	1									1	1
Northeastern region:											
Pennsylvania					1	1				2	2
New York					3			1		4	2
Canada:											
Manitoba								1		1	1
Total	16	1	1	5	15	3	1	3	1	48	9

SUMMARY OF SURVEY

A total of 533 single-uredium cultures were isolated from collections obtained in 29 States in the United States, 3 States in Mexico, and 3 Provinces in Canada, in the 6-year period 1927–32. Thirty-three distinct physiologic forms were identified among these 533 cultures by the reaction of the standard differential hosts previously described. The distribution and prevalence of these forms among the 35 States and Provinces are given in table 13.

A total of 22 physiologic forms have been identified among 151 cultures collected in Iowa in the period 1927–32. Sixty-one of these cultures were collected from naturally and artificially inoculated *Rhamnus* plants, 89 from naturally inoculated oat plants growing under field conditions, and 1 from artificially inoculated oats growing under greenhouse conditions. All except 3 of the cultures from *Rhamnus* and 52 of those from oats were collected at Ames, Iowa. Fourteen of the 22 forms from Ames were identified among the cultures from *Rhamnus* and 13 among those from oats. Although forms 1, 6, 16, and 19 were collected from oats at Ames, it is possible that they were initially disseminated from artificially inoculated *Rhamnus*. Hence only forms 1, 3, 7, 9, 12, 17, 20, 26, and 29 can be considered definitely as occurring naturally in Iowa. These 9 forms were represented in 32 cultures collected in parts of Iowa other than Ames or near the *Rhamnus* nursery at Ames. Therefore, in a discussion of the natural distribution of physiologic forms in the United States, consideration must be given to the fact that 14 of the 21 forms collected in Iowa may have been dependent upon *Rhamnus* for their dissemination and 12 of these dependent upon artificially inoculated *Rhamnus* species. As previously stated, form 33 probably originated as a mutation.

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TABLE 13.—*Distribution of physiologic forms of Puccinia coronata avenae in the United States, Canada, and Mexico, 1927–32, inclusive*

Region and State or Province	Number of collections of physiologic form—																														Number of total isolations	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Cultures	Forms
Western States:																																			
California	3						3													2					2									10	4
Oregon	4			4			7															2								1			18	5
Mexico:																																			
Coahuila							2																											2	1
Guanajuato							1																											1	1
Querétaro	1			1			1																											3	3
Southern Great Plains:																																			
Texas	28			1			7		1			1								3											1			42	7
Oklahoma	8			2	1		6													3													20	5
Kansas	14						22										1								1						1			39	5
South-central region:																																			
Louisiana	2		1				3													3										1			9	4
Arkansas	2					1										1																	5	4
Missouri	4		1				4										2														2			13	5
Mississippi	9	1					4																					1						15	4
Southeastern region:																																			
Florida	20					1	4				1					1								3					1		1			32	8
Georgia	21			1			10									4																		36	4
Alabama	2																																	2	1
Tennessee	9			1			10									1							2			2			1					26	7
Virginia	2						4																											6	2
West Virginia	3		5				3						1			7	2																	21	6
North-central region:																																			
Iowa	35	4	28	3	1	6	22	3	4		2	1	2	2		7	3	13	6	2			1		4				1				1	151	22
Illinois	1						1			1						1												2						6	5
Indiana							1																											1	1
Wisconsin																			2			2							1					5	3
Minnesota	1						3																	2	1									7	4
Michigan	1						2																											3	2
Northern Great Plains:																																			
Nebraska			1																															1	1
South Dakota							1																											1	1
North Dakota	2		6			1				1																		3						13	5
Northeastern region:																																			
Ohio			1																															1	1
Pennsylvania							1									1																		2	2
New Jersey																								2										2	1
New York		2					3																						6					11	3
Maine		2																																2	1
Canada:																																			
Manitoba		2	2			1														2	1			2		2				1		2		15	9
Ontario		2	1																															3	2
Quebec		1	2					2															1						1			2		9	6
Total	172	14	48	13	2	10	125	5	5	1	2	3	2	2	2	23	8	13	8	15	1	4	6	7	8	4	1	5	11	1	6	5	1	533	33

Physiologic forms 1 and 7 were by far the most prevalent and widely distributed of any during the period of this investigation. Form 1 was represented by 172 cultures collected in 21 States and Provinces, while form 7 was represented by 125 cultures from 24 States and Provinces. Twelve of the cultures indentified as form 1 were collected from artificially and naturally inoculated *Rhamnus*, while the remaining 160 cultures were collected from naturally inoculated oats growing under field conditions. All of the 125 cultures, representing form 7, were from naturally infected oat plants. Except in 1928, forms 1 and 7 were very similar in distribution and prevalence. In that year they were collected from the same regions, but form 1 was much more prevalent. Both forms were found to hibernate on fall-sown and volunteer oats in the South and on the Pacific coast as far north as Astoria, Oreg. Apparently, forms 1 and 7 spread northward in the spring and summer into the spring-oat region. In addition, form 1 is disseminated by naturally inoculated *Rhamnus lanceolata* in the lower Mississippi Valley. All cultures collected from naturally inoculated *R. lanceolata* have been identified as form 1.

Dietz and Leach (*11*), in describing the distribution of *Rhamnus lanceolata*, state:

> Its northern limit is the central parts of Iowa, Illinois, and Indiana, and the southern parts of Ohio and Pennsylvania, although along the rivers it may be found somewhat north of this line. It is commonly found as far south as Alabama and Texas, although in the Southern States it is largely replaced by *R. caroliniana*.

Form 7 is seemingly dependent upon hibernation for its survival; at least, it was not collected from naturally or artificially inoculated *Rhamnus*. The fact that forms 1 and 7 consistently appeared each year in the southern oat region and in decreasing prevalence northward seems to be further proof that these two forms hibernate in the fall-sown-oat region and spread northward in the spring and early summer. Form 1 was collected in 1 State and form 7 in 3 States in Mexico in 1931. With the exception of form 4, these were the only forms found in Mexico in 1931.

Form 3 was the next most prevalent and widely distributed. It and forms 1 and 7 were the only ones collected and identified in each of the years during the period 1927–32. With the exception of one culture collected on May 27, 1931, at Calhoun, La., form 3 was always collected in the spring-oat region from either naturally or artificially inoculated *Rhamnus* or from oats growing near naturally inoculated *R. cathartica*. A total of 48 cultures, representing form 3, were collected from 7 States in the United States and 3 Provinces in central and eastern Canada. Of these 48 cultures, 18 were collected from artificially and naturally inoculated *Rhamnus*. All the cultures collected from naturally inoculated *R. cathartica* were identified as form 3. *R. cathartica*, although a native of Europe, is widely grown as a hedge plant in the upper Mississippi Valley and the Northeastern States, where it has escaped from cultivation and become naturalized. Form 3 probably was almost entirely dependent upon *R. cathartica* and possibly other species of *Rhamnus* for its initial spring appearance. Apparently it seldom if ever hibernated in the winter-oat region, and the primary reason no doubt largely lies in the fact that most of the southern oat varieties, and especially the fall-sown ones, are resistant to form 3.

Of the remaining 29 forms, forms 6, 11, 16, 20, 22, 23, 24, 25, 26, 31, and 32 were widely distributed and not limited to either the spring-sown or fall-sown areas. These forms apparently are all aggressive enough to be able to hibernate on fall-sown and volunteer oats in the South. Forms 11, 20, 24, 31, and 32 are known to hibernate in the South because they were collected in winter and early spring before *Rhamnus* plants became infected. It is probable, because of their wide distribution and limited prevalence, that most of these forms also were disseminated from naturally inoculated *Rhamnus* in the Northern States.

Forms 4, 5, 9, 12, 13, 17, 27, and 30 were predominantly southern ones, although 9, 12, and 17 occurred naturally as far north as Iowa. These three forms, however, have been observed to hibernate in the South, and it is possible that favorable winds carried urediospores north from the points of hibernation. Among this group of southern forms was form 30, the most aggressive of the 33 identified. With the exception of forms 5 and 9 all these apparently southern forms are more aggressive than form 7, which, without doubt, hibernates in the South. Because of the small number of cultures representing each of them it is impossible to state definitely that they were limited to the Southern States. If, however, these forms were distributed to any extent in the North or disseminated from *Rhamnus* their prevalence must have been very limited.

In contrast to the forms just mentioned, forms 2, 8, 10, 19, 21, 28, and 29 were northern ones. With one exception they were collected only in the Northern States and Canada, and always in the spring-oat region where the various *Rhamnus* species function as alternate hosts. One culture of form 2 was collected at State College, Miss., in 1930. Forms 29, 2, 19, and 28 were very restricted, while form 10 was comparatively highly aggressive. All of these northern forms apparently were dependent upon *Rhamnus* for their initial dissemination.

Forms 14, 15, and 18 were collected only from artificially inoculated *Rhamnus*. Since the *Rhamnus* species from which these forms were obtained are not indigenous either to the United States or Canada and were artificially inoculated it is entirely possible that these three forms were not naturally distributed in the United States or Canada.

A total of 300 cultures were collected from Mexico and the States where crown rust may hibernate on fall-sown or volunteer oats, and 172 cultures (exclusive of those collected at Ames, Iowa, from or near infected *Rhamnus*) were collected in the Northern States and Canada where crown rust does not hibernate and where the alternate host is known to function. Twenty-four forms were identified among the 300 cultures from the South, while 31 were represented in the 172 cultures from the North. It is evident from these data and from tables 7 to 13, inclusive, that the South was more evenly and thoroughly represented each year than the North. Everything being equal, therefore, a much larger proportion of forms should have been represented in the South. The obvious explanation for this apparent predominance of forms in the North is the fact that those hibernating in the South remain stable, while forms in the North may be greatly affected by hybridization and segregation.

REACTION OF OAT VARIETIES

Our knowledge of the distribution and prevalence of the 33 physiologic forms of *Puccinia coronata avenae* identified in the period 1927–32 would be of greater value if something was known of the reaction of important commercial oat varieties to these same forms. Time and labor would not permit a determination of the reaction of these varieties to all of the 33 forms. Instead, forms 1, 3, 7, 16, 17, and 18 were selected. Forms 1, 3, 7, and 16 were used because they were widely distributed and prevalent. These four forms are apparently the most important from an economic standpoint. Forms 17 and 18 were, at the time of their selection, of particular interest because of their origin. These six forms range in versatility from the very aggressive form 1 to the very restricted form 18.

The seedling reaction of 266 varieties of oats to these 6 forms was determined. The reactions of any particular variety to the 6 forms were obtained simultaneously under identical conditions. The seed of each variety came from a single panicle, was sown simultaneously, and was grown side by side in the greenhouse. The inoculations with the six forms were made simultaneously, as were also the reaction determinations. There should be no variation, therefore, in the reaction of a particular variety to the six forms because of environmental differences or variability in the genetic constitution of the seed. The number of days from inoculation until the first appearance of telia was recorded for each variety inoculated with forms 3 and 7.

The reaction of adult plants under field conditions is in many respects more important than that of seedling plants to specific physiologic forms under greenhouse conditions. Sufficient crown rust had developed in 21 of the 33 uniform nurseries listed in table 2, at the time they were inspected, to show possible significant differences in the reaction of the varieties. Besides the varieties in these 21 uniform nurseries, others were observed at Ames, Iowa, in 1929–32, and at Manhattan, Kans., in 1930.

The infection coefficients were computed for each year that a variety was observed, and if the variety was observed at a particular station more than 1 year the average infection coefficient was computed for that station. The weighted average infection coefficient was also computed for each variety. These coefficients are of limited value, because certain varieties were not grown at all stations or in all of the years; moreover, the severity of the crown-rust epiphytotics varied greatly at the several stations in the different years. The same limitations would be less applicable to a percentage of weighted mean, which might be calculated for each variety.

In table 14 are shown the infection type on seedling plants of each variety artificially inoculated with forms 1, 3, 7, 16, 17, and 18 and the average infection coefficients for adult plants of each variety growing under field conditions at various locations in the United States.

TABLE 14.—*Reaction of 266 oat varieties to 6 physiologic forms of Puccinia coronata avenae, and infection coefficients on varieties grown under field conditions for the years indicated at 12 experiment stations*

[T = trace]

Variety tested	C.I. no.	Infection type on seedling plants inoculated with physiologic form—						Infection coefficients for the years indicated on varieties grown at—																										Times observed	Weighted average of infection coefficient
								Ames, Iowa					Manhattan, Kans.				Stillwater, Okla.			Fayetteville, Ark., 1931	Denton, Tex.				Calhoun, La., 1931	State College, Miss., 1929	Knoxville, Tenn., 1929	Clemson College, S.C., 1930	Experiment, Ga.			Tifton, Ga., 1929	Gainesville, Fla., 1931			
		1	3	7	16	17	18	1929	1930	1931	1932	Average[1]	1929	1930	1931	Average[1]	1929	1931	Average[1]		1929	1930	1931	Average[1]					1928	1929	Average[1]					
Alabama Hybrid	971	4	3	4	4	4	4	40	60	40	40	45.0	30			30.0	20		20.0		20			20.0		50	0		10	2	6.0	3		12	26.25
Alber	2766	4	0	0	0	0	0		4	2	2	2.7		2		2.0		0	0	3		0	2	1.0				T−						10	1.51
Albion	729	4	4	4	4	4	4	20	20	60	36	34.0	50			50.0																		5	37.20
Alcot White	3059	4	4	4	0	4	0	25	30			27.5	50			50.0	15		15.0		35			35.0		70	0		T−	10	5.0	30		10	26.51
Algerian	3066	4	3	4	4	4	4	12	10	16	36	18.5	25			25.0	15		15.0		15			15.0		10	0		T−	T	.1	0		12	11.60
Algerian Cape	1002	4	0	4	0	1	2	T−	5	10	5	5.0	35			35.0																		5	11.02
Algerian×Calcutta	2807	4	4	4	4	4	4	20	32		45	32.3	20	5		12.5	T−		.1		T−	50		25.0		T−	0	T	5	3	4.0	T−		14	12.90
Anthony	2143	4	4	0	0	0	0	45	24	32	45	36.5	20	6	3	9.7	10	T	5.1	9	20	15	4	13.0	20	25	T−	40		T−	.1	40	4	20	18.12
Argentine	993	4	4	4	2	2	2	14	15	70	40	34.8	50			50.0																		5	37.80
Aurora	831	4	4	4	4	4	4	50	60	91	85	71.5	65			65.0																		5	70.20
Avena brevis	1783	4	0	0	4	4	4	5	2	T−	3	2.5	3	4	0	2.3	0	0	0	3	0	T	0	.1		0	0	T		0	0	0		18	1.14
A. brevis	2513	4	0	3	4	3	4		20	40	40	33.3		15	0	7.5						20	0	20.0	0		30						8	18.33
A. strigosa	1782	3	0	4	4	4	4	4	3	5	2	3.5	6	3	0	3.0		0	0	5		0	0	0	6		10					0	14	3.14
Do	2525	4	4	4	4	4	4		30	2	3	11.7																						3	11.70
Avoine du Maroc	1789	4	4	4	0	0	0	T−	5	30		11.7	6			6.0																		4	10.28
Awnless Culred	2676	4	4	4	4	4	4	20	20			20.0	60			60.0																		3	33.33
Awnless Monarch	1879	4	4	4	4	4	4	11	5			8.0	35			35.0																		3	17.00
Awnless Probsteier	1888	4	4	4	4	4	4	50	5			27.5	40			40.0																		3	31.67
Bathurst	1810	4	0	4	0	4	0	3	30	24	21	19.5	5	6	0	3.7	0	0	0	9	T−	T	1	.7	9	50	0	T	T−	0	.1	10	T	21	8.04
Belar	2760	3	0	4	0	4	0	2	20	15	32	17.3	8	3	0	3.7	T	0	.1	8	3	T−	T−	1.6	50	10	0	10	1	T−	.6	0	15	21	8.45
Do	2770	4	1	4	1	4	1	3	30	30	32	23.8	8	4		6.0	T−		.1		4	T−		2.1		20	0	T		T−	.1	10		14	10.11
Belyak	1630	4	4	4	4	4	4	30	40	60	40	42.5	50			50.0																		5	44.00
Bicknell	206–151	4	2	4	0	4	0	40	50	70		53.3	50			50.0																		4	52.50
Biffen White Winter	2011	4	4	4	4	4	4	20	10			15.0	50			50.0	4		4.0		25			25.0		85	0		1	T−	.6	30		10	22.51
Do	2012	4	4	4	4	4	4	35	10			22.5	50			50.0	4		4.0		30			30.0		75	0		5	T−	2.6	30		10	23.91
Black Algerian	3065	4	1	4	0	4	0	T−	5	3		2.7	3		2	2.5		0	0	4	5		T	2.6	36	32	0		5	T−	2.6	5	4	16	6.53
Do	840–1	4	1	4	0	4	0	15	T	T	7	5.6		T+		.3						T		.2										6	3.27
Do	2015	4	1	4	1	4	1	3	3			3.0	30			30.0	3		3.0		10			10.0		45	0		2	T−	1.6	8	0	11	10.41

[1] Only those years for which there are reports on infection are included in the average, and where there is such a report for only one year the figure for that year is carried into the "Average" column.

TABLE 14.—*Reaction of 266 oat varieties to 6 physiologic forms of Puccinia coronata avenae, and infection coefficients on varieties grown under field conditions for the years indicated at 12 experiment stations*—Continued

[T = trace]

Variety tested	C.I. no.	Infection type on seedling plants inoculated with physiologic form—						Infection coefficients for the years indicated on varieties grown at—																										Times observed	Weighted average of infection coefficient
								Ames, Iowa					Manhattan, Kans.				Stillwater, Okla.			Fayetteville, Ark., 1931	Denton, Tex.				Calhoun, La., 1931	State College, Miss., 1929	Knoxville, Tenn., 1929	Clemson College, S.C., 1930	Experiment, Ga.			Tifton, Ga., 1929	Gainesville, Fla., 1931		
		1	3	7	16	17	18	1929	1930	1931	1932	Average	1929	1930	1931	Average	1929	1931	Average		1929	1930	1931	Average					1928	1929	Average				
Black Bell I	1767	4	4	4	4	4	4	12	40	48		33.3	50			50.0																		4	37.50
Black Bell II	1308	4	4	4	4	4	4	22	16	48		28.7	50			50.0																		4	34.00
Black Diamond	1878	4	3	4	4	4	4	12	50	40	60	40.5	50			50.0																		5	42.40
Black Mesdag	1877	4	4	4	4	4	4	18	20	80	65	45.8	70			50.0																		5	50.60
Black Mogul	1074	4	4	3	4	4	4	50	10	50	45	38.8																						4	38.75
Black President	1992	4	3	4	4	4	4	60	60	16		45.3	50			50.0																		4	46.50
Black Rival	807	4	4	4	4	4	4	40	40	60	80	55.0	60			60.0																		5	56.00
Black Speckled	1817	4	4	4	4	4	4	36	20			28.0	55			55.0																		3	37.00
Black Tartar	991	4	2	4	4	4	4	25	20	30		25.0	30			30.0	10		10.0		5			5.0		30	T		15	5	10.0	5		11	15.92
Black Winter	606	4	2	4	4	4	4	25	24	30	40	29.8	50			50.0																		5	33.80
Blue Stem	3070	4	0	4	0	4	0	20	40			30.0	40			40.0	5		5.0		20			20.0		55	0		5	T	2.6	60		10	24.51
Bond	2733	I	I	0	I	I	I			0	0	0	0			0																		3	0
Boswell	480	4	4	4	4	4	4	40	40			40.0	70			70.0																		3	50.00
Brunker	2054	4	4	4	4	4	4	20	8	30	24	20.5	30			30.0	5		5.0		12			12.0		85	0			T	.1	40		11	23.10
Buddah	2799	4	4	4	4	4	4	20	20	40	40	30.0	35	15		25.0	8		8.0		30	T		15.1		10		20	T	T	.1	8		14	17.60
Burt	1436	4	4	4	4	4	4	20	30	50	54	38.5	40			40.0	5		5.0		8			8.0		10	0				5	5.0	5		11	20.64
Do	1861	4	4	4	4	4	4	10	10	30	40	22.5	50			50.0																		5	28.00
Do	2043	4	4	4	0	4	0	25	35	50	40	37.5	45			45.0																		5	39.00
Calcutta	994	4	4	4	4	4	4	40	50	50	28	42.0	25			25.0																		5	38.60
Calcutta×Cape	2802	4	0	3	0	2	0	2	8	20		10.0	40	5	0	15.0	5	0	2.5	4	10	T	8	9.1		15	0	5	T	5	2.6	5		18	7.35
Capa	2765	3	0	3	0	0	0		9	10	15	11.3		8	0	4.0		0	0	2		T	T−	.1				T−						10	4.44
Canadian	1625	4	3	4	4	4	4	36	70	40		48.7	60			60.0																		4	51.50
Castleton Potato	1972	4	4	4	4	4	4	10	10			10.0	50			50.0																		3	23.33
Cassel	1859–4	4	0	4	0	3	1	20	50	40	65	43.8	50			50.0																		5	45.00
Chinese (hull-less)	1003	4	4	4	4	4	4	50	60	20	80	52.5	70			70.0																		5	56.00
Chorol	2060	4	4	4	4	4	4	3	5	10	40	14.5	50			50.0																		5	21.60
Coastblack	1025	4	4	4	4	4	4	23	10			16.5																						2	16.50
Cole	834	4	4	4	4	4	4		40	40	36	38.7																						3	38.67
Colburt	2019	4	4	4	4	4	4	70	50	80	50	62.5	50			50.0	25		25.0		40			40.0		90	T−		20	T−	10.1	90		12	47.10
College Algerians	2052	4	1	4	0	4	0	25	20	6	45	24.0	30	5	4	13.0	5	T	2.6	5	5	T+	5	5.2	27	10	0	5	5	T−	2.6	5	30	21	11.31
Colorado No. 37	1640	4	4	4	4	4	4		5	50	50	35.0																						3	35.00
Comewell	1317	4	4	4	4	4	4		20	40	45	35.0																						3	35.00

Cornellian	1842	4	4	4	4	4	4	5	5	10	28	12.0	40	10	2	17.3	5	0	2.5	T		5	9	7.0	5			5						14	9.23
Cowra	2761	4	0	4	0	4	0	28	30	40	80	44.5	50	15	25	30.0	5	T	2.6	20	20	40	15	25.0	50	25	0	25		5	2.5	0	10	20	24.16
Culberson	273	4	4	4	4	4	4	60	60	80	85	71.3	60			60.0	30		30.0		35			35.0		95	10		15	5	10.0	10		12	45.42
Culred	189-518	4	4	4	4	4	4	25	70			47.5	60			60.0																		3	51.67
Custis	2041	4	0	4	0	0	0	60	5			32.5	55			55.0	10		10.0		8			8.0		95	0		35	5	20.0	20		10	29.30
Danish Giant	1989	4	3	4	4	4	4	12	20			16.0	45			45.0																		3	25.67
Danish Island	1684	4	4	4	4	4	4	35	30	5	44	28.5	40			40.0																		5	30.80
Do	1897	4	4	4	4	4	4	12	20			16.0	60			60.0																		3	30.67
Daubeney	1621	4	4	4	4	4	4	25	20	80	65	47.5	50			50.0																		5	48.00
Dookie No. 10	2829	4	2	4	0	4	0	40	40	45	65	47.5	45			45.0	25		25.0		30			30.0		70	T—		20	20	20.0	60		12	38.25
Diamond (hull-less)	2640	4	4	4	4	4	4			20	30	25.0																						2	25.00
Dwarf Culberson	748	4	4	4	4	4	4	60	70	40	80	62.5	50			50.0																		5	60.00
Early Blonde	3060	4	2	4	1	4	0	35	50	20	85	47.5	50			50.0	20		20.0		25			25.0		24	T—		10	10	10.0	60		12	32.43
Early Burt	3061	4	0	4	0	4	0	10	10			10.0	36			36.0	5		5.0		12			12.0		10	0		30	5	17.5	8		10	12.60
Do	2763	4	0	4	0	4	0		30	10	10	16.7		15	4	9.5		0	0	4		10	14	12.0	40			10					15	12	13.50
Early Champion	1623	4	4	4	4	0	4	50	10	20	45	31.3	50			50.0																		5	35.00
Early Joanette	1092	4	4	4	4	4	4	16	20	30	40	26.5	60			60.0																		5	33.20
Do	1393	4	4	4	4	4	4		10			10.0																						1	10.00
Early May	2828	4	0	4	0	4	0	10	5	20	21	14.0	45			45.0	5		5.0		20			20.0		10	0			5	5.0	8		11	13.54
Early Mountain	1624	4	4	4	4	4	4	30	70	40	70	52.5	50			50.0																		5	52.00
Early Ohio	3073	4	4	4	4	4	4		20	80	80	60.0																						3	60.00
Early Ripe	2803	4	1	4	1	4	0	10	10	30	50	25.0	50	10		30.0	5		5.0		20	T		10.1		15	0	5	T—	50	25.6	40		15	19.69
Echo	1892	4	4	4	4	4	4	18	15	40	45	29.5	55			55.0																		5	34.60
Edkin	2330	4	4	4	1	4	0		40	20	50	36.7																						3	36.67
Empire	1974	4	4	4	4	4	4	40	5	10	40	23.8																						4	23.75
Extra Early	3062	4	0	4	4	0	4	25	T	5	35	16.3	60			60.0																		5	25.04
Ferguson Navarro	966	4	4	4	4	3	4	60	60	30	85	58.8	60			60.0																		5	59.00
Forward	2242	4	4	4	4	4	4	40	8	10	36	23.5																						4	23.50
Fowlds (hull-less)	1996	4	4	4	4	3	4	40	5	40	36	30.3																						4	30.25
Fortune	1983	4	4	4	4	4	4	16	8	6	36	16.5	55			55.0																		5	24.20
Frazier (Tex. No. 765)	3071	4	4	4	4	4	4	20	5	40	45	27.5	50			50.0																		5	32.00
Frazier (Tex. No. 765–19)	3072	4	0	4	4	4	4	30	5	35	50	30.0	60			60.0																		5	36.00
Frazier	2381	4	4	4	4	4	4	30	40	40	40	37.5		30	20	25.0		T	.1	27		60	5	32.5				20						11	28.38
Fulghum	650-203	4	3	4	4	4	4	30	50	40		40.0	70			70.0	55		55.0		35			35.0		75	0		10	T—	5.1			10	36.51
Do	650-204	4	3	4	4	4	4	40	40	20	50	37.5	25	40		32.5	25		25.0		24	5		14.5		70	0	60	10	5	7.5	12		15	28.40
Do	2498	4	4	4	4	0	4	40	50	40		43.3	45			45.0	30		30.0		45			45.0		65	T—		15	5	10.0	15		11	31.83
Do	2499	4	4	4	4	4	4	70	80	40		63.3	80			80.0	40		40.0		40			40.0		50	T—		25	10	17.5			10	43.51
Do	2500	4	4	4	4	4	4	60	60	40		53.3	80			80.0	45		45.0		35			35.0		65	T—		40	10	25.0			10	43.51
Do	3067	4	4	4	4	4	4	35		40		37.5	50			50.0	35		35.0		25			25.0		40	0		10	30	20.0	16		10	28.10
Do	708	4	3	4	4	4	4	50	40	50	45	46.3	60			60.0																		5	49.00
Do	708-204	4	4	4	4	4	4	70	90	80		80.0	80			80.0	45		45.0		40			40.0	0	70	T—		20	5	12.5	40		12	49.10
Do	1360-217	4	4	4	4	4	4	30	50	20	45	36.3	60			60.0	35		35.0		40			40.0		55	T—		10	5	7.5	50		12	33.34
Fulmer	1859-1	4	3	4	4	4	4	10	10	10	18	12.0	28	10		19.0						0		0				5						8	11.38
Garton No. 5	1884	4	4	4	4	4	4	7	24	20	35	21.5	40			40.0																		5	25.20
Garton No. 473	1613	4	4	4	4	4	4	25	30	20	25	25.0	70			70.0																		5	34.00
Garton No. 748	1862	4	4	4	4	4	4	35	40	30	36	35.3	50			50.0																		5	38.20
Garton Gray	1864	4	3	4	4	4	4	16	20	30	36	25.5	55			55.0																		5	31.40
Garton Yellow	1612	4	4	4	4	4	4	30	20	38	36	31.0	50			50.0	20		20.0		35			35.0		80	T—		15	15	15.0	0		12	28.26
Glabrota	2630	0	0	0	4	0	0	0	0	0	T—	0	0		0	0		0	0	0		0	0	0	0			T					2	13	.18
Glen Innes	980	4	4	4	4	4	4	5	10	2	50	16.8	5	6	1	4.0	0	0	0	3	0	T	0	.1	7	50	0	0	T—	0	.1	20	0	21	7.59
Gopher	2027	4	4	4	4	4	4	25	10	20	36	22.8	60			60.0																		5	30.20
Golden	2806	3	4	4	4	4	4	25	40	16	32	28.3	30	10		20.0	25		25.0		8	55		31.5		30	0	60	10	40	25.0	3		15	25.60

TABLE 14.—*Reaction of 266 oat varieties to 6 physiologic forms of Puccinia coronata avenae, and infection coefficients on varieties grown under field conditions for the years indicated at 12 experiment stations*—Continued

[T = trace]

Variety tested	C.I. no.	Infection type on seedling plants inoculated with physiologic form—						Infection coefficients for the years indicated on varieties grown at—																								Times observed	Weighted average of infection coefficient
								Ames, Iowa					Manhattan, Kans.				Stillwater, Okla.			Fayetteville, Ark., 1931	Denton, Tex.				Calhoun, La., 1931	State College, Miss., 1929	Knoxville, Tenn., 1929	Clemson College, S.C., 1930	Experiment, Ga.			Tifton, Ga., 1929	Gainesville, Fla., 1931		
		1	3	7	16	17	18	1929	1930	1931	1932	Average	1929	1930	1931	Average	1929	1931	Average		1929	1930	1931	Average					1928	1929	Average				
Golden Drop	1890	4	3	4	4	4	4	16	30	20	30	24.0	50			50.0																	5	29.20
Do	1988	4	4	3	4	4	4	25	8	50	40	30.8	35			35.0																	5	31.60
Golden Giant	1606	4	4	4	4	4	4	18	10	20		16.0	50			50.0																	4	24.50
Golden Sheaf	2056	4	3	4	4	4	4	20	20			20.0	25			25.0	15		15.0		20			20.0		95	0		T−	T−	0.1	30		10	22.52
Gothland	1898	4	4	4	4	4	4	21	5	60	40	31.5	55			55.0																	5	36.20
Gray	2014	4	0	3	0	2	1	35	10			22.5	60	3		31.5	20		20.0		25	0		12.5		60	T+	T	1	30	15.6	5		13	19.19
Green Mountain	1892	4	4	0	1	1	0	18	15	18	36	21.8	55	15	1	25.7		0	0	T		85	5	45.0	60			60	T−	0	.1		40	16	27.22
Green Russian	1040	4	4	4	4	4	4	8	T	5	21	8.6																					4	8.55
Do	1978	4	4	4	4	4	4	18	20	5	28	17.8	60			60.0																	5	26.20
Do	2342	4	4	4	4	4	4	40	20	70	40	42.5	45	15	5	21.7		0	0	7		25	5	15.0	60			3				10	14	24.64
Do	2344	4	3	4	4	4	4	1	8	24	18	12.8	2	0	0	.7		0	0	2		16	4	10.0	60			10					14	10.36
Do	2890	4	4	4	4	4	4			24	40	32.0			3	3.0		T	.2	T			4	4.0	48							20	8	17.43
Guyra	981	4	0	4	0	0	0	14	40	10	40	26.0	50	20		35.0	16		16.0		20	5		12.5		50	0	5	T−	5	2.6	20		15	19.67
Do	2034	4	3	3	4	3	3	7	10	32	40	22.3	50			50.0	T−		.1		8			8.0		10	0	5	T−	T−	.1	0		13	13.11
Do	2768	4	4	4	4	4	4	12	30		40	27.3	T−	20		10.1						5		5.0									6	15.33
Hajira	1001	4	4	4	4	4	4	20	20	8	36	21.0	28	32		30.0						20		20.0				15					8	22.38
Hamilton	2039	4	4	4	4	4	4	14	24	16		18.0	50			50.0	T−		.1		30			30.0		90	T−		15	T−	7.6	40		11	25.39
Hatchett	838	4	4	4	4	4	4	50	80	50	60	60.0	50			50.0																	5	58.00
Hay	1622	4	4	4	4	4	4	6	5	8	24	10.8	6	2	0	2.7						T		.2				50					9	12.65
Hawkeye (Iowa No. 102)	2464	4	4	0	0	4	0	16	20	54	32	30.5	40	12	8	20.0	5	0	2.5	10	20	10	10	13.3	70	5	0	50		10	10.0	15	20	20	20.35
Hundred Bushel (Hastings)	2797	4	0	4	0	0	0	25	10	5	7	11.8	30	5	5	13.3	T−	0	.1	10	5	T	5	5.1		5	0	35		T−	.1	T−		18	8.19
Idamine	1834	4	4	4	4	4	4	40	8	24	60	33.0																					4	33.00
Iogold	2329	4	4	4	4	4	4	25	40	30	65	40.0	50	50		50.0						20		20.0				30					8	38.75
Iogren	2024	4	4	4	4	4	4	27	30	40	18	28.8	31	12		21.5						20		20.0				50					8	28.50
Iomine	2827	4	4	4	4	4	4	36	16	40	32	31.0	40			40.0	10		10.0		20			20.0		20	T−			T−	.1	20		11	21.29
Iowa No. 67	2870	4	4	0	0	0	0	16	20	20	20	19.0																					4	19.00
Iowa No. 69	2463	4	4	0	0	0	0	24	40	50	28	35.5	45	5		25.0						40		40.0	30			40					15	10	31.70
Iowa No. 77	2813	4	4	0	0	0	0	16	50	60	25	37.8	40	20		30.0	5		5.0		20	30		25.0		8	0	30		10	10.0	15		14	23.50
Iowa No. 444	2331	4	4	4	4	4	4	18	15	10	36	19.8	31			31.0																	5	22.00
Iowar	847	4	4	4	4	4	4	25	10	20	40	23.8	50			50.0																	5	29.00
Irish Victor	1251	4	4	4	4	4	4	22	10	16	50	24.5	45			45.0																	5	28.60

Ithacan	2141	4	4	4	4	4	4	40	15	30	45	32.5																						4	32.50
Japan	1157	4	4	4	4	4	4	50	10	50	40	37.5																						4	37.50
Do	1889	4	4	4	4	4	4	18	70	20	45	38.3	50			50.0																		5	40.60
Joanette	549	4	4	4	4	4	4		30			30.0																						1	30.00
Do	1880	4	4	4	4	4	4	16	60	12	50	34.5	50			50.0																		5	37.60
"Joanette strain"	2660	4	4	3	4	4	4		90	18	50	52.7																						3	52.67
June	1902	4	4	4	4	4	4	40	18	30	36	31.0																						4	31.00
Kanota	839	4	4	4	4	4	4	50	50	20	54	43.5	45	40	25	36.7		5	5.0	20		20	10	15.0				50						12	32.42
Kansas No. 5213-7	2823	4	0	4	0	3	0		10	18	36	21.3		50	2	26.0		T	.2	20		50	15	32.5	24			50					50	12	27.10
Kareela	2774	4								0	14	7.0			0	0																		3	4.67
Keystone	2146	4	4	4	4	4	4	40	15	10	24	22.3																						4	22.25
Kherson	459	4	4	4	4	4	4	35	30	20	40	31.3	60			60.0																		5	37.00
Do	1885	4	4	4	4	4	4	40	10			25.0																						2	25.00
Do	1905	4	4	4	4	4	4	40	10			25.0																						2	25.00
King	850	4	3	4	4	4	4	40	60			50.0	30			30.0	15		15.0		40			40.0		60	0		15	5	10.0	8		10	27.30
Lachlan	983	4	4	4	4	4	4	40	60			50.0	40			40.0	15		15.0		20			20.0		75	0		15	T	7.6	15		10	28.02
Do	2805	4	1	4	0	4	0	45	10			27.5	60	2		31.0	10		10.0		30	5		17.5		30	0	T		T—	.1	40		12	19.36
Laurel (hull-less)	2231	4	4	4	4	4	4	40	40			40.0	40			50.0	20		20.0		19			19.0		20	0		50	5	27.5	60		10	30.40
Lee	2042	4	1	4	0	4	0	60	60	40	65	56.3	60	50	40	50.0	10	0	5.0	30	20	10	25	18.3		90	T—	10	25	5	15.0	20		19	32.64
Liberty (hull-less)	845	4	4	4	4	4	4	12	10	60	60	35.5	60			60.0																		5	40.40
Lincoln	1262	4	4	4	4	4	4	18	50	30	40	34.5	45			45.0																		5	36.60
Madrid	603	4	4	4	4	4	4	40	70	50	45	51.3	60			60.0																		5	53.00
Magistral	2460	4	4	0	0	0	0	3	T	4	7	3.7	1	0	0	0.3		0	0	1		T	0	.1	6			0					0	14	1.60
Mansholt IIB	1990	4	4	4	3	4	4	20	24	20		21.3	40			40.0																		4	26.00
Mansholt III	2046	4	4	4	4	4	4	27	20			23.5	50			50.0																		3	32.33
Markton	2053	4	4	4	4	4	4	40	70	60	40	52.5	70	50	25	48.3	5		5.0	40		70	25	47.5	80			75					20	14	47.86
Marvellous	1999	4	4	4	4	4	4	16	70	50	40	44.0	60			60.0																		5	47.20
Mortgage Lifter	2804	4	4	4	4	0	4	3	3	25		10.3	6	3	8	5.7	5	0	2.5	10	T—	T	15	7.7		T—	0	0	2	T—	1.6	15		18	5.31
Miami	2245	4	4	4	4	4	4	20	18	24	36	24.5																						4	24.50
Minota	1285	4	4	4	4	4	4	20	10	16	27	18.3	45			45.0																		5	23.60
Minnesota No. 295	1290	4	4	4	4	4	4	50	10		36	32.0																						3	32.00
Mogul	1074	4	4	4	4	4	4	10	10			10.0	65			65.0																		3	26.33
Monarch	1876	4	4	4	4	4	4	10	8	2	32	13.0	50			50.0																		5	20.40
Mongolian (hull-less)	1770	4	4	4	4	4	4	60	90	50	45	61.3																						4	61.25
Mulga	2796	4	1	4	0	4	0	3	T	20	32	13.8	6	10	2	6.0	20	0	10.0	10	10	5	5	6.7		15	0	T	1	T	.6	0		19	7.35
Myall	2800	4	4	4	4	4	4	3	T	8	21	8.1	24	5	0	9.6	8	0	4.0	7	25	T	0	8.4		25	0	T	T—	T—	.1	T—		19	6.68
Nortex	2382	4	0	4	0	4	0	13	20	4	23	15.0	5	5	1	3.6	10	0	5.0	8	T—	T		2.8	45	T	0	5		T	.2	30	9	19	9.41
North Finnish	1882	4	4	4	4	4	4	10	20	60	40	32.5	45			45.0																		5	35.00
O.A.C. Fo. 72	846	4	4	4	4	4	4	18	20	20	40	24.5	60			60.0																		5	31.60
O.A.C. No 144	2476	4	4	4	4	4	4	30	40	30	36	34.0	40			40.0																		5	35.20
Odal	2047	4	4	4	4	4	4	36	10	10	45	25.3	60			60.0																		5	32.20
Old Island Black	2035	3	3	0	4	0	4	12	20	10	65	26.8	50			50.0																		5	31.40
Do	1756	4	3	2	2	2	0		20	60		40.0																						2	40.00
Oriental	1598	4	4	4	4	4	4	30	40	10	20	25.0	60			60.0																		5	32.00
Orion	2048	4	4	4	4	4	4	22	20	30	65	34.3	60			60.6																		5	39.40
Pampa	2767	3	0	3	0	0	0		16	15	36	22.3		5	1	3.0		0	0	4		T—	2	1.5	4			0					0	12	6.93
Patterson	2147	4	4	4	4	4	4	40	18	30	32	30.0																						4	30.00
Pringle Progress	1717	4	4	4	4	4	4	40	10			25.0																						2	25.00
Probsteier	1656	4	4	4	4	4	4	9	10	20	36	18.8	60			60.0																		5	27.00
Rainbow	2345	4	4	3	4	3	4	1	3	10	25	9.8	2	3	0	1.7		0	0	5		0	5	2.5				T						12	4.52

TABLE 14.—*Reaction of 266 oat varieties to 6 physiologic forms of Puccinia coronata avenae, and infection coefficients on varieties grown under field conditions for the years indicated at 12 experiment stations*—Continued

[T=trace]

Variety tested	C.I. no.	Infection type on seedling plants inoculated with physiologic form—						Infection coefficients for the years indicated on varieties grown at—																										Times observed	Weighted average of infection coefficient
								Ames, Iowa					Manhattan, Kans.				Stillwater, Okla.			Fayetteville, Ark., 1931	Denton, Tex.				La., 1931	State College, Miss., 1929	Knoxville, Tenn., 1929	Clemson College, S.C., 1930	Experiment, Ga.			Tifton, Ga., 1929	Gainesville, Fla., 1931		
		1	3	7	16	17	18	1929	1930	1931	1932	Average	1929	1930	1931	Average	1929	1931	Average		1929	1930	1931	Average					1928	1929	Average				
Red Algerian	840	4	0	4	0	4	0	15	30	4	----	16.3	----	2	4	3.0	----	0	0	10	----	T	T	0.2	----	----	----	10	----	----	----	----	----	10	7.54
Do	977	4	4	1	4	4	4	T—	10	3	7	5.0	27	----	----	27.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	9.42
Do	1578	4	4	1	0	4	1	10	30	T—	40	20.0	30	3	----	16.5	----	----	----	----	----	T	----	.2	----	----	----	T	----	----	----	----	----	8	14.19
Do	1993–1	3	2	3	0	2	0	10	40	5	4	14.8	45	3	----	24.0	----	----	----	----	----	T	----	.2	----	----	----	T	----	----	----	----	----	8	13.43
Do	2033	3	3	4	4	4	3	2	20	T—	----	7.4	50	4	----	27.0	----	----	----	----	----	35	----	35.0	----	----	----	T	----	----	----	----	----	7	15.90
Do	2044	4	0	3	0	1	1	2	2	50	----	18.0	50	----	----	50.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	4	26.00
Do	2045	4	3	3	4	4	4	23	20	----	----	21.5	35	----	----	35.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	3	26.00
Red Rustproof	512	4	1	4	4	4	4	3	10	T	20	8.3	24	5	----	14.5	5	----	5.0	----	0	T	----	.1	----	8	0	T	T—	T—	0.1	5	----	15	5.39
Do	518–3	4	1	4	4	4	4	4	5	----	4	4.3	30	5	----	17.5	3	----	3.0	----	0	T	----	.1	----	10	0	0	----	T—	.1	T+	----	13	4.74
Do	844	4	0	4	0	0	0	7	1	4	4	4.0	30	----	----	30.0	5	----	5.0	----	4	----	----	4.0	----	5	0	----	----	1	1.0	2	----	11	5.73
Do	888	4	0	4	0	4	0	3	8	5	4	5.0	30	15	----	22.5	3	----	3.0	----	T+	T	----	.2	----	25	0	T	1	1	1.0	T+	----	15	6.40
Do	921	4	1	4	0	4	0	3	10	----	----	6.5	35	----	----	35.0	5	----	5.0	----	5	----	----	5.0	----	5	0	----	2	T—	1.1	3	----	10	6.81
Do	1008	4	2	4	4	4	4	5	20	----	----	12.5	40	----	----	40.0	10	----	10.0	----	5	----	----	5.0	----	10	0	----	2	T—	1.1	3	----	10	9.51
Do	1039	3	1	4	0	4	0	10	40	3	4	14.3	45	----	----	45.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	20.40
Do	1079	4	1	4	0	4	0	23	20	30	4	19.3	20	5	2	13.5	10	0	5.0	10	15	T+	5	6.8	18	20	0	T	T—	T—	.1	30	10	21	10.60
Do	1089	4	1	4	0	4	0	4	5	10	4	5.8	8	10	1	14.5	8	0	4.0	20	5	T	5	3.4	----	35	0	T	2	T—	1.1	8	----	19	6.60
Do	1450	4	3	4	4	4	4	50	50	----	----	50.0	50	----	----	50.0	10	----	10.0	----	35	----	----	35.0	----	48	----	----	20	5	12.5	----	----	8	33.50
Do	1571	4	0	4	0	4	0	3	10	----	----	6.5	35	----	----	35.0	15	----	15.0	----	16	----	----	16.0	----	45	T—	----	1	5	3.0	15	----	10	14.51
Do	1805	4	1	4	1	4	1	3	20	5	8	9.0	30	5	----	17.5	20	----	20.0	----	T—	T	----	.2	----	T—	0	T	----	T—	.1	8	----	14	7.12
Do	1815	4	0	4	0	4	0	3	----	4	20	9.0	----	----	3	3.0	----	0	0	4	----	4	----	4.0	6	----	----	----	----	----	----	----	10	9	6.00
Do	2808	4	1	4	0	4	0	3	20	40	5	17.0	50	5	10	32.5	----	0	0	30	----	10	15	12.5	----	----	----	T	----	----	----	----	----	12	15.68
Do	2809	4	1	4	0	4	0	T—	50	60	8	29.5	45	3	----	24.0	----	----	----	----	----	10	----	10.0	----	----	----	0	----	----	----	----	----	8	22.01
Richland	787	4	4	4	4	4	4	30	20	40	50	35.0	60	----	----	60.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	40.00
Ruakura	701	4	0	4	0	4	0	60	30	32	36	39.5	45	----	16	30.5	18	0	9.0	20	30	----	20	25.0	----	64	0	----	15	5	10.0	----	----	15	26.07
Do	1961	4	3	4	4	4	4	50	10	40	36	34.0	28	----	----	28.0	20	----	20.0	----	35	----	----	35.0	----	95	T—	----	10	5	7.5	30	----	12	29.93
Do	2025	4	1	4	1	0	0	50	60	40	36	46.5	40	30	----	35.0	30	----	30.0	----	20	85	----	52.5	90	80	T—	10	----	1	1.0	40	0	16	38.26
"Rustless selection" (Rustless)	724	4	4	4	4	4	4	45	T—	20	18	20.8	28	----	----	28.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	22.22
Schoolmam	2057	4	4	4	4	4	4	2	5	15	14	9.0	3	3	1	2.3	----	T	.2	2	----	0	T—	.1	----	----	----	0	----	----	----	----	----	12	3.78
Scottish Chief	1699	4	3	4	4	4	4	18	5	20	27	17.5	50	----	----	50.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	24.00
Seizure	1609	4	4	4	4	4	4	25	5	20	25	18.8	50	----	----	50.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	25.00

Sidney	3063	4	1	4	1	4	1	35	40	T—	----	25.0	45	----	----	45.0	10	----	10.0	----	5	----	----	5.0	----	24	0		10	5	7.5	0	----	11	14.92
Silvermine	1013	4	4	4	4	4	4	25	30	20	30	26.3	50	----	----	50.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	31.00
Silvermine selection	1894	4	4	4	4	4	4	14	8	----	----	11.0	35	----	----	35.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	3	19.00
Sir Douglas Haig	1987	4	3	4	4	3	4	35	10	40	----	28.3	40	----	----	40.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	4	31.25
Sixty-Day	1887	4	4	4	4	4	4	15	15	----	----	15.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	2	12.50
Do	1906	4	4	4	4	4	4	10	10	50	50	30.0	60	----	----	60.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	36.00
Sparrowbill	1604	4	3	4	4	4	4	18	10	40	40	27.0	50	----	----	50.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	31.60
Standwell	1975	4	4	4	4	4	4	30	5	40	24	24.8	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	4	24.75
State Pride	1154	4	3	4	4	4	4	18	20	40	40	29.5	50	----	----	50.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	33.60
Sterisel (sterilis selection)	2891	4	0	4	0	----	----	----	----	5	4	4.5	----	----	0	0	----	0	0	T—	----	----	T—	.1	60	----	----	----	----	----	----	----	7	8	9.53
Sunrise	982	4	0	4	0	4	0	3	20	4	5	8.0	3	3	0	2.0	0	0	0	5	10	T	T—	3.4	36	40	0	0	T—	0	.1	8	10	21	7.02
Do	1799	4	0	4	0	4	0	8	16	5	16	11.3	10	8	----	9.0	10	----	10.0	----	8	0	----	4.0	----	10	0	T—	----	0	0	8	----	14	7.08
Svalöf Victory	1145	4	4	4	4	4	4	45	8	30	24	26.8	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	4	26.75
Swedish Select	1375	4	4	4	4	4	4	22	5	40	27	23.5	50	----	----	50.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	28.80
Tabor	1777	4	4	4	4	4	4	T—	20	40	25	21.3	40	----	----	40.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	25.02
Tartar	991	4	4	4	4	4	4	18	----	----	----	18.0	45	----	----	45.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	2	31.50
Tartar King	1599	4	4	4	4	4	4	40	50	40	45	43.8	60	----	----	60.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	47.00
Tech	691	4	4	4	4	4	4	15	----	20	----	17.5	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	2	17.50
Do	947	4	4	4	4	4	4	15	40	----	----	27.5	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	2	27.50
Terry	602	4	4	4	4	4	4	40	50	30	60	45.9	70	----	----	70.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	50.00
Texas Red	3068	4	0	4	0	4	0	T—	T	20	----	6.8	45	2	1	16.0	----	----	----	----	----	T	----	.2	----	----	T	----	----	----	----	----	----	8	8.59
Tobolsk	1709	4	4	4	4	4	4	16	30	30	45	30.3	60	----	----	60.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	36.20
Upright	2142	4	4	4	4	4	4	----	20	20	45	28.3	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	3	28.33
Victor	803	4	4	4	4	4	4	50	40	40	40	42.5	60	----	----	60.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	46.00
Victoria	2401	1	0	0	0	0	0	0	0	T—	2	.5	T—	0	T—	.1	----	0	0	T	----	0	0	0	T—	----	----	0	----	----	----	----	0	14	.19
Victoria (Scasso)	2764	1	0	0	0	0	0	----	0	1	2	1.0	----	0	2	1.0	----	0	0	2	0	0	0	0	----	----	----	0	----	----	----	----	----	11	.70
Victory	1145	4	4	4	4	4	4	18	50	30	27	31.3	45	16	----	30.5	----	----	----	----	----	20	----	20.0	----	----	----	30	----	----	----	----	----	8	29.50
Do	1985	4	4	4	4	4	4	11	30	30	27	24.5	35	4	----	19.5	----	----	----	----	----	30	----	30.0	----	----	----	60	----	----	----	----	----	8	28.38
Warrigal	2798	4	1	4	0	4	0	16	10	6	10	10.5	20	10	0	10.0	T	0	.1	4	T—	T	T—	.1	----	5	0	T	T—	T—	.1	T—	----	19	4.32
Wayne	2567	4	4	4	4	4	4	10	10	40	27	21.8	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	4	21.75
Wernich Golden	1746	4	4	4	4	4	4	60	3	----	----	31.5	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	2	31.50
White Avalanche	1440	4	4	4	4	4	4	60	10	----	----	35.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	2	35.00
White Bonanza	1686	4	3	4	4	4	4	22	60	70	----	50.7	60	----	----	60.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	4	53.00
White Cross	2026	4	4	4	4	4	4	40	5	50	----	31.7	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	3	31.67
White Maine	1692	4	4	4	4	4	4	22	10	40	36	27.0	60	----	----	60.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	33.60
White Tartar	551	4	4	0	4	4	4	30	----	40	40	36.7	----	----	1	1.0	----	0	0	5	----	4	----	4.0	50	----	----	----	----	----	----	----	10	9	20.00
Do	1640	4	4	4	4	4	4	27	70	20	36	38.3	50	----	----	50.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	40.60
Winter Turf	1570	4	4	4	4	4	4	20	30	----	50	33.3	45	----	----	45.0	15	----	15.0	----	50	----	----	50.0	----	90	----	----	T	5	2.6	90	----	10	39.52
Wisconsin Wonder	1645	4	4	4	4	4	4	10	20	30	32	23.0	50	----	----	50.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	5	28.40
Do	3074	4	4	4	4	4	4	50	10	24	----	28.0	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	3	28.00
Wolverine	1591	4	4	4	4	4	4	30	8	40	32	27.5	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	4	27.50
Worthy	1590	4	4	4	4	4	4	27	10	24	36	24.3	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	4	27.50
Yarran	3064	4	3	4	3	3	3	25	30	80	24	39.8	64	----	----	64.0	20	----	20.0	----	45	----	----	45.0	----	30	0	----	10	20	15.0	50	----	12	33.17

A total of 266 varieties and selections of oats were inoculated in the seedling stage with physiologic forms 1, 3, 7, 16, 17, and 18. Of the 1,589 reactions observed and recorded, 1,329 were susceptible and 260 were resistant. Form 1 was by far the most virulent, only four varieties—Bond (C.I. 2733), Glabrota (C.I. 2630), Victoria (C.I. 2401), and Victoria ((Scasso) C.I. 2764)—being found resistant to it. Bond was apparently immune, showing no macroscopic evidence of infection. Glabrota was nearly immune, showing only slight chlorotic flecks. Both Victoria varieties were highly resistant, showing often only necrotic flecks, although minute uredia surrounded by heavy necrotic areas were usually present. Sixty-seven varieties were resistant to form 3, which apparently is the most common and widely distributed of the restricted forms. Eighteen varieties were resistant to form 7, a virulent and widely distributed form. Seventy, 31, and 70 varieties, respectively, were resistant to the less important forms 16, 17, and 18. Forms 16 and 18 apparently are very similar, although the differential reaction of Glabrota to these two forms was distinct and consistent.

Bond and the two Victoria varieties were the only ones resistant in the seedling stage to all 6 forms. Glabrota was resistant to all except form 16, and Alber (C.I. 2766) was resistant to all except form 1. Nineteen varieties were resistant to 4 of the 6 forms, 44 varieties were resistant to 3 forms, 7 varieties were resistant to 2 forms, and 14 varieties were resistant to 1 of the 6 forms. A total of 179 varieties were not resistant to any of the 6 forms.

The same plants observed for infection types were observed also for rapidity of telial development. An average of five plants was grown in a 3-inch clay flowerpot. These plants were not transplanted on becoming older; consequently, the development of telia on the older plants may have been hastened somewhat because of impaired growing conditions. For any particular variety, however, the plants infected with forms 3 and 7 were grown side by side under the same greenhouse conditions. There was a marked difference between forms 3 and 7 in their precocity of telial development. The average number of days following inoculation until telia appeared on those varieties infected with forms 3 and 7 was 14.4 and 31.3 days, respectively. It is obvious that the difference between these two averages is highly significant. Following the classification mentioned on page 14 these cultures representing forms 3 and 7 would be classified as groups 1 and 2, respectively.

Parker (*27*) first reported that early development of telia was positively correlated with the resistance of the host plant. This relationship was observed in the present investigation with both seedling and adult plants, although it was most pronounced with adult plants. Usually telia developed on susceptible seedling plants within a few days after they appeared on the resistant plants. Certain forms, however, developed telia only on resistant seedling plants, and other forms were not observed to produce telia on either resistant or susceptible seedling plants. A total of 266 varieties in the juvenile stage of development were inoculated with form 3; 199 were susceptible (type 3–4); 28 were resistant (type 1–2); and 39 were immune or nearly immune (type I–0). The average number of days until telia appeared on varieties susceptible and resistant to form 3 was 14.9 and 10.8, respectively, while the average number of days until telia

appeared on 247 varieties susceptible to and 3 varieties resistant to form 7 was 31.5 and 20.7, respectively.

Numerous investigators have studied the reaction of oat varieties to natural epiphytotics of crown rust under field conditions. These data are, however, of limited value because only percentages of infection were recorded, and no information is available concerning the distribution and prevalence of physiologic forms at the time the data were obtained. Levine, Stakman, and Stanton (*21*) found Green Mountain, Red Rustproof (C.I. 1815), Iowar, "Rustless selection" (Rustless), Burt (C.I. 2043), and Ruakura (C.I. 2025) to be the most resistant of 22 varieties observed throughout the United States in 1925, 1926, and 1927. In the present investigation Red Rustproof was the only variety of this group that showed high resistance, and it ranked nineteenth among the most resistant varieties. Durrell and Parker (*12*) observed the reaction of some 200 varieties of oats to field epiphytotics of crown rust in the period 1914–18. They found, as a whole, varieties belonging to *Avena byzantina* more resistant than those belonging to *A. sativa*. None of the varieties they observed showed less than 40 percent as a maximum of infection. Very few of these varieties were studied in the present investigation.

The infection coefficient, as previously described, arbitrarily expresses in a numerical manner both the type and percentage of infection combined. A variety may have a low infection coefficient either because of a resistant reaction or a low percentage of infection, or both. A low percentage of infection under field conditions in turn may be due either to external conditions, such as limited inoculum, unsuitable environmental conditions, etc., or to some functional or morphological resistance of the plant itself. There apparently is a definite relation between the age of certain varieties and the percentage of crown-rust infection under field conditions. This relation appears less evident under greenhouse conditions. Many varieties will not develop their maximum percentage of infection until they reach a certain advanced stage of development, even though inoculum and environmental conditions be optimum.

The infection coefficients recorded for Ames, Iowa, in the period 1929–32, and for Manhattan, Kans., in 1931, represent in each case the maximum for the year. Only one observation was made at the other stations. Maximum infections were not observed at Stillwater, Okla., Knoxville, Tenn., or Experiment, Ga., for any of the years indicated. The average intensity of infection was not the same at any of the stations observed. However, with the exception of Stillwater in 1931 and Knoxville in 1929 there was apparently sufficient inoculum in each nursery to expose all varieties equally.

The weighted average infection coefficients recorded in the last column of table 14 are the averages of each variety for all of the times they were observed. Unfortunately, all the varieties could not be grown at each of the stations for the years indicated. Consequently, a comparison of these average infection coefficients cannot be very specific. There is a marked tendency for the varieties to show the same relative resistance at the various stations. This probably is explained by the universal presence of form 1 and the dominance of forms 1, 3, 7, and 16. In the seedling stage many of the southern varieties, belonging mainly to *Avena byzantina*, are resistant to form 3, which is confined chiefly to the Northern States. These varieties

apparently were resistant to form 3 in the adult stage because this form was not collected from them but from varieties susceptible in their seedling stage. Moreover, certain of the northern varieties (belonging to *A. sativa* and *A. sativa orientalis*) were resistant to form 7 in the seedling stage as well as in the adult stage. In general, the infection coefficients show the effect of the resistance of the varieties to the forms present. However, the presence of an aggressive form, such as 1 or 7, makes it difficult to discern the effect of the more restricted forms.

Eighty-one of the 266 varieties given in table 14 have a weighted average infection coefficient of 20 or less and 43 have a coefficient of 10 or less. All the varieties of any apparent importance from the standpoint of crown-rust resistance, under field conditions in the United States, are included in this group of 81, and those that are outstanding for resistance are found among the 43 varieties with a coefficient of 10 or less. More than half of the varieties fall within the range of 20.01 to 40, inclusive. All these varieties as well as 36 varieties with a higher average coefficient must be considered as susceptible under field conditions in the United States, although many were doubtless resistant to one or more of the rarer forms. The distribution of the varieties in the various class ranges of weighted average infection coefficients is shown in table 15.

The ability of oat varieties to withstand epiphytotics of crown rust under field conditions is of major economic importance. The 25 varieties most outstanding in this respect are arranged in table 16 in the order of their resistance, on the basis of the weighted average infection coefficients given in table 14.

TABLE 15.—*Distribution of varieties in class ranges of weighted average infection coefficients*

Varieties (number)	Infection coefficient class range	Varieties (number)	Infection coefficient class range
43	0–10	20	40.01– 50
38	10.01–20	14	50.01– 60
77	20.01–30	1	60.01– 70
72	30.01–40	1	70.01–100

The first four varieties in table 16 are very outstanding for their resistance to crown rust in both juvenile and adult stages, and they were the only varieties uniformly resistant in the juvenile stage to important forms 1, 3, and 7. In the first-leaf stage, Bond was apparently immune, or nearly immune, from these three forms, from all the forms identified in 1931, and from all except one of the forms identified in 1932. In addition to extreme resistance to crown rust, Bond has desirable agronomic characters that enhance its value for hybridization. Glabrota, belonging to *Avena strigosa*, is of no commercial importance. It is resistant to 26 of the 33 forms described in table 4 and ranks next to Bond for resistance under field conditions. Because of its chromosome number, Glabrota is of little value for hybridization. The two Victoria varieties are apparently identical, both morphologically and pathologically. These two varieties were resistant in the first-leaf stage to all the 33 forms described in table 3 and have been highly resistant under field conditions in the central and southenr portions of the United States. The history, classification, and prob-

able agronomic importance of Bond, Glabrota, and the two Victoria varieties have been reported by Murphy and Stanton (*25*) and Stanton and Murphy (*35*). In addition to their unusual resistance to crown rust these four varieties have shown apparent immunity from or extreme resistance to *Ustilago avenae* (Pers.) Jens. and *U. levis* (Kell. and Sw.) Magn. at the cooperating stations where they were grown and to artificial inoculation with both smuts at Ames, Iowa. Unfortunately, all four varieties were completely susceptible to natural epiphytotics of *Puccinia graminis avenae* whenever present.

TABLE 16.—*Average-infection coefficient of 25 oat varieties arranged in the order of their resistance to epiphytotics of Puccinia coronata avenae under field conditions; and reaction of seedling plants of these varieties to 6 physiologic forms*

Variety tested	C.I. no.	Field observations		Infection type on seedling plants inoculated with physiologic form—					
		Number	Average-infection coefficient	1	3	7	16	17	18
Bond	2733	3	0	I	I	0	I	I	I
Glabrota	2630	13	.18	0	0	0	4	0	0
Victoria	2401	14	.19	1	0	0	0	0	0
Victoria (Scasso)	2764	10	.70	1	0	0	0	0	0
Avena brevis	1783	18	1.14	4	0	0	4	4	4
Alber	2766	10	1.51	4	0	0	0	0	0
Magistral	2460	14	1.60	4	4	0	0	0	0
Avena strigosa	1782	14	3.14	3	0	4	4	4	4
Black Algerian	840-1	7	3.27	4	1	4	0	4	0
Schoolmam	2057	12	3.78	4	4	4	4	4	4
Warrigal	2798	19	4.32	4	1	4	0	4	0
Capa	2765	10	4.44	3	0	3	0	0	0
Rainbow	2345	12	4.52	4	4	3	4	3	4
Kareela	2774	3	4.67	4					
Red Rustproof	518-3	13	4.74	4	1	4	4	4	4
Mortgage Lifter	2804	18	5.31	4	4	4	4	0	4
Red Rustproof	512	15	5.39	4	1	4	4	4	4
Do	844	11	5.73	4	0	4	0	0	0
Do	1815	9	6.00	4	0	4	0	4	0
Do	888	15	6.40	4	0	4	0	4	0
Black Algerian	3065	16	6.53	4	1	4	0	4	0
Red Rustproof	1089	19	6.60	4	1	4	0	4	0
Myall	2800	19	6.68	4	4	4	4	4	4
Red Rustproof	921	10	6.81	4	1	4	0	4	0
Pampa	2767	12	6.93	3	0	3	0	0	0

Avena brevis (C.I. 1783), Alber, and Magistral have very low infection coefficients. These three varieties were resistant to important form 7 in the seedling stage. *A. brevis*, because of its chromosome number and undesirable agronomic type, is of little commercial importance. The crown-rust resistance and probable agronomic importance of Alber already have been reported by Stanton and Murphy (*35*). Magistral, belonging to *A. sativa orientalis*, has many desirable qualities in addition to resistance to crown rust. The most important of these are its white grain and extreme resistance to natural epiphytotics of *Puccinia graminis avenae* at the stations where it was grown from 1929 to 1932.

On the basis of their average infection coefficients, the remaining 18 varieties in table 16 are very important from the standpoint of resistance to natural epiphytotics of crown rust. None of these varieties was resistant in the seedling stage to forms 1 or 7. Certain of these varieties, such as Schoolmam, Rainbow, and Red Rustproof, are grown commercially in the United States. Rainbow is of particular importance because it is highly resistant to stem rust; Schoolmam also is moderately resistant. The history, classification, and

probable agronomic value of Capa (C.I. 2765), Kareela (C.I. 2774), and Pampa (C.I. 2767), have been reported by Stanton and Murphy (*35*).

The reaction of seedling plants to specific physiologic forms is more easily obtained than that of adult plants. The value of such data is limited unless it is known whether there is a relation between the age of plants and their reaction to crown rust. Johnston and Melchers (*19*) found that certain varieties of wheat were susceptible to form 9 of *Puccinia triticina* Eriks. in the seedling stage but resistant at heading time. Gassner (*16*) studied naturally infected wheat and oat plants at Estanzuela, Uruguay, in 1927. He found the younger plants of wheat most susceptible to *Puccinia triticina* but noted a loss in resistance to *P. graminis* and *P. coronata* (*P. coronifera*), respectively, as wheat and oat plants became older. Gassner observed the reaction to *P. coronata* of seven oat varieties in various stages of development. He found the greatest resistance in the uppermost leaves of the plants. Oat variety 1091–a showed a more resistant infection type in the juvenile than in the adult stage, although it was resistant in all stages of development. The major difference in reaction of juvenile and adult plants and also the variability in reaction of different parts of the plant seemed to be a difference in amount of infection rather than in infection type. Gassner's oat varieties 64–s, 64–t, and 1095–a were of the same origin and apparently identical with Capa, Victoria (C.I. 2401), and Alber, respectively.

Pure-line selections of the differential hosts and additional varieties, in three stages of development, were uniformly and simultaneously inoculated with form 1 of *Puccinia coronata avenae*. When inoculated the three stages of development were: (1) Seedling plants in first-leaf stage; (2) juvenile plants with 5 to 7 leaves; and (3) adult plants in flowering to soft-dough stages. The plants were held at a temperature of 68° to 72° F., from the time of inoculation until infection types were recorded. The results are shown in table 17.

TABLE 17.—*Reaction at different stages of development of oat varieties inoculated with form 1 of Puccinia coronata avenae*

Variety tested	C.I. no.	Stage of development				
		First leaf	Fifth to seventh leaf	Fully headed		
				Lower leaves	Upper leaves	Flag leaf
Ruakura	2025	3+	3+	3	3+	4
Green Russian	2890	4	3–4	3–	3	3+
Hawkeye	2464	3+	3+	3	3+	4
Anthony	2143	4	3–to 3+	3–	3	3+
Sunrise	982	3	3	3–	3	3+
Green Mountain	1892	3+	2+to 3	2–	2	3–
White Tartar	551	3+	3+	3	3+	3+
Red Rustproof	1815	3+	3+	3	3+	4
Sterisel	2891	3+	3	3–	3	3+
Belar	2760	3+	3–	3–	3	3+
Glabrota	2630	[1] 0 n	[2] 0 c	I	0 c	0 n
Victoria	2401	1–	0–1	0 n	1–	1
Bond	2733	0 n	0 n	I	I	I
Markton	2053	4	3+	3+	4	4+
Nortex	2382	4–	3 to 3+	3	3+	4
Alber	2766	3+	3–to 3+	2+	3–	3
Kanota	839	3+	3 to 4	3–	3	4
Richland	787	3+	3 to 4	3+	4	4+
Schoolmam	2057	3+	2+	2	2+	3–
Kareela	2774	3+	3+	3	3+	4
"Joanette strain"	2660	3	3 +to 3	2+	3	3+
Rainbow	2345	3+	2 to 3	2	3	3+

[1] n=Necrosis. [2] c=Chlorosis.

Only a slight relation was evident between the stage of development and the reaction of the varieties to form 1. Juvenile plants in the fifth- to seventh-leaf stage were slightly more resistant than seedling plants in the first-leaf stage, whereas fully-headed plants usually showed a greater variation in reaction between different portions of the same plant than was evident between plants of the same variety in different stages of development. In general, it would seem that the stage of development of an oat plant has little effect on its reaction to form 1 of crown rust, although there was apparent a slight increase of resistance in most of the varieties as they developed from the first-leaf to the fifth- to seventh-leaf stage. The dominant reaction thereafter apparently is little affected by the stage of development of the host plant.

Johnston and Melchers (*19*) observed that those wheat varieties that changed in their reaction to leaf rust as they grew older showed their highest resistance in the uppermost leaves. The data presented in table 17 indicate that the contrary is true for oats inoculated with form 1 of crown rust. Although the difference is slight it seems constant enough to be significant. Usually the infection type was uniform for an entire leaf, although leaves of adult plants sometimes showed a more susceptible reaction on the base of the leaf, as compared with the tip. No variation was observed in the infection type on different parts of the first leaf of seedling plants when inoculated with pure cultures. Seedling plants in the first-leaf stage, with the tip of the second leaf just appearing from the whorl, at the time of inoculation sometimes developed a more susceptible infection type on the tip of this second leaf than that developed on the first leaf. This variation was not often observed on the differential varieties, but such a variation was frequently observed on hybrid plants, particularly those that were heterozygous for resistance to crown rust. Hybrid plants with a mesothetic reaction to crown rust showed the greatest variation in reaction, when plants in different stages of development were infected.

These data seem to indicate that the young tissue of the oat leaf tends to be more susceptible to crown rust than the older tissue. Apparently, the reaction of the younger tissue of an adult plant tends to be similar to that of the first leaf of the seedling plant. Neither the variation due to difference in age nor that due to the portion of the plant infected appears great enough to be of any importance to the plant breeder, except when plants heterozygous for rust reaction are being studied. A variety resistant in the seedling stage to a particular physiologic form is evidently resistant in the adult stage to the same form. A variety susceptible in the seedling stage may not, however, always be equally susceptible in the adult stage. On this basis a study of the reaction of seedling plants to a specific form is of definite, although somewhat limited, value insofar as it serves as an index of the reaction of adult plants to the same form.

In addition to this apparent protoplasmic resistance characterized by necrosis and small size or absence of pustules, certain varieties apparently have what may be a functional or morphologic resistance, characterized by a low percentage or amount of infection. Adult plants of certain varieties will develop only a trace of type 4 infection, while adult plants of another variety of the same age and stage of development and under identical environmental conditions will

develop the maximum percentage of the same type of infection. Insofar as initial infection on adult plants is concerned there seems to be little, if any, correlation between the infection type and the percentage of the leaf area infected. On the other hand, there may be a striking correlation between the type and percentage of infection in secondary and later infection.

GRAMINEOUS HOST RANGE OF CERTAIN PHYSIOLOGIC FORMS

An attempt was made to determine the gramineous host range of physiologic forms 1, 3, 7, 16, 17, and 18. As many as possible of the various gramineous species that have been reported as hosts for *Puccinia coronata* were secured. The seedling reaction of each of these and other species to the above-mentioned physiologic forms was determined.

The reaction of certain species of grass to a particular physiologic form of crown rust was not nearly so constant as was that of oat varieties. Abnormal types of reaction and much variation were observed on individual plants and between different plants of the same species.

In table 18 is shown the reaction of 70 species belonging to the tribes Agrostideae, Andropogoneae, Aveneae, Chlorideae, Festuceae, Hordeae, and Phalarideae to each of the physiologic forms mentioned above.

Thirty-seven of the 70 species were, to outward appearances, immune from each of the six physiologic forms tested. Thirteen species (including 10 species of *Avena*) were susceptible to each of the six forms. Three of these (*Achyrodes aureum* (L.) Kuntze, *Anthoxanthum odoratum* L., and *Festuca octoflora* Walt.) are wild-grass species. *Anthoxanthum odoratum* and *Festuca octoflora* are of common occurrence throughout the United States, while *Achyrodes aureum* is a native of Europe and naturalized only in southern California to Texas. *Dactylis glomerata* L. was susceptible to physiologic form 7, whereas minute uredia were produced when it was inoculated with forms 1 and 3. The other forms (16, 17, and 18) produced only necrotic areas on this species. Minute uredia were produced on *Poa annua* L. by each of the six physiologic forms. *Phleum pratense* L. was somewhat variable in reaction. Uredia were produced on this species by all forms, except form 17, repeated trials with this having failed to produce any infection whatever. There was much variation in the production of chlorotic and necrotic areas on the different species. Apparently this type of infection is greatly influenced by the age and condition of the host tissue. Newly developed leaves often gave a more susceptible reaction than older ones.

The data in table 18 show that certain of the species tested differ in their reaction when inoculated with different physiologic forms. Outside of the *Avena* group, however, this evidence of physiologic specialization is insignificant. Before physiologic forms could be accurately differentiated by means of gramineous hosts other than *Avena*, it would be necessary to secure pure lines of the various species.

TABLE 18.—*Reaction of seedling plants of 70 species of grains and grasses to 6 physiologic forms of Puccinia coronata avenae*

[For explanation of symbols, see Infection Types of Crown Rust, p. 6]

Species tested	C.I. no.	Infection type on juvenile plants inoculated with physiologic form—					
		1	3	7	16	17	18
Achyrodes aureum		2-4	2-4	2-4	2-4	2-4	2-4
Agropyron caninum		I-0	I-0	I-0	I-0	I-0	I-0
Agropyron repens		I-0	I	I	I-0	I-0	I-0
Agropyron smithii		I	I	I	I	I	I
Agrostis alba		I	I	I	I	I	I
Agrostis exarata		I-0	I-0	I-0	I-0	I-0	I-0
Agrostis maritima		I	I	I	I	I	I
Agrostis palustris		I	I	I	I	I	I
Agrostis stolonifera		I	I	I	I	I	I
Agrostis thurberiana		I	I	I	I	I	I
Aira caespitosa		I	I	I	I	I	I
Alopecurus pratensis		I	I-0	I	I-0	I	I-0
Anthoxanthum aristatum		I-0	I-0	I-0	I-0	I-0	I-0
Anthoxanthum odoratum		0-4	0-3	0-4	0-3	0-3	0-3
Arrhenatherum elatius		I-0	I	I-0	I	I-0	I
Arrhenatherum elatius (Avena elatior)		I	I	I	I	I	I
Avena abyssinica	2108-2	4	4	4	4	4	4
Avena barbata	2466	4	0	4	0	4	0
Avena brevis	1783	4	0	0	4	4	4
Avena diffusa segetalis	2137	4	4	4	4	4	4
Avena diffusa volgensis	2138	4	4	4	4	4	4
Avena nuda	845	4	4	4	4	4	4
Avena nudibrevis	2465	4	4	4	4	4	4
Avena sativa	2053	4	4	4	4	4	4
Avena sativa aristata	2123	4	4	4	4	4	4
Avena sativa aurea	2127	4	4	4	4	4	4
Avena sativa mutica	2121	4	4	4	4	4	4
Avena strigosa	1782	3	0	4	4	4	4
Avena strigosa glabrescens	2630	0	0	0	4	0	I
Avena wiestii	1994	4	4	4	4	4	4
Beckmannia erucaeformis		I	I	I	I	I	I
Bromus ciliatus		I	I	I	I	I	I
Capriola dactylon		I	I	I	I	I	I
Chloris gayana		I	I	I	I	I	I
Dactylis glomerata		0-1	0-1	0-4	I-0	I-0	I-0
Elymus canadensis		I	I	I	I	I	I
Festuca confinis		I	I	I	I	I	I
Festuca duriuscula		I	I	I	I	I	I
Festuca elatior		I-0	I-0	I-0	I-0	I-0	I-0
Festuca gigantea		I	I	I	I	I	I
Festuca obtusa		I	I	I	I	I	I
Festuca octoflora		2-4	2-4	2-4	0-3	2-4	0-3
Festuca ovina		I	I	I	I	I	I
Festuca rubra		I	I	I	I	I	I
Festuca subulata		I	I	I	I	I	I
Holcus halepensis		I	I	I	I	I	I
Hordeum distichon		I	I	I	I	I	I
Hordeum jubatum		I	I	I	I	I	I
Hordeum vulgare		I	I	I	I	I	I
Lolium italicum		I	I	I	I	I	I-0
Lolium multiflorum		I	I	I	I	I	I
Lolium perenne		I	I-0	I	I	I	I-0
Lolium temulentum		I-0	I	I	I	I	I
Melica mutica		I	I	I	I	I	I-0
Notholcus lanatus		I-0	I	I	I	I	I
Phleum pratense		0-3	0-2	0-2	0-2	I-0	0-2
Poa annua		0-1	0-1	0-1	0-1	0-1	0-1
Poa arachnifera		I	I	I	I	I	I
Poa compressa		I	I	I	0	I	0
Poa nemoralis		I	I	I	I	I	I
Poa pratensis		I	I	I	I	I	I
Poa trivialis		I	I	I	I	I	I
Secale cereale		I	I	I	I	I	I
Sporobolus cryptandrus		I	I	I	I	I	I
Trisetum spicatum		I	I	I	I	I	I
Triticum aestivum (T. vulgare)		I	I	I	I	I	I
Triticum compactum		I	I	I	I	I	I
Triticum durum		I	I	I	I	I	I
Triticum monococcum		I	I	I	I	I	I
Triticum spelta		I	I	I	I	I	I

Melhus, Dietz, and Willey (*23*), using *Puccinia coronata avenae*, obtained normal infection on *Alopecurus pratensis* L. and *Arrhenatherum elatius* Beauv., while in the present investigations the maxi-

mum infection observed on these species was an 0 type. It is possible that they were using a physiologic form to which these species were particularly susceptible, or it may be that the variance in results was due to variation within the two gramineous species.

Uredia of various size were produced on the following species when inoculated with one or more of the six physiologic forms under consideration: *Achyrodes aureum*, *Anthoxanthum odoratum*, *Avena abyssinica*, *A. barbata*, *A. brevis*, *A. diffusa segetalis*, *A. diffusa volgensis*, *A. nuda*, *A. nudibrevis*, *A. sativa*, *A. sativa aristata*, *A. sativa aurea*, *A. sativa mutica*, *A. strigosa*, *A. strigosa glabrescens*, *A. wiestii*, *Dactylis glomerata*, *Festuca octoflora*, *Phleum pratense*, and *Poa annua*.

DISCUSSION AND CONCLUSIONS

Although 33 physiologic forms of *Puccinia coronata avenae* were isolated from 533 cultures collected in North America in the 6-year period 1927–32, probably many more were present. Additional differential varieties might have been selected that would have made possible the determination of other forms. Rapidity of telial development could be used as a differentiating character for the identification of additional forms. Moreover, it would conceivably be possible, with controlled environmental conditions, to subdivide certain of the forms already described by employing more refined but constant differences in infection types. It is also obvious that the isolation of a larger number of cultures would have disclosed additional more or less rare forms. Other characters doubtless will be discovered that may be employed for differentiating physiologic forms of crown rust. There is, however, no present apparent need for a finer differentiation than that employed to describe the 33 forms herein reported. On the other hand, it would be possible to combine the forms described into groups of more or less similar forms.

It is evident from the data obtained during this investigation that the physiologic-form flora of North America is not fixed. Forms 1, 3, and 7 were present each year and other more or less rare forms probably were present throughout the period of the investigation; but, in general, there was considerable variation in the occurrence and distribution of the forms from year to year. The constant appearance of forms 1 and 7 is explained in part, at least, by their regular hibernation in the winter-oat region. The fact that form 3 was consistently disseminated by naturally inoculated *Rhamnus cathartica* also explains its constant appearance and indicates that it probably is a homozygous form. Similarly, form 1 was consistently disseminated from naturally inoculated *R. lanceolata*. When these two forms, however, were used to inoculate other species of *Rhamnus* additional forms appeared in the aecial stage. Possibly *R. cathartica* and *R. lanceolata* have a selective or differential effect.

The year-to-year variation in the physiologic-form flora is no doubt largely due to hybridization and segregation on the alternate host. Most of the forms studied apparently were sufficiently aggressive to allow hibernation on fall-sown and volunteer oats in the winter-oat region, but only a few forms appeared to hibernate successfully. It is probable that forms vary in their reaction to environmental conditions when hibernating and that certain forms survive where others cannot. Mutation also may be a source of origin for new forms, but such occurrences are probably rare.

The methods of origin of new and reappearance of old forms are doubtless as old as the species itself, and it would seem that the physiologic-form flora of a particular region would become more or less fixed. However, with varying environmental conditions, introduction of new *Rhamnus* species, and constant development and introduction of new and elimination of old oat varieties, it is evident that there is much to disturb the stability of the physiologic-form complex.

In Europe, Klebahn (*20*) first divided *Puccinia coronata* Corda into two species, *P. coronata* (Corda) Kleb. and *P. coronifera* Kleb. He differentiated these two species mainly on the basis of their ability to infect *Rhamnus frangula* and *R. cathartica*, respectively. In North America Melhus, Dietz, and Willey (*23*) and Fraser and Ledingham (*14*) have shown that certain species of *Rhamnus* act as differential hosts for the parasitic races of *P. coronata* Corda. It is apparent from data secured in the present investigation that certain species of *Rhamnus* also may act as differential hosts for physiologic forms of the parasitic race *P. coronata avenae*. Frenzel (*15*) and other German investigators recognize Klebahn's classification and designate crown rust of oats as *P. coronifera* Kleb. Frenzel (*15*), however, observed unusually heavy infection on *R. cathartica* in Germany in 1929 and was unable to secure uredia on oats inoculated with the aeciospores from *R. cathartica*, although he did obtain uredia on various grass species. With these data at hand it seems only logical to retain all parasitic races and physiologic forms of crown rust of oats under the one morphologic species *P. coronata* Corda. Physiologic specialization in the species is highly developed and is evident on both the alternate and gramineous hosts. Ruakura was resistant to all except 1 of Frenzel's (*15*) 33 forms, whereas in the present investigation this same variety was resistant to 16 of the 33 forms described. It is, therefore, evident that the physiologic-form floras of Germany and North America are radically different. There is, however, no apparent justification for the designation of crown rust of oats as different species in the two countries.

Resistance to crown rust among oat varieties was not common. None of the commercial oat varieties studied was outstanding for resistance to crown rust in either seedling or adult-plant stages of development. The varieties belonging to *Avena byzantina* were more resistant as a group than those belonging to *A. sativa* or *A. sativa orientalis*. Highly resistant varieties were, however, present in each species, such as Bond, Victoria (C.I. no. 2401), and Magistral, belonging to *A. byzantina*, *A. sativa*, and *A. sativa orientalis*, respectively. Bond, Victoria (C.I. nos. 2401 and 2764), and Glabrota were outstanding for their seedling and adult resistance. The two Victoria varieties showed no susceptibility in any of the tests, and Bond was susceptible only to form 33. Fortunately, these varieties also showed considerable resistance to *Ustilago avenae* and *U. levis*. Magistral and Rainbow were resistant to crown rust under field conditions and, in addition, were highly resistant to stem rust in all of the tests. These two were the only varieties that notably were resistant to both rusts under field conditions. Desirable agronomic varieties resistant to stem rust and smut have already been developed. Appropriate crosses between these and the above-mentioned crown-rust-resistant varieties have been made, and it is hoped that by back crossing and careful selection under epiphytotic conditions desirable

high-yielding agronomic strains resistant to all four of these major oat diseases will be developed.

SUMMARY

All the physiologic forms of *Puccinia coronata avenae* yet described in North America are compared and given a standardized numerical designation.

Thirty-three physiologic forms, occurring in North America in the 6-year period 1927–32, are described.

Physiologic forms differ not only in pathogenicity on oat varieties but also in rapidity of telial development. Certain forms could be subdivided on this basis. Restricted forms tend to develop teliospores more rapidly than aggressive forms. Telia usually appeared on resistant varieties a few days earlier than on susceptible ones.

The 33 forms varied in versatility from the very aggressive forms 1 and 30 to the very restricted forms 2 and 29.

Fourteen forms were collected from naturally and artificially inoculated *Rhamnus* species. Certain species tend to harbor specific forms.

Form 2 evidently is heterozygous. Five additional forms were isolated among aecial collections from species of *Rhamnus* inoculated with form 2. New forms apparently originate by hybridization and segregation on the alternate host.

The reaction of the differential varieties, and of Victoria, Bond, and Markton, when held at 55°, 65°, 75°, and 85° F., to forms 1 and 7 was determined. The reaction of these varieties to form 1 was not greatly affected by temperature, but the effect of temperature on their reaction to form 7 was striking. At 85° form 7 could hardly be distinguished from form 1. Certain varieties were resistant at low and susceptible at high temperatures, while at an intermediate temperature they developed a mesothetic reaction. Other varieties did not change from resistant to susceptible but exhibited a decrease in resistance or an increase in susceptibility as the temperature became higher.

The distribution and prevalence of the 33 forms in 1927–32 are reported. Forms 1, 3, and 7 were present each year. Forms 1 and 7, and a number of less important forms, hibernate on fall-sown and volunteer oats in the winter-oat region. Other forms apparently are entirely dependent upon the alternate host for initial dissemination in the spring. Form 7 apparently is dependent upon hibernation for survival. Forms 1 and 7 were the most widely distributed and most commonly prevalent forms.

The seedling reaction of 266 oat varieties to forms 1, 3, 7, 16, 17, and 18 and the adult reaction of these same varieties to natural epiphytotics of crown rust at various locations in the central and southern portions of the United States are presented. Form 1 was the most aggressive of the six forms studied, only 4 varieties—Bond, Glabrota, Victoria (C.I. 2401), and Victoria ((Scasso) C.I. 2764)—being resistant to it in the seedling stage. Bond and the two Victorias were the only varieties resistant to all six forms.

Certain oat varieties were slightly more resistant to form 1 in the juvenile (fifth- to seventh-leaf stage) than in the seedling (first-leaf stage). Adult plants exhibited a variation in reaction on different portions of an individual plant, usually equal to that found on plants of the same variety in the different stages of development. Whenever differences in reaction on an individual plant were evident, the

younger tissues appeared most susceptible and the older tissues most resistant. This difference, however, with the exception of plants heterozygous for reaction to crown rust, was always meager.

The reaction of 70 gramineous species to 6 forms was characterized by almost uniform immunity or extreme resistance. *Achyrodes aureum, Anthoxanthum odoratum, Dactylis glomerata, Festuca octoflora, Phleum pratense, Poa annua,* and 14 species of *Avena* developed uredia when inoculated with 1 or more of the 6 forms. There was evidence of slight differential reaction on *Anthoxanthum odoratum, D. glomerata, F. octoflora,* and *Phleum pratense.*

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