PHYSIOLOGIC SPECIALIZATION IN PUCCINIA GRAMINIS SECALIS[1]

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INTRODUCTION

The literature dealing with the physiologic specialization of *Puccinia graminis secalis* Eriks. and Henn. and *P. dispersa secalis* Eriks. and Henn. is exceedingly meager. Levine and Stakman (*4*)[4] reported in 1923 that *P. graminis secalis* comprised at least two, and probably three, distinct physiologic forms, identified by their parasitic effect on three commercial varieties of rye—Rosen, Swedish, and Prolific. Mains (*6*) in 1926 referred to two physiologic forms of *P. dispersa secalis*, which he distinguished by their parasitic effect on an inbred line of Abruzzes (Abruzzi) rye. This selfed line of rye was uniformly highly resistant to his physiologic form 1 and very susceptible to form 2. For obvious reasons the use of standard commercial varieties of cereals as differential hosts in the study of physiologic specialization of the grain rusts is highly desirable. But as rye naturally is cross-pollinated, the study of specialization in *P. graminis secalis* is more difficult than that of other varieties (races) of *P. graminis* for which pure lines of differential hosts may be obtained with comparative ease.

The particular object of the present investigation was to ascertain the number, geographic distribution, and parasitic nature of the physiologic forms of *Puccinia graminis* on rye. An attempt was made to obtain rust collections from as many localities as possible, to identify them, and to determine their parasitic behavior under varying conditions. Particular attention was paid to the rye-growing sections of the United States, the survey being especially concentrated in southeastern Minnesota.

MATERIALS AND METHODS

The first serious endeavor to study intensively physiologic specialization in stem rust of rye was started in 1918. It was not until 1921, however, that the first three differential hosts, mentioned in the introduction, were found. Later, two additional differential varieties, Dakold and Colorless, were added. These five differentials were selected from a dozen or more commercial varieties and inbred lines of rye that had been inoculated repeatedly. In addition to the five differential varieties, each of which reacted differently to different physiologic forms, should be mentioned Giant Winter, obtained from J. F. Brandon, superintendent of the United States Dry-Land Field

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[4] Reference is made by number (italic) to Literature Cited, p. 314.

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Station at Akron, Colo. Giant Winter has proved extremely susceptible to all forms of *Puccinia graminis secalis* so far discovered and consequently can not be properly considered a differential host for these forms.

DESCRIPTION OF DIFFERENTIAL HOSTS

The five commercial varieties of rye chosen as differential hosts are all members of *Secale cereale* L. A brief description of each and of Giant Winter follows:

ROSEN, MINN. ACCESSION No. 82.—Rosen rye was developed at the Michigan Agricultural Experiment Station by selection from Petkus rye obtained from Russia through J. A. Rosen, agricultural expert of the Agrojoint Colonization Committee, in 1909. It was first distributed in 1912. It matures late, has large spikes filled with large dark kernels, is not so winter-hardy as Swedish No. 2, and is well adapted for growing in Michigan, Wisconsin, and southern Minnesota.

SWEDISH, MINN. No. 2.—A very hardy, good-yielding variety, which was produced at the Minnesota Agricultural Experiment Station by selection from a sample of Swedish rye obtained in 1895 from John Brogard, Henning, Minn. Seed was selected from the hardy plants that survived the winter. The seed was first distributed to farmers in 1907, and this is now the leading variety in Minnesota and the eastern part of South Dakota. The plants have small heads with small dark kernels, borne on rather tall, slender culms.

PROLIFIC, MINN. ACCESSION No. 89.—Prolific is a spring rye, the origin of which was a mass selection made at the University of Saskatchewan from an unknown sample of seed received from Germany. It was registered in 1921 under the name "Prolific, Sask. 302," and a quantity of hand-picked seed has been distributed each season since that time. According to Champlin (*2*), it matures very late but is a high yielder and is now grown extensively in the Province of Saskatchewan.

DAKOLD, MINN. ACCESSION No. 93.—Dakold rye was originated by the North Dakota Agricultural Experiment Station in 1902, when a few plants were found in a field where winter wheat had been sown but had been winterkilled. It was first distributed as "N. Dak. No. 959," but was later named Dakold. It resembles Swedish No. 2 in appearance and is very hardy under northwestern conditions. It is widely grown in North Dakota and has produced the highest average yield in a 4-year test at Saskatchewan.

COLORLESS, MINN. No. 104.—Colorless rye was produced at the Minnesota Agricultural Experiment Station by continued, pedigreed selection for the pale-color character from Swedish No. 2, resembling the latter in every other respect.

GIANT WINTER.—Giant Winter rye was introduced into the United States from France by the United States Department of Agriculture in 1901. The variety resembles Swedish No. 2 but appears to be of minor economic importance. It is grown to a certain extent in southeastern Wyoming and northeastern Colorado.

INOCULATION TECHNIC AND CULTURE METHODS

In all, 147 cultures of rye stem rust were studied. Specimens were obtained from 12 States in the United States, extending from Maine to Colorado and from Kansas to Wisconsin; from Ontario, Canada; and from France, Scotland, and Sweden. The hosts on which the rust was orginally found comprised cultivated and volunteer rye, *Secale cereale;* the common barberry, *Berberis vulgaris* L.; and the following wild grasses: *Agropyron repens* (L.) Beauv., *A. smithii* Rydb., *A. tenerum* Vas., *Elymus* sp., *Hordeum jubatum* L., and *H. pusillum* Nutt. By means of inoculations, made for the past decade at University Farm, St. Paul, Minn., 104 of the cultures were separated into distinct physiologic forms. The inoculation technic was essentially that described by Stakman and Piemeisel (*10*). The identity of the forms was determined by a modification of the method used by Stakman and Levine (*8*) in their study of physiologic forms of *Puccinia graminis tritici* Eriks. and Henn. The various types of infection produced by *P. graminis secalis* on rye seedlings were used as a guide in the present study. (Fig. 1.) The host-reaction classes were adapted with some modification from Levine (*3*). The modifications were necessary because of the heterozygous nature of the differential varieties of rye. This heterozygosity also necessitated, in the majority

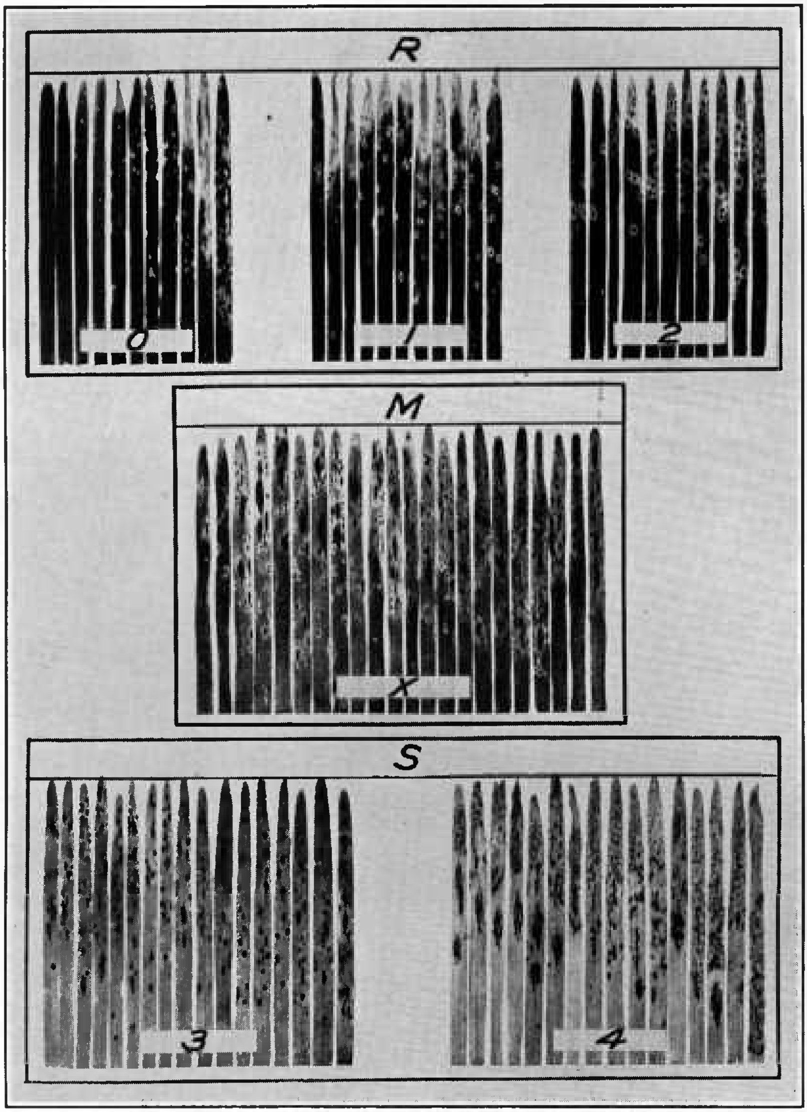

FIGURE 1.—Reaction classes of differential varieties of rye as indicated by infection types produced by *Puccinia graminis secalis:* Class R, resistant, embracing type 0 (no infectiou whatever or pronounced necrotic flecks), type 1 (minute uredia surrounded by solid necrotic areas), and type 2 (small pustules in green islands surrounded by necrotic halos); class M, mesothetic, consisting of type X (infection heterogeneous and ill defined); class S, susceptihle, composed of type 3 (medium-size uredia with slight chlorosis hut no necrosis), and type 4 (large confluent uredia, resulting in very heavy infection)

of cases, the testing of rather large numbers of individuals of each differential variety. On an average, more than 200 plants of each variety were infected before the identity of a rust culture was established, although there were some unavoidable exceptions.

CLASSIFICATION OF HOST REACTIONS

Three host-reaction classes—resistant, mesothetic, and susceptible—are recognized in the identification of physiologic forms of *Puccinia graminis secalis*. This classification is based on the different types of infection produced by the rust on seedlings and on the relative number of individuals in a given variety reacting in a definite manner. The following is a schematic description of the reaction classes and infection types:

CLASS R.—A variety is considered resistant when less than 25 per cent of the infected plants show normal development of rust, or conversely, when the rust-infection types produced on 75 per cent or more of the infected plants are, individually or severally, 0, 1, and 2, with their plus and minus fluctuations:

Type 0.—Plants virtually immune; no uredia are developed, but sharply defined necrotic flecks or necrotic lesions usually are present.

Type 1.—Plants extremely resistant; infection very light; uredia minute and scattered, surrounded by clearly defined, continuous necrotic areas.

Type 2.—Plants moderately resistant; infection light; uredia isolated and small to medium in size; hypersensitive areas in the form of necrotic halos or circles; pustules usually in green, though slightly chlorotic, islands.

CLASS M.—The host reaction is considered mesothetic when more than 25 and less than 75 per cent of the infected plants have rust pustules of types 3 and 4, or when the infection on all or most of the plants is heterogeneous as indicated by infection type X with its accompanying plus and minus fluctuations:

Type X.—Infection heterogeneous; uredia very variable, apparently including all types and degrees of infection on the same blade; no mechanical separation seems possible, since on reinoculation spores from small uredia may produce large ones, and vice versa.

CLASS S.—When 75 per cent or more of the infected plants of a given variety are moderately to heavily rusted, i. e., when the infection on them is of either type 3 or 4, or both, including their plus and minus variations, the variety is designated susceptible:

Type 3.—Plants moderately susceptible; infection medium; uredia mid sized with slight tendency to coalesce; true hypersensitiveness absent but light chlorotic areas usually present, especially under unfavorable cultural conditions.

Type 4.—Plants completely susceptible; infection normal and heavy; uredia large and generally confluent; hypersensitiveness normally absent, but chlorosis may be present when cultural conditions are not favorable.

Plus and minus signs indicate a slightly greater or smaller amount of rust than the nearest figure representing the infection type. Necrotic lesions are designated by a dot (.), necrotic flecks by a semicolon (;), and necrotic islands by a colon (:). The sign of equality denotes double minus.

The determination of the rust reaction of a given variety to *Puccinia graminis secalis* is rather simple when a great many plants are tested. The individual plants are examined first for infection types; then they are grouped according to the reaction classes, and the number in each class is recorded. The relative susceptibility of the variety is determined by the quotient obtained from dividing the number of susceptible plants by the total number of infected plants. Thus, for example, Colorless was considered highly susceptible to the Litchfield (Minn.) culture (form 11), because 461, or 91.47 per cent, of the 505 plants that became infected had rust pustules of types 3 and 4; of the remaining infected plants, 43, or 8.51 per cent, were placed in the resistant class, and 1 was classified as mesothetic. Dakold, on the other hand, was considered resistant to this culture, because only 25, or 8.93 per cent, of the 280 infected plants were really susceptible. Similarly, the Swedish variety was classified as mesothetic to the Litchfield culture because 32.08 per cent of the infected plants, i. e., more than 25 but less than 75 per cent, were heavily infected.

However, when the number of plants was unavoidably small, the susceptibility quotient ceased to be effectively operative. In such cases a numerical equivalent, as presented in Table 1, was assigned to each infected plant according to the degree and type of infection produced on it. From these the relative susceptibility of the variety was determined by calculating the average percentage equivalent. For instance, in the case of Rosen, inoculated with the culture from Haddington, Scotland (form 11), 19 plants became infected; 3 of these were marked type 3, 3 were 4−, and the remaining 13 were recorded as 4+. The total numerical equivalent for the 19 plants, according to Table 1, was $3\times50+3\times82+13\times94=1,618$, with an average for the variety of $1,618\div19$, or 85.16 per cent.

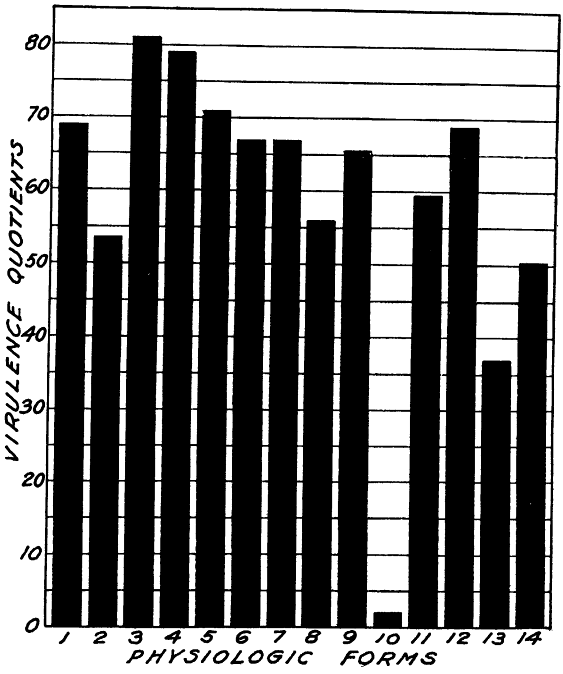

FIGURE 2.—Successive series of the physiologic forms of *Puccinia graminis secalis* indicating their respective virulence quotients

TABLE 1.—*Graduated scale showing numerical equivalents for host reactions, corresponding to symbols representing types and degrees of infection,*[a] *used as a means to determine the relative susceptibility of differential varieties*

Immune to moderately resistant				Mesothetic to extremely susceptible			
Infection index	Numerical equivalent	Infection index	Numerical equivalent	Infection index	Numerical equivalent	Infection index	Numerical equivalent
0	0	x.	8	x=	28	x+	65
0;	½	x;	10	x−	32	x++	70
0:	1	2=	12	x	36	4=	76
1=	2	2−	15	3=	40	4−	82
1−	3	2	18	3−	45	4	88
1	4	2+	21	3	50	4+	94
1+	5	2++	24	3+	55	4++	100
1++	6			3++	60		

[a] For explanation of symbols see p. 300.

EXPERIMENTAL RESULTS

Data regarding the pathogenicity of collections of rust used in these studies are presented in Table 2. In Table 3 are recorded the extreme and mean reactions of the differential varieties and the virulence quotient, of the physiologic forms. The latter are illustrated in Figure 2.

TABLE 2.—*Geographic distribution and parasitic behavior of physiologic forms of Puccinia graminis secalis isolated during the period 1921–1931*

Physiologic form No.	Place of origin	Original host	Stage of rust	Collected by—	Rosen: Number of plants: Total infected	Rosen: Resistant	Rosen: Mesothetic	Rosen: Susceptible	Rosen: Degree of relative susceptibility	Swedish: Number of plants: Total infected	Swedish: Resistant	Swedish: Mesothetic	Swedish: Susceptible	Swedish: Degree of relative susceptibility	Prolific: Number of plants: Total infected	Prolific: Resistant	Prolific: Mesothetic	Prolific: Susceptible	Prolific: Degree of relative susceptibility	Dakold: Number of plants: Total infected	Dakold: Resistant	Dakold: Mesothetic	Dakold: Susceptible	Dakold: Degree of relative susceptibility	Colorless: Number of plants: Total infected	Colorless: Resistant	Colorless: Mesothetic	Colorless: Susceptible	Colorless: Degree of relative susceptibility
									Per cent					*Per cent*					*Per cent*					*Per cent*					*Per cent*
1	St. Paul, Minn.	Secale cereale	Uredial	E. O. Horn, M. N. Levine.	67	55		12	17.91	122	12	4	106	86.89	44	2		42	95.45										
2	Madison, Wis.	Agropyron repens	do	H. B. Humphrey	28	3	3	22	78.57	10	10			3.40	24	15		9	37.50										
	Massy, France	Secale cereale	do	E. C. Stakman	39	2		37	94.87	28	22		6	21.43	41	15	9	17	41.46										
3	Caledonia, Ontario.	Agropyron repens	do	I. L. Conners	15			15	94.00	27			27	88.00	16			16	82.00										
	Gurnee, Ill.	do	do	J. L. Seal	16			16	78.44	14			14	82.21	12			12	82.00										
	do	Secale cereale	do	do	15			15	82.00	14	1		13	82.64	18	4		14	77.78										
	Ithaca, N. Y.	Agropyron repens	do	R. S. Kirby	26			26	88.00	15			15	82.00	18			18	88.00										
	Marshall, Wis.	Hordeum jubatum	do	J. L. Seal	10			10	94.00	12	1		11	80.75	18			18	80.00										
	Northfield, Minn.	Agropyron repens	do	J. J. Christensen	23			23	92.69	11			11	77.00	12			12	85.00										
	Red Wing, Minn	do	do	E. D. Sylvester	21			21	79.33	15			15	82.00	13			13	82.92										
	Rosemount, Minn.	Berberis vulgaris	Aecial	F. R. Rasmussen, E. M. Hansing.	377	44	14	319	84.62	471	72	22	377	80.04	306	67	6	233	76.14	458	130	49	279	60.92	386	24	21	341	88.34

4	Briançon, France	do	do	E. C. Stakman	19	--	--	19	84.21	16	--	--	16	88.00	11	4	--	7	63.64	--	--	--	--	--	--	--	--	--	--
	Minneapolis, Minn.	Agropyron repens	Uredial	H. C. Gilbert	30	1	3	26	86.67	11	2	--	9	81.82	13	5	--	8	61.54	--	--	--	--	--	--	--	--	--	--
	do	do	Telial	R. U. Cotter	142	13	1	128	90.14	210	35	8	167	79.52	85	17	6	62	72.94	433	127	46	260	60.05	184	8	--	176	95.65
	Northfield, Minn.	Berberis vulgaris	Aecial	J. J. Christensen	303	15	--	288	95.05	213	37	--	176	82.63	188	78	1	109	57.98	127	44	--	83	65.34	200	4	--	196	98.00
5	Commerce, Mich.	Agropyron repens	Uredial	W. F. Reddy, M. N. Levine.	34	5	--	29	85.29	17	17	--	--	2.00	18	3	--	15	83.33	--	--	--	--	--	--	--	--	--	--
	Presque Isle, Me.	Berberis vulgaris	Aecial	Donald Folsom	20	1	--	19	82.30	9	7	--	2	19.00	15	--	--	15	88.00										
6	Stockholm, Sweden.	Agropyron repens	Uredial	E. C. Stakman	19	1	2	16	84.21	31	2	--	29	93.55	23	19	--	4	17.39	--	--	--	--	--	--	--	--	--	--
7	Anoka, Minn.	Berberis vulgaris	Aecial	L. W. Melander, R. U. Cotter.	155	14	16	125	80.65	219	75	11	133	60.73	188	29	32	127	67.50	370	199	38	133	35.95	445	62	36	347	77.98
	Bancroft, S. Dak.	Agropyron repens	Telial	R. O. Bulger	150	11	--	139	92.67	108	33	--	75	69.44	155	70	3	82	52.90	163	112	5	46	28.22	137	6	--	131	95.62
	Belleville, Kans.	Agropyron smithii	Uredial	D. G. Fletcher	213	17	--	196	92.02	129	47	--	82	63.57	161	66	2	93	57.76	279	179	9	91	32.62	149	7	--	142	95.30
	Blooming Prairie, Minn.	Berberis vulgaris	Aecial	L. W. Melander, J. M. Walter.	190	18	5	167	87.89	343	100	33	210	61.22	156	34	11	111	71.15	478	212	52	214	44.77	357	29	16	312	87.39
	Bloomington, Wis.	Secale cereale	Uredial	W. J. Seymour	321	7	--	314	97.82	348	112	--	236	67.82	287	102	--	185	64.46	192	108	--	84	43.75	254	13	--	241	94.88
	Charlevoix, Mich.	Agropyron repens	Telial	W. F. Reddy	168	12	1	155	92.26	118	41	--	77	65.25	248	107	14	127	57.21	136	76	5	55	40.44	329	15	--	314	95.44
	Chatham, Mich.	do	do	B. R. Churchill	170	3	2	165	97.06	487	152	4	331	67.96	342	99	--	243	71.05	285	164	5	116	40.70	238	1	--	237	99.58
	Chatfield, Minn.	do	do	L. W. Melander	290	14	29	247	85.17	549	216	70	263	47.91	238	74	25	139	58.40	661	420	68	173	26.17	585	18	50	517	88.38
	Cherrygrove, Minn.	Berberis vulgaris	Aecial	V. F. Peterson, B. C. Dettman.	253	13	--	240	94.86	268	106	2	160	59.70	416	172	--	244	58.65	323	224	2	97	30.03	228	16	--	212	92.98
	Decorah, Iowa	Agropyron repens	Telial	P. W. Rohrbaugh, L. W. Melander.	192	12	4	176	91.67	385	85	69	231	60.00	168	56	12	100	59.52	517	270	97	150	29.01	261	21	21	219	83.91
	Faribault, Minn.	Berberis vulgaris	Aecial	L. W. Melander, J. J. Christensen.	479	57	32	390	81.42	434	81	42	311	71.66	302	68	38	196	64.90	529	177	87	265	50.09	591	71	36	484	81.90
	Fond du Lac, Wis.	do	do	E. C. Barsch	601	30	80	491	81.70	544	127	100	317	58.27	267	64	84	119	44.57	840	392	163	285	33.93	580	26	106	448	77.24
	Fort Collins, Colo.	Agropyron tenerum.	Telial	E. A. Lungren	61	8	--	53	86.89	43	21	--	25	54.35	130	50	1	79	60.77	94	60	3	31	32.98	178	22	--	156	87.64
	Ganges, Mich.	Agropyron repens	Uredial	E. A. Weimer	381	2	--	379	99.48	374	114	2	258	68.98	255	95	--	160	62.75	432	213	23	196	45.37	346	41	--	305	88.15
	Gilman City, Mo.	Hordeum jubatum	do	D. G. Fletcher	256	29	--	227	88.67	220	83	4	133	60.45	382	146	3	233	60.99	164	93	--	71	43.29	479	44	--	435	90.81
	Lake City, Minn.	Agropyron repens	Telial	L. W. Melander, R. U. Cotter.	271	11	--	260	95.94	103	27	6	70	67.96	140	51	4	85	60.71	106	52	9	45	42.45	287	2	--	285	99.30
	Lebanon, Kans.	Hordeum pusillum.	Uredial	D. G. Fletcher	197	4	--	193	97.97	356	97	14	245	68.82	286	112	4	170	59.44	247	137	2	108	43.72	119	8	--	111	93.28
	Lesueur Center, Minn.	Agropyron repens	do	H. B. Humphrey, L. W. Melander.	127	22	--	105	82.68	501	105	20	376	68.74	625	217	10	398	63.68	429	256	2	171	39.86	262	13	--	249	95.04
	Lewiston, Minn.	Secale cereale	do	L. H. Person	154	3	--	151	98.05	201	66	2	133	66.17	150	64	--	86	57.33	115	57	11	47	40.87	113	7	--	106	93.81
	Lydia, Minn.	Berberis vulgaris	Aecial	F. R. Rasmussen, W. C. Hanson.	502	81	15	406	80.88	300	94	4	202	67.33	202	95	3	104	51.49	317	137	10	170	53.63	284	39	1	244	85.92
	Plainview, Minn.	Agropyron repens	Uredial	V. F. Peterson, B. C. Dettman.	188	9	--	179	95.21	297	105	15	177	59.60	220	100	6	114	51.82	184	85	12	87	47.28	124	12	--	112	90.32
	Red Wing, Minn.	do	Telial	L. W. Melander, R. U. Cotter.	158	8	--	150	94.94	184	77	7	100	54.35	157	54	4	99	63.06	165	108	--	57	34.55	273	26	4	243	89.01
	do	Berberis vulgaris	Aecial	M. N. Kelso, H. G. Ukkelberg.	61	4	--	57	93.44	25	6	--	19	51.24	61	18	--	43	70.49	88	58	--	30	34.09	133	8	--	125	93.98

TABLE 2.—*Geographic distribution and parasitic behavior of physiologic forms of Puccinia graminis secalis isolated during the period 1921–1931*—Continued

Physiologic form No.	Place of origin	Original host	Stage of rust	Collected by—	Rosen: Total infected	Rosen: Resistant	Rosen: Mesothetic	Rosen: Susceptible	Rosen: Degree of relative susceptibility	Swedish: Total infected	Swedish: Resistant	Swedish: Mesothetic	Swedish: Susceptible	Swedish: Degree of relative susceptibility	Prolific: Total infected	Prolific: Resistant	Prolific: Mesothetic	Prolific: Susceptible	Prolific: Degree of relative susceptibility	Dakold: Total infected	Dakold: Resistant	Dakold: Mesothetic	Dakold: Susceptible	Dakold: Degree of relative susceptibility	Colorless: Total infected	Colorless: Resistant	Colorless: Mesothetic	Colorless: Susceptible	Colorless: Degree of relative susceptibility
									Per cent					*Per cent*					*Per cent*					*Per cent*					*Per cent*
7	Rochester, Minn.	Agropyron repens	Telial	L. W. Melander	143	15	1	127	83.81	146	75	2	69	47.26	207	76	33	98	47.34	645	298	140	207	32.09	512	16	50	446	87.11
	Salina, Kans.	Agropyron smithii	Uredial	D. G. Fletcher	52	4	---	48	92.31	91	51	---	40	43.96	165	63	---	102	61.82	45	32	---	13	28.89	213	11	1	201	94.37
	Saratoga, Minn.	Agropyron repens	do	L. W. Melander	110	8	1	101	91.82	327	157	---	170	51.99	338	96	1	241	71.30	156	104	1	51	32.69	211	10	---	201	95.26
	Sauk Center, Minn.	do	do	C. L. Lefebvre	196	45	---	151	77.04	239	65	12	162	67.78	304	125	4	175	57.57	348	165	18	165	42.99	468	52	---	416	88.89
8	Belleville, Kans.	Elymus sp	do	G. L. Peltier	164	74	---	90	54.88	133	91	1	41	30.83	341	131	4	206	60.41	233	196	4	33	14.16	357	77	---	280	78.43
	do	Hordeum pusillum.	do	F. J. Scrivner	233	60	---	173	74.25	352	201	---	151	42.90	287	120	---	167	58.19	150	134	---	16	10.67	153	17	---	136	88.89
	Goodhue, Minn.	Secale cereale	do	L. W. Melander	244	29	56	159	65.16	147	69	2	76	51.70	436	136	2	298	68.35	115	84	9	22	19.13	328	52	29	247	75.31
	Invergrove, Minn.	Berberis vulgaris	Aecial	S. P. Swenson, C. P. Shumway.	310	58	24	228	73.55	159	70	21	68	42.77	156	56	8	92	58.97	253	207	15	31	12.25	251	30	19	202	80.48
	Presque Isle, Me.	Agropyron repens	Uredial	Donald Folsom	94	32	4	58	61.70	88	59	1	28	31.82	103	34	10	59	57.28	---	---	---	---	---	---	---	---	---	---
9	Cherrygrove, Minn.	Berberis vulgaris	Aecial	L. F. Wasson, W. D. Swenson.	481	50	25	406	84.41	534	143	61	330	61.80	516	44	34	438	84.86	641	452	53	136	21.22	473	34	24	415	87.74
	Decorah, Iowa	Agropyron repens	Telial	P. W. Rohrbaugh, L. W. Melander.	235	21	---	214	91.06	208	109	5	94	45.19	247	37	5	205	83.00	458	365	6	87	19.00	209	38	13	158	75.60
	Kenyon, Minn.	Berberis vulgaris	Aecial	L. F. Wasson, W. D. Swenson.	357	40	5	312	87.12	241	120	23	98	40.66	141	21	4	116	82.27	315	239	13	63	20.00	333	26	18	289	86.79
	Marengo, Ill.	Agropyron repens	Telial	I. L. Brakansiek, L. J. Ham.	102	9	---	93	91.08	186	89	2	95	51.08	175	38	---	137	78.29	107	88	---	19	17.76	326	43	8	275	84.36
	Ponca, Nebr.	Secale cereale	Uredial	A. F. Thiel	144	32	---	112	77.78	174	94	---	80	48.41	148	28	4	116	78.38	140	115	---	25	17.86	203	26	---	177	87.19
	Union Lake, Minn.	Berberis vulgaris	Aecial	L. W. Melander, J. J. Christensen.	318	20	8	290	91.19	280	88	29	163	58.21	187	25	9	153	81.82	312	221	21	70	22.44	503	19	11	473	94.04
	Wanamingo, Minn.	Agropyron repens	Telial	L. W. Melander	185	21	---	164	88.65	200	105	---	95	47.50	369	66	20	283	76.89	152	135	---	17	11.18	505	70	9	426	84.36

10	Akron, Colo.	Secale cereale	Uredial	M. N. Levine	26	26	---	---	1.85	18	18	---	---	2.22	16	16	---	---	2.50	---	---	---	---	---	---	---	---	---	---
	Belleville, Kans.	Berberis vulgaris	Aecial	D. G. Fletcher	175	25	---	150	85.71	377	208	1	168	44.56	136	79	---	57	41.91	332	264	---	68	20.48	146	10	---	136	93.15
	do	do	do	G. H. Starr	399	51	16	332	83.21	220	125	4	91	41.36	288	103	1	184	63.89	292	236	13	43	14.73	203	20	2	181	89.16
	do	Hordeum jubatum	Uredial	G. L. Peltier	162	20	---	142	87.65	204	100	---	104	50.98	276	107	11	158	57.25	278	211	16	51	18.35	379	52	5	322	84.96
	Chatfield, Minn.	Agropyron repens	Telial	L. W. Melander	651	82	2	567	87.10	1,038	369	94	575	55.39	742	157	96	489	65.90	1,091	773	74	244	22.36	1,514	118	83	1,313	86.72
	Decorah, Iowa	do	do	P. W. Rohrbaugh, L. W. Melander.	250	9	---	241	96.40	237	91	5	141	59.49	165	56	3	106	64.24	347	272	18	57	16.43	235	13	2	220	93.62
	East Lansing, Mich.	Elymus sp.	do	W. F. Reddy	144	4	---	140	97.22	126	58	1	67	53.14	166	73	---	93	56.02	171	127	2	42	19.52	236	22	---	214	90.68
	Faribault, Minn.	Berberis vulgaris	Aecial	L. W. Melander, J.J.Christensen.	574	94	25	455	79.27	267	145	15	107	40.07	223	85	16	122	54.71	465	405	15	45	9.68	466	64	28	374	80.26
	Haddington, Scotland.	Agropyron repens	Uredial	E. C. Stakman	19	---	---	19	85.16	11	---	6	5	43.82	24	---	13	11	42.42	---	---	---	---	---	---	---	---	---	---
	Ishpeming, Mich.	Berberis vulgaris	Aecial	H. S. Hunter	385	25	24	336	87.27	238	110	14	114	47.90	90	32	5	53	58.89	308	260	19	29	9.42	248	27	8	213	85.88
	Litchfield, Minn.	Hordeum jubatum	Telial	L. W. Melander, R. U. Cotter.	143	22	2	119	84.40	427	260	30	137	32.08	288	166	7	115	39.93	280	255	---	25	8.93	505	43	1	461	91.47
	Loyalton, S. Dak.	Agropyron repens	Uredial	G. W. Eade, H. C. Batson, et al.	413	38	28	347	84.02	384	187	32	165	42.97	293	72	30	191	65.19	556	467	21	68	5.56	378	37	36	305	80.69
	do	Berberis vulgaris	Aecial	G. W. Eade	361	43	11	307	85.04	287	108	9	170	59.23	303	83	24	196	64.69	303	239	9	55	18.15	380	34	28	318	83.68
	Mankato, Minn.	do	do	F. R. Rasmussen	336	33	26	277	82.44	257	110	14	133	51.75	207	49	17	141	68.12	323	247	21	55	17.03	370	36	7	327	88.38
	Marquette, Mich.	do	do	H. S. Hunter	328	33	11	284	86.58	225	68	56	101	44.89	118	34	6	78	66.11	270	168	59	43	15.85	222	21	19	182	81.98
	Minneapolis, Minn.	Agropyron repens	Telial	R. U. Cotter	223	30	---	193	86.55	266	156	---	110	41.35	173	80	3	90	52.02	220	182	1	37	16.82	175	24	---	151	86.29
	do	do	do	do	239	20	1	218	91.21	189	102	2	85	44.97	194	72	---	122	62.89	222	198	1	23	10.36	291	24	1	266	91.41
11	do	do	do	D. G. Fletcher	113	1	---	112	99.11	199	90	8	101	50.75	90	50	1	39	43.33	256	195	7	54	16.70	102	8	---	94	92.15
	Minnetrista, Minn.	do	do	L. W. Melander, F. R. Rasmussen.	102	4	---	98	96.08	130	72	6	52	40.00	140	45	10	85	60.71	253	194	---	59	23.32	275	36	6	233	84.73
	New Brighton, Minn.	do	do	R. U. Cotter	50	1	---	49	98.00	186	86	21	79	42.47	86	27	3	56	65.12	217	158	18	41	18.89	122	7	4	111	90.98
	Orono, Minn.	do	do	L. W. Melander	204	17	---	187	91.67	196	117	3	76	38.78	138	66	---	72	52.17	164	141	3	20	12.20	206	20	4	182	88.35
	Petoskey, Mich.	Secale cereale	Uredial	R. E. Warner	99	18	---	81	81.82	78	47	2	29	37.18	72	44	1	27	37.50	52	49	---	3	5.77	116	27	---	89	76.72
	Redding, Iowa	Hordeum jubatum	do	D. G. Fletcher	156	15	---	141	90.38	135	59	19	57	42.23	181	77	---	104	57.46	137	113	---	24	17.52	379	82	---	297	79.41
	Rochester, Minn.	Agropyron repens	Telial	L. W. Melander	245	9	8	228	93.13	260	123	39	98	37.69	202	55	45	102	50.50	272	199	45	28	10.29	483	17	75	391	80.95
	do	do	do	L. W. Melander, R. U. Cotter.	118	20	---	98	83.05	561	268	17	276	49.20	330	128	9	193	58.48	117	103	---	14	11.97	383	64	---	319	83.29
	Rochester, N. Y.	do	Uredial	R. S. Kirby	155	27	---	128	82.58	101	57	7	37	36.63	47	27	---	20	42.55	32	27	---	5	15.63	28	2	---	26	92.86
	Rosetown, Minn.	do	Telial	R. U. Cotter	173	7	---	166	95.95	396	186	23	187	47.22	254	67	5	182	71.65	511	377	18	116	22.70	468	41	10	417	89.10
	St. Paul, Minn.	do	do	do	153	17	---	136	88.89	201	74	10	117	58.21	125	52	---	73	58.40	344	251	15	78	22.67	572	55	5	512	89.51
	do	Secale cereale	Uredial	H. E. Brewbaker	61	7	---	54	88.52	69	23	7	39	56.52	41	11	2	28	68.29	---	---	---	---	---	---	---	---	---	---
	Salina, Kans.	Berberis vulgaris	Aecial	W. A. Walker	135	16	---	119	88.02	731	291	198	242	33.11	249	108	10	131	52.61	187	158	6	23	12.30	354	32	---	322	90.96
	Traverse City, Mich.	Secale cereale	Uredial	R. G. Smith	239	9	---	230	96.23	309	137	---	172	55.66	192	95	---	97	50.52	133	98	---	35	22.97	215	14	---	201	93.49
	Wells, Minn.	Agropyron smithii	do	C. L. Lefebvre, V. F. Peterson.	168	24	7	137	81.55	201	102	16	83	41.29	223	80	14	129	57.85	143	123	---	20	13.99	497	40	2	455	91.55
	Woodstock, Ill.	Hordeum jubatum	do	L. R. Davis	209	32	---	177	84.69	307	101	16	190	61.89	210	71	9	130	61.90	387	258	46	83	21.19	599	87	5	507	84.64
	Zumbra Heights, Minn.	Agropyron repens	Telial	L. W. Melander	106	8	---	98	92.45	95	37	6	52	54.74	140	45	10	85	60.71	253	194	---	59	23.32	275	36	6	233	84.73

TABLE 2.—*Geographic distribution and parasitic behavior of physiologic forms of Puccinia graminis secalis isolated during the period 1921–1931*—Continued

Physiologic form No.	Place of origin	Original host	Stage of rust	Collected by—	Reaction of differential varieties																								
					Rosen					Swedish					Prolific					Dakold					Colorless				
					Number of plants				Degree of relative susceptibility	Number of plants				Degree of relative susceptibility	Number of plants				Degree of relative susceptibility	Number of plants				Degree of relative susceptibility	Number of plants				Degree of relative susceptibility
					Total infected	Resistant	Mesothetic	Susceptible		Total infected	Resistant	Mesothetic	Susceptible		Total infected	Resistant	Mesothetic	Susceptible		Total infected	Resistant	Mesothetic	Susceptible		Total infected	Resistant	Mesothetic	Susceptible	
									Per cent					*Per cent*					*Per cent*					*Per cent*					*Per cent*
	Haycreek, Minn.	Berberis vulgaris	Aecial	J. J. Christensen, L. W. Melander.	360	39	22	299	83.06	344	68	71	205	59.59	290	43	24	223	76.90	613	294	112	207	33.35	327	27	23	277	84.71
	Invergrove, Minn.	do	do	P. L. Holmberg, C. Marti.	273	18	2	253	92.67	292	68	32	192	65.75	113	10	4	99	87.61	224	140	15	69	30.80	286	10	---	276	96.50
	Minneapolis, Minn.	Agropyron repens	Telial	D. G. Fletcher	44	4	---	40	90.91	20	7	---	13	65.00	9	---	---	9	82.00	46	15	---	31	67.39	50	1	---	49	98.00
12	do	Hordeum jubatum	Uredial	H. C. Gilbert	17	---	---	17	88.00	11	---	11	---	65.00	16	---	---	16	82.00	---	---	---	---	---	---	---	---	---	---
	Northfield, Minn.	Agropyron repens	do	F. R. Rasmussen	477	50	20	407	85.32	516	125	37	354	68.60	375	56	16	303	80.80	727	367	68	292	40.17	487	34	22	431	88.50
	do	Hordeum jubatum	do	do	407	18	41	348	85.50	507	73	75	359	70.81	339	30	23	336	86.38	605	173	143	289	47.77	516	38	41	437	84.46
	Ord, Nebr.	Berberis vulgaris	Aecial	G. A. Feather	255	22	30	203	79.61	289	67	67	155	53.63	117	9	19	89	76.07	261	135	56	70	26.82	309	19	38	252	81.55
	Potosi, Wis.	Secale cereale	Uredial	L. G. Strom	468	27	36	405	86.54	401	65	90	246	61.35	316	34	33	249	78.80	454	191	122	141	31.06	433	17	21	395	91.22
	Redfield, S. Dak.	do	do	M. N. Levine	119	10	---	109	91.60	63	25	---	38	60.32	31	5	---	26	83.87	43	26	---	17	39.53	221	28	---	193	87.33
	Westfield, Minn.	Berberis vulgaris	Aecial	J. M. Walter, L. W. Melander.	211	25	3	183	86.73	212	74	13	125	58.96	274	39	18	217	79.20	308	196	23	89	28.90	263	24	10	229	87.07
13	Morris, Minn.	Secale cereale	Uredial	M. N. Levine	280	153	24	103	36.79	447	331	23	93	20.80	365	174	18	173	47.40	342	317	9	16	4.68	565	164	42	359	63.54
14	Brookings, S. Dak.	Berberis vulgaris	Aecial	R. O. Bulger	310	41	2	267	86.13	359	214	1	144	40.11	214	85	---	129	60.28	316	281	3	32	10.13	183	54	---	129	70.49
	Central Lake, Mich.	Agropyron repens	Telial	W. F. Reddy	48	8	---	40	83.33	100	61	---	39	39.00	137	77	---	60	43.79	72	62	---	10	13.88	167	57	---	110	65.87

TABLE 3.—*Relative susceptibility of differential varieties of Secale cereale and comparative virulence of physiologic forms of Puccinia graminis secalis*

Physiologic form No.	Relative susceptibility of—										Virulence quotient
	Rosen		Swedish		Prolific		Dakold		Colorless		
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
1	0.43–24.87	17.91	74.54–94.00	86.89	82.47–93.00	95.45					68.67
2	78.57–94.87	88.06	3.40–21.43	15.79	37.50–41.46	40.00					53.53
3	78.44–94.00	88.47	77.00–88.00	83.42	76.14–88.00	81.36	56.34–71.43	60.92	84.50–91.67	83.34	80.55
4	84.21–95.05	93.32	79.52–88.00	81.78	57.98–72.94	62.63	60.05–65.34	61.25	95.65–98.00	96.88	79.18
5	82.30–85.29	84.29	2.00–19.00	6.86	83.33–88.00	85.67					70.80
6	82.00–94.00	84.21	88.00–96.00	93.55	.87–22.75	17.39					67.12
7	77.04–99.48	89.29	43.96–71.66	62.72	44.57–71.30	60.35	26.17–53.63	38.01	77.24–99.58	88.76	66.90
8	54.88–74.25	67.75	30.83–51.70	41.41	57.28–68.35	62.13	10.67–19.13	13.58	75.31–88.89	79.43	56.24
9	77.78–91.19	87.32	40.66–61.80	52.39	76.89–84.86	81.21	11.18–22.44	19.62	75.60–94.04	86.72	65.55
10	1.00– 2.00	1.85	1.00– 3.00	2.22	1.00– 3.00	2.50					2.13
11	79.27–99.11	87.35	32.08–61.89	46.70	37.50–71.65	58.68	5.56–23.32	17.35	76.72–93.62	86.60	59.53
12	79.61–92.67	86.05	53.63–70.81	63.54	76.07–87.61	81.20	26.82–67.39	36.73	81.55–98.00	87.79	69.18
13	25.58–56.49	36.79	15.37–24.13	20.80	31.25–71.96	47.40	2.53–13.24	4.68	49.75–71.27	63.54	37.22
14	83.33–86.13	85.75	39.00–40.11	39.87	43.79–60.28	53.85	10.13–13.88	10.82	65.87–70.49	63.29	50.37
Weighted average	85.88		54.85		63.96		28.29		86.55		63.57

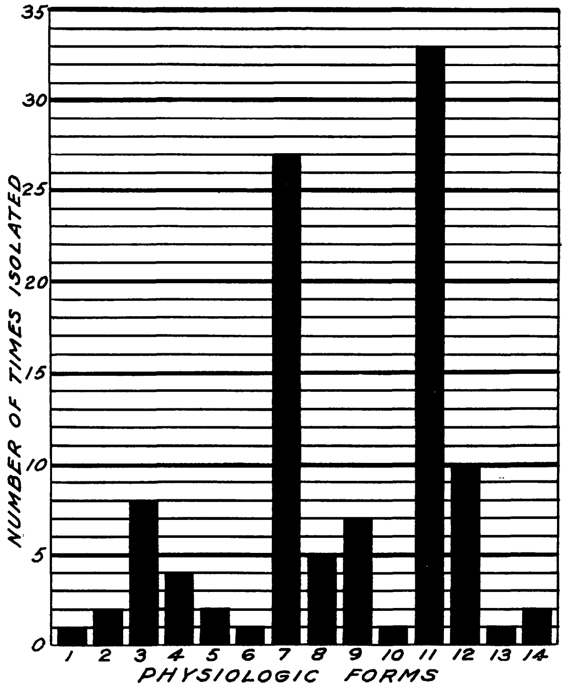

FIGURE 3. —Frequency distribution of physiologic forms of *Puccinia graminis secalis* identified during the period 1921–1931

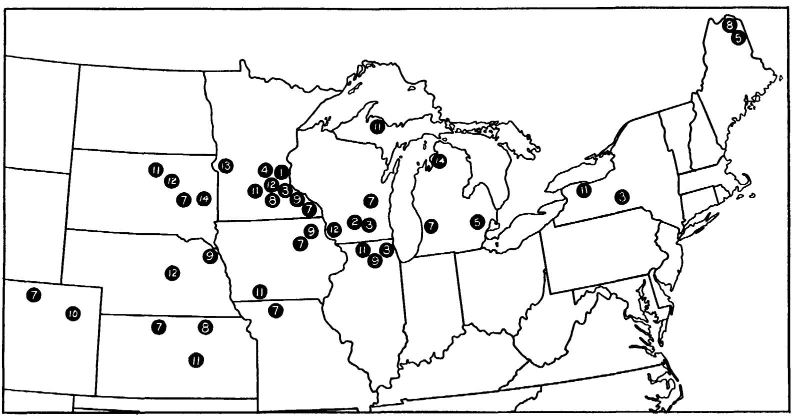

FIGURE 4. —Distribution of physiologic forms (numerals in circles) of *Puccinia graminis secalis* in the United States as represented by individual collections made and identified during the period 1921–1931

Data on the prevalence and distribution of the physiologic forms are presented in Figures 3 and 4 and in the following list:

Places where the different physiologic forms of Puccinia graminis secalis were collected, 1921–1931, and the number of times each was isolated

	Times isolated
Form 1	1
1921—St. Paul, Minn.	
Form 2	2
1922—Madison, Wis.	
Massy, France.	
Form 3	8
1921—Gurnee, Ill.	
1922—Caledonia, Ontario.	
Gurnee, Ill.	
Ithaca, N. Y.	
Marshall, Wis.	
Northfield, Minn.	
Red Wing, Minn.	
1931—Rosemount, Minn.	
Form 4	4
1922—Briançon, France.	
Minneapolis, Minn.	
1927—Northfield, Minn.	
1930—Minneapolis, Minn.	
Form 5	2
1922—Presque Isle, Me.	
1923—Commerce, Mich.	
Form 6	1
1922—Stockholm, Sweden.	
Form 7	27
1925—Gilman City, Mo.	
Red Wing, Minn.	
1926—Bancroft, S. Dak.	
Charlevoix, Mich.	
Chatham, Mich.	
Fort Collins, Colo.	
Lake City, Minn.	
Sauk Center, Minn.	
1927—Belleville, Kans.	
Bloomington, Wis.	
Cherrygrove, Minn.	
Decorah, Iowa.	
Ganges, Mich.	
Lebanon, Kans.	
Lesueur Center, Minn.	
Lewiston, Minn.	
Plainview, Minn.	
Red Wing, Minn.	
Salina, Kans.	
Saratoga, Minn.	
1929—Chatfield, Minn.	
Rochester, Minn.	
1930—Lydia, Minn.	
1931—Anoka, Minn.	
Blooming Prairie, Minn.	
Faribault, Minn.	
Fond du Lac, Wis.	
Form 8	5
1922—Presque Isle, Me.	
1924—Belleville, Kans.	
Goodhue, Minn.	
1927—Belleville, Kans.	
1931—Invergrove, Minn.	
Form 9	7
1924—Wanamingo, Minn.	
1926—Marengo, Ill.	
Ponca, Nebr.	
1927—Decorah, Iowa.	
1931—Cherrygrove, Minn.	
Kenyon, Minn.	
Union Lake, Minn.	
Form 10	1
1923—Akron, Colo.	
Form 11	33
1922—Haddington, Scotland.	
Rochester, N. Y.	
St. Paul, Minn.	
1924—Redding, Iowa.	
1925—Belleville, Kans.	
Litchfield, Minn.	
1926—East Lansing, Mich.	
Minneapolis, Minn.	
Petoskey, Mich.	
Salina, Kans.	
Wells, Minn.	
Woodstock, Ill.	
1927—Belleville, Kans.	
Decorah, Iowa.	
Rochester, Minn.	
Traverse City, Mich.	
1928—New Brighton, Minn.	
Zumbra Heights, Minn.	
1929—Chatfield, Minn.	
Minnetrista, Minn.	
Orono, Minn.	
Rochester, Minn.	
Rosetown, Minn.	
St. Paul, Minn.	
1930—Minneapolis, Minn. (twice)	
1931—Belleville, Kans.	
Faribault, Minn.	
Ishpeming, Mich.	
Loyalton, S. Dak. (twice).	
Mankato, Minn.	
Marquette, Mich.	
Form 12	10
1922—Minneapolis, Minn.	
1925—Redfield, S. Dak.	
1928—Minneapolis, Minn.	
1931—Haycreek, Minn.	
Invergrove, Minn.	
Northfield, Minn. (twice).	
Ord, Nebr.	
Potosi, Wis.	
Westfield, Minn.	
Form 13	1
1926—Morris, Minn.	
Form 14	2
1926—Central Lake, Mich.	
1927—Brookings, S. Dak.	

The number of forms identified in each year was as follows: In 1921, 2; in 1922, 8; in 1923, 2; in 1924, 3; in 1925, 3; in 1926, 5; in 1927, 6; in 1928, 2; in 1929, 2; in 1930, 3; in 1931, 6; total, 14.

It is noteworthy that each of all but two of the collections studied consisted of a single physiologic form. The exceptions were telial collections on *Agropyron repens*, one from Decorah, Iowa, and the other from Chatfield, Minn. *Berberis vulgaris* was inoculated with sporidia of these collections, and the resulting aecia yielded three distinct forms from the Decorah collection (forms 7, 9, and 11) and two forms from the Chatfield collection (forms 7 and 11).

PHYSIOLOGIC SPECIALIZATION

When the type and degree of infection and the relative susceptibility of each differential variety have been determined, the physiologic forms are identified with the aid of a key similar to those used for the identification of physiologic forms of *Puccinia graminis tritici* and *P. graminis avenae* (*8*, *1*). The key is here included. Only the reaction class of each variety is considered. For example, if Rosen is resistant and Swedish susceptible, the key would indicate that the culture producing this reaction is *P. graminis secalis* form 1. On the other hand, if Rosen is susceptible, Swedish and Prolific mesothetic, Dakold resistant, and Colorless susceptible, the rye stem rust causing these reactions would be identified as form 11. The key does not indicate the reaction of the complete set of differentials in every instance. It is therefore necessary to check the tentative identification with the known action of the corresponding forms as indicated in Table 3. If the relative susceptibility of each of the differential hosts approximates that designated for the physiologic form in question, the identification is considered complete; if it does not, then either the form has not yet been described or the culture consists of a mixture of forms, which must be separated before correct identification can be made.

Identification of Physiologic Forms

Analytical key for the identification of physiologic forms of *Puccinia graminis secalis* on the basis of their parasitic behavior on five differential varieties within the species *Secale cereale*.

	Form No.
Rosen resistant:	
Swedish resistant	10
Swedish susceptible	1
Rosen mesothetic:	
Swedish resistant	13
Swedish mesothetic	8
Rosen susceptible:	
Swedish resistant—	
Prolific mesothetic	2
Prolific susceptible	5
Swedish mesothetic—	
Prolific mesothetic—	
Dakold resistant—	
Colorless mesothetic	14
Colorless susceptible	11
Dakold mesothetic	7
Prolific susceptible—	
Dakold resistant	9
Dakold mesothetic	12
Swedish susceptible—	
Prolific resistant	6
Prolific mesothetic	4
Prolific susceptible	3

PATHOGENICITY

It will be seen from Tables 2 and 3 that some of the physiologic forms of *Puccinia graminis secalis* are very virulent, whereas others are extremely weak on the differential varieties of rye. The behavior of the first 3 of the 14 identified forms on Rosen, Swedish, and Prolific has been briefly described by Levine and Stakman (*4*) as follows:

> One form [form 3] is quite virulent, possessing the capability of attacking heavily all of the three varieties; another form [form 2] attacks Rosen very heavily, Prolific only moderately and Swedish very weakly; while still another form [form 1] produces normal infection on Swedish and Prolific, but only weak infection on Rosen.

Judging from its virulence quotient (Table 3 and fig. 2), it would seem that form 3 is the most virulent of all known forms, but only slightly more so than form 4. Next in order of virulence is form 5. It must be remembered, however, that the reaction of Dakold and Colorless to this form is unknown; consequently its exact virulence quotient is not fully established. Form 12, with a virulence quotient of 69.18, follows very closely behind form 5, whose quotient is 70.80 on the basis of the three varieties tested. Each of these quotients is considerably lower than that of form 3, whose quotient is 80.55, or that of form 4, whose quotient is 79.18. Unlike form 5, forms 3, 4, and 12 have been tested on all of the differentials. The weakest in virulence, as far as has been determined, is form 10, whose quotient is only 2.13, the next being form 13 with a quotient of 37.22. However, it must be borne in mind that form 10, like form 5, has been tested on only three differential hosts.

PREVALENCE AND DISTRIBUTION

More than half of all collections identified consisted of only forms 7 and 11. These two forms in the main closely resemble each other in their pathogenicity on the five differentials. The only outstanding difference is furnished by Dakold, a variety mesothetic to Form 7 and resistant to form 11. The difference in virulence quotient of the two forms is slightly more than 7 points. Forms 7 and 11 resemble each other not only in frequency distribution, 27 and 33 isolations respectively (see p. 309, Table 4, and fig. 3), but also in extent of distribution geographically. Both forms were for the most part found in only three States—Kansas, Michigan, and Minnesota (Table 4); form 7 was collected in these States twenty-one times, and form 11, twenty-six times. In addition, form 7 was found also in Colorado, Iowa, Missouri, South Dakota, and Wisconsin; while form 11 was collected also in Illinois, Iowa, New York, South Dakota, and Scotland. Form 7 was isolated twice in 1925, six times in 1926, twelve times in 1927, twice in 1929, once in 1930, and four times in 1931, whereas form 11 appeared three times in 1922, once in 1924, twice in 1925, six times in 1926, four times in 1927, twice in 1928, six times in 1929, twice in 1930, and seven times in 1931.

TABLE 4.—*Prevalence and distribution of physiologic forms of Puccinia graminis secalis identified during the period 1921–1931*

Distribution	Number of times indicated form was found														Total number of—	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Cultures	Forms
United States:																
Colorado							1			1					2	2
Illinois			2						1		1				4	3
Iowa							1		1		2				4	3
Kansas							3	2			4				9	3
Maine					1			1							2	2
Michigan					1		3				5			1	10	4
Minnesota	1		3	3			15	2	4		17	7	1		53	9
Missouri							1					1			1	1
Nebraska									1						2	2
New York			1								1	1			2	2
South Dakota							1				2	1		1	5	4
Wisconsin		1	1				2								5	4
Foreign countries:																
Canada			1												1	1
France		1		1											2	2
Scotland											1				1	1
Sweden						1									1	1
Total	1	2	8	4	2	1	27	5	7	1	33	10	1	2	104	14

The only other forms that were fairly common, besides those just discussed, were forms 3 and 12. Form 3 was isolated only during three years of the investigation, once in 1921, six times in 1922, and once in 1931, but it occurred in New York, also through Ontario to Minnesota, in an almost straight line. Form 12 was found once each in 1922, 1925, and 1928, but was isolated seven times in 1931. As is true of the physiologic forms of stem rusts of wheat and of oats (*3*, *5*, *9*), the same forms of *Puccinia graminis secalis* did not recur with any regularity year after year, nor were they uniformly distributed in any definite area.

All the forms except form 6 have been found in the United States. Form 6 came from Stockholm, Sweden. However, since this study by no means constitutes a complete survey of the status of rye stem rust, it is unlikely that all of the forms that may have been present were collected.

DISCUSSION AND CONCLUSIONS

Notwithstanding the heterozygous nature of commercial varieties of rye, it was possible to establish the existence of at least 14 physiologic forms of *Puccinia graminis secalis* by the use of certain standard varieties of *Secale cereale*. In many cases great numbers of plants must be tested to be certain of the results. However, when the results of inoculation are clear-cut and uniform, smaller numbers may suffice. In the identification of form 7, for example, where three of the five differential varieties are mesothetic or intermediate in reaction, not less than 200 seedlings of each variety were found to be necessary. In the case of form 10, on the other hand, apparently reliable results were obtained with a tenth of the required number of plants tested. The infection types in the last instance were very definite and absolutely uniform. The maximum infection on any one plant was (1 −), the minimum (0;). It seemed reasonable to accept these results as conclusive and as a basis for considering the existence of form 10 as highly probable. That this form is a component part of *P. graminis secalis* is evidenced by the fact that the original culture came from heavily infected Giant Winter rye. At any rate, the majority of the forms described in this paper were identified after a considerable number of individuals of the various differential hosts had been tested. Forms 7 and 11 were found most widely distributed and of most frequent occurrence, representing about 26 and 32 per cent, respectively, of the total number of cultures identified. Form 12 was third, with a 10 per cent ratio in the frequency distribution, and form 3 was fourth, with approximately 8 per cent of the total number identified. The remaining 11 forms gradually tapered down from seven isolations to only a single one.

Seventy-four of the collections were identified directly from the original material, for they were either in the uredial (46 cultures) or aecial (28 cultures) stages. The remaining 30 cultures were of telial origin and had to pass through the aecial stage on barberry (*Berberis vulgaris* L., *B. oblonga* Schn., or *B. notabilis* Schn.) before their behavior on the differentials could be ascertained. It was from two telial collections on quack grass that three different forms (7, 9, and 11), in one case, and two forms (7 and 11), in another case, were isolated on passing through the aecial stage on the common barberry. Inasmuch as it is not known whether the original material in either case consisted of a single physiologic form, it would be hazardous to assume that a genetic change had occurred. There is evidence, however, of hybridization in the aecial stage, resulting from crossing *Puccinia graminis secalis* with *P. graminis tritici*.

Changes in environmental conditions affect perceptibly the degree of infection and virulence quotients of forms of rye stem rust but not their physiologic specialization. Pathogenically these forms appear to remain genetically constant under varying conditions of temperature and luminescence. L. W. Melander [5] observed yellow pustules in a brown culture of rye stem rust, supplied to him by the writers and grown by him under constant light (162 foot-candles) at 20° C. The yellow pustules also were present at the same time in the original culture grown by the writers under ordinary greenhouse conditions. This would tend to show the presence of color mutation in *Puccinia graminis secalis*, similar to that described by Newton and Johnson (7) for *P. graminis tritici*. Extensive tests proved the two varicolored cultures to be pathogenically identical, namely, *P. graminis secalis* form 7.

Many varieties of barley and all the differential varieties of wheat, as well as the oat differentials, were subjected to a thorough test with the *secalis* forms. The oat varieties were extremely resistant throughout. All the differential varieties of wheat reacted in like manner, except Little Club. This variety reacted heterogeneously to a few collections of *Puccinia graminis secalis* when first inoculated. In all these tests the presence of forms of *P. graminis tritici* was detected. In one instance, however, the presence of the wheat stem rust was not discovered until after many tests had been made. Its occurrence may therefore have resulted from a subsequent accidental contamination, and the moderate development of rust on Little Club evidently was entirely due to the rye rust. Unfortunately, this rust strain was

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[5] Associate Pathologist, Division of Barberry Eradication, Bureau of Plant Industry.

destroyed before monosporous cultures could be obtained for further intensive analysis. However, reasonably pure cultures of forms 7 and 11 of *P. graminis secalis* recently have been identified that infected Little Club wheat in an indeterminate (mesothetic) manner, although all other wheat differentials definitely proved to be extremely resistant to these forms.

Between 30 and 40 varieties of barley belonging to the species *Hordeum vulgare* L., *H. intermedium* Kcke., *H. distichon* L., and *H. deficiens* Steud., reacted variously to the different tested forms of *Puccinia graminis secalis*. A detailed study of the reaction of barley varieties to the different cereal rusts is at present being completed.

SUMMARY

During the period from 1921 to 1931, inclusive, close to 150 collections of *Puccinia graminis secalis* were studied to determine the physiologic specialization within this rust variety.

Fourteen physiologic forms have been distinguished, and the characteristic parasitic behavior of each has been ascertained on several differential varieties of *Secale cereale*.

Because rye is cross-pollinated, the identification technic is more involved than in the case of stem rust of either wheat or oats, but apparently is not less certain.

Some of the physiologic forms identified occurred frequently and were widely distributed, others occurred rarely and in restricted areas.

Form 11 was isolated from the largest number of localities and was an important factor in the rye stem-rust epidemics of 1926, 1927, 1929, and 1931, occurring with approximately even frequency in all these years except 1927.

Although form 7 was collected almost as often as form 11; it appeared to be scattered over a greater geographic area and was isolated at different times for six, instead of nine, years of the present investigation. It was especially common in 1927.

Forms 1, 6, 10, and 13 were collected only once each; the remaining eight forms were isolated from two to ten times each.

The frequency of the occurrence of the different physiologic forms was not always coextensive with their distribution, nor was the prevalence of a given physiologic form paralleled by its virulence on the differential varieties.

The pathogenicity of the physiologic forms of *Puccinia graminis secalis* was but slightly and only temporarily affected by external conditions, such as temperature and light.

There seems to be strong circumstantial evidence of the occurrence of color mutations in the rye stem rust, but none so far of mutations in parasitic behavior.

The possibility of the origin of rye stem-rust forms through hybridization in the aecial stage is supported by the evidence of the production of new forms of wheat stem rust by crossing *Puccinia graminis secalis* with *P. graminis tritici*.

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