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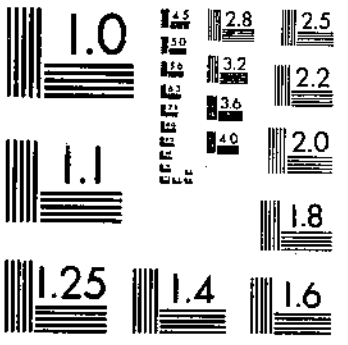

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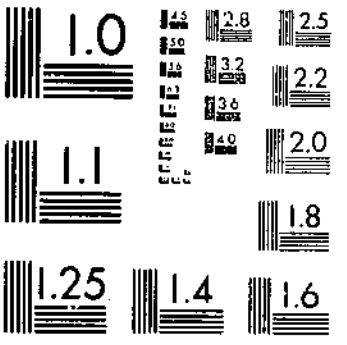

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Physiologic Specialization in the Oat Smut Fungi and Its Relation to Breeding Oats for Smut Resistance[1]

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RACE specialization in the oat smut fungi has been thoroughly established, and its relation to the development of improved varieties of oats is generally recognized. A knowledge of the number and distribution of these races in any given area is helpful in an oat-improvement program, especially for workers having inoculum and facilities available for testing promising new hybrid selections and varieties of oats for smut resistance.

Experiments were begun in 1936 for the purpose of systematizing the identification of oat smut races occurring in the principal oat-producing regions of the United States and establishing facilities for the systematic determination of varietal reaction to these races. This bulletin presents the results of these experiments, together with data on the reaction of certain newly developed varieties of oats to the races of oat smuts that have been identified.

REVIEW OF LITERATURE

Physiologic specialization in *Ustilago avenae* (Pers.) Rostr. and *U. kolleri* Wille (*U. levis* (Kell. and Swing.) Magn.) has been recognized

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[2] Grateful acknowledgment is made to those agronomists and plant pathologists whose cooperation in supplying seed and smut collections made this study possible.

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since 1924, when Reed (*5*)[3] described two races of each species, two of which came from Missouri and two from Wales. Sampson (*13*) tested these same four races in Wales and confirmed Reed's results. Subsequently these investigators (*6*, *7*, *14*) identified other races of *U. avenae* and *U. kolleri* on the basis of host reaction, and other workers (*1*, *12*, *19*) distinguished between races of these species on the basis of culture characteristics. The investigations of Nicolaisen (*3*), Schattenberg (*16*), and Leitzke (*2*) in Germany and Rădulescu (*4*) in Rumania have revealed the presence of specialized races of *U. avenae* in those countries.

For a long time Reed and his coworkers emphasized the identification of new races, giving little attention to the development of a standard system for race identification and designation. In 1924, Reed (*5*) described two races of each species on the basis of the resistant and susceptible reaction of certain species and varieties of the host and designated them, according to the source of the inoculum, as the Missouri and Wales races. Later, Reed (*6*) identified two additional races of *U. avenae* on the basis of the resistance or susceptibility of Fulghum and Red Rustproof oats, which he designated, this time according to pathogenicity, as the Fulghum and Red Rustproof races. These were distinct from the Missouri and Wales races, and all were identified on the basis of two classes of reaction, namely, the resistance or the susceptibility of the differential hosts.

In 1930, however, Reed (*7*) published the results of more extensive investigations in which 11 races of *Ustilago avenae* and five of *U. kolleri* were identified on the basis of six numbered classes of infection percentages. These classes were designated as 0 for no infection; 1 for 1 to 10 percent; 2 for 11 to 25 percent; 3 for 26 to 50 percent; 4 for 51 to 75 percent; and 5 for 76 to 100 percent. Roman numerals were used to designate these races, and the Missouri, Wales, Red Rustproof, and the Fulghum races mentioned were included in this group. Later Reed and Stanton (*9*) described a new race of *U. kolleri*, which they designated as the Fulghum race of covered smut because of its ability to infect Fulghum oats. In 1936, it was shown by these same authors (*10*) that the Fulghum and Red Rustproof races of *U. avenae* and *U. kolleri* could, in some cases, be further divided into subraces, although no definite race or subrace numbers were assigned. In these later articles Reed and Stanton (*9*, *10*) did not follow the system of race identification and designation used by Reed (*7*) in 1930, but simply referred to the races by collection numbers and identified them by the resistance and susceptibility of their respective hosts.

The most extensive classification of races of the oat smuts yet published was presented by Reed (*8*) in 1940, when he assigned numbers to 29 races of *Ustilago avenae* and to 14 races of *U. kolleri*. Of these races, 17 of *U. avenae* and 8 of *U. kolleri* were found in the United States. These races, designated by Arabic numerals, were identified by the resistance and susceptibility of the differential varieties, of which there were 17 for the *U. avenae* races and 10 for those of *U. kolleri*. This superseded his earlier classification (*7*), in which he

[3] Italic numbers in parentheses refer to Literature Cited, p. 15.

used 6 infection classes as the basis for race differentiation and Roman numerals for race designation. The races that were included in the earlier classification (*7*) were included in the later classification under the same numbers, but in Arabic numerals. Thus, all the races that Reed had identified from time to time were grouped according to a single standard of classification. Recently, however, Reed and Stanton (*11*) have identified a new race of *U. avenae*, designated as "A–30."

The adaptability of a system of classification of races depends to a great extent upon the constancy of the reaction of the differential varieties to the established races; otherwise, it becomes difficult to recognize new races. Apparently Reed (*8, p. 142*) found no significant variability in the behavior of the races he identified, as indicated by his statement that—

> All races of both loose and covered smuts have shown a remarkable consistency in their behavior, having given uniform results on a series of hosts for many successive generations, extending over several years.

In contrast, Tervet (*17*) observed much variation in the range of pathogenicity of certain oat smut collections from year to year, and he regarded this as the major problem in physiologic race determination in these organisms. Thus, according to Tervet, range of pathogenicity, as a criterion for the separation of races, is a variable quality that depends upon the interaction of host and pathogen, which in turn may be affected by various environmental factors. Consequently, much variation might be expected. It is important, therefore, to determine the limits of variability under the conditions to be used in race determination (*17*). Although Tervet (*17*) was of the opinion that the host need not be a factor in variations, later studies (*18*) demonstrated that it can be a factor unless care is exercised always to obtain pure seed of the same variety from the same source.

Tervet (*17*) discussed fully the various factors that contribute to variation in pathogenicity of races of the oat smuts from year to year and pointed out that this variation was not sufficient to prevent recognition of races. He was able to classify 3 races of each species in 79 collections studied, originating primarily from the Mississippi Valley. It is worthy of note, however, that he (*17*) based the identity of these races on the general trend of their ranges of pathogenicity over a period of several years and not according to sharply defined limits. In view of the variable results that he obtained in several tests, this appears to have been the logical procedure. Since the results and observations of the writers were similar to those reported by Tervet, his method of analysis has been applied to the data reported in this bulletin.

MATERIAL AND METHODS

During the course of the present studies, 218 collections of oat smut were tested, of which 148 were *Ustilago avenae*, 60 were *U. kolleri*, and 10 were species mixtures. With the exception of 12 races previously identified by other workers (*3, 17, 20*), this material represented field collections from 29 States in the United States and 2 Provinces in Canada. In these studies 27 varieties of oats were used, of which 18 were *Avena sativa* L.; 6, *A. byzantina* C. Koch; 2, *A. orientalis* Schreb.; and 1, *A. nuda* L. Ten of these proved valuable as differential vari-

eties. The complete list of species and varieties, with their respective C. I.[1] numbers, is given below. Those that were used as differential varieties in tables 1 and 2 are marked with an asterisk (*).

Avena sativa	C. I. No.
*Anthony	2143
*Black Diamond	1878
*Victory	500
Canadian	1625
*Gothland	1898
*Monarch	1876
*Black Mesdag	1877
*Camas	2905
*Nicol	2925
*Lelina	3404
Black Norway	1874
Joanette	1762
Richland	787
Monarch Selection	1879
Early Champion	1866
Avena sativa—Continued	C. I. No.
Bicknell	3218
South Dakota 334	2884
Markton	2053
Avena byzantina	
*Fulghum	708
Red Rustproof (Ala. Sel.)	1355
Appler	1815
Calcutta	994
Bond	2733
Victoria	2401
Avena orientalis	
Green Mountain	1892
Selzuri	1609
Avena nuda	
Large Hull-less×Markton	3209

The inoculated seed was grown in field plots one or more years at Pullman, Wash.; Aberdeen, Idaho; Arlington Farm, Rosslyn, Va.; and Beltsville, Md.; and in the greenhouse 2 years at Beltsville. The percentages of smut were based on total number of panicles in a row, which number usually ranged from 100 to more than 300 (depending upon the variety), at Pullman, and somewhat less at the other field stations; while in the greenhouse tests the number of panicles averaged approximately 50 to the row. In the greenhouse tests at Beltsville, lights were used to bring plants to maturity in a shorter time. Consequently, there was little or no tillering and the number of panicles corresponds closely to the number of plants in a row.

Two methods of inoculating oat seed with chlamydospores are known to be satisfactory. One of these consists in removing the glumes and dusting the naked seed with dry spores. The other one, known as the partial-vacuum method, consists in immersing the seed in a spore suspension and subjecting it to partial vacuum for a definite period and then releasing the vacuum, thus forcing the spores beneath the glumes into direct contact with the embryo or close to it. Both methods are satisfactory from the standpoint of producing high infection percentages, but the former method has the disadvantage of being too time-consuming for large-scale field tests. Furthermore, it results in poor stands. Consequently, the partial-vacuum method was used in these studies. The procedure in making the inoculations was as follows: The chlamydospore suspension was prepared by placing one or more smutted oat panicles (depending on size) in a flask containing enough tap water for the quantity of suspension required and then shaking the flask vigorously until the spore density was sufficient to blacken the water. For *Ustilago kolleri*, it was necessary to macerate the smut balls by soaking and stripping them from the panicles. The spore suspension was strained through cheesecloth to remove fragments of host tissue and smut balls. Seed of the varieties to be inoculated was then placed in screw-capped glass vials of suitable size, and enough spore suspension was added to each to extend about half an inch above the seed. The tops were screwed on loosely, the vials

[1] C. I. refers to accession number of the Division of Cereal Crops and Diseases.

placed in a desiccator, and partial vacuum applied for 20 minutes and then released. The excess spore suspension was then poured off and the inoculated seed emptied onto paper towels and allowed to dry, after which it was placed in coin envelopes and stored until planting time.

After the spore suspension of each race or collection was prepared, all flasks, vials, and other equipment used were washed and then sterilized in the autoclave, and all other necessary precautions were taken to prevent the mixing of spores of different races.

Obviously it was not possible by the method used to calculate a uniform density of the spore suspensions of different races and collections. In lieu of this, each suspension was made sufficiently dense to insure the minimum spore load for maximum infection on a susceptible check variety. The uniformly successful results obtained over a period of years should indicate that the differences in infection percentages obtained were not due to differences in spore load.

Before inoculating, the seed of the differential varieties was freed from any natural contamination with smut spores or mycelium by soaking it in a 1:320 solution of commercial formaldehyde for 10 to 20 minutes. A few of the varieties were given either a long treatment (1 hour) or a second treatment, when it had been noted that smut had occurred in any uninoculated row of the previous crop. After treatment, the seed was washed thoroughly in running water and then spread out to dry.

Inoculum of the different races was maintained by collecting it from the same variety each year, and usually the variety chosen was the one that most nearly identified each race by its susceptible reaction. For example, a race that is characterized by the susceptibility of Black Mesdag was maintained by taking inoculum from that variety. When the collections were made from either the field or greenhouse plots the smutted panicles were picked just as they were beginning to break from the enclosing sheaths, which were then removed and the panicles placed in a leakproof parchment bag. The bags were allowed to remain open in the laboratory until the specimens were dry, after which they were closed.

Race identity was based on the resistance and the susceptibility of the differential varieties. An average of 10 percent or less of smut for all the tests was regarded as a resistant reaction, and more than 10 percent was regarded as a susceptible reaction. Different degrees of susceptibility were recognized, but intermediate reactions had no value in race differentiation, owing to the problem of variable pathogenic reaction already discussed.

The data presented in tables 1 and 2 show clearly the differentiation of 15 races of *Ustilago avenae* and 7 of *U. kolleri*, respectively. The races of the former species are designated A–1 to A–15 (table 1) and the latter, K–1 to K–7 (table 2). None of the differential varieties was uniformly susceptible to all races, but 3 of them (Anthony, Black Diamond, and Victory) were highly susceptible to about half of the races. These varieties, however, were useful in the separation of the other half of the races.

As shown in table 1, the first seven races of *Ustilago avenae* are similar in their high virulence on Anthony, Black Diamond, and Victory, but differ in the reactions of certain other varieties. For example, A–1 differs from A–2 by the susceptibility of Camas to the latter race;

and A–3 differs from the first two by its high virulence on Monarch. Race A–4 is similar to A–3 but differs by its high virulence on Black Mesdag; and A–5 differs from the preceding four races by its high virulence on Gothland. Race A–6 is simlar to A–3 but differs from it in the degree of virulence on Gothland. It also is similar to A–5 but differs from this race in the susceptibility of Monarch. Thus, A–6 is characterized chiefly by the common susceptibility of Gothland and Monarch and the resistance of Camas; whereas, A–7, though similar to A–6, differs from it by its pathogenicity on Camas and Nicol. Race A–8 is similar to A–1, differing only in the resistance of Victory to the former, and A–9 differs from A–8 by its pathogenicity on Fulghum. Race A–10 differs from A–5 by the resistance of Black Diamond; and the similarity of A–10 to A–11 is broken by the susceptibility of Nicol to the latter. The resistance of Anthony to A–12 distinguishes this race from A–9, while A–13 is characterized by the resistance of all the differential varieties except Anthony and Monarch. Races A–14 and A–15 are readily distinguished from all others by the susceptibility of Lelina, while they differ from each other by the susceptibility of Monarch and Gothland to A–15 and of Anthony only to A–14.

TABLE 1.—*Reaction of 10 differential varieties of oats in the greenhouse and the field to races of Ustilago avenae*

Smut race	Test No.[1]	Smut percentages on—									
		Anthony	Black Diamond	Victory	Gothland	Monarch	Fulghum	Black Mesdag	Camas	Nicol	Lelina[2]
A–1	1	98	96	100	0	0	0	0	0	0	-----
	2	100	95	97	0	0	7	0	0	0	-----
	3	83	70	94	4	0	2	0	0	0	0
	4	73	87	76	0	0	0	0	0	0	0
A–2	1	98	70	93	0	0	0	0	97	0	-----
	2	87	64	46	0	0	0	0	100	0	-----
	3	76	61	66	0	0	0	0	98	0	0
	4	69	64	67	0	0	0	0	94	0	0
A–3	1	98	76	94	11	93	3	0	0	2	-----
	2	87	75	77	12	71	0	2	0	3	-----
	3	68	30	55	2	71	0	0	0	0	0
	4	60	26	41	13	84	0	0	0	0	0
A–4	1	98	74	91	0	100	0	91	0	14	-----
	2	98	83	90	0	100	0	83	0	15	-----
	3	87	47	44	0	95	0	71	0	0	0
	4	71	43	35	0	86	0	93	0	0	0
A–5	1	100	93	98	94	0	0	0	0	0	-----
	2	35	41	50	72	0	7	0	0	0	-----
	3	90	83	91	69	0	0	0	0	0	0
	4	80	63	65	64	0	0	0	0	0	0
A–6	1	95	90	89	90	71	6	0	0	0	-----
	2	85	64	77	45	81	0	0	0	0	-----
	3	87	66	50	50	98	0	0	0	0	0
	4	33	24	19	11	60	0	0	0	0	0
A–7	1	96	96	85	94	98	4	0	30	13	-----
	2	89	77	59	52	87	3	0	36	10	-----
	3	70	25	31	59	74	0	0	61	8	0
	4	29	16	11	57	71	0	0	24	0	0

[1] Tests made as follows: Nos. 1 and 2, in greenhouse at Beltsville, Md., 1942 and 1943, respectively; Nos. 3 and 4, in field at Pullman, Wash., 1943 and 1944, respectively; and No. 5, in greenhouse at Pullman, 1945.

[2] The reaction indicated for Lelina in test No. 3 was obtained in 1942.

TABLE 1.—*Reaction of 10 differential varieties of oats in the greenhouse and the field to races of Ustilago avenae*—Continued

Smut race	Test No.	Smut percentages on—									
		Anthony	Black Diamond	Victory	Gothland	Monarch	Fulghum	Black Mesdag	Camas	Nicol	Lelina
A–8	1	74	55	0	6	0	0	0	0	0	-----
	2	79	82	0	0	0	3	0	0	0	-----
	3	41	26	0	0	0	0	0	0	0	0
	4	54	57	1	0	0	0	0	0	0	0
A–9	1	43	24	0	10	0	59	0	0	0	-----
	2	44	68	3	0	0	68	4	0	0	-----
	3	44	31	3	11	-----	33	0	0	1	0
	4	13	21	3	5	0	75	0	0	0	0
A–10	1	98	0	88	62	0	5	0	0	0	-----
	2	100	0	87	29	0	0	0	0	0	-----
	3	70	0	63	44	0	0	0	0	0	0
	4	70	0	15	34	0	0	0	0	0	0
A–11	1	100	0	100	28	0	2	0	2	40	-----
	2	98	0	78	25	0	0	0	0	56	-----
	3	93	0	93	50	0	5	0	0	28	0
	4	76	0	61	16	3	0	0	0	9	0
A–12	1	0	91	0	9	0	78	0	0	3	-----
	2	0	88	0	34	0	90	0	0	0	-----
	3	0	63	0	0	0	46	0	0	0	0
	4	0	28	0	0	0	77	0	0	0	0
A–13	1	13	0	0	5	97	0	0	0	0	-----
	2	8	0	9	6	64	6	0	0	0	-----
	3	18	0	0	0	48	1	0	0	0	0
	4	1	0	0	0	35	0	0	0	0	0
A–14	4	32	28	1	0	0	12	0	0	0	91
	5	50	87	37	0	0	86	0	0	6	100
A–15	4	0	19	0	8	90	29	0	0	0	81
	5	0	92	0	80	97	93	0	2	0	93

Apparently only two of the seven races of *Ustilago kolleri*, differentiated in table 2, represent pathogenic factors different from those contained in the races of *U. avenae*. Race K–4 is distinguished from all other races of both species by the common susceptibility of Monarch, Fulghum, and Black Mesdag. Race K–7 is similar to A–14 and A–15 in the susceptibility of Lelina, but differs from them in that Gothland is susceptible to K–7 and resistant to A–14, and Monarch is resistant to K–7 and susceptible to A–15. The reaction of the differential varieties to races K–1, K–2, K–3, K–5, and K–6 is almost identical with that to races A–1, A–3, A–5, A–4, and A–8, respectively.

At least four other collections of *Ustilago avenae* and one of *U. kolleri* appeared to represent races different from those described, but the results obtained were so variable that it seems best to subject them to further tests before assigning race numbers.

It would seem that the majority of races described here probably are identical with races described by others. There has been no opportunity to compare these with all the races of others, but, as already mentioned, 12 of the collections used represented previously described races. Included among these were Reed's (*8*) races 1, 10, and A–30 of *Ustilago avenae* and races 1 and 13 of *U. kolleri;* Tervet's (*17*) races 1

and 2 of *U. avenae* and 1, 2, and 3, of *U. kolleri;* and Vaughan's (*20*) Black Mesdag races 1 and 2 of *U. avenae.* The results obtained indicate that, of the races listed in tables 1 and 2, A–11, A–15, and K–2 are the same as Reed's races 1 and A–30 of *U. avenae* and race 1 of *U. kolleri*, respectively. (The inoculum of A–15 was obtained from Dr. Reed as his A–30.) Races A–11, A–5, and K–2 are the same as Tervet's races 1 and 2 of *U. avenae* and race 1 of *U. kolleri*, respectively; and A–4 is the same as Vaughan's race 2. (Inoculum of A–4 was obtained from the Minnesota Agricultural Experiment Station as Vaughan's Black Mesdag race 2.) Further tests are necessary before other equivalents can be determined.

TABLE 2.—*Reaction of 10 differential varieties of oats in the greenhouse and the field to races of Ustilago kolleri*

Smut race	Test No.[1]	Smut percentages on—									
		Anthony	Black Diamond	Victory	Gothland	Monarch	Fulghum	Black Mesdag	Jamas	Nicol	Lelina[2]
K–1	1	92	76	89	2	0	0	0	0	0	-----
	2	100	100	81	4	0	5	0	0	0	-----
	3	88	50	43	0	0	0	0	0	0	0
	4	86	'24	74	0	0	0	0	0	0	0
K–2	1	98	67	89	0	93	3	0	0	0	-----
	2	91	100	100	0	100	0	0	0	0	-----
	3	79	30	91	3	89	1	0	0	0	0
	4	72	56	59	0	97	0	0	0	0	0
K–3	1	100	69	91	100	6	0	0	0	0	-----
	2	100	94	100	97	17	10	0	0	0	-----
	3	82	37	79	81	0	1	0	0	0	0
	4	62	14	16	73	0	0	0	0	0	0
K–4	1	63	19	8	0	98	74	73	0	0	-----
	2	38	56	0	0	93	85	95	0	0	-----
	3	29	10	3	0	79	49	22	0	0	0
	4	31	5	1	0	78	70	22	0	0	0
K–5	1	98	4	93	2	100	0	84	0	0	-----
	2	100	80	80	0	100	0	40	0	0	-----
	3	81	15	50	0	91	0	20	0	0	0
	4	75	1	11	0	84	0	15	0	0	0
K–6	1	94	80	0	0	0	0	0	0	0	-----
	2	100	96	0	0	0	5	2	0	3	-----
	3	75	87	1	0	0	0	0	0	0	0
	4	82	33	0	0	0	0	0	0	0	0
K–7	4	56	2	5	25	0	0	0	0	0	45
	5	70	50	91	80	3	8	0	0	0	36

[1] Tests made as follows: Nos. 1 and 2, in greenhouse at Beltsville, Md., 1942 and 1943, respectively; Nos. 3 and 4, in field at Pullman, Wash., 1943 and 1944, respectively; and No. 5, in greenhouse at Pullman, 1945.
[2] The reaction indicated for Lelina in test No. 3 was obtained in 1942.

It will be noted that none of the races identified here represent the Red Rustproof type described by Reed (*8*) as race 10 of *Ustilago avenae.* Several collections of *U. avenae* from Red Rustproof oats have been tested and found to be capable of infecting Appler or Alabama Red Rustproof selections. Invariably, however, these collections were unable to perpetuate themselves more than 2 to 3 years and consequently were lost. A similar experience was had with Reed's race 10

of *U. avenae*, which infects Red Rustproof. Consequently, it would seem that this race type is extremely difficult to maintain, at least under the conditions of these tests, and for this reason it is not included. There is no doubt, however, that such a race exists, and it should be given consideration in a program of breeding smut-resistant Red Rustproof varieties.

EXPERIMENTAL RESULTS

Physiologic Races

A total of 218 collections of smut were tested on approximately 28 varieties of oats in the 8-year period from 1937 to 1944. A complete tabulation and presentation of the data obtained is beyond the scope of this bulletin. From an analysis of the data accumulated up to 1941, it was apparent that about 20 races of *Ustilago avenae* and *U. kolleri* could be identified on the basis of the differential reaction of 9 varieties of oats. Later, a tenth variety, Lelina, was added. These tentatively identified races along with new collections were then tested in the greenhouse and in the field for 3 years. The results obtained from these studies were used as the basis for race identification and are summarized in tables 1 and 2.

Distribution of Races

The 22 races identified were found to be distributed in 28 States, as shown in table 3. The number of races found in individual States ranged from 1 to 8, the greatest number being found in Minnesota. Individual races were found in from 1 to 13 States, A–6 and K–2 ranking first and second, respectively. In relative prevalence, however, these 2 races reversed their positions, being represented by 19 and 23 collections, respectively. A wide range in relative prevalence is indicated by the fact that 6 races were represented by only 1 collection each.

The race identity of only 141 of the 218 collections of smut was determined. A few of the remaining 77 collections apparently represented the Red Rustproof type of race, but most of them were discarded as possible duplicates. Owing to changes in differential varieties, these collections could not be properly classified in the final analysis, and, consequently, had to be omitted from the study on distribution.

Varietal Resistance

Information on the number and distribution of physiologic races of the oat smut fungi is useful for determining the adaptability of a variety to a given region and for the selection of appropriate parent varieties to use in breeding for smut resistance. This study of physiologic specialization was therefore supplemented each year by tests with a few varieties and hybrid selections of oats for the purpose of determining the scope of their resistance. To date (1946), 28 named varieties and 19 hybrid selections have passed through these individual race tests. The accumulated data on the varieties are presented in tables 4 and 5. Obviously these data are not strictly

TABLE 3.—*Distribution and prevalence of 15 physiologic races of Ustilago avenae (A–1 to A–15) and of 7 U. kolleri (K–1 to K–7)*

State	Race and number of times identified from each State																					
	A races															K races						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	1	2	3	4	5	6	7
Alabama										1												
Arkansas						1							1									
California								1														
Colorado	1	2																				
Florida						1																
Georgia			2			1																
Idaho					2	3	1				3					1	6					
Illinois					1			1		1											1	
Indiana	1									1	1							1		1		1
Iowa	1		1		3						1							1				
Kansas									1			3			1							
Michigan					1	1													1			
Minnesota	1				2	1					2		2			1	4	1				
Mississippi								1														
Missouri					1	2	2		1		1	2					1					
Montana			3																			
Nebraska					1					3	1						1					
Ohio					1	1				2												
Oklahoma				1		1									1							
Oregon																	1					
North Dakota					2	3	1									4	2					
South Carolina						1								1			1					
South Dakota	1						3				2					1	1					
Texas						2																
Utah		1																				
Washington	3	1	1		1								1			2	5					
Wisconsin			1		1												1					
Wyoming			2			1																

comparable, since they were not obtained from a single uniform test. Each year, however, the tests were made under conditions favorable for smut development, as indicated by the fact that upwards of 50 percent smut usually developed in varieties known to be susceptible. Consequently, it is believed that the tests were sufficiently reliable to determine the smut reaction of the varieties tested.

TABLE 4.—*Oat varieties and hybrid selections that were smut-free in a test made to determine varietal reaction to 22 individual races of Ustilago avenae and U. kolleri*

Variety (with pedigree) and hybrid selection	C. I. No.
Benton (D69×Bond)	3910
Boone (Victoria×Richland)	3305
Clinton (D69×Bond)	3971
Huron (Markton×Victory)	3756
Marion (Markton×Rainbow)	3247
Markton	2053
Marvic (Markton×Victory)	2597
Neosho (Fulghum-Markton×Victoria-Richland)	4141
Rangler (Nortex×Victoria)	3733
Bond×Anthony Sel	4004
D69×Bond Sel	3662
Do	3663
Do	3841
Do	3846
Do	4285
Do	4272
Fulghum-Markton×Victoria-Richland Sel	4001
Markton×Rainbow Sel	3350
Red Rustproof×(Victoria-Richland) Sel	3720
Richland×Fulghum Sel	3966
Victoria-Richland×Markton-Rainbow Sel	3609
Victoria-Richland×Morota-Bond Sel	4301

The procedure followed in testing the varieties was the same as that described for the physiologic race study, except that all tests were conducted in the field at Pullman, Wash. The inoculated seed was planted in single rows 4 to 5 feet long. The smut percentages were based on the total number of panicles to the row and were calculated to the nearest whole number, except that fractional percentages of less than 0.5 were recorded as 1. Usually the number of panicles in a row ranged from 250 to 350, but occasionally it was as low as 150 and as high as 500. No data were recorded for rows lacking a complete stand of plants.

A high degree of resistance to all races was exhibited by the majority of varieties and selections tested. No smut was produced by any of the races on the 9 named varieties and 13 hybrid selections listed in table 4. The reaction of 25 other varieties and hybrid selections to individual races is presented in table 5. Though not smut-free, several of these were highly resistant to all races, while others were highly resistant to the majority of races but highly susceptible to others.

Royal Scot exhibited the widest range of susceptibility, being infected by 16 of the races. Several other varieties, however, showed a greater degree of susceptibility to certain races. Notable in this respect is the susceptibility of Bridger and Victoria to A–2 and A–14,

TABLE 5.—*Reaction of varieties and hybrid selections of oats to individual physiologic races of Ustilago avenae and U. kolleri*

Variety (with pedigree) and hybrid selection	C. I. No.	Percentage of panicles smutted by—																					
		U. avenae (A races)															*U. kolleri* (K races)						
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	1	2	3	4	5	6	7
Bannock (Markton×Victory)	2592	0	9	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bridger (Markton×Victory)	2611	0	81	0	0	0	0	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DeSoto (Lee×Victoria)	3923	0	0	0	0	0	0	0	0	0	0	0	0	0	73	50	0	0	0	0	0	0	36
Erban (Banner×Early Ripe)	3477	0	0	0	0	5	20	2	0	0	2	0	0	1	0	0	0	0	8	0	0	0	0
Fultex (Fulghum×Victoria)	3531	0	0	0	0	0	0	0	0	0	0	0	0	0	64	77	0	0	0	0	0	0	63
Fulton (Fulghum×Markton)	3327	0	0	0	0	0	12	0	1	0	0	0	0	0	---	---	0	0	0	0	0	0	---
Hancock (Markton×Rainbow)	3346	0	0	0	0	0	0	12	0	0	0	5	0	0	---	---	0	0	0	0	0	0	---
Marida (Markton×Idamine)	2571	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Osage (Victoria-Richland×Fulton)	3991	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Richland	787	0	0	3	0	0	3	16	0	0	10	21	0	0	0	0	0	0	1	0	0	8	0
Royal Scot	3836	25	18	23	5	18	18	12	3	10	4	12	0	4	0	0	15	25	0	0	0	10	5
Sac (D69×Bond)	3907	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Vanguard (Hajira×Banner Sel.)	3837	5	8	12	0	8	4	0	7	4	9	12	0	0	0	0	0	10	0	0	2	16	11
Vanguard 339	------	0	6	0	0	0	4	0	1	1	6	7	6	0	---	---	0	0	0	0	0	0	---
Ventura ([Victoria-Richland]×Fulton)	3989	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vicland (Victoria×Richland)	3611	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	7
Victorgrain (Victoria×Fulgrain)	3692	0	0	0	0	0	0	0	0	0	0	0	0	0	19	27	0	0	0	0	0	0	50
Victoria	2401	0	0	0	0	0	0	0	0	0	0	0	0	0	89	24	0	0	0	0	0	0	0
Vikota (Victoria×Richland)	3602	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	3
Bannock×Victoria-Richland Sel.	3916	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Do.	4181	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bond×D67 Sel.	4327	0	0	1	1	0	2	3	3	2	5	0	0	0	2	1	1	1	0	1	0	1	1
D69×Bond Sel.	4532	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Fulghum×Victoria Sel.	3967	0	0	0	0	1	0	0	0	0	0	0	0	0	79	17	0	0	0	0	0	0	49
Hancock×(Morota-Bond) Sel.	3972	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

respectively. A high degree of specialization to varieties derived from hybrids involving Victoria and Fulghum is shown by A–14, A–15, and K–7. Thus, from the standpoint of developing smut-resistant oat varieties, A–2, A–14, A–15, and K–17 are highly significant races.

That high resistance to these and all other races can be obtained, however, is shown by the varietal reactions indicated in tables 4 and 5. Among these, the parental varieties and selections that have contributed to the production of highly smut-resistant varieties are Markton, Victoria, Richland, Fulghum, Bond, and D69.

DISCUSSION AND CONCLUSIONS

Consistency in the behavior of physiologic races on a given set of differential hosts under comparable conditions for a period of years is important in a long-time program of race identification. This is especially true when the maintenance of race identity and the identification of newly occurring races are primarily an integral part of a general crop-improvement effort. The real value of such a program should be measured more by the applicability of the results than by their uniformity. For example, if a group of races can be clearly identified and used as a basis for determining varietal resistance, it probably is not highly important from the practical standpoint if these races do not always react in exactly the same way on the different varieties, so long as the identity of each is maintained. Therefore, in this series of tests with oat smuts, emphasis has been placed on the broad objective of identifying representative races from the principal oat regions of the United States and organizing facilities for determining the reaction of newly developed oat varieties to these races. It would seem that this has been satisfactorily accomplished.

As mentioned, Tervet (*17*) has considered the problems encountered in the determination of physiologic races of the oat smuts both intensively and extensively, and he points out that variability in pathogenicity is the most important problem. Similar observations were made during the course of these studies. Some of the races showed a greater tendency toward variability than others, but, with a few exceptions, those included in tables 1 and 2 were fairly consistent in pathogenicity on the varieties used in the tests reported. There seems to be no entirely satisfactory explanation for the inconsistent reactions that did occur, but some possible reasons may be suggested. Lower infections usually were obtained in field tests than in greenhouse tests of susceptible varieties. Furthermore, there were greater inconsistencies in the results from the two field tests than in those from the two greenhouse tests, as exemplified by race A–6 (table 1). Results of this type might be expected, since it obviously is easier to maintain conditions favorable for infection in the greenhouse than in the field. The number and degree of inconsistencies in results from inoculation experiments with oat smut races probably could be greatly reduced if all testing could be done in the greenhouse.

Variability in reaction was greater in some varieties than in others, as shown by the fact that Anthony and Camas exhibited a significantly higher degree of susceptibility to A–7 in test 3 than in test 4, while Gothland and Monarch were about equally susceptible to this race in both tests. Similarly, for A–9, Anthony was more susceptible in test

3 than in test 4, whereas the reverse was true with Fulghum. It appears that when two varieties are susceptible to the same race, conditions that favor high infection of one are not necessarily conducive to high infection of the other. It would seem, therefore, that environmental variability possibly might modify varietal response to certain races and thereby account for some of the inconsistencies found.

The importance of purity of the differential varieties is obvious and has been emphasized by Reed (*8*) and Tervet (*18*). Tervet has shown not only that the same strain should be maintained, but also that the same lot of seed of a given strain should be used so far as possible. The majority of tests carried on in this study were made with the same strain of each variety from one source. In some instances, however, shortages necessitated getting seed from other sources, and possibly some of the variability in results was due to this difference in source. There is no specific evidence in the results, however, to indicate that the seed was at fault. A constant supply of uniform seed of the differential varieties has been produced by the Aberdeen (Idaho) station for many years.

Genetic purity and stability of oat smut races are no less important than seed purity of the host in maintaining the identity of races from year to year. Field collections of oat smut sometimes contain both species—*Ustilago avenae* and *U. kolleri*—and probably frequently two or more races. Race identity, therefore, is contingent first upon the degree to which the pathogenicity of field collections can be purified. The difficulty of obtaining genetic purity and stability is emphasized by Leitzke's (*2*) studies with race mixtures of *U. avenae*. He obtained highly divergent results with race mixtures, including reduced, unchanged, and increased pathogenicity and the production of new pathogenic types. Furthermore, by succeeding inoculations, the manifestation of these various pathogenic attributes was immediate in some cases and delayed in others, retained in some and lost in others, and reduced in some and intensified in others.

Thus, the purification of some of these pathogenic types might be exceedingly difficult. In this connection, Sampson and Western (*15*) pointed out that, in the absence of hybridization, varietal screening and the use of monochlamydospore cultures for inoculum are convenient ways of approaching purity of races.

A third method, suggested but not used by Sampson and Western (*15*), is to inoculate with paired monosporidial cultures from a single chlamydospore. This method was tried in these studies but was found to be unsuitable, because it eliminated certain pathogenicity complexes that are needed in varietal resistance tests. Varietal screening was finally adopted as the most suitable method for approaching pathogenic purity of races, and it seems that the results are satisfactory, at least for the purpose for which they are intended to serve.

The failure of the Red Rustproof type of race to perpetuate itself under the conditions of these experiments is difficult to explain and no attempt at an explanation will be made here. Nevertheless, the existence of this type of race should be taken into consideration in breeding for smut-resistant oats of the Red Rustproof type.

A knowledge of the prevalence and distribution of oat smut races is an important consideration in the development and introduction of new oat varieties. Since all important oat varieties of recent and current

production are highly resistant to almost all races, however, the significance of race distribution, and prevalence centers for the most part around relatively few races. For example, only two races—A–2 and A–7—are important in determining the adaptability of varieties, such as Bridger (C. I. 2611), that have been derived from the cross Markton × Victory. Similarly, varieties of the Lelina type would be limited in adaptability for smut resistance by the distribution and relative prevalence of A–14, A–15, and K–7. Limited tests with several new collections suggest a wider distribution and greater relative prevalence of these races than is indicated by the data in table 3. Unfortunately, both Bridger and Lelina represent varieties that are agronomically adapted to the regions where the races to which they are susceptible are prevalent. This emphasizes the need of adequate facilities for determining the smut reaction of new oat varieties. Obviously, the effectiveness of such facilities will depend upon availability of races and adequate information regarding their distribution and relative prevalence.

SUMMARY

In 218 collections of oat smut obtained from various oat-producing regions of the United States and Canada, 15 races of *Ustilago avenae*, designated A–1 to A–15, and 7 races of *U. kolleri*, designated K–1 to K–7, were identified. These races are differentiated by the resistance and susceptibility of 10 oat varieties. Intermediate reactions were of no value for the separation of races.

Seven of these races apparently are identical with certain races described by other workers, while three races (A–2, A–15, and K–7) are believed to be described here for the first time. The rest could not be classified into previously known races.

The races identified in this study were found to be distributed in 28 States, with the number in individual States ranging from 1 to 8, the greatest number being found in Minnesota. The most widely distributed race was A–6, which was found in 13 States, while the most prevalent was K–2, which was represented by 23 collections.

The majority of 47 varieties and hybrid selections of oats tested were found to be highly resistant to all the races used. In tests with individual races 9 named varieties and 13 hybrid selections remained smut-free. No variety was highly susceptible to more than 2 races, although 1 variety, Royal Scot, was somewhat susceptible to the majority of races. Among varieties contributing to the production of highly smut-resistant varieties are Markton, Victoria, Bond, Richland, Fulghum, and D69.

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