PHYSIOLOGIC RACES OF USTILAGO HORDEI[1]

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INTRODUCTION

Covered smut of barley (*Ustilago hordei* (Pers.) Kell. and Sw.) in the United States has long been recognized as an important hazard in the culture of barley (*Hordeum vulgare* L.). In the years from 1918 to 1935 for which records are available,[2] its estimated toll averaged over 2¼ million bushels annually, and twice during these years the estimated annual loss exceeded 5 million bushels. Despite recent notable advances in the control of barley covered smut through seed treatment, as shown by Leukel (*10*),[3] relatively little progress has been made in combating the disease through selecting and breeding barleys having inherent resistance to various physiologic races in the smut species. Until recently, progress in this direction had been almost completely blocked by the lack of an effective and easily applied method of artificial inoculation of the seed for producing high percentages of smutted plants. Despite the general belief of long standing that barley is inoculated, in threshing, by the spread of the spores to the surface of the seed, the artificial blackening of seed with millions of spores usually has failed to result in high percentages of smutted plants. Jensen (*9*) first reported this difficulty nearly 50 years ago. In 1934, the writer (*15*) devised a spore-suspension method of inoculating seed barley in which spores are washed beneath the hulls. The method is similar in principle to Haarring's (*5*) "evacuation" method of inoculating oats with smut, but it employs no vacuum or nutrient solution. The spore-suspension method is effective, fairly easy to apply, and approaches the natural method of inoculation as recently reported (*17*). The way thus was opened for the studies on physiologic races presented herein.

PREVIOUS INVESTIGATIONS

Faris (*3*, *4*) first reported physiologic races in *Ustilago hordei* in 1924. Five pathogenic races were isolated. Rodenhiser (*11*), in 1928, described seven cultural races, and a further test of two of these

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[2] UNITED STATES BUREAU OF PLANT INDUSTRY. ESTIMATE OF CROP LOSSES DUE TO PLANT DISEASES. 1917 U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bull. 2:1-18, 1918. [Mimeographed.]

——— CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES. 1918-35. U. S. Bur. Plant Indus. Plant Disease Reptr. Sups. 6:186-213. 1919; 12:307-332, 1920; 18:317-338, 1921; 24:489-510, 1922; 30:462-490, 1923; 36:318-348, 1924; 43:381-410, 1925; 49:382-412, 1926; 56:394-423, 1927; 64:370-399, 1928; 83:1-68, 1932; 87:1-82, 1935; 89:1-45, 1935; 94:1-75, 1936. [Mimeographed.]

[3] Reference is made by number (italic) to Literature Cited, p. 691.

showed differences in their pathogenicity on Lion and Himalaya barleys. Recently Aamodt and Johnston (*2*) found two races in Alberta, Canada. Apparently this report completes the list of available contributions. The fact that there have been relatively few investigations of physiologic races of *U. hordei* doubtless is due largely to the difficulties with seed inoculation, as noted previously.

MATERIALS AND METHODS

The experiments were conducted at Ithaca, N. Y., during the 3-year period 1934–36. Eight pure-line varieties of spring barley were used as differential hosts, namely, Excelsior (C. I.[4] 1248), Gatami (C. I. 575), Hannchen (C. I. 531), Lion (C. I. 923), Nepal (C. I. 595), Odessa (C. I. 934), Pannier (C. I. 1330), and Trebi (C. I. 936). The selection of these varieties was based largely on unpublished studies of the late Dr. J. A. Faris. Faris conducted an experiment at Fargo, N. Dak., in 1933, to determine suitable differential barleys and physiologic races of *Ustilago hordei*. Thirty varieties inoculated with each of 65 smut collections comprised the test. The maximum percentage of smutted heads was 28, in the variety Odessa, which proved to be susceptible to every smut collection. In most of the other varieties the maximum smut infection rarely exceeded 15 percent. Although the data were inadequate to warrant definite conclusions, they were useful to the writer in indicating that certain collections of smut were representative of distinct races and that the varieties named above should make good differential hosts. Faris (*3*, *4*) also had found that Hannchen and Nepal well differentiated two smut races which he numbered "1" and "2."

For differential hosts, the writer chose, so far as possible, from the varieties listed by Harlan and Martini (*6*), those that are outstanding for certain characteristics and representative of some barley-growing region of the world. In the course of study, the following additional species and varieties also were tested for their suitability as differential hosts: Hillsa (C. I. 1604), *Hordeum deficiens* Steud. (C. I. 668–1), *H. intermedium* Koern. and Wern. (C. I. 4377), Lyallpur (C. I. 3403), Club Mariout (C. I. 261), Oderbrucker (C. I. 1529), Summit (C. I. 929), and White Smyrna (C. I. 910). The first four proved too highly resistant to be useful, and the remainder failed to further or better differentiate any of the smut races thus far isolated with the varieties selected. Twenty-eight winter varieties or selections were also tested to determine their possible value in differentiating physiologic races of covered smut.

The 8 selected varieties, during the 3-year test period, were inoculated with each of 200 collections of covered smut obtained from 26 States. Preparatory to inoculation, seed of the differential hosts was soaked in a formaldehyde solution (1 part of formaldehyde to 320 parts of water) for 2 hours, washed in running water for one-half hour to remove all traces of formaldehyde, and spread in thin layers until

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

thoroughly dry. Each year five check rows of uninoculated seed of each variety so treated produced smut-free plants. In view of the occurrence of mixed collections of the different barley smuts, the spores of the collections used each year were first examined to determine the character of the epispore and the type of germination on 2-percent potato-dextrose agar. Later, the smutted heads resulting from seed inoculation with each collection were examined in the different varieties. All collections that were suspected or determined to be other than true barley covered smut were eliminated.

In 1934, 1935, and 1936, respectively, 75, 60, and 65 new smut collections were tested. The 1934 collections comprised six races; in 1935 two other races were isolated, but in 1936 no additional races were obtained. Two collections of each of the six races obtained in 1934 were further tested in 1935 and 1936, and two collections of each of the two races obtained in 1935 were again tested in 1936. In these further tests of the isolated races, the inoculum of each race to be used in the succeeding year's test was collected on the same date and subsequently stored in a cool room. Whenever possible, the inoculum was collected from the variety which most clearly differentiated each race to aid in screening out any other races that might have occurred in the original collection. A month or less before seeding, the seed was inoculated by the spore-suspension method previously described (*15*).

The inoculated seed in each year's test was planted at the rate of 6 g to the 5-foot row. The new collections were tested in duplicated systematically distributed rows. In the further tests, in 1935 and 1936, of previously isolated races, triplicated systematically distributed rows were employed. In preparing the inoculum, in inoculating, and in planting the seed, adequate precautions were observed to prevent mixing of spores of different collections. The smut percentages obtained were based on counts of the total number of heads per row in 1934 and 1935 and of 300 heads per row in 1936.

In the analysis of data three infection classes were used, as follows: 0–5 percent infection=resistant class (R); 6–35 percent infection=intermediate class (I); 36 percent infection and above=susceptible class (S).

The classification is arbitrary and the limits of the infection classes have been selected to fit the present data. The purpose of the classification is to present in a convenient way the host reactions in the present study that differentiated the various races of covered smut. As shown in table 1, increase in susceptibility frequently is accompanied by an increase in the variability of infection. The progressive widening in limits of the intermediate and susceptible classes accommodates these variations. In some previous studies of cereal smuts, narrower infection ranges have been considered significant for separating physiologic races. In the present study, however, the variations in different years and between replications in a single year frequently were too great to warrant the use of a classification with more than three classes of infection. In the three seasons in which the tests

were conducted at Ithaca, N. Y., extremes of drought, precipitation, and heat occurred during the growing seasons of 1934, 1935, and 1936, respectively. Under such conditions, the separation of smut races doubtless should be based only on differences in pathogenicity that are fairly wide and reasonably consistent.

In each of the 3 successive years of the experiment, the maximum percentages of smutted heads in the susceptible variety Odessa were 62, 54, and 50, respectively. In Nepal, the maximum percentages were 60, 45, and 58, respectively. The conditions for infection thus appear to have been adequate for the differentiation of physiologic races.

RESULTS

IDENTIFICATION OF PHYSIOLOGIC RACES

The annual and average percentages of smut produced by each of the eight races of *Ustilago hordei*, in 2 or 3 years of the tests, are given in table 1. In each year the two collections of each race produced similar results. Data for only one collection of each race therefore are recorded. As noted previously, some of the smut collections used were collected by Faris. These collections were numbered, but their physiologic race identity was unknown except that one collection was labeled "form 1" and another "form 2." In the present experiments the reaction of these races on the varieties Hannchen and Nepal was similar to that described by Faris (*4*), and Faris' numbers were therefore retained. The varietal reactions which differentiate the races are given in table 2, and this is followed by a key to facilitate the identification of the races. Table 2 and the key show that the eight smut races may be identified with only five of the eight varieties used. However, two of the varieties omitted, Gatami and Trebi, have given good differential reactions with some races and have been useful in confirming their identity. Odessa, also omitted from the key, is needed to perpetuate race 8.

The total number of collections obtained from each of the 26 States that served as sources of the collections, and also the number of races and their relative prevalence in each of these States as indicated by the collections used in these experiments, are given in table 3.

TABLE 1.—*Percentages of smutted heads in 8 varieties of spring barley inoculated with 8 physiologic races of Ustilago hordei, and grown at Ithaca, N. Y., 1934–36*

Race No.	Year tested	Smutted heads in—							
		Excelsior (C. I. 1248)	Gatami (C. I. 575)	Hannchen (C. I. 531)	Lion (C. I. 923)	Nepal (C. I. 595)	Odessa (C. I. 934)	Pannier (C. I. 1330)	Trebi (C. I. 936)
		Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
1	1934	0.0	0.0	8.2	0.0	0.0	34.3	0.0	9.8
	1935	0	0	18.6	0	0	36.9	0	2.4
	1936	0	0	18.8	0	0	44.9	0	2.2
	Average	0	0	15.2	0	0	38.7	0	4.8
2	1934	4.0	12.8	2.2	10.2	40.5	41.2	0	3.6
	1935	0	7.7	0	17.8	43.0	30.8	0	0
	1936	0	13.5	0	12.5	58.2	38.4	0	0
	Average	1.3	11.3	7	13.5	47.2	36.8	0	1.2
3	1934	20.0	0	0	7.1	60.0	25.0	4.2	0
	1935	30.3	.6	0	15.7	45.1	40.8	0	.6
	1936	29.3	0	0	11.6	46.5	49.3	0	0
	Average	26.5	.2	0	11.5	50.5	38.4	1.4	.2
4	1934	0	0	8.8	0	18.8	45.2	13.8	24.2
	1935	.9	0	13.2	0	32.0	29.7	13.5	9.6
	1936	0	0	10.5	0	33.1	29.5	6.9	4.2
	Average	.3	0	10.8	0	28.0	34.8	11.4	12.7
5	1934	0	0	0	15.6	0	61.8	0	27.9
	1935	0	0	0	19.1	0	27.0	0	18.8
	1936	0	0	0	12.7	0	21.4	0	10.4
	Average	0	0	0	15.8	0	36.7	0	19.0
6	1934	0	0	30.4	25.5	0	52.6	0	45.8
	1935	0	0	17.4	20.2	0	34.3	0	29.5
	1936	0	0	32.1	19.3	0	50.2	0	31.1
	Average	0	0	26.6	21.7	0	45.7	0	35.5
7	1935	.8	0	0	0	24.3	53.5	1.5	3.6
	1936	.3	0	0	0	29.5	26.9	0	.3
	Average	.6	0	0	0	26.9	40.2	.8	2.0
8	1935	0	0	0	0	.5	39.7	0	0
	1936	0	0	0	0	0	28.3	0	0
	Average	0	0	0	0	.3	34.0	0	0

TABLE 2.—*Reactions of 5 varieties of spring barley which differentiate 8 physiologic races of Ustilago hordei*

Race No.[1]	Reaction[2]—				
	Excelsior (C. I. 1248)	Hannchen (C. I. 531)	Lion (C. I. 923)	Nepal (C. I. 595)	Pannier (C. I. 1330)
8	R	R	R	R	R
1	R	I	R	R	R
7	R	R	R	I	R
4	R	I	R	I	I
5	R	R	I	R	R
6	R	I	I	R	R
2	R	R	I	S	R
3	I	R	I	S	R

[1] The race numbers are presented in the order given to facilitate comparison with the key to 8 physiologic races of *Ustilago hordei* that follows.

[2] R (resistant)=0–5 percent of smutted heads; I (intermediate)=6–35 percent; S (susceptible)=36 percent or more.

Key to eight physiologic races of Ustilago hordei

	Physiologic race
Lion resistant:	
Nepal resistant:	
Hannchen resistant	8
Hannchen intermediate	1
Nepal intermediate:	
Pannier resistant	7
Pannier intermediate	4
Lion intermediate:	
Nepal resistant:	
Hannchen resistant	5
Hannchen intermediate	6
Nepal susceptible:	
Excelsior resistant	2
Excelsior intermediate	3

TABLE 3.—*Number and distribution of physiologic races of barley covered smut in 200 collections from 26 States*

Location	Collections of race No. —								Total collections
	1	2	3	4	5	6	7	8	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Arizona					1				1
California	1		1		34	1			37
Colorado						1			1
Georgia	3								3
Idaho		1	1		2	13			17
Illinois						1	2		3
Iowa			1			9			10
Kansas			1		1	1			3
Louisiana						1			1
Michigan						1			1
Minnesota	1					19			20
Missouri			1			1			2
Montana				1		2			3
Nebraska						9			9
New York						10			10
North Carolina	2					1			3
North Dakota				1		18			19
Oklahoma						1			1
Oregon		1			1				2
South Dakota						2			2
Texas	1								1
Utah					1	14			15
Virginia	7					1		1	9
Washington				1	17	5			23
West Virginia								1	1
Wisconsin						3			3
Total	15	2	5	3	57	114	2	2	200

The data in table 1 show, in general, a high degree of consistency in the percentages of infection with each of the races during the 2 or 3 years of the test. In some instances certain races produced a low percentage of smutted heads in certain varieties in 1934 but did not cause smut in these varieties in the following years. This may have been due to mixtures in the original collections that were screened out as a result of passage through selected hosts in the following years.

Despite the fact that environmental conditions were marked by unusual variations in temperature and precipitation in the three seasons in which the tests were conducted at Ithaca, the spore-suspension method of seed inoculation proved effective and the degree of smut infection was reasonably uniform.

Two facts are apparent from table 3: (1) The wide distribution of race 6 and (2) the predominance of race 5 in California and Washington.

WINTER VARIETIES AS DIFFERENTIAL HOSTS

In the fall of 1935, the 28 winter varieties or selections listed in table 4 were inoculated with the eight races of covered smut and sown in triplicated, systematically distributed rows at Statesville, N. C. In other respects the general conduct of the test was similar to that with the spring barleys. The results of the test are given in table 4. In general, these winter barleys displayed little clear-cut differential reaction to the smut races except that about two-thirds of them were resistant to race 2. The Nakano Wase selections, including Esaw, however, were moderately susceptible to race 2 and highly resistant or immune to all other races. The Smooth Awn selections 86 and 203 were the most uniformly resistant, showing less than 5 percent of heads smutted by any of the races. Unfortunately, Esaw and the Nakano Wase and Smooth Awn selections are highly susceptible to the brown loose smut (*Ustilago nuda* (Jens.) Kell. and Sw.) which is prevalent in the humid winter barley region.

Doubtless as a preface to further studies on the use of winter barleys as differential hosts, a better knowledge of the influence of winter injury on the incidence of covered smut should be acquired. Tisdale (*18*) and Faris (*3*) have shown that plants of certain winter barleys are more susceptible to winter injury when infected with covered smut than when not infected. In the experiment just described there were wide differences in the degree of winter injury sustained by the different varieties and this may have obliterated differential responses to the races of smut that otherwise would have been apparent.

TABLE 4.—*Percentages of smutted heads in 28 varieties of winter barley inoculated with 8 physiologic races of Ustilago hordei and grown at Statesville, N. C., 1935–36*

Race No.	Smutted heads in—													
	Alaska (C. I. 4106)	Beardless No. 6 (C. I. 2746)	Cusado (C. I. 895)	Esaw (C. I. 4090)	Gaddis (C. I. 6003)	Garren	Han River (C. I. 2163)	Kashmir	Kentucky No. 2 (C. I. 6148)	Kentucky Smooth Awn (C. I. 6021)	Khayyam (C. I. 1117)	Nakano Wase selection 33	Nakano Wase selection 68	Orel (C. I. 351)
	Pct.	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
1	10.2	3.3	11.0	0.0	5.3	6.0	22.3	15.1	4.9	36.1	7.9	1.2	0.0	6.8
2	6.3	6.3	1.7	12.3	7.4	1.3	3.1	3.4	.2	9.2	2.4	7.3	10.9	2.1
3	14.4	16.2	6.0	.0	12.2	10.5	16.9	12.3	2.9	34.8	8.1	.0	.0	4.6
4	25.8	17.1	11.5	.0	15.8	13.3	21.2	18.6	7.7	24.6	11.4	.0	.0	16.8
5	40.8	2.6	19.4	.4	7.3	9.4	45.8	30.9	13.8	34.3	25.4	3.0	.6	24.7
6	40.9	5.8	22.3	2.2	5.1	6.5	47.3	28.2	12.8	28.8	26.8	.0	.0	20.3
7	30.5	14.0	28.1	.8	22.5	9.3	38.8	22.4	15.1	27.9	35.0	.0	1.2	22.6
8	39.5	4.9	26.1	1.9	9.2	6.8	32.2	33.1	12.7	28.6	26.6	.0	.0	19.3

TABLE 4.—*Percentages of smutted heads in 28 varieties of winter barley inoculated with 8 physiologic races of Ustilago hordei and grown at Statesville, N. C., 1935–36*— Continued

Race No.	Smutted heads in—													
	Pidor (C. I. 901)	Scottish Pearl (C. I. 277)	Smooth Awn selection 86	Smooth Awn selection 203	Smooth Awn selection 205	Squarehead (C. I. 252)	Tenkaw (C. I. 646)	Tennessee Winter (C. I. 3534)	Tennessee Winter (C. I. 3546)	Tennessee Winter (C. I. 6034)	Tennessee × Abyssinia (37) (C. I. 6236)	Texas Winter (C. I. 554)	Wisconsin Winter (C. I. 2159)	Woods Hooded (C. I. 6235)
	Pct.	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
1	11.8	12.5	0.0	0.0	0.5	11.5	8.8	16.9	25.1	10.5	22.9	13.6	13.3	13.2
2	11.3	4.0	1.1	1.6	15.0	.9	2.2	2.9	6.8	.5	10.3	2.8	2.9	3.3
3	3.6	7.9	.0	.0	.0	6.8	11.8	12.8	23.7	6.0	16.7	10.1	12.1	11.1
4	19.1	19.4	1.4	.0	.0	21.7	16.6	20.0	37.4	11.9	20.8	16.0	16.6	19.2
5	27.6	25.5	4.7	3.1	5.1	24.7	28.1	25.3	45.7	7.9	29.6	26.1	39.3	10.6
6	39.6	35.0	1.7	.0	.0	36.2	35.8	31.6	57.2	8.5	37.4	38.1	33.3	14.9
7	13.6	31.1	.0	.0	4.8	32.8	37.3	33.2	45.8	10.2	29.4	32.1	34.2	21.1
8	16.5	37.7	.0	.0	2.5	30.7	29.3	27.6	54.5	7.7	35.5	29.1	30.1	11.7

Another factor that seems due to assume greater importance in future studies of physiologic races is the influence of environmental conditions on the response of the host after infection. The results of Faris (*3*) seem to indicate that after the smut has penetrated the seedling environmental conditions may influence the host response in a way other than through winter injury; and, as Faris notes, "the reaction of barley varieties to such environmental changes may not be the same." Aamodt (*1*), Smith (*13*), Rodenhiser and Holton (*12*), and Holton and Heald (*8*) have reported that environmental conditions after infection may affect the incidence of bunt in wheat.

DISCUSSION

Eight physiologic races of *Ustilago hordei* have been isolated on the basis of differences in their pathogenicity on eight varieties of barley. Although sufficient data are not yet available to permit a detailed discussion of the distribution of these races, it seems evident that the race designated No. 6 is the most widely distributed. It was found in 21 of the 26 States from which collections have been obtained. It was also the most frequently collected, occurring in 114 of a total of 200 collections. However, in California and Washington race 5 was outstanding, occurring 34 times in 37 collections from California and 17 times in 23 collections from Washington. The predominance of race 5 in California may be linked with the antiquity and survival of Coast barley in that State. As noted by Harlan and Martini (*7*), when North America was discovered there were no barleys here. The early Spanish missionaries introduced Coast barley into California about 1770, and it is still widely grown there. Of the 37 covered smut collections obtained from California, 26 came from Coast and the two Coast-type varieties Atlas and California Tennessee Winter. Twenty-three of these twenty-six collections proved to be race 5. The early importations of Coast seed in California may have harbored this particular race of smut, which has survived and spread with its susceptible and popular host.

Despite the apparent restriction of certain smut races to limited areas, the probability that the different races will be spread through wind dissemination of spores and through the interchange of infected seed makes it highly desirable to breed barleys resistant or immune to all the known races of smut. To date Pannier (C. I. 1330) has proved highly resistant or immune to seven races and only moderately susceptible to one. *Hordeum deficiens* (C. I. 668–1) and *H. intermedium* (C. I. 4377), used only in the test of 1934, were highly resistant or immune to the six races occurring in the collections of that year. These two and Pannier also have proved highly resistant or immune to two races of the black loose smut (*Ustilago nigra Tapke*) of barley recently described (*14, 16*). In these experiments no smut has been observed in Hillsa (C. I. 1604) and Lyallpur (C. I. 3403), yet the former was inoculated with 65 collections of *U. hordei* in 1933 by Faris and both were inoculated with eight races of *U. hordei* and two of *U. nigra* in 1935 by the writer (*16*). In the light of the results of the present investigation, it appears that physiologic races of *U. hordei* are not more numerous than those of other small-grain smuts and that the breeding of barleys for resistance to covered smut should not be hampered by lack of resistant parental material.

SUMMARY

Eight physiologic races of *Ustilago hordei* were found in 200 collections from 26 States. Race separation was based on differences in pathogenicity on five varieties of spring barley.

The most widely distributed race was collected in 21 of the 26 States. It was also the most generally prevalent race, occurring 114 times in the 200 collections.

In California and Washington another race was conspicuously prevalent and widespread. It occurred 51 times in 60 collections from these States.

Under the conditions of a 1-year test with 28 winter varieties or selections, little clear-cut differential host response to the 8 races of covered smut was obtained. Marked differences in varietal response to winter injury occurred. A better knowledge of the influence of this factor on the incidence of covered smut in winter barleys is needed.

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