INHERITANCE OF RESISTANCE IN OATS TO USTILAGO LEVIS [1]

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INTRODUCTION

The control of oat smuts through the breeding of resistant strains is of wide interest because of the economic importance of these diseases. This paper presents the results of studies on the inheritance of resistance to infection by *Ustilago levis* (Kell and Sw.) Magn. Genetic data were obtained on six crosses, and some rather fragmentary data on three others. Approximately 140,000 plants were observed. Data were recorded on (1) the percentage of individuals resistant to *U. levis* in F_2 and later generations, (2) the relation of infection in F_3 lines to infection in selections from them in later generations, and (3) the relation between certain morphological characters and resistance to smut infection in progeny plants. The study was conducted during 1925, 1926, and 1927, and data collected at five widely separated points are presented.

REVIEW OF LITERATURE

Wakabayashi (*15*)[2] published the first report in this country on the inheritance of the resistance of oats to infection by smut. He crossed Red Rustproof (resistant) with Black Tartarian (susceptible). The indicated dominance of resistance was attributed to three independent dominant factors. His results indicated that correlation existed between lemma color and resistance to smut infection in the cross studied.

Barney (*1*) concluded that resistant varieties contained either one, two, or three factors for resistance to smut. Gaines (*3*) studied crosses between Red Rustproof and Black Tartarian, Abundance, Large Hull-less, and Chinese Hull-less. He reported that Red Rustproof has three factors for resistance. Reed and Stanton (*13*), studying the cross Fulghum × Swedish Select, observed no correlation between the morphological characters studied and resistance to smut. Gaines (*4*) concluded that the smut-resistant Markton probably contains three factors for smut resistance. In crosses between Black Mesdag, resistant to both loose and covered smuts, and Hull-less, susceptible to both, Reed (*9*) observed that resistance was dominant to susceptibility. Segregation in the F_2 indicated a single-factor difference between the parents. In later experiments Reed (*11*) observed similar results from crosses of Hull-less × Black Mesdag, and Silvermine × Black Mesdag. He studied the inheritance of resistance to smut infection in several other crosses, and

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[2] Reference is made by number (italic) to Literature Cited, p. 1099.

states that "In all crosses involving varieties differing in their behavior to smut, resistance was dominant and susceptibility recessive, and segregation in the F_2 appeared to occur on the basis of a single-factor difference."

Hays, Griffee, Stevenson, and Lunden (*6*) studied resistance in crosses of Black Mesdag with homozygous strains from the cross Minota × White Russian. They state that "immunity to smut in oats is dominant to susceptibility." No correlation was found between glume color, awn development, hairs on the rachilla segment, and smut resistance. They found it impossible to state the exact genetic constitution of their material as to smut resistance.

Garber, Giddings, and Hoover (*5*) found in the cross Gopher × Black Mesdag that no relation existed between smut susceptibility and earliness. They suggest a possible linkage between black seed color and a supplementary factor for transgressive segregation of smut susceptibility, but little if any linkage between leaf width and resistance to smut. They conclude that Gopher and Black Mesdag differ in their reaction to smut infection by a single main factor, and in addition by at least one modifying factor, presumably present in Black Mesdag, which resulted in transgressive segregation for susceptibility.

MATERIALS AND METHODS

Markton, so far as known, is immune under field conditions to both the loose and covered smut strains generally found in the United States. Data were obtained on crosses of this variety with the susceptible varieties Early Champion, Ligowa, Scottish Chief, Swedish Select, Iogren, and Aurora. Some data also were obtained on crosses of Markton with Victory, Idamine, and Silvermine. Several strains of the Iogren and Silvermine varieties were tested by Reed, Griffiths, and Briggs (*12*). Iogren is a selection from Green Russian, and Idamine a selection from a commercial strain of Silvermine known as Funk. Morphological descriptions of all these varieties are available.

In studies of the relative susceptibility of oats to *Ustilago avenae* and *U. levis*, respectively, Reed et al. (*12*) classified the above varieties, or varieties closely related to them, as follows:

Highly susceptible to both smuts: Early Champion, Silvermine.
Moderately susceptible to both smuts: Green Russian, Ligowa, Swedish Select, Silvermine, Victory.
Less resistant to *U. avenae* than to *U. levis:* Aurora, Green Russian, Scottish Chief.

All the crosses were made at the Aberdeen substation, Aberdeen, Idaho. The inoculum used in 1925 and 1926 was collected almost entirely at Aberdeen. It was identified as *Ustilago levis* with a very slight admixture of *U. avenae*. Later, field cultures proved this identification correct. The smut inoculum used in 1927 at all stations and on all crosses except those involving Iogren was isolated and cultured in the greenhouse at the Arlington Experiment Farm, Rosslyn, Va., during the winter of 1926–27. The Iogren crosses grown in 1927 were inoculated with smut furnished by Dr. George M. Reed, curator, Brooklyn Botanic Garden, Brooklyn, N. Y.

The inoculum was prepared by grinding the smutted panicles. Inoculations were made by thoroughly blackening the oat seed with smut spores and shaking the seed and spores in envelopes.

It was shown by Jensen (*7*) as early as 1887, subsequently by others, and more recently by the present writers (*2, 14*), that removing the lemma and palea from the oat kernel prior to inoculation with *Ustilago levis* increases the percentage of smut-infected plants. Except in the case of occasional undersized F_2 plants, 100 kernels from each F_2 plant were sown in growing the F_3 of three of the six crosses studied. Two were sown at the rate of 33 and one at the rate of 50 kernels from each F_2 plant. In growing the F_4 and F_5 in each of two crosses, 80 kernels of each plant chosen were sown, and in each of the remaining crosses usually 40 kernels were sown. In one cross all seed of a single panicle was sown. The glumes were removed from all kernels prior to inoculation in cases where less than 100 were sown per family. When 100 kernels were sown the glumes were removed from half the number.

The F_1 plants of all hybrids were grown in the greenhouse at the Arlington Experiment Farm. The F_2 generations of all but two crosses were grown at the Aberdeen substation in 1924 or 1925. The F_2 generation of the others was grown at the Sherman County branch station, Moro, Oreg., in 1924. Data on smut infection in the F_2 were obtained only on the crosses Markton × Iogren and Markton × Silvermine. Studies were made on subsequent generations of the different crosses at Aberdeen, Idaho; Ames, Iowa; Moro, Oreg.; Dickinson, N. Dak.; and Moccasin, Mont. At Aberdeen the crop was grown under irrigation. The climate at Ames is humid and moisture usually is ample. At the other stations subhumid or dry-land conditions prevail. Climatic conditions were comparatively normal at all stations while the experiments were in progress.

In this study any plant that showed any degree of smut was considered infected.

INHERITANCE DATA

Data on the susceptibility to smut infection of the parent varieties grown as checks are given in Table 1. Data for the inheritance of resistance to smut infection in the different crosses are given in Table 2. Data for distribution of F_3 lines according to degree of infection are given in Table 3. The data for each cross are discussed separately.

TABLE 1.—*Percentage of infection by Ustilago levis in susceptible parent varieties grown adjacent to the six crosses studied genetically*

[Markton produced no smutted plants at any station in any season]

Susceptible parent variety	Station where grown	Percentage of infection			
		1925	1926	1927	Maximum
Early Champion	Moro, Oreg	100.0	99.0	------	100.0
Ligowa	----do	86.6	78.9	------	86.6
Scottish Chief	----do	24.6	20.6	------	24.6
Swedish Select [a]	Dickinson, N. Dak	80.6	74.2	20.0	80.6
Iogren	Aberdeen, Idaho	93.0	------	[b] 96.6	96.6
Do	Ames, Iowa	------	39.0	------	------
Do	Moccasin, Mont	------	------	[b] 78.0	------
Aurora	Aberdeen, Idaho	55.0	19.2	------	55.0
Do	Ames, Iowa	------	12.8	------	------

[a] Swedish Select smutted 63.0 per cent at Moro, Oreg., in 1926.

[b] Inoculum used was obtained from the Brooklyn Botanic Garden. In all other tests the smut strain originally obtained at Aberdeen, Idaho, was used as inoculum.

TABLE 2.—*Number and percentage of progeny lines from F_2 plants of oats infected by Ustilago levis in crosses between the smut-resistant Markton and six susceptible varieties grown in tests at five experiment stations in 1925, 1926, and 1927*

Variety crossed with Markton	Station where grown	Year grown	Generation tested	Number of progeny lines—			Summary of comparable data for cross		
				Smut free	Infected	Total	Number of lines grown	Lines infected	
								Number	Per cent
Early Champion	Moro, Oreg	1925	F_3	38	101	139			
Do	do	1926	F_4	35	3	38			
Summary							139	104	74.8
Ligowa	Moro, Oreg	1925	F_3	21	48	69			
Do	do	1926	F_4	20	1	21			
Summary							69	49	71.0
Scottish Chief	Moro, Oreg	1925	F_3	47	48	95			
Do	do	1926	F_4	44	3	47			
Summary							95	51	53.7
Swedish Select	Dickinson, N. Dak.	1925	F_3	57	78	135			
Do	do	1926	F_4	46	11	57			
Do	do	1927	F_5	44	2	46			
Do	do	1927	F_3 [a]	80	14	94			
Summary							135	93	68.9
Iogren	Aberdeen, Idaho	1925	F_2	171	12	183			
Do	Ames, Iowa	1926	F_3	136	35	171			
Do	Aberdeen, Idaho [b]	1927	F_3 [a]	42	35	77			
Do	Moccasin, Mont. [b]	1927	F_3 [a]	30	40	70			
Summary							183	96	52.5
Aurora	Aberdeen, Idaho	1925	F_3	74	72	146			
Do	do. [c]	1926	F_4	62	2	64			
Do	Ames, Iowa [c]	1926	F_4	74	0	74			
Summary							146	74	50.7

[a] Recheck of previously tested F_3 material using remnant seed.
[b] Inoculum used was from a different source from that used in other tests.
[c] Duplicate seedings so far as seed was available.

TABLE 3.—*Distribution of F_3 progeny lines of crosses of Markton oats with six varieties based on percentage of plants infected by Ustilago levis*

[Markton sown for comparison was free from smut in all tests]

Variety crossed with Markton	Number of F_3 lines in infection percentage indicated (class centers)												Total F_3 lines	F_3 lines infected	Mean of infection in F_3 lines	Infection in susceptible parent
	0	5	15	25	35	45	55	65	75	85	95	100				
													Number	*Per cent*	*Per cent*	*Per cent*
Early Champion	38	22	22	13	7	15	5	4	3	5	1	4	139	72.7	24.2	100.0
Ligowa	21	7	17	6	9	4	3			2			69	69.6	18.4	86.6
Scottish Chief	47	21	15	6	4	1				1			95	50.5	7.9	24.6
Swedish Select [a]	57	50	15	6	4	3							135	57.8	6.7	80.6
Do	44	25	8	4	2	1	2	1					87	49.4	7.3	63.0
Iogren [b]	136	23	7	2		2						13	183	25.7	9.1	39.0
Do	42	14	6	7	5			1	1		1		77	45.5	9.7	96.6
Do	30	14	11	9	5	1							70	57.1	9.7	78.0
Aurora	74	51	15	5	1								146	49.3	4.4	55.0

[a] The first group of these strains was grown at Dickinson, N. Dak., in 1925, the second group at Moro, Oreg., in 1926.
[b] The first group of these F_3 strains was grown at Ames, Iowa, in 1926; the second and third groups include data obtained in rechecking experiments by sowing remnant F_2 seed at Aberdeen, Idaho, and Moccasin, Mont., in 1927. In the first group of this cross are included as 100 per cent infected 12 infected F_2 plants grown at Aberdeen, Idaho, in 1925.

MARKTON × EARLY CHAMPION

The cross Markton × Early Champion was studied at the Sherman County branch station in 1925 and 1926. A total of 139 F_3 families was grown, of which 101 showed infection. When the 38 smut-free

F_3 populations were further tested in the F_4, three additional strains produced smut. Of the original 139 F_2 plants, 104 were shown by their breeding behavior to be smut susceptible or heterozygous, and 35 to be smut free. These data, though limited, show that susceptible and segregating strains predominated, and might indicate a single-factor difference for resistance.

MARKTON × LIGOWA

Of 69 F_3 populations of the cross Markton × Ligowa, grown at Moro, Oreg., in 1925, 48 produced smut and 21 were smut free. In the F_4 generation one of the 21 strains not infected in F_3 was smutted. Of the 69 F_2 plants 49 were shown by their breeding behavior to be smut susceptible or heterozygous. The susceptible and segregating strains predominated, and a single-factor difference for resistance between the parents is indicated.

MARKTON × SCOTTISH CHIEF

Of 95 F_3 populations of the cross Markton × Scottish Chief grown at Moro, Oreg., in 1925, 48 produced smut and 47 were smut free. In the F_4 3 of the 47 families smut free in F_3 contained smut-susceptible plants. Of the original 95 F_2 plants 51 were shown to be susceptible or heterozygous and 44 remained smut free.

These results might indicate a 9:7 genetic ratio involving two factors for resistance in this cross. As shown in Table 1, the Scottish Chief parent seems to possess more resistance to smut infection than does either Early Champion or Ligowa, indicating that these varieties may differ from the Scottish Chief variety in their genetic constitution.

MARKTON × SWEDISH SELECT

In 1925, 135 F_3 lines of the cross Markton × Swedish Select were grown at the Dickinson substation, Dickinson, N. Dak. Smutted plants were produced in 78 families and 57 families were smut free. Of the 57 smut-free families in F_3, 11 produced smutted plants in the F_4. When further tested in the F_5 two additional lines produced smut. A recheck of the F_3 made by sowing remnant F_2 seed showed two lines to be susceptible which had not contained smutted individuals in the previous tests.

Summarizing the results of the cross, 93 of the 135 F_2 plants were shown to be susceptible or heterozygous, and 42 produced progeny free from smut. The data might indicate a ratio of 3 susceptible and heterozygous to 1 resistant, but if so, the deviation from the expected is wide. However, more than twice as many lines were infected as were smut free.

In addition to the above study, 87 F_2 plants of this cross not grown at Dickinson in 1925 were studied in the F_3 at Moro, Oreg., in 1926. Of these, 44 lines were free from smut and 43 were infected. The smut-free lines of this group were not tested further. These data are not included in Table 2.

The data on this cross from the two stations if added together would give little definite genetic information. There is reason to believe that the data from the two stations are not comparable. Owing to a difference in the virulence of the inoculum, the age of the seed, or a climatic condition, the infection at Moro in 1926 was less than at Dickinson in either year. Even the susceptible Swedish

Select parent showed only 63 per cent infection at Moro, while at Dickinson infection percentages were 80.6 and 74.2 in 1925 and 1926, respectively. Considering all the data, however, it is evident that susceptible and heterozygous strains were more numerous than resistant ones.

IOGREN × MARKTON

The F_2 of the cross Iogren × Markton was grown from smutted seed at Aberdeen, Idaho, in 1925. Of the 183 F_2 plants, 12 were infected with smut.

An F_3 generation from the smut-free F_2 plants was grown at Ames, Iowa, in 1926. Of the 171 F_3 lines, 35 produced smut.

In a recheck of the F_3, in which remnant seed of the F_2 plants was used, 70 F_3 families were grown at Moccasin, Mont., and 77 F_3 families at Aberdeen in 1927. Inoculum used in 1927 was supplied by George M. Reed, of the Brooklyn Botanic Garden. Of the 70 lines grown at Moccasin 40 produced smut. Of these 40 infected lines 12 had been infected at Ames in 1926. Two lines producing smut at Ames were not grown at Moccasin, and one line infected at Ames was smut free at Moccasin. Of the 77 lines grown at Aberdeen 35 produced smutted plants. Two lines infected at Ames were smut free at Aberdeen, and 14 lines were smutted in both tests. Three lines producing smut at Ames were not grown at Aberdeen, because of lack of seed.

Of 183 F_2 plants 12 were infected in the F_2; including all F_3 data, an additional 84, or a total of 96, proved susceptible or heterozygous. The Iogren parent smutted 96.6 per cent at Aberdeen in 1927. Evidently the study should have been continued in order to obtain reliable genetic information.

AURORA × MARKTON

Of the 146 F_3 populations of the cross Aurora × Markton grown at Aberdeen in 1925, 72 produced smut and 74 were smut free. An F_4 generation of the 74 smut-free lines was grown at Ames in 1926, and a comparable F_4 test of 64 of the same lines at Aberdeen the same year. Conditions were unfavorable at Ames, and none of the families produced smut. Two of the families grown at Aberdeen produced smut.

Of the 146 strains on which data were obtained, 74 were susceptible or heterozygous and 72 did not become infected in two tests. Much of the material of this cross was grown at Ames, but for some unknown reason poor stands and poor infection make the data obtained at Ames of doubtful significance. However, the data from both stations show that susceptible and segregating strains were slightly more numerous than noninfected strains. Data obtained under conditions more favorable for infection might show results conforming essentially to those of the other crosses. On the basis of lower infection percentages there is some reason to believe that Aurora itself differs genetically from Early Champion and Ligowa in resistance to smut infection.

ADDITIONAL CROSSES

Some data were obtained on the inheritance of resistance to smut in three additional crosses. The number of F_2 plants from which populations could be produced was too small to give results of much genetic significance, and the data obtained are not presented in tabular form.

Of 39 F_3 families of the cross Markton × Victory grown at Aberdeen in 1925, 19 produced some smut and 20 produced only smut-free plants. Seed from random-selected plants of 14 of the 20 smut-free families and of 1 smut-susceptible line was divided, half the seed of each plant being sown at Aberdeen and half at Ames. No smut infection occurred in the material grown at Ames, but 2 of 14 lines produced smut at Aberdeen. The line susceptible in F_3 also produced smut in F_4. When tested further in F_5, none of the lines that were smut free in previous generations showed susceptibility. Of the 39 lines of this cross, 21 were smut susceptible or heterozygous. Of the 18 smut-free lines, 6 were tested but once. Freedom from smut in some of these 6 may have been merely "escapes." Too few lines were available to give data of significant genetic value. Susceptible and heterozygous strains, however, did predominate. The Victory parent tested in comparison with the hybrids smutted 93.0, 76.8, and 85.4 per cent at Aberdeen in 1925, 1926, and 1927, respectively, and 40.3 per cent at Ames in 1926.

Of 27 F_3 lines of a Markton × Idamine cross, 5 produced smut. Of the 22 lines free from smut in F_3, 10 were tested further, half the seed of each chosen progeny plant being sown at Aberdeen and half at Ames. Of the 10 lines, 4 produced smut at Aberdeen only, 1 produced smut at both Aberdeen and Ames, and 5 were smut free at both stations. A further test of the 5 lines that were smut free in F_4 showed no smut in these previously smut-free lines.

The genetic value of the above data is doubtful. They differ from those previously presented in this paper in the predominance of smut-free strains, but this difference probably is more apparent than real. While 17 out of 27 lines were free from smut during the period of the experiments, only 10 of the 22 lines not infected in F_3 were tested further. Of these 10 lines 5 became infected in F_4. As these 10 strains were chosen at random, it seems reasonable to assume that had all 22 lines been fully tested the number of infected lines would have exceeded the 10 actually shown by the data.

The Idamine parent smutted 76.6, 61.2, and 64.5 per cent at Aberdeen in 1925, 1926, and 1927, respectively, and 61.8 per cent at Ames in 1926.

An F_2 generation of the cross Silvermine × Markton was grown from inoculated seed at Aberdeen in 1925. Of 56 plants 3 were infected and 53 were smut free. An F_3 generation of the 53 smut-free plants was grown at Ames in 1926. Six of the 53 F_3 families produced smut. In a second F_3 test 45 lines were grown from remnant F_2 seed at Aberdeen in 1927. In this test 17 families produced smut. One line not grown at Aberdeen in 1927 became infected at Ames in 1926, and 5 lines that smutted at Ames in 1926 again smutted at Aberdeen in 1927. By combining F_2 and F_3 data, 21 smutted to 35 smut-free segregates were observed in this cross. This result is similar to that obtained for Markton × Idamine, the latter a close relative to Silvermine, and might seem to substantiate a genetic condition in Idamine and Silvermine differing from that in the other varieties studied. It must be borne in mind, however, that the present cross was not studied in F_4 for a further checking of susceptibility. The doubtful reliability of the data for the cross Markton × Idamine has already been pointed out. Until better evidence is forthcoming,

therefore, there is no proof of any distinct genetic difference in the smut resistance of these two varieties and the others previously considered.

The Silvermine parent smutted 35.7 and 76.7 per cent in 1925 and 1927, respectively, at Aberdeen, and 47.7 per cent at Ames in 1926.

CORRELATION OF RESISTANCE IN F_3 AND F_4

Several investigators have classified F_2 plants genetically on the basis of the percentage of infection in the F_3 and later progenies; that is, it has been assumed that the F_2 parent plant of an F_3 line in which 30 per cent of the plants became infected differs in factorial constitution from the F_2 parent plant of an F_3 line in which only 10 per cent of the plants were infected.

The smut reaction of F_4 populations of families from each of four crosses was studied statistically by the writers in an attempt to determine the relationship in reaction between different generations of the same cross. The hulls were removed from all seed prior to inoculation. Not less than 40 and in most cases 50 or more kernels were sown from each F_3 plant. The inoculum and methods were the same as those discussed in the foregoing pages. Data presented in Table 4 are discussed separately for individual crosses. To make the study as complete as possible, all data from the F_4 progeny rows grown from smut-free F_3 populations are included. As a result, the classes of progeny grown that had no infection (0) in the F_3 are very large as compared with the others.

TABLE 4.—*Distribution of progeny of different F_3 lines of oats according to percentages of infection in F_4 progeny of four crosses of Markton (resistant) with the smut-susceptible varieties named*

Variety crossed with Markton and F_3 plant No.	Infection in F_3 plant	Number of F_4 progeny in infection percentage class indicated (class centers)												F_4 lines grown	Mean infection	Correlation for cross; r=
		0	5	15	25	35	45	55	65	75	85	95	100			
Early Champion:	*Per cent*													*Number*	*Per cent*	
1071a–x	0	111	3											114	0.1	
1071a–1–10	1.3	11												11	0	
1071a–2–19	6.3	15												15	0	
1071a–3–42	15.4	3	2	1	3	2								11	15.5	
1071a–2–5	28.4	9		1										10	1.5	
1071a–3–25	36.4	7	1											8	0.6	
1071a–2–14	44.7	7		1		3								11	10.9	
1071a–2–18	56.1	4			1	1	2				1	1		10	33.0	
1071a–3–15	66.6	3	2	2	1									8	8.1	
1071a–2–54	76.3	1		1										2	7.5	
1071a–2–29	85.2	1		1	1									3	13.3	
1071a–2–44	92.2					1							1	2	67.5	
1071a–2–23	92.9												2	2	100.0	+0.574±0.031
Swedish Select:																
1069a–x	0	211	4	6	5	1	1							228	1.4	
1069a–5–4	2.4	36	2											38	.3	
1069a–6–10	9.4	18	2	4	4	4	5	4	5	2	2		2	52	30.8	
1069a–6–43	18.9	26	3	4	1	2	3	2		2				43	13.1	
1069a–4–20	30.2	14	1	6	7		7		4	2			1	44	28.8	+.458±.026
Aurora:																
1072a–x	0	220	1	1										222	.1	
1072a–2–12	8.6	55	2											57	1.2	
1072a–2–23	9.5	67	10	4	2									83	1.9	
1072a–2–13	16.7	38	24	18	1		1							82	5.6	
1072a–3–47	23.4	29	22	24	8									83	8.1	+.507±.022
Scottish Chief:																
1065a–x	0	138	3											141	.1	
1065a–2–39	1.6	39												39	0	
1065a–3–9	15.9	25	2	1	1		1							30	3.2	
1065a–2–19	34.3	9	8	3	6	3	2	2	3	1	1			38	23.6	
1065a–2–1	82.5					1	1	2	7	7	6	11	5	40	80.6	+.913±.007

MARKTON × EARLY CHAMPION

The study of the cross Markton × Early Champion was made at Moro in 1926. The infection percentages of 12 parent F_3 strains chosen for study varied from very low to very high by approximately 5 to 10 per cent gradations. In addition, three plants were selected from each of the 38 smut-free lines for testing in F_4. Infection in the F_4 progeny showed significant correlation with infection in the F_3, $r = +0.574 \pm 0.031$. The F_4 lines naturally showed some tendency toward less infection than the F_3 lines, since F_4 populations could be grown only from smut-free or partially smutted F_3 plants.

MARKTON × SWEDISH SELECT

A study of the cross Markton × Swedish Select was made at Dickinson in 1926. The four F_3 lines chosen for study in the F_4 varied in the percentage of smut infection present. In addition to the smutted plants, three plants were selected for study from each of the 57 smut-free F_3 lines. Correlation between F_3 and F_4 infection in this cross was $r = +0.458 \pm 0.026$. It is interesting to note that one of the most heavily infected F_4 populations was from an F_3 line having a comparatively light infection percentage. The total infection range, however, was only 28 per cent. Transgressive segregation for susceptibility to smut infection occurred in progeny of this cross. Higher percentages of infection were observed in some of the hybrid lines than in the susceptible Swedish Select parent.

AURORA × MARKTON

Data on the cross Aurora × Markton were obtained at Aberdeen in 1926. The four F_3 lines chosen for study in the F_4 varied in smut infection percentages. Also a total of 222 lines, or three lines from each of 74 F_3 lines, was tested. The range in infection percentages between the various lines was only 12.8 per cent. Significant correlation was found between F_3 and F_4 infections, $r = +0.507 \pm 0.022$.

MARKTON × SCOTTISH CHIEF

The cross Markton × Scottish Chief was studied at Moro in 1926. All the plants from four infected lines and three plants each from 47 smut-free lines were tested in F_4. Duplicate seedings of each F_3 line of this cross had been grown; one inoculated with smut, the other not inoculated. Seed used for growing the F_4 generation was taken from the material not inoculated in F_3. As a result, susceptible individuals had not been eliminated in the F_3 and there was a higher correlation between F_3 and F_4 infections in this cross than in any of the others studied. Correlation was relatively high, $r = +0.913 \pm 0.022$. It is of interest to observe in connection with these studies that transgressive segregation for susceptibility to smut infection, as in the Markton × Swedish Select cross, was also indicated in the progeny of this cross. Some progeny lines produced higher percentages of smut than were observed in the susceptible Scottish Chief parent. This observation was made by Garber, Giddings, and Hoover (*5*) in the cross Gopher × Black Mesdag.

RELATION BETWEEN MORPHOLOGICAL CHARACTERS AND RESISTANCE TO SMUT INFECTION

A knowledge that linkage exists between a morphological character and either disease resistance or susceptibility is of definite service to the plant breeder. Linkage of this type in oats was indicated by Wakabayashi (*15*), although others have observed little or no correlation between morphological characters and smut reaction in this crop. Data are here presented on the relationship between the characters susceptibility to smut infection and panicle length, kernel length, kernel width, awns, prominence of nerves, and lemma color. The differences of the means are computed for the characters susceptibility to smut infection and panicle and kernel length. The value of Q has been computed for the characters susceptibility to smut infection and kernel width, awns, prominence of nerves, and lemma color. The association coefficients were computed by the method described by Yule (*16*).

PANICLE LENGTH

The relation between panicle length of the F_2 and resistance to smut infection in F_3 and later generations was studied in the crosses Markton × Swedish Select and Aurora × Markton. Markton, the resistant parent of these crosses, has a much longer panicle than either of the other varieties. The distribution for the two crosses is presented in Table 5. The data indicate no relationship between panicle length in the F_2 and smut infection in the F_3 progeny. Differences between the mean of infected and smut-free plants in the two crosses were 0.16 ± 0.09 and 0.30 ± 0.13, respectively.

TABLE 5.—*Mean panicle lengths of F_2 plants shown to be susceptible and of those shown to be resistant to smut infection by later generation progeny populations*

Cross and smut reaction of progeny	Number of progeny from parents having indicated panicle length (inches)									
	4. 1–5	5. 1–6	6. 1–7	7. 1–8	8. 1–9	9. 1–10	10. 1–11	11. 1–12	Total	Mean
Markton×Swedish Select:										
Infected		1	2	10	43	67	22	7	152	9. 26±0. 06
Smut free		0	0	6	27	26	11	0	70	9. 10± . 07
Difference										. 16± . 09
Aurora×Markton:										
Infected	1	6	9	23	17	16	0	0	72	7. 85± . 10
Smut free	0	1	10	22	27	10	3	1	74	8. 15± . 09
Difference										. 30± . 13

KERNEL LENGTH

The crosses studied in the experiment on kernel length were the same as those in the experiment on panicle length. The resistant Markton has unusually long kernels, while those of the other varieties are very short. In determining kernel length, five primary kernels taken at random from each plant were measured and averaged. The data are given in Table 6. There was no apparent relation between kernel length and resistance or susceptibility to smut in these two crosses. Differences between the mean of infected and smut-free plants of the two crosses were 0.03 ± 0.08 and 0.06 ± 0.12, respectively.

TABLE 6.—*Mean kernel lengths of F_2 plants shown to be susceptible and of those shown to be resistant to smut infection by later generation progeny populations*

Cross and smut reaction of progeny	Number of progeny from parents having indicated kernel length (mm.)								
	14. 1–15	15. 1–16	16. 1–17	17. 1–18	18. 1–19	19. 1–20	20. 1–21	Total	Mean
Markton×Swedish Select:									
Infected	-------	6	38	80	26	2	-------	152	17. 37±0. 04
Smut free	-------	2	24	28	15	1	-------	70	17. 34± . 07
Difference	-------	-------	-------	-------	-------	-------	-------	-------	. 03± . 08
Aurora×Markton:									
Infected	1	5	22	25	15	2	2	72	17. 36± . 09
Smut free	1	6	16	32	13	6	0	74	17. 42± . 08
Difference	-------	-------	-------	-------	-------	-------	-------	-------	. 06± . 12

KERNEL WIDTH

The same two crosses also were studied for relation between kernel width and resistance to smut. Kernel width was determined by measuring in millimeters five primary kernels taken at random and averaging the results. All kernels 3 mm. or more in width were grouped as wide, and those less than 3 mm. as narrow. The data are presented in Table 7. Little or no relation is indicated in the crosses studied. In one cross $Q = +0.037 \pm 0.045$, and in the other $Q = -0.357 \pm 0.049$.

TABLE 7.—*Association between kernel width in F_2 plants and susceptibility to smut infection of progeny of these plants in later generations*

Cross and smut reaction of progeny	Number of progeny of parents having indicated kernel widths			Q
	Wide (3 mm. or over)	Narrow (less than 3 mm.)	Total	
Markton×Swedish Select:				
Infected	81	71	152	-------
Smut free	36	34	70	+0. 037±0. 045
Aurora×Markton:				
Infected	59	13	72	-------
Smut free	67	7	74	− . 357± . 049

AWNS

The smut-resistant parent Markton is awned. The susceptible parent Aurora is almost completely awnless. The coefficient of association between awns and smut infection for the cross Aurora×Markton was $Q = -0.052 \pm 0.056$.

PROMINENCE OF NERVES

The nerves, the fibrovascular bundles running longitudinally through the oat lemma, are much more prominent and more easily observed in some varieties of oats than in others. In the resistant Markton they are readily identified, while in the susceptible Swedish Select, Scottish Chief, and Aurora they blend into the adjacent tissue and are somewhat obscured. A study of relationship of lemma

nerves to smut infection in crosses of Markton with these three varieties was made. The coefficients of association for the three crosses, $Q = -0.214 \pm 0.043$, $+0.202 \pm 0.066$, and $+0.083 \pm 0.055$, respectively, indicate that prominence of nerves has no relation to resistance to smut.

LEMMA COLOR

The lemmas of the resistant Markton are yellow; those of the susceptible Swedish Select and Scottish Chief are white. The relationship of lemma color to smut infection in the crosses Markton × Swedish Select and Markton × Scottish Chief was studied. The coefficient of association for the first cross, $Q = +0.094 \pm 0.045$, would indicate no relation between these characters. The coefficient for the second cross, $Q = +0.632 \pm 0.042$, would indicate a high degree of correlation.

DISCUSSION

The results presented differ from those of previous studies, owing possibly in part to the use of different technic. The removal of hulls prior to inoculation resulted in unusually high infection percentages both in susceptible parents and in hybrid populations. This procedure has not been followed before in genetic studies, nor have the varieties employed in the experiments been used previously in reported studies of this nature. Except for a statement by Gaines (*4*), nothing relative to the genetic nature of the smut immunity of Markton appears to have been published. Gaines states:

> Data on F_3 families of Markton × Large Hull-less and Markton × Banner, grown at Pullman, Washington, in 1926, and as yet not completely analyzed, show the immunity of Markton to be dominant but controlled by multiple factors—probably three.

Reed (*8, 10*) has demonstrated the existence of several physiologic forms of *Ustilago levis*. Differences in the reaction of host varieties to various physiologic forms might give different genetic results in the same oat cross from inoculum of different forms.

Seasonal and place variations in smut infection also may modify apparent segregations. It seems evident that until a more certain technic is evolved care should be exercised in drawing conclusions relative to the factors involved in the inheritance in oats of resistance to infection by smut in field experiments. Moreover, conclusions should be specifically limited to the smut strains used, and some consideration should be given to climatic conditions and other factors affecting infection.

The data herein given show that, with the present technic of artificial inoculation for smut infection in oats, genetic interpretations based on the percentage of smut-infected individuals in F_3 may not be accurate. As pointed out, the effect of seasonal fluctuations in infection certainly can not be ignored. In all but one cross in the experiments reported herein the growing of F_4 populations from seed produced by the inoculated F_3 probably reduced true association. Completely susceptible F_3 plants were destroyed by smut, and the F_4 progenies were grown, therefore, only from wholly or partially smut-free plants.

The foregoing remarks indicate the difficulty of determining differences in infection caused by environmental or hereditary factors. The division of infection data such as are presented in Tables 3 and 4

into any but very general genetic classes seems unsafe to the writers. Since infection of all susceptible plants is rarely attained in a single test with present technic, a factorial genetic interpretation based on the percentage of infection seems of doubtful validity.

In this study little or no evidence of correlation between morphological characters and resistance to smut infection was observed. This finding corresponds with that obtained in most previous studies of this nature, and indicates that resistance probably is not linked with any character that would interfere with the breeding of resistant varieties having desirable agronomic characters.

SUMMARY AND CONCLUSIONS

The smut-resistant Markton variety of oats was crossed with Early Champion, Ligowa, Scottish Chief, Swedish Select, Iogren, Aurora, and also with Victory, Idamine, and Silvermine. More than 140,000 progeny plants were studied.

In these studies the lemma and the palea were removed from the oat kernel in most cases prior to inoculation with smut. Results have led the writers to the following conclusions:

Markton is extremely resistant to, if not actually immune from, the *Ustilago levis* strain used in these experiments.

The percentages of infection in the nine susceptible varieties varied with the varieties, and the infection percentage of individual varieties was subject to wide fluctuations from year to year.

In seven of nine progeny populations of crosses of Markton (smut free) with smut-susceptible varieties, smut-susceptible and heterozygous plants predominated in F_2, as shown by the breeding behavior of their progenies. In the remaining two, however, in which small populations were grown, the reverse was true.

In three crosses approximately one-fourth of the progeny lines from F_2 plants were smut free and three-fourths infected. In three other crosses almost equal percentages of smut-free and infected progeny lines from F_2 plants were observed.

The results obtained from a study of the several crosses give reason to doubt the existence in Markton of three factors for resistance to all *Ustilago levis* strains.

Such complete gradation of smut percentages occurred within F_3 lines that it seems impracticable to divide these progenies into genetic classes on the basis of percentage of infection.

Correlation between infection percentages in F_3 and F_4 was especially high in the Markton × Scottish Chief cross of which random F_3 material was available for study in F_4. In three other crosses correlation was shown, although random material of the F_3 generation was not available for testing in F_4.

Transgressive segregation for smut infection was observed; that is, the infection percentages in some F_4 lines of the crosses Markton × Scottish Chief and Markton × Swedish Select exceeded the infection percentages of the susceptible parents.

There was little or no correlation between (1) panicle length, (2) kernel length, (3) kernel width, (4) presence of awns, (5) prominence of nerves in lemmas, and (6) lemma color in F_2 plants and the resistance of their progeny to infection by covered smut, *Ustilago levis*.

LITERATURE CITED

(1) BARNEY, A. F.
1924. THE INHERITANCE OF SMUT RESISTANCE IN CROSSES OF CERTAIN VARIETIES OF OATS. Jour. Amer. Soc. Agron. 16: 283–291, illus.

(2) BAYLES, B. B., and COFFMAN, F. A.
1928. EFFECTS OF DEHULLING SEED AND OF DATE OF SEEDING ON GERMINATION AND SMUT INFECTION IN OATS. Jour. Amer. Soc. Agron. 21: 41–51, illus.

(3) GAINES, E. F.
1925. THE INHERITANCE OF DISEASE RESISTANCE IN WHEAT AND OATS. Phytopathology 15: [341]–349.

(4) ———
1927. THE RELATION OF TRIPLOID FACTORS AND CHROMOSOME GROUPS IN WHEAT AND OATS. Jour. Amer. Soc. Agron. 19: 202–205.

(5) GARBER, R. J., GIDDINGS, N. J., and HOOVER, M. M.
1929. TRANSGRESSIVE SEGREGATION FOR SUSCEPTIBILITY TO SMUT IN AN OAT CROSS. Jour. Agr. Research 39: 953–962.

(6) HAYES, H. K., GRIFFEE, F., STEVENSON, F. J., and LUNDEN, A. P.
1928. CORRELATION STUDIES IN OATS OF THE INHERITANCE OF REACTION TO STEM RUST AND SMUTS AND OF OTHER DIFFERENTIAL CHARACTERS. Jour. Agr. Research 36: 437–457.

(7) JENSEN, J. L.
1888. THE PROPAGATION AND PREVENTION OF SMUT IN OATS AND BARLEY. Jour. Roy. Agr. Soc., England (2) 24: 397–415.

(8) REED, G. M.
1924. PHYSIOLOGIC RACES OF OAT SMUTS. Amer. Jour. Bot. 11: 483–492.

(9) ———
1925. THE INHERITANCE OF RESISTANCE OF OAT HYBRIDS TO LOOSE SMUT. Mycologia 17: 163–181.

(10) ———
1927. FURTHER EVIDENCE OF PHYSIOLOGIC RACES OF OAT SMUTS. Mycologia 19: 21–28.

(11) ———
1928. THE INHERITANCE OF RESISTANCE OF OAT HYBRIDS TO LOOSE AND COVERED SMUT. Ann. N. Y. Acad. Sci. 30: 129–176.

(12) ——— GRIFFITHS, M. A., and BRIGGS, F. N.
1925. VARIETAL SUSCEPTIBILITY OF OATS TO LOOSE AND COVERED SMUTS. U. S. Dept. Agr. Bul. 1275, 40 p., illus.

(13) ——— and STANTON, T. R.
1925. RELATIVE SUSCEPTIBILITY OF SELECTIONS FROM A FULGHUM-SWEDISH SELECT CROSS TO THE SMUTS OF OATS. Jour. Agr. Research 30: 375–391, illus.

(14) STANTON, T. R., COFFMAN, F. A., TAPKE, V. F., WIEBE, G. A., SMITH, R. W., and BAYLES, B. B.
1930. INFLUENCE OF HULLING THE CARYOPSIS ON COVERED-SMUT INFECTION AND RELATED PHENOMENA IN OATS. Jour. Agr. Research 41: 621–633.

(15) WAKABAYASHI, S.
1921. A STUDY OF HYBRID OATS, AVENA STERILIS × AVENA ORIENTALIS. Jour. Amer. Soc. Agron. 13: 259–266.

(16) YULE, G. U.
1900. ON THE ASSOCIATION OF ATTRIBUTES IN STATISTICS: WITH ILLUSTRATIONS FROM THE MATERIAL OF THE CHILDHOOD SOCIETY, ETC. Roy. Soc. [London], Phil. Trans., Ser. A 194: 257–319, illus.