



UNITED STATES DEPARTMENT OF AGRICULTURE  
WASHINGTON, D. C.

FIELD STUDIES ON RESISTANCE OF  
HYBRID SELECTIONS OF OATS TO  
COVERED AND LOOSE SMUTS

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North Dakota, Montana, Idaho, and Oregon  
Agricultural Experiment Stations)

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INTRODUCTION

Smuts take an estimated toll of approximately 45,000,000 bushels of oats annually.<sup>2</sup> The formaldehyde seed treatment, long recommended for the control of oat smuts, is effective, yet the annual loss of oats caused by smuts continues to be heavy. This indicates that, in general, seed treatment is not commonly practiced. Another method of reducing oat losses is by breeding and developing smut-resistant varieties.

<sup>1</sup> The writers express their appreciation to L. C. Burnett, chief in cereal breeding, Iowa Agricultural Experiment Station, and agent, Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, for assistance in conducting experiments at Ames, and to the following members of the Division of Cereal Crops and Diseases for assistance in conducting field experiments: R. W. Smith, associate agronomist, at Dickinson, N. Dak.; B. B. Bayles, associate agronomist, formerly at Moccasin, Mont., and Moro, Oreg.; G. A. Wiebe, assistant agronomist, formerly at Aherdeen, Idaho; and D. E. Stephens, senior agronomist, at Moro, Oreg.

<sup>2</sup> Estimates based on the following:

UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. ESTIMATES OF CROP LOSSES DUE TO PLANT DISEASES. 1917. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bull. 2, no. 1, 18 pp. 1918.

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— CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES. 1919-27. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bull. (or Rptr.) Sups. 12, 13, 24, 30, 36, 43, 49, 56, 64. 1920-28. [Mimeographed.]

Some of the most important commercial oat varieties in the United States are highly susceptible to covered smut (*Ustilago levis* (Kell. and Sw.) Magn.), or loose smut *U. avenae* (Pers.) Jens., or both. Markton, however, is an exception. The object of the studies reported herein has been to combine, through hybridization and selection, the near smut immunity of Markton with the desirable agronomic characters of some of the susceptible varieties. The tests were conducted for one or more years at stations in the arid, semiarid, and humid sections of the country, affording an opportunity to test the resistance of the selections under a wide range of environmental conditions. In the tests reported herein, the inoculum, in the form of chlamydo-spores of the loose and covered smut fungi of oats, was applied to seed from which the hulls had been removed. This method, as shown by Stanton et al. (13),<sup>3</sup> tends materially to increase smut infection in susceptible oats. Some promising selections were obtained which have both the smut resistance of Markton and the special value of the susceptible parent.

#### REVIEW OF LITERATURE

Reed (3) was the first to publish extensive data on the resistance of species and varieties of *Avena* to both covered and loose smuts. Later Reed, Griffiths, and Briggs (9) reported studies on varietal resistance and susceptibility of oats to covered and loose smuts. In general, similar results were obtained from the strains and varieties when grown at widely separated stations. Reed and Stanton (10) reported that selections from a Fulghum-Swedish Select cross reacted similarly toward both smuts, thus in general agreeing with the results of Reed (3) and Reed, Griffiths, and Briggs (9). Gaines (2) presented data on the resistance of varieties and hybrids of oats to *Ustilago levis*. Of 210 varieties and selections tested for resistance to this smut, 21 proved nearly immune. In the remaining sorts the incidence of smut ranged from a mere trace to nearly 100 percent.

The breeding experiments for smut resistance reported in part in this bulletin were begun mainly on the basis of the results obtained by Reed and Stanton (10). More recently Reed (4,5,7) and Reed and Stanton (11) have shown that there are distinct physiologic races of the oat smuts and that the problem of breeding for smut resistance is more complex than it originally appeared to be. For example, Fulghum is resistant to the physiologic forms of *Ustilago levis* and *U. avenae* from Missouri, but is highly susceptible to *U. avenae*-Fulghum and *U. levis*-Fulghum from the Southeastern States.

#### MATERIALS AND METHODS

The materials and methods used in this study have been fully described (1, 13). The number of physiologic forms making up the inoculum of the two smut species used in these experiments is not known. However, since the original collections were from various localities in the Northern States, the common smut forms occurring on the varieties of *Avena sativa* L. grown in these States were undoubtedly represented.

<sup>3</sup>Italic numbers in parentheses refer to Literature Cited, p. 9.

## RESISTANCE OF PARENT VARIETIES

In these experiments the parent varieties were grown from artificially inoculated seed at widely separated stations for one or more years. Their reaction to smut under different environmental conditions was thus obtained.

Data on the resistance to covered and loose smut of nine varieties used as parents of hybrids obtained at five agricultural experiment stations in one or more years from 1925 to 1927, inclusive, are presented in table 1. The total number of plants and the number and percentage of smutted plants are also shown.

TABLE 1.—Resistance and susceptibility of 9 parent oat varieties to covered and loose smuts when grown for 1 or more years at the agricultural experiment stations listed

[Plants grown from seed artificially inoculated with hulls removed]

Location of station	Variety	Year	Plants grown from seed inoculated with—					
			Ustilago levis			Ustilago avenae		
			Total plants	Smutted plants		Total plants	Smutted plants	
			Number	Percent	Number	Number	Percent	
Aberdeen, Idaho	Idamine	1925	158	121	76.6			
Do.	do.	1926	235	158	67.2			
Do.	do.	1927	62	40	64.5	63	44	69.8
Ames, Iowa	do.	1926	140	88	62.9			
Aberdeen, Idaho	Victory	1925	151	140	92.7			
Do.	do.	1926	177	136	76.8			
Do.	do.	1927	41	35	85.4	30	30	100.0
Ames, Iowa	do.	1926	72	29	40.3			
Aberdeen, Idaho	Iogren	1925	43	40	93.0			
Do.	do.	1927	88	85	96.6	80	70	87.5
Ames, Iowa	do.	1926	41	16	39.0			
Do.	do.	1927				41	19	46.3
Moccasin, Mont.	do.	1927	50	39	78.0			
Aberdeen, Idaho	Silverinine	1925	42	15	35.7			
Do.	do.	1927	60	46	76.7	58	43	74.1
Ames, Iowa	do.	1926	44	21	47.7			
Dickinson, N. Dak.	Swedish Select	1925	103	83	80.6			
Do.	do.	1926	97	72	74.2			
Do.	do.	1927	35	7	20.0	37	15	40.5
Moccasin, Mont.	do.	1927	79	77	97.5	98	89	90.8
Moro, Oreg.	do.	1926	251	158	62.9			
Do.	Scottish Chief	1925	114	28	24.6			
Do.	do.	1926	243	31	12.8			
Moccasin, Mont.	do.	1927	70	0	0	95	47	49.5
Moro, Oreg.	Early Champion	1925	283	280	98.9			
Do.	do.	1926	46	46	100.0			
Moccasin, Mont.	do.	1927	302	230	76.2	378	297	78.6
Moro, Oreg.	Ligowa	1925	15	13	86.7			
Do.	do.	1926	90	71	78.9			
Moccasin, Mont.	do.	1927	146	138	94.5	233	223	95.7
Aberdeen, Idaho	Markton	1925	159	0	0			
Do.	do.	1926	217	0	0			
Do.	do.	1927	65	0	0	69	0	0
Ames, Iowa	do.	1926	71	0	0			
Do.	do.	1927	88	0	0	80	0	0
Dickinson, N. Dak.	do.	1926	59	0	0			
Do.	do.	1927				33	0	0
Moro, Oreg.	do.	1925	78	0	0			
Do.	do.	1926	332	0	0			
Moccasin, Mont.	do.	1927	123	0	0	150	0	0
Total or average for Markton.			1,192	0	0	332	0	0

The data in table 1 show that in the *Ustilago levis* series every variety with the exception of Scottish Chief and Markton produced over 50 percent of smutted plants in one or more years. The data for Scot-

tish Chief agree with the results reported by Reed et al. (9), both in relatively low infection and in greater susceptibility to *U. avenae* than to *U. levis*. The negative data for Scottish Chief when inoculated with covered smut at Moccasin, Mont., in 1927 are traceable to unfavorable climatic and soil conditions at and immediately following seeding. Markton was consistently free from either smut at all stations in all years. Since these experiments were conducted, Smith and Bressman (12) have reported the occurrence of smut in Markton, evidently produced by a hitherto unidentified physiologic form. In general, the parent varieties reacted similarly to both smuts in the one year (1927) in which tests were made.

#### RESISTANCE OF SELECTIONS FROM THE UNNAMED OAT C.I. NO. 357

At Aberdeen, Idaho, in 1925, 200 selections from the unnamed oat C.I.<sup>4</sup> no. 357 were grown in head rows and tested for resistance to *Ustilago levis*. The purpose was twofold: To determine the heterogeneity of resistance to smut in this oat from which Markton was selected, and to isolate, if possible, smut-resistant strains superior to Markton. Of the 200 progenies, 112 were entirely free from covered smut. The susceptibility of 88 lines to *U. levis* shows that the original C.I. no. 357, consists of a mixture of strains. Incidentally, it may be noted that this variability in relation to the smut pathogen is paralleled by considerable variation in many minor plant characters.

In order to test further the resistance of the 112 lines, seed from each was sown at Aberdeen, Idaho, and Moro, Oreg., in the spring of 1926. Forty seeds of each line inoculated with spores of *U. levis* were sown at each station. Forty-four of the lines failed to show resistance to covered smut that year. Summary data are presented in table 2. Lines free from smut at both stations are not included in the summary.

TABLE 2.—Infection in the 44 susceptible progenies of the unnamed oat C.I. no. 357, grown at Aberdeen, Idaho, and Moro, Oreg., in 1926 from seed inoculated with *Ustilago levis*

Location of station	Progenies infected		Plants grown in infected families			Range of infection in progenies	
			Total	Infected		Minimum	Maximum
			Number	Number	Percent	Percent	Percent
Aberdeen, Idaho.....	37	84.1	1,271	94	7.4	2.4	35.5
Moro, Oreg.....	21	47.7	489	46	9.4	3.2	34.8
Both stations.....	14	31.8	795	90	11.3	2.8	34.8

The data of table 2 show that 44 of 112 selections which escaped infection at Aberdeen, Idaho, in 1925 were infected in 1926. A range of infection in the different progenies from 2.4 to 35.5 percent at Aberdeen and from 3.2 to 34.8 percent at Moro was obtained. A higher percentage of plants showed smut at Moro than at Aberdeen. The data emphasize the importance of conducting tests for resistance at different stations and in different years. The large number of the original 200 lines that became smutted shows the heterogeneity for smut resistance in the unnamed mass variety C.I. no. 357, from which Markton was selected.

<sup>4</sup>O.I. indicates accession number of the Division of Cereal Crops and Diseases.

It is evident that in the selection of Markton, one of the very best strains of the original mass population, C.I. no. 357, was isolated. The smut-resistant lines resulting from the experiment reported above have been tested for yield at numerous stations, but so far only a few have shown even equality with Markton. Most of them have been decidedly inferior.

## RESISTANCE OF HYBRID SELECTIONS

Numerous hybrid selections have been tested one or more years for resistance to covered smut. The smut-free selections have been further tested for resistance to both covered and loose smuts. In the latter tests lines inoculated with *Ustilago levis* were sown in a series adjacent to the same lines inoculated with *U. avenae*. In several hybrids, remnant F<sub>2</sub> seed was tested in F<sub>3</sub>, furnishing additional results on the reaction of selections to the two smuts.

Experiments were conducted at Aberdeen, Idaho, on the smut reaction of selections from crosses of Iogren × Markton, Silvermine × Markton, Markton × Idamine, and Markton × Victory; at Dickinson, N.Dak., on selections from Markton × Swedish Select; and at Moccasin, Mont., on selections from Markton × Scottish Chief, Markton × Ligowa, Early Champion × Markton, and Markton × Swedish Select. Summarized results are presented in table 3. Data on the smut-free selections are not included.

TABLE 3.—Percentages of covered and loose smuts in susceptible families of oat hybrids grown in 1927

Varieties crossed	Genera-tion	Station	Families tested	Seed inoculum								
				Ustilago levis			Ustilago avenae			Ustilago levis and U. avenae		
				Families in-fected	Plants infected	Maximum in-fec-tion	Families in-fected	Plants infected	Maximum in-fec-tion	Families in-fected	Plants infected	Average maxi-mum infection
				No.	No.	Pct.	Pct.	No.	Pct.	Pct.	No.	Pct.
Iogren × Markton.....	F <sub>3</sub>	Aberdeen, Idaho..	52	35	22.0	95.7	50	30.2	94.7	33	30.2	92.9
Silvermine × Markton.....	F <sub>3</sub>	do.....	45	16	13.7	60.7	33	12.7	52.2	14	15.3	52.0
Markton × Idamine.....	F <sub>3</sub>	do.....	45	1	2.3	2.3	6	10.0	30.8	1	16.6	16.6
Markton × Victory.....	F <sub>3</sub>	do.....	63	1	2.5	2.5	15	11.2	55.3	1	12.3	12.3
Markton × Swedish Select.....	F <sub>3</sub>	Dickinson, N.Dak..	102	13	9.1	25.0	36	21.1	85.7	8	22.4	49.1
Markton × Scottish Chief.....	F <sub>3</sub>	Moccasin, Mont....	44	5	32.0	63.6	9	17.1	45.8	5	25.8	47.9
Do.....	F <sub>3</sub>	do.....	96	7	15.3	38.4	18	21.2	94.7	4	35.4	89.7
Markton × Ligowa.....	F <sub>3</sub>	do.....	63	29	19.7	74.2	43	23.7	77.3	25	26.3	65.8
Do.....	F <sub>3</sub>	do.....	15	5	12.3	33.3	6	20.1	81.8	4	20.0	57.6
Early Champion × Markton.....	F <sub>3</sub>	do.....	127	60	22.1	190.0	88	22.1	2100.0	58	26.2	86.2
Do.....	F <sub>3</sub>	do.....	59	18	16.0	30.8	10	11.9	38.5	6	17.3	27.0
Markton × Swedish Select.....	F <sub>4</sub>	do.....	41	17	30.0	81.8	18	21.0	46.7	13	29.2	60.7

## IOGREN × MARKTON

An F<sub>3</sub> test of the Iogren × Markton cross at Ames, Iowa, for resistance to *Ustilago levis* was low in smut infection and is not reported. In 1927, 52 families were grown from remnant seed of F<sub>2</sub> plants at Aberdeen, Idaho. Only 2 remained free from loose smut, 17 being free from covered smut. On a plant-unit basis 30.2 and 22 percent of the plants were infected with *U. avenae* and *U. levis*, respectively.

Of the 33 families infected with both smuts, 30.2 percent of the plants were smutted.

#### SILVERMINE × MARKTON

Remnant seed of 45 of 53 F<sub>2</sub> plants of the Silvermine × Markton cross was inoculated with covered and loose smuts and sown at Aberdeen. Smut occurred in 35 of the 45 F<sub>3</sub> families. The summary data are shown in table 3. The average number of plants infected was 12.7 percent for loose smut and 13.7 percent for covered smut. Thirty-three of the thirty-five infected families were smutted by *Ustilago avenae* and only 16 by *U. levis*. The two families that showed no loose smut were slightly infected by *U. levis*.

#### MARKTON × IDAMINE

In the Markton × Idamine cross 45 F<sub>4</sub> selections not infected with *Ustilago levis* were tested with both loose and covered smuts in the F<sub>5</sub>. Six families became infected with loose smut and one succumbed to both smuts.

#### MARKTON × VICTORY

Sixty-three F<sub>5</sub> selections from previously smut-free families were inoculated with *Ustilago avenae* and *U. levis*. Fifteen of the sixty-three families proved susceptible to loose smut. One family was smutted by both species. These results are similar to those of the Markton × Idamine cross, in that the reaction of a selection to one smut is not an indication of its reaction to the other.

#### MARKTON × SWEDISH SELECT

The incidence of loose and covered smuts in the Markton × Swedish Select cross grown from inoculated seed at Dickinson, N.Dak., in 1927 is summarized in table 3. Forty-one of the one hundred and two F<sub>3</sub> families were smutted by *Ustilago avenae* or *U. levis* or both. Loose smut developed in 36 of the families and covered smut in 13. Populations from 41 smut-free F<sub>3</sub> families were tested at Moccasin, Mont., for resistance to both *Ustilago avenae* and *U. levis*. Of the 41 F<sub>4</sub> families, 19 were free from both smuts, while 22 showed one or the other. Of the 22 F<sub>4</sub> families 18 were smutted by *U. avenae* and 17 by *U. levis*. A considerably larger number of families succumbed to *U. levis* at Moccasin than at Dickinson.

The greater susceptibility of the Swedish Select parent to loose smut under the conditions at Dickinson, N.Dak., may explain why so much more loose than covered smut occurred in the F<sub>3</sub> hybrid families. However, at Moccasin, Mont., Swedish Select was equally susceptible to both smuts. At Dickinson, certain F<sub>3</sub> families showed high susceptibility to loose smut, yet high resistance to covered smut.

#### MARKTON × SCOTTISH CHIEF

Thirty-five of forty-four F<sub>3</sub> families grown at Moccasin, Mont., were free from both smuts, 9 were susceptible to loose smut, and 5 to covered smut. A summary of the susceptible families is shown in table 3.

Selections from 96 previously smut-free families were tested at Moccasin in F<sub>5</sub> with both *Ustilago avenae* and *U. levis*. Seventy-five families were free from smut. A summary of the 21 families susceptible to one or both smuts is shown in table 3. Suspects cannot be completely eliminated by testing under field conditions for 1 or 2

years. Even in the  $F_5$  7 of the 96 families that were smut-free the previous year became smutted. In this cross the susceptibles to covered smut were almost completely eliminated in  $F_3$  and  $F_4$ .

#### MARKTON $\times$ LIGOWA

$F_3$  populations were grown at Moccasin from remnant seed of 63  $F_2$  plants that had been tested with *Ustilago levis*. Of the 63 lines, 47 were susceptible to one or the other of the smuts. Summarized data are given in table 3. Of the 47 lines that proved susceptible to one or the other smut, 43 were infected with *U. avenae* and 29 with *U. levis*.

Fifteen of the most promising  $F_4$  lines, selected on the basis of freedom from smut and other desirable characters, were further tested with both smuts. Eight were again smut free, but seven proved susceptible to loose or to covered smut. Summarized data are presented in table 3. The occurrence of smut in so large a proportion of these  $F_5$  lines shows the difficulty encountered in weeding out the susceptibles. Five of the seven lines infected with covered smut were resistant to the causal pathogen in tests in two previous generations.

#### EARLY CHAMPION $\times$ MARKTON

The resistance to covered smut of selections from the Early Champion  $\times$  Markton cross was studied at Moro, Oreg., and at Moccasin, Mont. No tests were made with *Ustilago avenae* in Oregon.

At Moccasin 40 seeds of each of 127  $F_2$  plants were inoculated with spores of *U. levis* and a like number of each  $F_2$  plant with spores of *U. avenae*. Summarized data are presented in table 3. Of the 127 families grown, 90 succumbed to one or the other of the smuts. A somewhat greater number of families was susceptible to *U. avenae* than to *U. levis*, although the average percentage of plants infected per family is almost identical. Of the 90 families infected with one or the other smut, only 2 were free from loose smut. Twenty-nine families infected with loose smut were free from covered smut.

At Moro 140  $F_3$  progenies of the above cross were grown, of which 103 were smutted. Progenies from each of 3  $F_3$  plants of the 38 smut-free rows in the  $F_4$  produced only 3 families that showed covered smut. Of the 101 smut-free  $F_4$  families, 59 were tested in the  $F_5$  for resistance to both loose and covered smuts at Moccasin, Mont., in 1927. Of the 59 families, 19 were smutted with one or the other or both pathogenes. A summary is presented in table 3.

#### DISCUSSION OF RESULTS

The data for hybrid populations inoculated with both loose and covered smuts are of interest in showing the lack of linkage in reaction to the two smuts. These results are somewhat at variance with the conclusions reached by Reed and Stanton (11), who found hybrid selections appearing to react in a similar fashion to both smuts. Reed (6, 8) has shown that nearly all the selections from hybrids between Hull-less, a variety highly susceptible to either smut, and Black Mesdag, a variety highly resistant to or nearly immune from both smuts, after retesting certain ones, reacted similarly to the two smuts. The data on selections of Iogren  $\times$  Markton, Silvermine  $\times$  Markton, Markton  $\times$  Swedish Select, Markton  $\times$  Ligowa, and Early Champion  $\times$  Markton, reported in this bulletin, do not agree

with those obtained by Reed (8). The pistillate parents of these crosses all are highly susceptible to both smuts, yet many selections from their crosses with the highly resistant Markton do not show uniformity in their reaction to the two smuts. Further testing might have shown a similar behavior for some of the apparently dissimilar selections, but since conditions in most of the tests were exceedingly favorable for infection the results seem to be significant.

Average infection percentages for the two smuts in the hybrid selections suggest a slightly greater virulence for the loose smut. This difference is not sufficient, however, to account for the marked dissimilarity in the reaction of some of the selections to the two smuts.

In any effective program of breeding for resistance, the known races of both smuts occurring in a particular region must be used conjointly for satisfactory progress. Furthermore, it is desirable that the selections be tested for smut resistance under several different environments or at different stations. This conclusion is supported by the data on the  $F_3$  populations of Markton  $\times$  Idamine and Markton  $\times$  Victory crosses shown in table 3. A rather high infection of loose smut was obtained in a few families that showed no infection of covered smut.

#### VALUE OF RESISTANT SELECTIONS

As already stated, many of the smut-resistant selections resulting from the studies herein reported are being tested extensively for crop value. There are indications that in some of these selections the smut resistance of Markton has been combined satisfactorily with other desirable characters of the susceptible parents.

Sufficient data are not yet available for definite conclusions relative to these selections, yet so far the highest yielding lines have equalled or slightly exceeded the parent varieties in yield. It is believed that in the end desirable varieties will result that should make possible the commercial growing of smut-free varieties in many sections. New physiologic forms of the smut fungi capable of infecting the present resistant oats might, of course, delay this attainment.

Several of the smut-resistant selections from the unnamed oat C.I. no. 357 have about equaled or slightly exceeded Markton in average yield in the Northern Pacific Coast and Intermountain States. These strains are not adapted in the Corn Belt because of susceptibility to stem and crown rusts.

#### SUMMARY AND CONCLUSIONS

The loss of oats from smut approximates 45,000,000 bushels annually. Smut-resistant varieties will help to reduce this loss. The combining of the near-immunity from smut of Markton oats with the other valuable characters of leading commercial varieties is most important.

Crosses of Iogren  $\times$  Markton, Silvermine  $\times$  Markton, Markton  $\times$  Idamine, Markton  $\times$  Victory, Markton  $\times$  Swedish Select, Markton  $\times$  Scottish Chief, Markton  $\times$  Ligowa, and Early Champion  $\times$  Markton were grown from seed blackened with smut. The smut spores were applied to seed with the hulls removed. The susceptible hybrids were weeded out in each successive generation. In some cases, however, smutted plants still occurred in the  $F_5$ .



Promising hybrids have been obtained from the various crosses which combine the near-immunity of Markton with the other desirable characters of the susceptible parent.

Two hundred selections were isolated from the unnamed oat C.I. no. 357, from which Markton originated, and were tested for resistance to covered smut. In the 2 years of the test 156 of the lines became smutted. With this heterogeneity for resistance, considerable variation in morphological characters also occurred. Numerous strains highly resistant to smut, similar to Markton in plant and kernel characters, were among the 200 isolated. The preponderance of selections of this type indicates that Markton probably is representative of the dominant morphological form of the original mass strain. Observations indicated, however, that there was no correlation between the Markton form and smut resistance.

Conditions at the arid (irrigated) and semiarid (dry land) stations in Idaho, North Dakota, Montana, and Oregon were more favorable for the occurrence of smut than were conditions in Iowa.

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