Inheritance of Resistance to Loose Smut of Oat

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ABSTRACT

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The percentage of plants infected with loose smut (*Ustilago avenae*) was determined in oat (*Avena sativa*) parental cultivars and lines and in progenies after kernels were inoculated with water suspensions of teliospores by a vacuum procedure. Inheritance of resistance was studied with F_4 populations of three crosses. In cross Ogle/ND 820559 (susceptible/moderately resistant), the distribution of F_4 progenies appeared bimodal, with more of the progeny clustered around ND 820559 than around Ogle. Twenty-one percent of the F_4 lines displayed fewer infected plants than the resistant parent. In Don/Starter (resistant/resistant), the distribution of F_4 lines was skewed toward low incidence of infection, with many lines more susceptible than either parent. This suggested that resistance was probably conditioned by at least two genes. In Ogle/MN 85230 (susceptible/resistant), the distribution of F_4 lines appeared multimodal, with many lines similar to MN 85230, the resistant parent. The reaction of F_4 lines was verified by testing F_5 lines. Realized heritability, estimated from the Ogle/ND 820559 cross, was 0.93. The incidence of loose smut in Ogle and ND 820559 was not reduced by reselection.

Loose smut, caused by *Ustilago avenae* (Pers.) Rostr., was severe during 1972 in the oat (*Avena sativa* L.) cultivar Froker, which was the most widely grown cultivar in Minnesota. Since 1977, loose smut has been controlled in Minnesota by the widespread use of resistant oat cultivars (5–10). Because the inheritance of resistance to oat loose smut has not been evaluated for many years, this paper reports on it in selected Minnesota oat cultivars and breeding lines infected with the Minnesota population of *U. avenae*.

MATERIALS AND METHODS

Procedures for inoculation and disease evaluation. Kernels from parental oat cultivars, advanced breeding lines, and progenies of crosses were inoculated in test tubes (2.54 × 15.24 cm) that were placed in wire baskets (30–40 tubes per basket) and filled with water suspensions of inoculum of *U. avenae*. The inoculum was a mixture of teliospores: 12.5 g of spores per liter of water containing 10 ml of Tween 20. The tubes were plugged with metal gauze to prevent the loss of kernels during the inoculation process, and the baskets were placed in a chamber for vacuum infiltration of the teliospores (2,3,11). A vacuum of about 127 mm of mercury (12,868 kPa) was drawn for 3 min and released. This vacuum procedure was repeated three times in rapid succession. After inoculation, the kernels were placed on a paper towel and allowed to dry overnight, then placed in envelopes for planting.

The inoculum for this study was a mixture of teliospores collected the year prior to the tests and held at 5 C until used. Teliospores were first collected for our breeding program in 1972, primarily from Froker and from unknown cultivars in farm fields throughout Minnesota. Since 1973 the pathogen has been collected primarily from cultivars and breeding lines in the oat loose smut nursery of the University of Minnesota, with some teliospores from cultivars in farm fields.

Planting was during the last week of April or the first week of May at Rosemount, Minnesota, with a seeder set to drop kernels about 6 cm deep in rows 3.1 m long and 30 cm apart. Weeds were controlled manually and with recommended amounts of bromoxynil (ME 4 Brominal), propachlor (Ramrod), and dicamba (Banvel) applied preemergence and with propanil (Stampede) applied 3 wk after planting. Plots were sprinkler irrigated when necessary to maintain vigorous plant growth.

Inheritance of resistance. Three populations of F_2-derived F_4 lines were evaluated. The first population resulted from a cross between susceptible Ogle and moderately resistant ND 820559. In previous tests, 70–80% of Ogle plants were infected, whereas only 30–40% of ND 820559 plants were. The second population was from a cross between resistant cultivars Don and Starter, which both had 5% or fewer infected plants in previous tests. The third population was from a cross between Ogle and resistant MN 85230. In previous tests, MN 85230 had 5% or fewer infected plants. These crosses represent the range of a breeding program to develop smut-resistant cultivars.

In each cross, four kernels from random F_2 plants were advanced to the F_3 generation. All kernels from the four F_3 plants per selection were bulked to provide enough kernels for loose smut evaluations.

The parents of each cross and approximately 300 F_2-derived F_4 lines of each cross were evaluated for reaction to loose smut. Six replicates of each parent (five for ND 820559) were used. Each F_4 entry and each replicate of the parents consisted of 100 kernels inoculated by the standard vacuum procedure. Entries were evaluated for percentage of infected plants during the last week of June 1988, approximately 50 days after planting.

Verification of F_4 evaluations. The loose smut reaction of selected F_4 lines from the Ogle/ND 820559 cross was verified by testing F_4-derived F_5 lines. Ten F_4 lines that had less than 12% infected plants in the 1988 field test were selected for the study. From each F_4 line, 10 panicles were randomly selected (a total of 100 panicles), and about 50 kernels per panicle were inoculated by the standard vacuum procedure and planted in the glasshouse in winter 1988–89. The percentage of infected plants was determined when plants headed. Realized heritability was estimated in cross Ogle/ND 820559 with the formula: H_R = selection response in F_5 (selected population mean − base population mean)/selection differential in F_4 (selected population mean − base population mean).

A second evaluation was made to verify the loose smut reactions of the F_4 lines in the 1988 test using F_5 lines from Ogle/ND 820559 and Ogle/MN 85230. These F_5 lines were obtained by harvesting kernels of F_4 lines that displayed 20% or fewer infected plants (Group A F_5 lines) and from F_4 lines with 80% infected plants (Group B F_5 lines). The parents and check cultivars Don, Hazel, Moore, and Starter were also studied. There were 12 replicates of Ogle, six of ND 820559 and MN 85230, and four of the check cultivars. Kernels were inoculated by the standard vacuum procedure and planted in the field in summer 1990. Disease was evaluated when heading was completed.

Selection to improve smut reactions in cultivars or lines. The loose smut reactions of Ogle and ND 820559 were

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Table 1. Loose smut (*Ustilago avenae*) reactions of parents and F_4 populations in three oat crosses

Cross[a] Parents	No. tested[b]	Standard error (%)	No. lines and parents/% smut 0	10	20	30	40	50	60	70	80	90	100	Smut mean (%)	Midparent value (%)
Cross 1	277		0 5	5 10	23 10	19 17	24 16	24 8	23 14	18 18	16 8	16 3	0	50.1	59.7
Ogle	6	2.25									1 4	1		80.0	
ND 820559	5	4.21			1	3				1				30.0	
Cross 2	293		37	101 90	39 16	8 1	1							7.4	2.9
Don	6	1.74	1	4 1										4.6	
Starter	6	1.19	3	3										1.2	
Cross 3	280		0	36 20	19 13	13 16	11 19	11 25	6 15	5 12	12 8	7 27	2 3	41.3	41.0
Ogle	6	3.46							1		2 1	2		80.8	
MN 85230	6	1.86	4	1 1										2.5	

[a] F_4 populations.
[b] Number of F_4 lines and of replicates of parents.

obtained in the 1988 field test and verified in the glasshouse. This test also determined whether reselection might improve the resistance of Ogle (susceptible) and ND 820559 (moderately resistant). From each of these oats, 20 noninfected plants were randomly selected from each replicate, and 50 kernels from each plant were inoculated by standard vacuum procedures and planted in the glasshouse in winter 1988–89. The percentage of infected plants was determined after the plants headed.

RESULTS

Inheritance of resistance. *Ogle/ND 820559 cross.* The range of infected plants in six replicates of Ogle was 75–90% with a mean of 81%; whereas with ND 820559, the range was 26–36% of plants infected, with a mean of 30%. Standard errors for Ogle and ND 820559 were 2.25 and 4.21%, respectively. Infection of F_4 progeny ranged from 5 to 95% of plants per line. The progeny mean was 50%, and the midparent value was 60%. The low number of lines with 55% infection suggested that the distribution may be bimodal with 155 of the F_4 lines clustered around ND 820559 and 122 around Ogle (Table 1). A total of 21% of the F_4 lines displayed fewer infected plants than ND 820559. With the percentage of infected plants of ND 820559 as a basis for estimating resistance, F_4 lines with less than 27% infected plants were considered more resistant than ND 820559.

Don/Starter cross. The range of infected plants in six replicates of Don was 0–10% with a mean of 4.6%, and the range in Starter was 0–5% with a mean of 1.2%. Standard errors for Don and Starter were 1.74 and 1.19%, respectively. Infection of the F_4 progeny ranged from 0 to 35%, with the distribution skewed toward low percentage of infection (Table 1). However, a number of progeny had a higher infection percentage than either parent, suggesting different genes for resistance in the parents. The mean infection level for the progeny was 7%, which exceeded the midparent value of 3%.

Table 2. Mean percentage of plants of putative resistant F_4 lines of the cross Ogle/ND 820559 and of parents infected with *Ustilago avenae* in the field compared with the mean and range for the percentage of infected plants of F_5 lines derived from resistant F_4 lines and of the next parent generation in the glasshouse in 1988–89

Entry	F_4 smut infection[a] (%)	F_5 lines[b] Mean (%)	F_5 lines[b] Range (%)
1043[c]	10	04.9	0–28
1081	02	03.6	0–29
1093	05	15.8	0–87
1137	06	05.6	0–16
1147	11	08.1	0–25
1155	10	11.8	0–54
1179	04	10.0	0–43
1242	12	13.5	4–30
1245	05	05.1	0–21
1274	10	08.3	0–24
Parents			
ND 820559	30	14.0[d]	10–26
Ogle	80	58.0[d]	39–72

[a] Based on 100 plants per entry.
[b] Based on 500 plants per entry (10 F_4 plants per entry and 50 kernels per plant).
[c] Entries with 12% or less infected plants.
[d] Based on 100 plants for ND 820559 and 120 plants for Ogle.

Ogle/MN 85230 cross. The range of infection in Ogle in this test was 60–90% with a mean of 81%, and in MN 85230 the range was 0–10% with a mean of 2.5%. Standard errors for Ogle and MN 85230 were 3.46 and 1.86%, respectively. The incidence of infection in F_4 progeny ranged from 5 to 100% infected plants (Table 1). The distribution appeared multimodal, with many of the progeny having infections similar to one of the parents, particularly the resistant parent.

Verification of F_4 results. The loose smut reactions of F_4-derived F_5 lines of cross Ogle/ND 820559 were similar to those of their parental F_4 lines (Table 2). The percentages of loose smut in the F_4 lines selected in the field varied from 2 to 12% (Table 2). The mean in the F_4-derived F_5 lines varied from about 4.0 to 16.0%. In the F_5 lines the range of percentage infection was from 0.0 up to 28% in six sets of lines, from 0.0 up to 87% in three sets, and 4–30% in one set (Table 2).

The percentage of infected plants indicated moderate resistance for ND 820559 when tested as F_4 lines, and resistance to moderate resistance when tested as F_5 lines. Ogle was susceptible when tested both as F_4 and F_5 lines (Table 2).

Realized heritability in cross Ogle/ND 820559 was estimated by Pearson correlation analysis of similarities of the infection percentage means of lines in the field and in the glasshouse. Realized heritability was 0.93.

The loose smut reactions of F_4 lines of crosses Ogle/ND 820559 and Ogle/MN 85230, of the parents, and of check cultivars were verified in field trials in 1990 (Table 3). The mean percentage of plants infected in F_5 lines of group A (F_4 lines had 20% or less infection) of both crosses was lower than in F_5 lines of group B (F_4 lines had 80% infection) (Table 3). The mean and range of the percentage of smut-infected plants in Ogle were 64% and 50–80%, repectively; and in ND 820559 and MN 85230, mean and range were about 5% and 2–10%, respectively, as in previous tests (Table 3). The reactions of the check cultivars were also similar to those observed in previous tests: in resistant Don and Starter, the mean and range of percentage of infected plants was low; whereas

in susceptible Hazel and in intermediate Moore, the mean and range were high (Table 3).

Selection to improve smut reactions in cultivars or lines. In 1988, the smut reactions of Ogle and ND 820559 observed in the field were similar to those observed in glasshouse tests (Table 4). Mean and range percentages of smut-infected plants were greater in Ogle than in ND 820559 in both tests. Reselection did not increase the number of smut-free plants in lines of Ogle or ND 820559 (Table 4).

DISCUSSION

The virulence of the Minnesota population of *U. avenae* differed from that reported by others (1–3), as indicated by the reactions of smut differential cultivars between 1979 and 1990. Each year, the percentage of infected plants in differential cultivars Anthony, Black Diamond, Black Mesdag, and Victory was 30–90%; in Camas, Markton, Monarch, and Navarro the percentage was 0–10%; in Fulgam and Nicol it was 1–20%, somewhat higher than in the previous three cultivars; in Gothland it was 2–30%; and in Clintland 64 and Victoria it was 10–30%. Although we attempted to create diversity of virulence in the Minnesota population by adding, from time to time, teliospores collected from unknown cultivars, we did not succeed. Our data suggest that the Minnesota population of *U. avenae* has been relatively stable for a number of years.

Because the incidence of loose smut in oat cultivars is seldom 100%, it is possible that healthy plants derived from inoculated kernels may be resistant. This possibility was investigated with Ogle and ND 820559, both of which appeared to be homozygous and homogeneous. However, reselection in Ogle did not increase the incidence of healthy plants. The reselections contained high percentages of loose smut infected plants, and the mean infection percentage exceeded that of nonselected Ogle. Apparently, healthy plants derived from inoculated Ogle kernels escaped infection.

Lines of ND 820559 that were smut-free in the field and reevaluated in the glasshouse were highly variable compared to Ogle. This may indicate a residual heterogeneity. Perhaps the results may be explained as follows: a line or cultivar might display an intermediate incidence of smut infection if some plants successfully prevent development of the pathogen. This ability may be influenced by different environmental factors and growth rates of the shoot. Despite the fact that ND 820559 was more variable than Ogle, the mean infection percentages of reselections were similar to those of the nonselected check, suggesting that reselection is unlikely to produce much improvement for smut resistance.

The high value for realized heritability and the close agreement between F_4 lines and F_4-derived F_5 lines suggest that the low smut reaction of the F_4 lines was due to resistance and not to escape. This also was indicated with F_5 lines harvested from F_4 lines that had high or low incidence of loose smut.

There are no recent studies on the inheritance of resistance in oat to loose smut. Reed and Stanton (4) in 1938 reported that resistance is highly heritable and is conditioned by one to three genes (4). Our study confirms these conclusions. We identified many resistant lines and observed a high realized heritability, and reactions of F_4 and F_5 lines were in agreement. Results obtained with the population from the Don/Starter cross suggest at least two different genes are operative.

The crosses made in this study produced three distinct distributions of F_4 lines. F_4 progenies of cross Ogle/ND 820559 (susceptible/moderately resistant) formed a bimodal distribution, with many progeny being similar to ND 820559. This cross also demonstrated that a moderately resistant oat may be a useful source of resistance. F_4 progenies of Don/Starter (both resistant) formed a distribution that was skewed toward low incidence of smut. However, many of the lines were less resistant than either parent, and the mean of the lines was greater than the midparent value, suggesting that different resistance genes may be present in the parents. F_4 progenies of Ogle/MN 85230 (susceptible/resistant) formed a multimodal distribution with many of the lines having an incidence of infection similar to that of MN 85230.

Our selection studies demonstrated the feasibility of early generation selection for loose smut reaction in the progeny of crosses. Selection of F_4 lines was effective in each of our crosses.

Table 3. Mean and range of the percentage of infection of F_5 lines of two crosses, parents of the crosses, and check cultivars infected with *Ustilago avenae* in the field 1990

Cultivar or line	Total samples or lines (no.)	Mean (%)	Range (%)
Checks			
Don	4	1.25	0–5
Hazel	4	55.00	50–60
Moore	4	35.00	30–40
Starter	4	1.25	1–5
Parents			
Ogle	12	64.17	50–80
ND 820559	6	7.50	5–10
MN 85230	6	5.00	2–10
F_5 lines of Ogle/ND 820559			
Group A[a]	47	9.89	0–50
Group B	35	58.29	30–80
F_5 lines of Ogle/MN 85230			
Group A[a]	49	4.80	0–50
Group B	40	62.50	20–80

[a] Group A F_5 lines obtained by harvesting F_4 lines with 20% or less smut-infected plants. Group B F_5 lines from F_4 lines with 80% infected plants.

Table 4. Mean and range percentages of plants infected with *Ustilago avenae* in lines of oat cultivar Ogle and line ND 820559 in the field in 1988 and in the glasshouse in 1988–89

Cultivar Line	Field test mean[a] (%)	Glasshouse test[b] Mean (%)	Glasshouse test[b] Range (%)
Ogle			
1301	80	72	20–100
1302	75	63	27–100
1303	80	64	0–100
1304	78	66	36–100
1305	80	78	46–100
1306	79	69	33–91
Mean of lines	79	69	
Mean nonselected Ogle	80	58	39–72
ND 820559			
1307	36	30	2–81
1308	26	24	2–88
1309	36	29	4–80
1311	33	22	0–70
Mean of lines	33	26	
Mean nonselected ND 820559[c]	30	14	10–26

[a] Based on infected plants in a single row in 1988 field nursery.
[b] Based on 20 panicles from each F_4 line.
[c] Based on 20 samples obtained from an unselected seed lot.

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LITERATURE CITED

1. Hansing, E. D., Heyne, E. G., and Stanton, T. R. 1946. Reactions of oat varieties and selections to four races of loose smut. Phytopathology 36:433-445.
2. Holton, C. S., and Rodenhiser, H. A. 1948. Physiologic specialization in the oat smut fungi and its relation to breeding oats for smut resistance. U.S. Dep. Agric. Tech. Bull. 952.
3. Nielsen, J. 1977. A collection of cultivars of oats immune or highly resistant to smut. Can. J. Plant Sci. 57:199-212.
4. Reed, G. M., and Stanton, T. R. 1938. Inheritance of resistance to loose and covered smut in Markton oat hybrids. J. Agric. Res. (Washington, D.C.) 56:159-175.
5. Stuthman, D. D., Moore, M. B., Rothman, P. G., and Wilcoxson, R. D. 1977. Registration of Lyon Oats. Crop Sci. 18:356.
6. Stuthman, D. D., Moore, M. B., Rothman, P. G., Wilcoxson, R. D., and Rines, H. W. 1979. Registration of Moore oats. Crop Sci. 20:550.
7. Stuthman, D. D., Wilcoxson, R. D., and Rines, H. W. 1990. Registration of Starter Oat. Crop Sci. 30:1365-1366.
8. Stuthman, D. D., Rothman, P. G., Wilcoxson, R. D., and Rines, H. W. 1987. Registration of Proat oat. Crop Sci. 27:816.
9. Stuthman, D. D., Rothman, P. G., Wilcoxson, R. D., Rines, H. W., and Moore, M. B. 1984. Registration of Preston oats. Crop Sci. 24:383-384.
10. Stuthman, D. D., Wilcoxson, R. D., Rothman, P. G., Moore, M. B., and Rines, H. W. 1980. Registration of Benson oats. Crop Sci. 20:550.
11. Tervet, I. W. 1941. The relative susceptibility of different lots of oat varieties to smut. Phytopathology 31:672-673.

at the end of the season (August 1989).