THE INHERITANCE OF REACTION TO LOOSE SMUT IN THE SEGREGATING GENERATIONS OF CERTAIN BARLEY HYBRIDS

by

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INTRODUCTION

Loose smut of barley, Ustilago nuda (Jens.) Rostr. is an important disease in many barley producing areas. The reduction in yield is approximately equivalent to the percentage of smut (18). In 1939 Craigie (3) estimated that the average incidence of loose and covered smut in Manitoba was 3 per cent. This indicated an annual loss of 1,466,000 bushels. Plant Diseases Committee Reports (2) indicate that loose smut infection in barley has been increasing to the extent that in 1950 it alone averaged 3 per cent infection in Manitoba. Individual losses may be greater as fields showing 20 per cent loose smut have been reported (2).

While the percentage of infection generally is not high, the tendency of the disease, once established, to increase year by year increases the seriousness of the problem. Control is difficult as loose smut is intraseminal and cannot be controlled by the surface sterilization methods which are effective against surface borne smut spores. The disease can be controlled by the hot water seed treatment but this method is difficult to use and often seriously reduces the germination of the seed.

The breeding of resistant varieties offers the best practical means of control. Considerable work towards this objective has been done. The reaction of a number of varieties to loose smut has been reported (16) and resistant varieties are available for use as parental material. Utilization of these sources of resistance would be facilitated by knowledge of the mode of their inheritance and by knowledge of their linkage relations.

Physiological specialization has been shown to occur in the pathogen; this complicates the plant breeding problem and makes it desirable to have knowledge of the occurrence and nature of different sources of resistance.

This study was undertaken in an effort to provide some information regarding inheritance and linkage relations of resistance from certain sources used in the University of Manitoba barley breeding program.

REVIEW OF LITERATURE

Smith (19) presented a brief review of the work of a number of investigators on the inheritance of reaction to loose smut.

Tapke (21) distinguished Ustilago nigra from Ustilago nuda and described the former. Of these two he found that Ustilago nigra could be controlled by surface sterilization of the seed.

Artificial inoculation with Ustilago nuda which is a floral infecting smut consists of placing the chlamydospores into the florets of the host at flowering time. Various techniques have been used to accomplish this purpose and the relative efficiency of the different inoculation methods has been tested.

Schands and Schaller (16) reviewed thoroughly the methods which had been used in making artificial inoculations with loose smut and retested the more promising of these methods. They described a method whereby dry spores were "puffed" from a small rubber bulb, through a hypodermic needle, to the stigma after the lemma was pierced. Poehlman (10) used a hypodermic needle in a similar manner except that an aqueous suspension of spores was used. Moore (7) described a vacuum method whereby a spore suspension is forced into the florets by a sudden release of air into a partial vacuum formed above the suspension covering the spike. Ross et al (14) compared these three methods and found that injection of an aqueous suspension of chlamydospores was most effective. Under the comparatively dry conditions in Alberta, dry spores produced lower percentages of infection than had been obtained at Wisconsin (17).

Later Cherewick and Popp (1) modified Moore's partial vacuum method and succeeded in increasing the speed of inoculation as well as raising the percentage of infection.

Generally, in crosses between resistant and susceptible varieties, resistance appears to be due to a single dominant or incompletely dominant gene. However, modifying genes have been postulated to account for the lack of clear cut segregations (6). It is also possible that these results were due to a lack of efficiency in the inoculation methods that were available to early genetic investigators.

Zeiner (22) studied 8 crosses between barley varieties showing various degrees of resistance and susceptibility to Ustilago nuda. Although the evidence was not conclusive, resistance appeared to be dominant and controlled by a single factor. When two susceptible varieties were crossed there was no evidence of transgressive segregation toward greater resistance.

Nahmmacher (8) confirmed many of Zeiner's results; the uncertainty of the infection method, however, made it difficult to obtain an accurate analysis of the factors governing the reaction of the F_3 progenies.

Livingstone (6) found evidence for the presence of a single dominant factor for resistance in Hordeum deficiens and the Hordeum vulgare variety Trebi. No evidence of association between the genes for resistance and those for hoods and kernel row number was found.

Schands (15) reported a close linkage between the genes for the stem rust resistance of Chevron and the loose smut resistance of Trebi.

Schaller (17) showed that Trebi, Jet, Dorset and selection

X173-10-5-6-1 each possessed a single gene which conferred its own degree of resistance. The genes in Trebi and Jet gave the highest degree of resistance and were dominant in effect.

Transgressive segregation obtained in the cross between Trebi and Jet suggested that these genes were independently inherited. The Dorset gene and the weak gene in selection X173-10-5-6-1 were also independent. Linkage between the Dorset and Jet genes was suggested.

The following morphological characters which are located on the linkage groups indicated were studied:

Character	Linkage Group
non-6-rowed vs. 6-rowed spike	I
black vs. white lemma and pericarp	II
hulled vs. naked caryopsis	III
awns vs. hoods	IV
rough vs. smooth awns	V
long vs. short haired rachilla	V
normal seedling color vs. xantha	VII

No evidence of association between the genes conditioning any of these characters and the genes for smut resistance was found.

MATERIALS AND METHODS

Varieties

The resistant varieties studied are being utilized for smut resistance in the barley breeding program at the University of Manitoba. Titan (C.I. 7055) has been used for a number of years; Jet (C.I. 967) and Valkie (C.I. 5748) were obtained from the Canadian Accession Bureau at the time this investigation was initiated. Montcalm, the susceptible variety, has been used as a source of yield and malting quality characteristics.

Information regarding the reaction of these varieties to physiological races of Ustilago nuda was supplied by Cherewick (1*).

1* Unpublished data by W. J. Cherewick, Laboratory of Plant Pathology, Winnipeg, Manitoba.

Montcalm originated from the cross (Michigan 31604 x Common Six-Rowed 4307 M. C.) x Mandscheuri 1807 M. C. It is resistant to several collections of loose smut but is highly susceptible to the one used in this experiment.

Jet is a two-rowed, black, hulless barley of Abyssinian origin. It appears to be highly resistant to all the existing races of loose smut since none has been observed on it in either inoculated or uninoculated material (17).

Titan originated from the cross Trebi x Glabron. It is susceptible to some collections of smut but immune to the smut used in this experiment (loc. cit.).

Valkie is a yellow aleurone, two-row barley. It is resistant to a number of collections of smut including the one used in this study (loc. cit.).

Hybrid Populations

Hybrid populations were obtained from the following crosses which were made during the summer 1950:

Montcalm x Jet
Jet x Montcalm

Montcalm x Titan
Titan x Montcalm

Valkie x Montcalm
Montcalm x Valkie

Valkie x Titan
Titan x Valkie

Two generations of plants from these crosses were grown in the greenhouse during the winter 1950-1951. All the material that was to be inoculated was planted in January 1951 so that the parental varieties, F_1 and F_2 of each cross could be grown and inoculated under similar conditions. Due to unfavorable circumstances some of the F_1 plants did not reach maturity and therefore the population of these was not extensive.

The hybrid material was tested for reaction to the smut in the F_2 and F_3 generations. Since genetically susceptible plants may escape infection, classification of F_2 plants was based on the percentage of smutted plants in F_3 progeny rows. This was done to minimize the effect of escapes on the ratio of resistant to susceptible in F_2. The F_2 data were used to provide an estimate of the percentage of smut expected on segregating F_3 lines. When two parents differ by a single factor pair, the segregating F_3 lines and the F_2 populations are genetically alike hence the percentage of smut in the F_2 population should be approximately equivalent to the percentage in the segregating F_3 lines.

Inoculation Procedure

During flowering, approximately 60 F_2 plants from each of the reciprocal crosses were taken at random for inoculation. An attempt was made to inoculate a sufficient number of heads to produce a minimum of 30 inoculated seeds from each plant. About 20 heads from each parental variety and the available heads of F_1 plants were inoculated during the same period of time.

The original inoculum was provided by W. J. Cherewick of the Dominion Laboratory of Plant Pathology. It was originally obtained from Napanee, Ontario, and was designated as collection 45-30, of *Ustilago nuda*. Several heads from Montcalm plants grown in the field in 1950 were inoculated with it. Approximately 20 progenies from each of 10 of these heads were grown during the winter 1951. As it has been suggested that virulence may differ within a smut collection, the inoculum which was used throughout this study was taken from the progeny of the inoculated head that produced the highest percentage of infected plants. Freshly collected inoculum was used and spore germination was tested repeatedly.

The needle method was used for making inoculations. A hypodermic needle was inserted through the lemma of each individual floret and an aqueous spore suspension was injected into the florets.

Mature Plant Examination

For various reasons the F_3 progeny rows consisted of fewer plants than is desirable for genetic analysis. Tillering which was not profuse under greenhouse conditions, partial sterility especially in the inoculated heads and dormancy in a portion of the seed which was planted in the field combined to reduce the number of plants in the F_3 progeny lines.

Nevertheless all the inoculated material was grown and used for collecting data. This course was followed because elimination of the short lines would tend to introduce a bias into the ratio for kernel row number by elimination of 2-rowed segregates.

All the inoculated material was grown in the field during the summer of 1951. Before planting, all the seed was treated with Ceresan to minimize the possibility of infection with false loose or covered smut and to give protection against root rot organisms. The inoculated seed from individual F_2 plants was grown in separate rows; and when uninoculated seed was available, corresponding rows were grown from it so that the segregation of morphological characters could be observed in F_3. The inoculated seed from the F_1 plants and from the parental varieties was grown in headrows.

After the plants had grown to maturity they were pulled to determine the number of smutted and non-smutted plants in each line. A plant having even a single smutted tiller was regarded as susceptible. The percentage of smutted plants in each row was calculated from the totals obtained.

Association of Characters

The parents of two of the crosses involving resistance and susceptibility to loose smut differed in several morphological characters known to be simply inherited. The variety Jet has a black lemma and pericarp, 2-rowed spike and short glume awns. In contrast, Montcalm has a white lemma, 6-rowed spike and long glume awns. Valkie differs from Montcalm in having a 2-rowed spike, yellow aleurone and short glume awns.

These characters were observed in F_2 populations grown from uninoculated seed. Data were collected by determining the phenotype, and where possible the genotype, of individual F_2 plants which were inoculated. Genotype for aleurone color could be obtained in F_2 since aleurone color is an endosperm character; similarly awn pointed laterals served to distinguish plants heterozygous for the factor conditioning kernel row number. All F_2 determinations except those for aleurone color were checked again in the F_3 lines grown from the individual F_2 plants.

The data collected were used in an attempt to verify the reported mode of inheritance of these characters in the varieties studied; the relationship of the genes conditioning these characters to each other and to the genes for resistance and susceptibility to loose smut. For this purpose tests of goodness of fit and independence were made by means of the chi square. A probability value greater than .05 was regarded as indicating a satisfactory fit.

RESULTS AND DISCUSSION

Inheritance of Resistance to Loose Smut in the Cross Jet x Montcalm

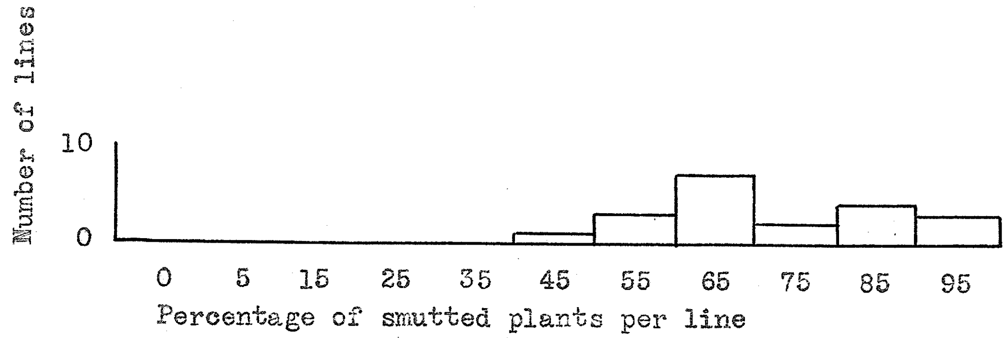
The distribution of loose smut infection by percentage classes for the parental rows and F_2 and F_3 progenies is shown in Table I and is illustrated graphically in Figure I. The data from the reciprocals of this cross were combined as shown in Table I since their distributions are essentially alike.

TABLE I Distribution of Loose Smut Infection by Percentage Classes for the Parental Rows and F_2 and F_3 Progenies of the Cross Jet x Montcalm

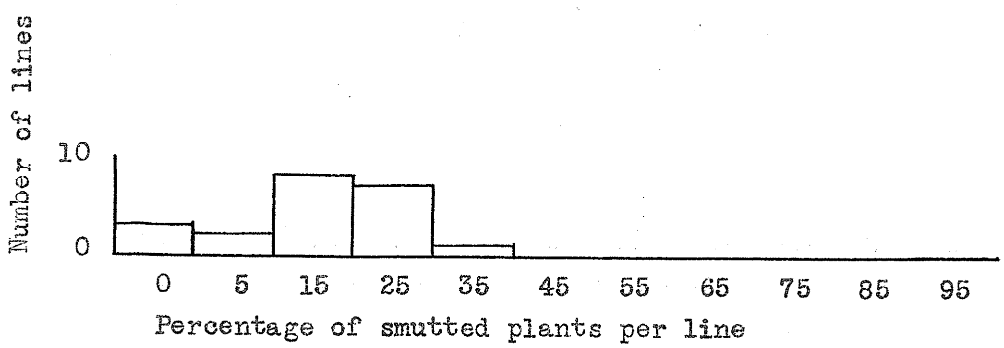
Parent or Cross	Class mark of per cent infection classes											Total no. of lines
	0	5	15	25	35	45	55	65	75	85	95	
Montcalm						1	3	7	2	4	3	20
Jet	18											18
Jet x Montcalm F_2	3	2	8	7	1							21
Jet x Montcalm F_3	41	7	22	23	14	2	3	6	7	9	5	139

The progeny of the 18 inoculated heads of Jet which contained 231 plants showed no smut. This substantiated previous observations since no loose smut has been observed on Jet here or at Wisconsin (17). Therefore Jet is regarded as immune to the race of smut used in this investigation.

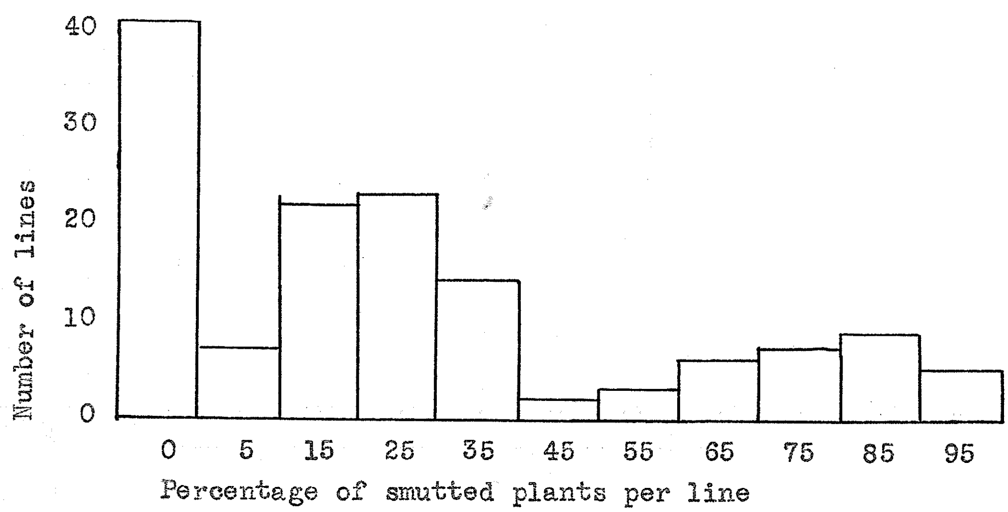
The progeny of the 20 inoculated heads of Montcalm consisting of a total of 345 plants showed an average of 72.2 per cent smut. This percentage of infection showed that Montcalm is susceptible to collection 45-30 of loose smut. The range of infection in the individual rows which was from 50 to 93 per cent showed that inoculations had been carried out with a reasonable degree of efficiency.



DISTRIBUTION OF SMUTTED PLANTS IN MONTCALM



DISTRIBUTION OF SMUTTED PLANTS IN F_2 LINES OF JET x MONTCALM



DISTRIBUTION OF SMUTTED PLANTS IN F_3 LINES OF JET x MONTCALM

Figure 1

When a single dominant gene is responsible for resistance $\frac{1}{4}$ of the F_2 plants of a cross between resistant and susceptible varieties are expected to be genetically susceptible. The average percentage of smutted plants in plants grown from artificially inoculated seed of the susceptible parent was 72.2. Assuming the same degree of infection in the F_2 plants, 18 per cent (72.2 x $\frac{1}{4}$) of them would be expected to show smut. Inoculated seed from 21 F_1 plants was grown and 74 of the 338 F_2 plants obtained or 19.1 per cent were smutted. The actual percentage of smutted plants obtained in F_2 closely approaches the expected.

The distribution of F_3 lines on a percentage infection basis is shown in Table I and Figure I. On the assumption that lines showing no smut are homozygous for the resistance of Jet and those that show any degree of smut possess some susceptibility, these lines may be divided into two groups; 41 resistant and 98 susceptible. The chi square value 1.4988 with a probability value between .30 and .20 indicates reasonable agreement to a 3:1 ratio.

Since no Montcalm rows (Figure I) showed less than 40 per cent smut and no F_2 lines contained more than 40 per cent, the F_3 lines were divided at that point into three classes representing the resistant, segregating and susceptible lines which are expected if smut resistance is simply inherited. The numbers in each class respectively are then; 41:66:32.

If inheritance of reaction to smut is due to a single factor, the percentage of smut in the segregating F_3 lines is expected to be approximately equal to the percentage in the F_2. Actually the F_2

showed an average of 19.1 per cent smut while the 66 F_3 lines classified as segregating showed 21.3 percent.

Two more comparisons between theoretically expected and actual numbers are made possible by the division of the F_3 lines into three classes. The results of the chi square tests for goodness of fit of mode of inheritance of reaction to smut are summarized in Table II.

TABLE II A Summary of Chi Square Tests for Mode of Inheritance of Reaction to Smut in the Cross Jet x Montcalm

Character and Cross	Assumption	X^2	P
Jet x Montcalm (n=139)			
susc. & seg. vs. res. lines	3:1	1.4988	.30-.20
res. & seg. vs. susc. lines	3:1	.2902	.70-.50
res.: seg.: susc. lines	1:2:1	.6324	.90-.80

As all the probability values (Table II) are in excellent agreement with a single factor hypothesis, the evidence indicates that the resistance of Jet to collection 45-30 of *Ustilago nuda* is conditioned by a single gene.

While no F_1 plants were grown from inoculated seed, the low percentage of infection in F_2 and the large low infection class in F_3 indicate that the gene is dominant in effect.

Inheritance of Resistance to Loose Smut in the Cross Titan x Montcalm

The distribution of loose smut infection by percentage classes for the parental rows and F_3 progenies is shown in Table III. Due to the similarity of the distributions, the data from both reciprocals of the cross were combined. Only a limited amount of information regarding the smut infection of the F_2 of this cross is available since most of the F_1 plants grown for inoculation failed to reach maturity. However 36 plants were obtained from inoculated F_1 seed; 8.3 per cent of these plants showed smut in F_2.

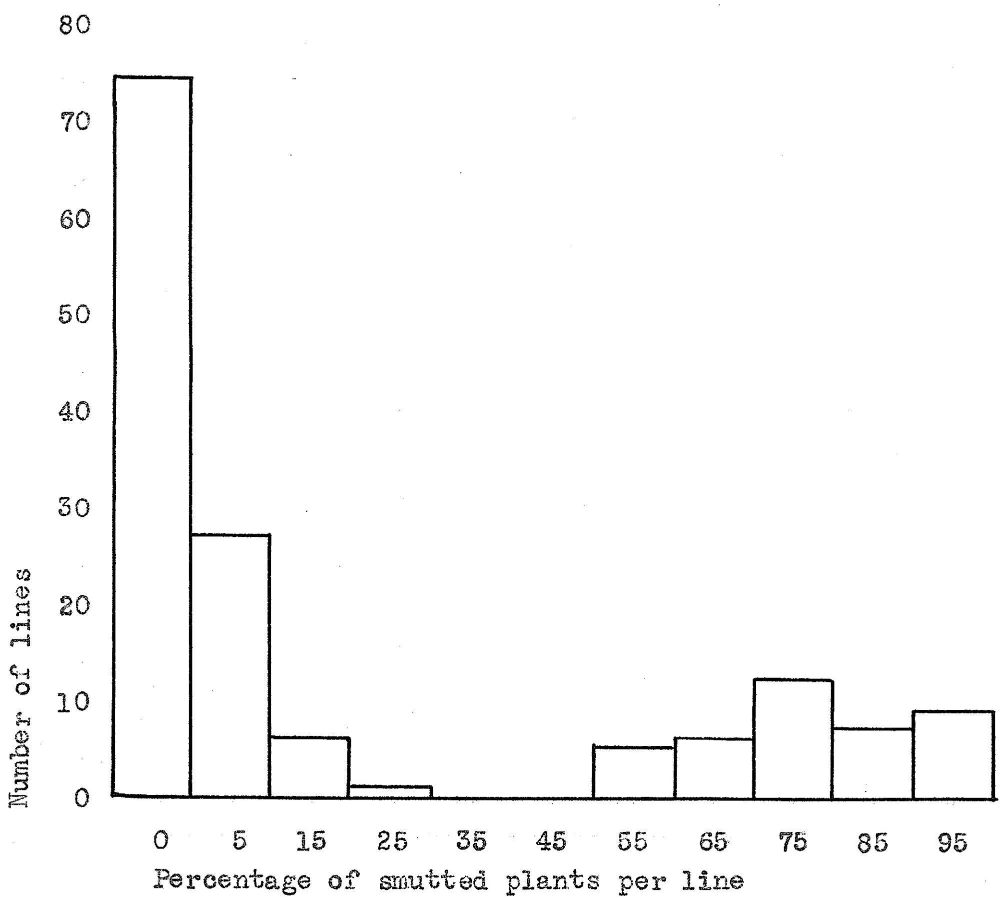
TABLE III Distribution of Loose Smut Infection by Percentage Classes for the Parental Rows and F_3 Progenies of the Cross Titan x Montcalm

	Class mark of per cent infection classes											Total
Parent or Cross	0	5	15	25	35	45	55	65	75	85	95	no. of lines
Montcalm						1	3	7	2	4	3	20
Titan	18											18
Titan x Montcalm F_3	75	27	6	1			5	6	12	7	9	148

The progeny of the 18 inoculated heads of Titan showed no smut. This agrees with results obtained by Cherewick (loc. cit.) and shows that Titan is immune to collection 45-30 of Ustilago nuda.

The progeny of the 20 inoculated heads of Montcalm previously mentioned were used again to represent the distribution of smutted plants in the susceptible parental variety.

As shown in Table III the absence of any F_3 lines in the 30 to 50 per cent infection classes divides the progenies into two groups, approximating a 3:1 ratio. Such a ratio would be expected if resistance is conditioned by a single factor. When classified in this manner there are



DISTRIBUTION OF SMUTTED PLANTS IN F_3 LINES OF TITAN x MONTCALM

Figure 2

109 resistant and segregating lines and 39 susceptible lines. Goodness of fit to a 3:1 ratio was tested by means of the chi square. A chi square value of .1441 with a probability of .80-.70 was obtained. This indicates satisfactory fit to a single factor ratio.

Examination of the distribution of F_3 lines in Table III and Figure II shows a preponderance of lines without any smut. The low percentage of infection in F_2 suggests that a larger number of plants than was available in some of the F_3 lines would be required to distinguish segregating lines from resistant ones.

In this cross Titan x Montcalm, only 8.2 per cent of smut was obtained in F_2 and 6.3 in F_3 lines that could be classified as segregating. The percentages of smut in F_2 and in the segregating F_3 lines are approximately equal as is expected when resistance is conditioned by a single gene. However the percentage is considerably lower than the 18 per cent which is expected when reaction to smut is conditioned by a single dominant gene.

Two hypothesis have been advanced to account for similar low percentages of infection in the progeny of inoculated plants which were heterozygous for resistance. A higher mortality rate in smut infected seeds and seedlings than in uninfected ones would tend to decrease the percentage of smut in segregating lines. Schaller (17) found some evidence indicating that a higher death rate occurs in infected seedlings. Increased mortality sometimes does occur as a very high rate of mortality has been observed in infected seedlings of Titan inoculated with a certain collection of loose smut (loc. cit.). It is also possible that resistant maternal tissue surrounding the embryo in plants heterozygous for resistance, in some way hinders infection of the embryo in hybrids involving Titan.

Both of these hypothesis were advanced by Schaller (17) in the study of the smut reaction of hybrids from crosses involving Trebi. Trebi is one of the parents of Titan and it has been suggested that Titan has derived a gene for smut resistance from Trebi (16). If this is the case, hybrids involving each of Titan and Trebi can be expected to show similarity in reaction to loose smut.

Inheritance of Resistance to Loose Smut in the Cross Valkie x Montcalm

The distribution of loose smut infection by percentage classes for the parental rows and F_3 progenies is shown in Table IV and in Figure III. The data from both reciprocals of this cross were combined since the distributions were similar. While most of the F_1 plants intended for inoculation failed to reach maturity, the progeny of one inoculated plant showed 7 per cent smut; this line consisted of 1 smutted and 13 non-smutted plants.

TABLE IV Distribution of Loose Smut Infection by Percentage Classes for the Parental Rows and F_3 Progenies of the Cross Valkie x Montcalm

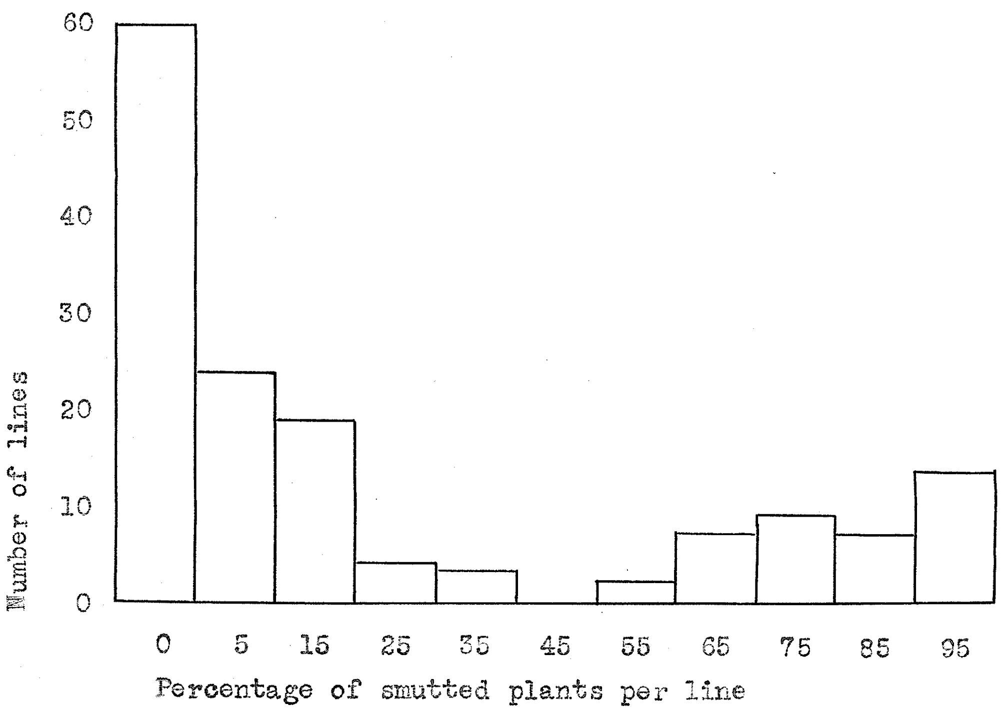
Parent or Cross	Class mark of per cent infection classes											Total no. of lines
	0	5	15	25	35	45	55	65	75	85	95	
Montcalm						1	3	7	2	4	3	20
Valkie	10										1	11
Montcalm x Valkie F_3	60	24	19	4	3		2	7	9	7	14	149

Evidence obtained by Cherewick (loc. cit.) indicated that Valkie was immune to the collection of smut used in this experiment. However the progeny of 11 inoculated heads of Valkie which were grown in separate rows produced 10 rows which showed no smut while all the plants in the eleventh row were smutted. Thus while the majority of Valkie plants are resistant to smut, susceptible plants do occur within the variety.

A cross between a susceptible Valkie plant and Montcalm would be expected to produce susceptible progeny only. One such susceptible group, consisting of four F_3 lines descended from a simgle crossed seed, was found. As it is highly improbable $[(1/4)^4$ or $.0039]$ that these lines resulted from a cross with a resistant Valkie plant, these lines were eliminated from the data used in this study.

The distribution of F_3 lines (Table IV) shows a break between the 40 and 50 per cent infection classes; this break divides the progenies into two groups, approximately in a 3:1 ratio. Such a ratio is expected if resistance is conditioned by a single gene. Actually there are 110 F_3 lines that may be resistant or segregating and 39 susceptible lines. A comparison of actual and expected numbers in these groups gave a chi square value of .1096 with a probability of .80-.70. This indicates agreement with a single factor hypothesis.

Examination of the distribution of F_3 lines in Table IV shows an excess of apparently resistant lines. As the F_2 showed a low percentage of infection a larger number of plants than were available in some of the F_3 lines would be required to distinguish segregating lines from resistant ones.



DISTRIBUTION OF SMUTTED PLANTS IN F_3 LINES OF VALKIE x MONTCALM

Figure 3

Those lines which could be classified as segregating showed an average of 11.1 per cent of smutted plants. This may be a better estimate of the amount of smut expected in F_2 than the 7 per cent obtained as the F_2 population was quite small. Although not as pronounced as in the cross between Titan and Montcalm, the tendency toward a low percentage of smut in lines segregating for resistance is evident here. The same hypotheses that were advanced to account for the low percentage of infection in the segregating lines of the Titan cross are again suggested to account for these results.

<u>Inheritance of Resistance to Loose Smut in the Cross Valkie x Titan</u>

The distribution of loose smut infection of the parental rows and F_3 progenies of the cross Valkie x Titan is shown in Table V. Examination of this table shows that most of the susceptible plants occurring in the cross are the progeny of a single F_1 plant. The progeny of this plant consisted of nine F_3 lines which are distributed in a manner which suggests segregation for a single factor. As it seems probable that this progeny resulted from a cross with a susceptible Valkie plant these lines were eliminated from the data as shown in Table V.

Examination of the data (Table V) from the remaining 102 F_3 lines of both reciprocals of the cross shows that there are no lines which can be classified as susceptible, 3 that may be considered segregating and 99 that appear to be resistant. Such a distribution would be expected if the genes conditioning resistance in each of Valkie and Titan are closely linked.

TABLE V Distribution of Loose Smut Infection by Percentage Classes for the Parental Rows and F_3 Progenies of the Cross Valkie x Titan

Parent or Cross	Class mark of per cent infection classes											Total no. of lines
	0	5	15	25	35	45	55	65	75	85	95	
Titan	18											18
Valkie	10										1	11
Valkie x Titan F_3 (excluding the progeny of F_1 plant no. 1)	99	2	1									102
Valkie x Titan F_3 (progeny of F_1 plant no. 1)	3	1	1			1					3	9

Two other explanations could conceivably account for the low percentages of smut found in the three F_3 lines. Chance infection from naturally occurring loose smut and impurity in the smut collection which was used could have produced these results. It is unlikely that either of these possibilities occurred. If loose smut which could infect Titan or Valkie was present either in the greenhouse or as an impurity in the inoculum the parental varieties should have shown a low percentage of smut infection. But as these possibilities cannot be eliminated, the gene conditioning resistance to collection 45-30 of loose smut in Titan and the one in Valkie may be alleles, but probably are located on closely linked loci.

Association of Characters

The results of the chi square tests on F_2 data are summarized in

Table VI. Independence tests based on F_3 data generally confirmed the F_2 results.

With one exception, the segregation of morphological characters fit monohybrid ratios; this agrees with published results (12,13). In the cross Valkie x Montcalm the segregation of non-6-rowed and 6-rowed spikes did not fit a 3:1 ratio due to an excess of 6-rowed segregates. While no selection was practiced in taking plants for inoculation, the use of a plant was necessarily subject to the condition that it produce sufficient seed for F_3 tests. This would tend to favour the 6-rowed types. Since there was no evidence for association between the genes conditioning smut reaction and kernel row number (Table VI) the differential selection of 6-rowed types would not affect the analysis of the genes conditioning resistance and susceptibility to smut.

Association tests between all but two of the morphological characters studied gave evidence of completely independent inheritance. In the cross Jet x Montcalm, the chi square for independence between glume color and kernel row number gave a probability value just exceeding the 5 per cent level (Table VI). Caution should probably be used in interpreting this apparently significant deviation from independence since the characters involved fitted a 9:3:3:1 ratio. In any case earlier investigators (12,13) showed that the genes conditioning glume color and kernel row number are located on different linkage groups.

The kernel row number and glume awn length characteristics were not expected to show independent inheritance since linkage between the genes conditioning glume awn length and kernel row number has been

TABLE VI A Summary of Chi Square Tests for Mode of Inheritance and Relationship of Characters in the Crosses Indicated

Characters and Crosses	Assumption	X^2	P
Jet x Montcalm (n=139)			
2-rowed vs. 6-rowed (V,v)	3:1	.6930	.50-.30
long vs. short glume awns	3:1	2.6115	.20-.10
black vs. white glumes (B,b)	3:1	.2902	.70-.50
res. & seg. vs. smut sus. lines (Un,un)	3:1	.2902	.70-.50
glume color, smut reaction	9:3:3:1	1.1631	.80-.70
	Independence	.6109	.90-.80
glume awn length, smut reaction	9:3:3:1	6.2789	.10-.05
	Independence	3.1868	.10-.05
kernel row number, smut reaction	9:3:3:1	1.8537	.70-.50
	Independence	.7872	.50-.30
glume awn length, glume color	9:3:3:1	3.1327	.50-.30
	Independence	.1537	.70-.50
kernel row number, glume color	9:3:3:1	5.9720	.20-.10
	Independence	5.0714	.05-.02
kernel row number, glume awn length	9:3:3:1	3.9768	.30-.20
	Independence	.7112	.50-.30
Valkie x Montcalm (n=149)			
2-rowed vs. 6-rowed (V,v)	3:1	4.1365	.05-.02
long vs. short glume awns	3:1	1.6309	.30-.20
res. & seg. vs. smut sus. lines (Un,un)	3:1	.1096	.80-.70
glume awn length, smut reaction	9:3:3:1	9.6518	< .01
	Independence	7.0880	< .01
kernel row number, smut reaction	9:3:3:1	6.6689	.10-.05
	Independence	1.5398	.30-.20
kernel row number, glume awn length	9:3:3:1	7.8620	.05-.02
	Independence	1.1791	.30-.20
(n=134)			
blue vs. yellow aleurone (Bl,bl)	3:1	.0100	.95-.90
aleurone color, smut reaction	9:3:3:1	1.9602	.70-.50
	Independence	1.5474	.30-.20
aleurone color, glume awn length	9:3:3:1	2.2786	.50-.30
	Independence	.0301	.90-.80
aleurone color, kernel row number	9:3:3:1	2.8093	.50-.30
	Independence	.4734	.50-.30
Titan x Montcalm (n=148)			
res. & seg. vs. smut sus. lines (Un,un)	3:1	.1441	.80-.70

reported. Swenson and Wells (20) studied awnless versus awned outer glumes and found the genes for awnedness and kernel row number linked with the recombination value, 30.0 ± 1.1. Robertson et al (11) studied fully awned outer glumes (awns coarse and long similar to the awns ordinarily found on the lemma) versus short outer glumes. Short awned glumes appeared to be dominant over the long ones since the genotype of the long awned variety was designated ee while that of the short one was written EE. Immer and Henderson (5) studied glume characteristic and obtained similar results.

The glume characteristics described by these investigators differ from the glume awn characteristics of the varieties used in this study. In each of Jet and Valkie the ratio of glume awn length to glume length is approximately 1:1 while in Montcalm the ratio is slightly more than 2:1. Furthermore the F_1 plants showed the long type of glume awn suggesting that the long type is dominant.

The glume length characteristics involved in the cross studied by Neatby (9) appear to be quite similar to the ones used in this study. His interpretation indicated that glume length was conditioned by two factors one of which was linked with the factor for naked seed. However examination of his data showed that it could be explained almost as well by a single factor hypothesis involving linkage with the factor for naked seed.

The chi square values shown in Table VI indicate complete independence between the genes conditioning smut reaction and those for each of the three characters; kernel row number, lemma color and aleurone color. In the cross Valkie x Montcalm, a probability value less than .01 suggests association between glume awn length and smut reaction. Linkage intensity was calculated by Immer's method (4,5) from F_2 and F_3 data and the recombination values obtained are respectively, 32.3±7.0 and 36.0±1.4.

SUMMARY AND CONCLUSIONS

The inheritance of reaction to collection 45-30 of loose smut was studied in hybrid populations derived from the three crosses between each of the resistant varieties Jet, Titan and Valkie and the susceptible variety Montcalm. A cross between two of the resistant varieties Valkie and Titan was also included in the study.

The evidence which was obtained indicated that the loose smut resistance of Jet was conditioned by a single dominant gene. In crosses with Montcalm, the resistance of each of Titan and Valkie also appeared to be due to a single dominant gene. The small amount of transgressive segregation obtained in the progeny of the cross of the two resistant varieties, Valkie and Titan, suggested that the genes for smut resistance in these two varieties are closely linked.

The segregation of four morphological characters was studied in the F_2 and F_3 generations of the hybrid populations. Each of the characters, kernel row number, lemma color, aleurone color and glume awn length appeared to be conditioned by a single gene. Association tests did not indicate linkage between the genes conditioning any of these characters.

Association tests indicated complete independence between the genes conditioning smut reaction and those for each of the characters; kernel row number, lemma color and aleurone color. Independence tests suggested linkage between glume awn length and reaction to smut in the Valkie x Montcalm cross. A recombination value of 36.0 ± 1.4 was obtained when linkage intensity was calculated from F_3 data.

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