

Inheritance of Resistance to Loose Smut in Three Winter Barleys¹

HENRY SHANDS, FRED L. PATTERSON and
JOHN F. SCHAFER, Purdue University

Loose smut of barley, caused by *Ustilago nuda* (Jens.) Rostr., is an important disease in humid and subhumid regions. The most practical control is by use of resistant varieties, but many commercial barley varieties do not have satisfactory resistance. Breeding for resistance is facilitated by knowledge of inheritance of available resistance and the contribution of each genetic factor concerned. Knowledge of the chromosome bearing each factor, its location on the chromosome, and linkages to easily identified marker genes is also desirable.

Studies, primarily with spring barleys, indicate that resistance generally is inherited simply. One factor pair, sometimes 2, usually dominant, controls resistance. Of 7 genes assigned symbols, only un_1 is recessive. Genetic symbols assigned and varietal sources of resistance are: Un_1 (Trebis), Un_2 (Missouri Early Beardless), Un_3 (Jet), Un_4 (Dorsett), Un_5 (Wis. X173-10-5-6-1), Un_6 (Jet), and un_1 (Anoidium) (1, 5, 6, 7, 8, 9, 10, 15, 16, 20). Genetic studies also have been reported for other sources of resistance, but the relation of these resistances to those assigned symbols has not been established (4, 6, 10, 11, 12, 23).

Loose smut resistance, Un , is linked to stem rust reaction, Tt (1, 18). Attempts to find associations of other marker genes with resistances were unsuccessful (7, 8, 11, 16) except for a possible linkage of the 2-row character VV with Abyssinian resistance (11). The value and uses of chromosomal interchange stocks, hereafter referred to as translocation stocks, for placing unlocated genes in linkage groups have been described by Burnham (2).

Materials and Methods

Saru (CI 5185) from Korea, Milton (CI 4966) from Russia, and Missouri B696 from a cross of Missouri Early Beardless x Kentucky 2, all obtained from J. M. Poehlman, University of Missouri, were studied in crosses with Mars translocation stocks and susceptible Purdue 466A7-7-7-2-2-7. Saru, Milton, and Missouri B696 were reported free from or low in smut infection (3, 10, 13). A covered-type selection, Saru-16, was used rather than the mixed naked and covered Saru parental stock. Natural infection in Purdue 466 at Lafayette, Indiana, has ranged from 4 to 20% over the last 8 years.

Translocation stocks of Mars (CI 7015) utilized were T1-5b, T1-6a, T2-6a, T3-4a, T3-7a and T4-5a (14). Chromosomes 2 and 7 were represented once in translocations in these stocks; all others twice. An indication of linkage of a resistance factor with the breakpoints of 2 translocation stocks would establish the resistance factor on the common interchange chromosome and localize the position from recombination

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values. Plants heterozygous for translocations were identified by semi-sterility of the spike.

Other marker genes were utilized where available. Distinguishing characteristics of the varieties are presented in Table 1. All are 6-

TABLE 1.
Distinguishing characteristics of five parental varieties.

| Variety or selection | C.I. number | Awns ¹ | Rachilla hairs | Stem rust resistance | (S) smut ² or winter (W) habit |
|------------------------|-------------|-------------------|----------------|----------------------|---|
| Milton | 4966 | r | S | t | W |
| Missouri B696 | | R | s | t | W |
| Saru-16 | 5185-16 | R | s | t | W |
| Purdue 466A7-7-7-2-2-7 | 10666-7 | R | S | t | W |
| Mars (translocations) | 7015 | r | S | T | S |

¹Genetic symbols: Rough vs. smooth awns (R,r); Long vs. short rachilla hairs (S,s); Stem rust resistance vs. susceptibility (T,t).

rowed barleys with white kernels and adherent lemma and palea. The selections of Milton and Saru differ from descriptions of the original introductions but are similar to selections made by other workers.

Race 1 of *U. nuda* (21) present in the Lafayette, Indiana, area was used. Initial inoculum was low in viability, and the first inoculated population showed low infection. For this reason, populations grown in the field and greenhouse in 1960 were considered together. Subsequent inoculum obtained fresh from susceptible Purdue 466 was highly viable, and other populations grown are considered in a second group (Table 2). Inoculation was with dry teliospores using a 20-gauge shortened hypodermic needle and medicine dropper bulb as described by Shands and Schaller (17). Hybrids were inoculated approximately 24 hours after pollination.

Part of the hybrid seed was smut-inoculated to obtain an F₁ infection level. Inoculation of approximately ½ of the heads on an F₁ plant provided an F₂ smut-infection test, and the noninoculated heads provided a sister F₂ population which could be inoculated, classified at harvest for the genetic markers, and carried to an F₃ smut-infection test.

Crosses of the smut-resistant winter barleys with each other and with susceptible Purdue 466 were grown in the greenhouse or field as follows. Parents, F₁, F₂, and backcross progenies for a greenhouse smut-infection reading were vernalized in flats in a 36° F cold room for 60 days and transplanted to 4-inch pots or left thinly planted in flats. Parental, F₁, and F₂ populations were spaced in the field at 3 inches in rows 1 foot apart in the fall of 1960 and 1961. Limited winter damage occurred in 1960, and severe winter damage eliminated most F₁ plants as well as an F₃ planting in 1961.

F₂ populations of crosses of the 3 smut-resistant winter lines to the 6 spring translocation stocks were spring-sown in 1960, 1961 and 1962. Each plant of the noninoculated F₂ populations was classified for fertility versus partial sterility and for marker genes segregating in the specific cross. In the subsequent spring the smut-inoculated seed

TABLE 2.
Reactions of parental and F₁ and F₂ hybrid plants to artificial inoculations with *Ustilago nuda*, averaged into 2 groups on the source of inoculum.

| Parent or cross | Generation | Group I* | | Group II | |
|--|----------------|---------------------|---------------------|---------------------|---------------------|
| | | plants tot† inf‡ | plants tot† inf‡ | plants tot† inf‡ | plants tot† inf‡ |
| | | No. | % | No. | % |
| Purdue 466 | parent | 87 | 35 | 254 | 51 |
| Mars (translocation stocks) | parent | 63 | 13 | 896 | 28 |
| Milton (C.I. 4966) | parent | 70 | 0 | 406 | 0 |
| Purdue 466 x Milton | F ₁ | — | — | 39 | 0 |
| Purdue 466 x Milton | F ₂ | 124 | 3 | 153 | 12 |
| Purdue 466 x F ₁ (Pur. 466 x Milton) | F ₁ | — | — | 19 | 63 |
| Mars (trans.) x Milton | F ₁ | 48 | 0 | — | — |
| Mars (trans.) x Milton | F ₂ | 199 | 3 | 1093 | 17 |
| Mo. B696 | parent | 71 | 3 | 300 | 7 |
| Purdue 466 x Mo. B696 | F ₁ | — | — | 6 | 67 |
| Purdue 466 x Mo. B696 | F ₂ | 117 | 12 | 124 | 44 |
| Purdue 466 x F ₁ (Pur. 466 x Mo. B696) | F ₁ | — | — | 8 | 63 |
| Mars (trans.) x Mo. B696 | F ₁ | 45 | 31 | — | — |
| Mars (trans.) x Mo. B696 | F ₂ | 331 | 8 | 1541 | 36 |
| Saru-16 (C.I. 5185-16) | parent | 37 | 0 | 308 | 5 |
| Purdue 466 x Saru-16 | F ₁ | — | — | 33 | 42 |
| Purdue 466 x Saru-16 | F ₂ | 107 | 16 | — | — |
| Purdue 466 x F ₁ (Pur. 466 x Saru-16) | F ₁ | — | — | 34 | 85 |
| Mars (trans.) x Saru-16 | F ₁ | 52 | 39 | — | — |
| Mars (trans.) x Saru-16 | F ₂ | 345 | 12 | 1942 | 40 |
| Saru-16 x Mo. B696 | F ₁ | 16 | 6 | 38 | 5 |
| Saru-16 x Mo. B696 | F ₂ | — | — | 176 | 19 |
| Saru-16 x Milton | F ₁ | 17 | 0 | 1 | 0 |
| Saru-16 x Milton | F ₂ | — | — | 250 | 13 |
| Mo. B696 x Milton | F ₁ | 17 | 0 | 9 | 0 |
| Mo. B696 x Milton | F ₂ | — | — | 237 | 13 |

* Group I = low viability inoculum. Group II = high viability inoculum.

† tot. no. = total number of plants examined at flowering time.

‡ inf % = % of total number of plants infected.

from each F₂ plant of the 1960 and 1961 series was planted in an F₃ progeny row. Smut percentages were calculated for rows containing 10 or more plants. Where insufficient plant numbers occurred in 1961, the row was repeated in 1962 if reserve seed was available, and the data were combined. A cool, wet spring in 1961 vernalized nearly all the winter habit plants of these segregating populations. In both 1961 and 1962, the young heads of the winter-type plants were examined for smut infection with the aid of a dissecting needle.

Races 15B and 56 of *Puccinia graminis* Pers. f. sp. *tritici* were inoculated into spreader rows of Manchuria (CI 2947) to test for stem

rust resistance conditioned by the T gene, with good tests obtained in 1961 and 1962.

Genetic symbols, used for convenience in the analysis, are not intended for permanent assignment.

Results and Discussion

INHERITANCE OF RESISTANCE—Infection percentage data are presented in Tables 2 and 3. Data in Table 2 are not comparable

TABLE 3.

Frequency distribution of smut infection percentages in progenies of F_2 plants from crosses of resistant varieties with Mars translocation stocks, artificially inoculated with *U. nuda*.

| Cross | F_2 smut infection percentages classes | | | | | |
|--------------------------|--|------|-------|-------|-------|-------|
| | 0 | 1-10 | 11-20 | 21-30 | 31-40 | 41-50 |
| Mars (trans.) x Milton | 133 | 85 | 64 | 36 | 28 | 21 |
| Mars (trans.) x Mo. B696 | 56 | 112 | 127 | 116 | 105 | 58 |
| Mars (trans.) x Saru-16 | 39 | 97 | 110 | 111 | 77 | 73 |

| Cross | F_2 smut infection percentages classes | | | | | Total plants |
|--------------------------|--|-------|-------|-------|--------|--------------|
| | 51-60 | 61-70 | 71-80 | 81-90 | 91-100 | |
| Mars (trans.) x Milton | 15 | 9 | 3 | 0 | 1 | 395 |
| Mars (trans.) x Mo. B696 | 47 | 34 | 26 | 18 | 11 | 710 |
| Mars (trans.) x Saru-16 | 36 | 23 | 19 | 4 | 0 | 589 |

between groups I and II; group I involved low viability smut inoculum, and group II high viability inoculum. The frequency distribution data in Table 3 were obtained from detailed data by summing the number of F_2 plants having progenies in each smut infection class for the crosses of each resistant variety with the 6 Mars translocation stocks. The division of frequency distributions into genetic classes is arbitrary although the choices appear valid in consideration of parental data. The simplest hypothesis in keeping with the data was selected, and the fit of the data to that hypothesis is shown in Table 4.

Purdue 466, the susceptible parent, had 35 and 51% infection in groups I and II, respectively, and was sufficiently susceptible in all tests for the level of infection to be distinguished from infection levels of the 3 resistant parents (Table 2). Levels for the resistant parents were, for groups I and II: Milton, 0 and 0%; Missouri B696, 3 and 7%; and Saru-16, 0 and 5%. Mars translocation stocks had 13 and 28% infection in groups I and II. Although the translocation stocks served in the role of a susceptible parent, the difference obtained in infection level between Mars and each resistant parent was not great.

Neither the translocation stocks nor Mars itself were crossed with Purdue 466, but the differences of infection indicated a physiological difference in susceptibility between the 2 varieties, possibly attributable to a factor or factors conditioning moderate resistance in Mars. Such weak factors, Un_2 and Un_5 , have been proposed by Livingston (7) and Schaller (16) to explain similar levels of resistance. The data from crosses with Mars translocation stocks are analyzed 2 ways, either con-

TABLE 4

Assigned resistance factors and proposed class divisions for progenies of F_2 plants from crosses of resistant varieties with Mars translocation stocks, artificially inoculated with *U nuda*.

| | Milton | Missouri B696 | Saru-16 |
|----------------------------------|--|---------------------|-----------------|
| | Analysis of resistant parents based on Mars having no resistance factor | | |
| % infection of resistant parents | 0 | 7 | 5 |
| Total progenies of F_2 plants | 395 | 710 | 589 |
| Proposed class division | 0-20:21-100 | 0-10:11-100 | 0-10:11-100 |
| Observed ratio | 282:113 | 168:542 | 136:453 |
| Expected ratio | 3:1 | 1:3 | 1:3 |
| P value | .05-.10 | .4-.5 | .2-.3 |
| Class genotypes | AA-:aa | cc:C- | dd:D- |
| Assigned parental genotypes | AA x aa | cc x CC | dd x DD |
| Resistance factor | A | c | d |
| | Analysis of resistant parents based on Mars having a weak resistance factor | | |
| % infection of resistant parents | 0, 28* | 7, 28 | 5, 28 |
| Total progenies of F_2 plants | 395 | 710 | 589 |
| Proposed class division | 0-20:21-50:51-1000-10 | 10:11-50:51-1000-10 | 10:11-45:46-100 |
| Observed ratio | 282:85:28 | 168:406:136 | 136:334:119 |
| Expected ratio | 12:3:1 | 4:9:3 | 4:9:3 |
| P value | .2-.3 | .6-.7 | .4-.5 |
| Class genotypes | A—:aaB-:aabb | cc—:C-B-:C-bb | dd—:D-B-:D-bb |
| Assigned parental genotypes | AAbb x aaBB | ccbb x CCBB | ddbb x DDBB |
| Resistance factor | A, B* | c, B | d, B |

*First entry represents parent; second entry represents Mars parent.

sidering the Mars infection as the level of susceptibility or considering Mars to have a weak factor for resistance. The P value for the suggested ratio along with class divisions and possible class genotypes of the F_2 frequency distribution are presented in Table 4 for each hypothesis. Because of the somewhat arbitrary class divisions, frequency distributions have not been divided into more than 3 classes for any hypothesis. Using the hypotheses proposed for the F_2 data from Mars crosses, F_2 infection percentages for both Mars and Purdue 466 crosses are predicted from parental values and are shown in Table 5 along with the observed infection percentages for the given cross.

Milton—The value of Milton resistance is suggested by the immune reaction of the parent and F_1 populations from crosses of Milton with susceptible Purdue 466 and the other resistant parents. The im-

mune reaction of the parent and F_1 populations from crosses of Milton parents indicates complete dominance.

TABLE 5
Observed reaction of F_2 plant population artificially inoculated with *U. nuda* and predicted reaction from parental data for proposed mode of inheritance of resistance.

| Cross | Expected F_2 ratio | Group I* | | Group II | |
|--------------------------|-------------------------|----------|-----------|----------|----------------|
| | | Observed | Predicted | Observed | Pre- dicted |
| | | % | | % | % |
| Purdue 466 x Milton | 3:1 | 3 | 9 | 12 | 13 |
| Mars (trans.) x Milton | 3:1 | 3 | 3 | 17 | 7 |
| Purdue 466 x Mo. B696 | 1:3 | 12 | 28 | 44 | 41 |
| Mars (trans.) x Mo. B696 | 1:3 | 8 | 10 | 36 | 23 |
| Purdue 466 x Saru-16 | 1:3 | 16 | 27 | — | — |
| Mars (trans.) x Saru-16 | 1:3 | 12 | 9 | 40 | 22 |

*Group I = low viability inoculum; Group II = high viability inoculum.

The hypothesis that the resistance in Milton is controlled by a single, completely dominant factor is suggested by the F_2 data of the Mars translocation crosses. With Mars at 28% infection representing the homozygous recessive condition for the Milton factor, F_2 lines having more than 20% infection might reasonably be considered susceptible and those with 20% or less, resistant (Table 3). The ratio, 282 resistant: 113 susceptible, fits a 3:1 Chi-square test with a P value of .05-.10 (Table 4).

Considering Milton to have a single dominant factor, A, and Mars a weak but dominant factor different from that in Milton, B, the F_2 distribution might be divided as follows. The 0-20% infection classes would represent A- individuals, the 21-50% classes the Mars types aaB-, and the 51-100% classes, aabb. The expected 12:3:1 ratio is fit by these data with a P value of .3-.4 for the Chi-square goodness of fit test.

The low infection percentages in all F_2 populations from crosses with Milton may indicate the presence of more than one dominant factor, or resistance of the maternal tissue of the F_1 plants. On the contrary, 63% infection in the backcross Purdue 466 x F_1 (Purdue 466 x Milton) is equal to that of the susceptible parent for the same test and is greater than would be expected with a single, dominant factor.

Metcalf and Johnson (10) found a single dominant gene governing resistance to races 1, 2, and 3 in a spring-type derivative from the Milton variety in publication since completion of this research. They showed that the gene was independent of the resistances of Jet (Un_6 and Un_8) and of Valkie.

The evidence from these 2 studies in general supports the hypothesis of a single, completely dominant resistance gene in Milton.

Missouri B696—The infection levels of Missouri B696 were 3 and 7% in groups I and II (Table 2). The 6 F_1 plants from the cross with Purdue 466 gave 67% infection, comparing closely to a 63% infection

in Purdue 466 in the same test. The backcross Purdue 466 x F_1 (Purdue 466 x Missouri B696) had 63% infection. These data indicate that Missouri B696 may contain a recessive factor. The combined group II F_2 infection level of 44% approximates the predicted 41% (Table 5). The expected F_2 value for group I of 28% is not closely approximated by the 12% observed but this could be explained by the low viability inoculum.

In the F_3 distribution of the cross with Mars (Table 3), the 1-10% infection class is similar in reaction to Missouri B696. Considering the 0-10% classes to be resistant, the observed ratio of 168 resistant: 542 susceptible fits the expected 1:3 ratio with a P value of .4-.5 for the Chi square test (Table 4).

Again considering Mars to possess a dominant, weak factor for resistance, B, and denoting resistance from Missouri B696 as c, the 0-10% classes might represent homozygous resistant genotypes cc—. The 11-50% classes contain C-B- genotypes having their distribution around the Mars infection level. The 51-100% classes characterize susceptible genotypes, C-bb. The data fit the 4:9:3 expected ratio with a P value of .6-.7 and again support the hypothesis of a single recessive factor in Missouri B696.

Saru-16—This variety reacted similarly to Missouri B696. Saru-16 had 0 and 5% infection in groups I and II. The F_1 of the cross with Purdue 466 showed 42% infection while the backcross Purdue 466 x F_1 (Purdue 466 x Saru-16) had 85% infection in group II (Table 2). These values suggest the presence of a recessive factor.

The F_2 infection level in group I was 16%. Although no group II data were available, it might be estimated from the increased F_2 infection in group II of the cross of Mars and the similarly reacting Missouri B696 that the infection level would be in the range of the predicted 41% (Table 5). The group I value of 16% is below that predicted from the parental reactions, as it was for Missouri B696, and may be due to the low viability inoculum.

The F_3 distribution from crosses with the Mars translocations also appears similar to that of Missouri B696 (Table 3). The Saru-16 infection falls into the 1-10% level, and the 0-10% classes might be considered resistant. The observed ratio, 136 resistant: 453 susceptible, fits the expected 1:3 ratio with a P value for the Chi-square test of .2-.3 (Table 4).

Denoting the Saru-16 resistance as d, and retaining B for the Mars factor, the distribution may again be divided with the 0-10% classes representing Saru-16 resistance, dd—. Using a 5% interval, the 11-45% classes would comprise D-B-. The susceptible classes, 46-100%, contain D-bb. The 4:9:3 expected ratio is fit with a P value of .4-.5 for the Chi-square test.

IDENTITY OF RESISTANCES—The similar mode of inheritance of resistance in Missouri B696 and Saru-16 suggested that the same factor might be controlling resistance in each. F_1 progeny from the cross of Saru-16 and Missouri B696 showed infection similar to that of the 2 parents (Table 2). The 19% infection obtained in the F_2 of Saru-16 x Missouri B696 was considerably higher than that of either parent or

the F_1 . It is suggested that the factors in Saru-16 and Missouri B696 are different.

The immune reaction of F_1 plants of crosses of Missouri B696 and Saru-16 with Milton was expected from the proposed completely dominant Milton factor. Both F_2 populations had 13% infected plants, indicating the factors of Missouri B696 and Saru-16 are distinct from that of Milton.

The conclusion that these factors are different is reasonable from consideration of the geographical source areas. Saru, introduced from Korea in 1930, would be unlikely to have the same resistance as Missouri Early Beardless from which Missouri B696 was derived. Missouri Early Beardless originated from a mass selection made in 1932 from a hooded winter barley whose origin was unknown but believed to be from one of the southern states (22). Milton, introduced from Russia in 1927, would in turn have an independent source.

LOCATION OF RESISTANCE FACTORS—Infection data from crosses of Milton, Missouri B696, and Saru-16 with the Mars translocation stocks are presented in Table 3. The number of F_2 plant progenies falling into 11 F_2 smut-infection classes was tabulated by F_2 phenotype for each marker character studied. Awn barbing and rachilla hair length (chromosome 7) and stem rust reaction (chromosome 1) were classified in the Missouri B696 and Saru-16 crosses. Only stem rust reaction was classified in the Milton crosses. The fertility versus partial sterility resulting from crossing to the translocation stocks was classified for all crosses. These data were tested with a Chi-square test for goodness of fit. Although a few ratios did not fit the expected, they appear the result of small populations or failure of semisterile plants to produce sufficient progeny for loose smut infection analysis.

To visually demonstrate possible associations, frequency distributions for each character for each cross were plotted with the number of F_2 plants possessing a given character as the ordinate and the F_2 smut infection classes (0, 1-10, 11-20,....., 91-100) as the abscissa. The frequency distributions by infection classes for the 2 F_2 phenotypes of a character were plotted on the same graph. A close resemblance between the 2 distributions for each character indicated homogeneity of the entire population and consequently implied no linkage of loose smut reaction to the genetic character against which it was plotted. To confirm the visual conclusion as to the homogeneity of these populations, the Mann-Whitney U Test as described by Siegel (19) was chosen. One of the most powerful nonparametric statistical tests, it is used to test whether 2 independent groups have been drawn from the same population.

The frequency distribution graphs and statistical tests showed no associations with translocation breakpoints or marker genes. Failure to detect such linkage, if present, might also result from the fact that Mars and its translocation derivatives could be classed as only moderately susceptible to loose smut (Table 2), resulting in a lack of separation of the resistant and susceptible distribution peaks on the graph, or that there were small populations in some crosses of Milton with the translocation stocks. With the exception of the Trebi factor (1, 18) and

possibly a factor in Abyssinian (11), smut resistance genes have eluded placement by linkage analysis in previous studies also (7, 8, 11, 16).

Summary

Milton, Missouri B696, and Saru-16 each possessed a high level of resistance to a collection of race 1 of *U. nuda*. Parental, F₁, backcross, and F₂ data from hybrids of these resistant varieties x susceptible Purdue 466A7-7-7-2-2-7 and F₃ data from hybrids of the resistant varieties x Mars translocation stocks, suggested resistance to be conferred by a dominant factor pair in Milton and a recessive factor pair each in Missouri B696 and Saru-16. Resistant x resistant hybrids indicated the resistances to be distinct from each other. Crosses of the 3 resistant varieties with Mars translocation stocks T1-5b, T1-6a, T2-6a, T3-4a, T3-7a, and T4-5a showed independent inheritance of the resistance factors from the translocation interchange points and marker genes controlling stem rust reaction, rachilla hair length, and awn barbing.

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