

INVESTIGATIONS ON THE INHERITANCE  
AND INTERRELATIONSHIPS OF THE GENES CONDITIONING  
THE JET TYPE OF RESISTANCE TO CERTAIN CULTURES  
OF THE SMUTS THAT ATTACK BARLEY

by

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ABSTRACT

The mode of inheritance and interrelationships of the genes in the variety Jet, (C.I.967), conditioning reaction to single cultures of Ustilago nuda (Jens.) Rostr., Ustilago nigra Tapke, and Ustilago hordei (Pers.) Lagerh. were studied in the F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> generations of hybrids between Jet and the varieties Vantage (C.A.N.1162) and Plush (C.A.N.1106). It was concluded that Jet has a single dominant gene pair conditioning resistance to U. nuda and single recessive gene pairs conditioning resistance to U. nigra and U. hordei. The gene pairs conditioning resistance to U. nigra and U. hordei were found to be closely linked. No associations were detected between the gene pair conditioning resistance to U. nuda and those conditioning resistance to the other two smut species.

The Jet gene pair conditioning reaction to U. nigra was assigned the symbols ung ung.

The mode of inheritance of the genes conditioning the immune type of reaction of the barley varieties Bifarb, (C.I.3951-3), Kitchin (C.I.1296-1), Nigrinudum, C.I.5798 and Jet, to a Trebi-attacking culture of U. nuda, was studied in the F<sub>2</sub> and F<sub>3</sub> generations of hybrids involving the immune varieties and the U. nuda susceptible variety Newal (C.A.N.1089). The interrelationships of the genes conditioning immunity in the five varieties were investigated by studying

the  $F_3$  and  $F_4$  generations of hybrids involving the immune varieties. Interrelationships between the gene or genes conditioning U. nuda immunity in Jet with the genes conditioning resistance in the varieties Valkie (C.I.5748) and Brachytic-119 were investigated by studying the  $F_3$  generations of hybrids involving Jet and Valkie-trd. and Jet and Brachytic-119. It was concluded that single dominant genes, each located at the same locus, conditioned the immune type of resistance to U. nuda in the varieties Bifarb, Kitchin, Nigrinudum, C.I.5798 and Jet. The gene conditioning the immunity of Jet to U. nuda was found to differ from the factors conditioning the resistances of Brachytic-119 and Valkie. Because of the similarity of the genetics of reaction to U. nuda it was concluded that the morphologically identical varieties Jet and Nigrinudum were one variety.

The mode of inheritance of the factors governing nine barley linkage group marker-characters and the interrelationships of the genes conditioning the marker-characters with those responsible for the resistance of Jet to U. nuda, U. nigra and U. hordei were investigated in the  $F_2$  and  $F_3$  generations of hybrids between Jet and six barley varieties. It was found that each of the marker characters was conditioned by a single factor pair. No associations were demonstrated between the genes conditioning resistance to U. nuda, U. nigra and U. hordei and those responsible for the following marker-characters: resistance vs. susceptibility to Puccinia graminis Tritici Eriks. and Henn. (Tt), two-vs. six-row character (Vv), naked vs. hulled kernel (Nn), and black vs. white lemma and pericarp (Bb).

The Jet factor pair conditioning reaction to U. nuda was also found to be independent of the factor pairs conditioning the marker-characters rough vs. smooth awns (Rr), hoods vs. awns (Kk), normal vs. orange-lemma color (Oo), normal vs. chlorina-seedling (Fc fc), and normal vs. glossy-seedling (Gl<sub>2</sub> gl<sub>2</sub>).

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## INTRODUCTION

Smut resistance in barley involves resistance to the embryo-infecting loose smut caused by Ustilago nuda (Jens.) Rostr., and to the seedling-infecting smuts, caused by Ustilago hordei (Pers.) Lagerh., and Ustilago nigra Tapke. Because of the wide-spread occurrence of loose smut and the difficulties involved in controlling this disease, investigations involving this form of smut have been more extensive than those concerned with covered smut caused by U. hordei and false loose smut caused by U. nigra.

The spring barley variety Jet (C.I.967)<sup>1</sup>, has been used extensively by barley breeders in Western Canada during the past few years as the major source of resistance to loose smut. This variety is immune to U. nuda and has been reported a good source of resistance to U. nigra and to U. hordei (43).

Considerable work has been reported on the inheritance of resistance to U. nuda (13,15,17,34,35,39,41), and to U. hordei (38,47). However, no attempts have been made to relate the inheritance of resistance to one smut species with that of the other. There is also no reported evidence concerning the mode of inheritance of resistance to U. nigra.

The unique ability of Jet to resist the barley smuts provides the opportunity for simultaneous investigations on the inheritance of resistance to the three smut species, and also the interrelation of the resistance factors involved.

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1) C.I. refers to Accession Number, Cereal Section, U.S.D.A.

Physiologic specialization within the organism causing loose smut has been known for some time (30,31,33). Instances of so-called "breakdown" of resistance have also been reported (39). Because of the wide-spread use of the variety Jet as a source of resistance to U. nuda, it is essential that other potential sources of resistance be explored and that the relationships of the genes for resistance be understood.

Favorable linkages between the resistance factors and those conditioning readily recognizable characters of barley would greatly facilitate breeding for smut resistance.

This report presents information obtained through investigations in three aspects of inheritance involving the smuts of barley:

- 1) the determination of the mode of inheritance and the interrelationships of the Jet genes conditioning resistance to the three smut species that attack barley;
- 2) a study of the inheritance and interrelationships of different varietal sources of resistance to U. nuda;
- 3) a study of possible linkage relationships of the smut resistance genes of Jet with those responsible for specific characteristics of certain of the barley linkage group tester stocks.

REVIEW OF LITERATURE

The success of investigations on the inheritance of smut resistance in barley has depended almost entirely on the reliability of methods used in establishing infection in the susceptible plants (13,15,17,34,35,38,39,41).

Artificial inoculation with U. nuda consists of placing chlamydospores of the pathogen into the florets of the host at flowering-time. Inoculation of the seedling-infecting smuts is usually carried out by placing the chlamydospores in close proximity to the embryo of the seed. Various techniques have been used to accomplish these purposes.

Shands and Schaller (36) reviewed and re-tested the methods used up to 1946 in making artificial inoculations with U. nuda. They described as the most effective, a method whereby chlamydospores were "puffed" from a small rubber bulb through a hypodermic needle to the stigma of the host after the lemma had been pierced. Poehlman (21) used a hypodermic needle in a similar manner except that an aqueous suspension of spores was used. Ross et al. (32) compared the two needle-inoculation methods and found that the injection of an aqueous suspension was the most effective under the drier conditions of Western Canada. Cherewick and Popp (2) and Cherewick and Cunningham (4) modified Moore's "partial vacuum method" (18) and succeeded in increasing speed of inoculation and percentage of U. nuda infection. Moore and Munnecke (19) described a simple, rapid and effective method of inoculating wheat and barley

with U. nuda by squirting the heads at flowering-time with minute, powerful jets of a spore suspension.

Probably the most widely used method of inoculating with U. hordei consists of exposing the embryo and contaminating the seed with chlamydospores (12,38,47,48). Popp and Cherewick (23) described a "Waring Blendor" method of inoculating oats and barley with the seedling-infecting smuts. This method and Allison's "partial vacuum" method, as described by Hallisky (9), ensure penetration of the chlamydospore inoculum beneath the lemma and palea of the kernel.

Because of the manner of infection peculiar to the seedling infecting smuts, the effect of environment on the success of inoculation is more pronounced with these smuts than with loose smut. Tapke (42), Fischer and Holton (6), and Cherewick (3) have reviewed the information on the influence of environmental factors on the development of smut diseases. Optimum conditions for seedling smut infection include: well aerated soil; seed bed temperatures ranging from 20° to 25° C. and soil moisture content ranging from 20 to 40 percent of moisture holding capacity.

With respect to the loose smut organism U. nuda, cool, highly humid conditions during the blossoming period favor infection (3,7,42). The most optimum period for inoculation is during the first two days following anthesis (36).

Vanderwalle (46) and Cherewick (3) point out that environmental conditions conducive to rapid growth of the host could result in loose smut infected seedlings outgrowing the parasite and producing

normal seed.

The literature dealing with the inheritance of resistance to U. nuda will be presented separately from that pertaining to U. hordei. No genetic studies on the resistance to U. nigra have been encountered.

Smith (40) presented a brief review of the work of a number of investigators on the inheritance of resistance to loose smut. He indicated, in studies of crosses between resistant and susceptible varieties, that resistance appeared to be governed by a single dominant gene.

Livingstone (15) found evidence of the presence of a single dominant factor for resistance in Hordeum deficiens and Hordeum vulgare var. Trebi (C.I.936). This gene and a minor gene for resistance in Missouri Early Beardless were designated Un and Un2 respectively (28). Schaller (35) showed that the spring barley varieties Trebi, Jet, Dorsett (C.I.4821), and Sel. X 173-10-5-6-1 each possessed different single genes, each of which conditioned its own degree of resistance. The gene in Trebi and that of Jet gave the highest degrees of resistance and were dominant in effect. Schaller (35) suggested the symbols Un3, Un4 and Un5 for the genes in Jet, Dorsett and X 173-10-5-6-1 to the "race" of smut which he used. In compliance with this suggestion, Skoropad and Johnson (39) designated the gene in Jet which conditioned resistance to the "race" of U. nuda attacking Trebi as Un6. Mohajir et al (17) obtained indication of transgressive segregation in crossing highly resistant and moderately resistant varieties. This was thought to be due to recessive genes in the moderately resistant



varieties. The smut resistance of Abyssinia (C.I.668) and Jet to the "race" of smut (non-Trebi attacking) which they used, was found to be conditioned by two factor pairs in each variety. It was suggested that one of the Abyssinia genes was different to the Un gene in Trebi and that the genes for resistance in Abyssinia were different to the Jet genes.

Konzak (13) presented evidence which demonstrated that resistance to different loose smut "races" may be inherited differently depending on the physiologic "race" of the pathogen and the host variety. He inoculated crosses involving the two immune varieties Jet and Valkie (C.I.5748), and the susceptible variety Odessa (C.I. 938), to eight "races" of U. nuda to which Jet and Valkie were immune. Resistance to "race" 1 was found to be determined by a single dominant gene present in each of the varieties Jet and Valkie. Jet and Valkie each possessed two dominant genes for resistance to "races" 3 and 7. Both genes of Valkie were required to confer resistance whereas either Jet gene sufficed. Resistance to "races" 4 and 8 was conditioned by either of two dominant independent genes present in both of the resistant varieties. Resistance to "race" 6 was conditioned by a single dominant gene in Jet but by two complimentary dominant genes in Valkie.

The inheritance of reaction to "race" 1, revealed by Konzak (13), confirmed the results of investigations by Stefansson (41) with the immune varieties Valkie and Jet.

Schaller (34) found that one incompletely dominant and one

recessive gene were responsible for resistance to U. nuda in a cross between Brachytic-119, a smut resistant mutant from Himalaya (C.I.620), and Persicum, a susceptible variety.

Early attempts made to determine the mode of inheritance of resistance to U. hordei were limited in success because of the difficulties involved in obtaining sufficiently high infection of susceptible material (12, 24, 40). Recently Shands (38) found that resistance to "race" 6 of U. hordei was conditioned by one major dominant factor pair, Uh Uh, in the crosses Chevron x Brachytic and Colsess x Brachytic. Wells (47) found that a dominant gene for resistance to "race" 6 of U. hordei was common to the varieties Titan (C.I.7055), and O.A.C. 21 (C.A.N.1086)<sup>1</sup>, Ogalitsu (C.I.7152) and Anoidium (C.I.7269). Anoidium was found to carry a second dominant gene for resistance designated Uh2, and Ogalitsu a second recessive gene for resistance designated uh3. The variety Jet was found to possess a single recessive gene for resistance to U. hordei which was designated uh4 (47).

Six of the seven linkage groups in barley have been established. Recent work by Kramer et al. (14), Haus (10), and Tsuchiya (45) has indicated that the groups formerly designated as III and VII should be considered as one. Tsuchiya (45) referred to a new

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1) C.A.N. refers to Canadian Accession Number

linkage group VII composed of the gene pair  $Xn\ xn$  which conditions xantha seedling and  $Ec\ ec$ , a factor pair for earliness. Tsuchiya has located this new group on what he refers to as his chromosome 6. Burnham<sup>1</sup> refers to this chromosome as the "g" chromosome.

Robertson, Wiebe and Shands (28,29), Smith (40), and Woodward (49) have summarized the data on barley linkages and compiled maps on each linkage group.

Shands (37) reported a linkage between the genes conditioning the loose smut resistance and stem rust susceptibility of Trebi in a cross of this variety with Chevron (C.I.1111). Mohajir et al. (17) observed a suggestion of an association of loose smut reaction with spike row character in crosses where Abyssinian (C.I.668), or Jet were involved. Poehlman (22), found that most of the hooded barley varieties that he tested were resistant, whereas most of the awned varieties tested were susceptible to loose smut. Unfortunately the genetics of the correlation was not studied.

Several investigators have failed to reveal linkages of genes conditioning resistance to U. hordei with various linkage markers (12,38,47).

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1) Dr. C. R. Burnham, University of Minnesota, Minn. U.S.A.

## SECTION ONE

### DETERMINATION OF THE MODE OF INHERITANCE AND THE INTERRELATIONSHIPS OF THE JET GENES CONDITIONING RESISTANCE TO THE THREE SMUT SPECIES THAT ATTACK BARLEY

#### MATERIALS AND METHODS

##### Varieties

The inheritance and interrelationships of the Jet genes conditioning resistance to Ustilago nuda, Ustilago nigra and Ustilago hordei were studied in hybrids between Jet and the varieties Vantage (C.A.N.1162), and Plush (C.A.N.1106). Table 1 shows the smut reactions of the parental varieties inoculated to cultures of U. hordei, U. nigra and U. nuda. The reactions to the smuts were obtained from classifiable plants obtained from lots of one hundred inoculated seeds sown in the greenhouses at the Canada Department of Agriculture, Research Branch, Experimental Farm, Brandon, Manitoba in the fall of 1958 and the spring of 1959. Inoculations with U. nuda were carried out in the field in 1958; inoculations with the seedling infecting smuts were carried out immediately prior to seeding.

Jet is a naked-kernelled, two-rowed variety of Abyssinian origin with rough awns and black lemma, palea and pericarp. It was introduced into the United States by H. V. Harlan prior to 1920.

Plush and Vantage are white six-rowed feed barley types of commercial importance in Canada. Plush was derived from the cross Lion x Bearer; Vantage from the cross Newal x Peatland, 2 x Plush.

Table 1. Smut reactions of three barley varieties artificially inoculated with virulent cultures of U. hordei, U. nigra and U. nuda.

Variety	Infection in Percent								
	U. hordei			U. nigra			U. nuda		
	1957	1958	Ave.	1957	1958	Ave.	1957	1958	Ave.
Vantage	38.7	52.6	45.7	53.4	55.4	54.4	84.4	79.6	82.0
Plush	67.4	49.7	58.6	74.0	74.7	74.4	83.2	69.0	76.1
Jet	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Smut Cultures and Methods of Inoculation

Smut ohlamydospores of cultures Uh 47-64-4 of U. hordei, Ung 49-6-2 of U. nigra and Un 49-68 of U. nuda were supplied by Dr. W. J. Cherewick<sup>1</sup>. A high degree of stability for the genetic factors conditioning pathogenicity in both the seedling infecting smut cultures and the Trebi attacking U. nuda culture had been previously established by Cherewick (pers. comm.).

The individual smut cultures were increased on the susceptible variety Newal (C.A.N.1089). Chlamydospores of the seedling infecting smuts were stored at a temperature of approximately 38° F., while the U. nuda fungus was maintained in the form of mycelium within the inoculated seed of the susceptible variety. Inoculum of U. nuda was obtained by growing plants from infected seed when required and using the chlamydospores from the freshly harvested, smutted spikes. The viability of the cultures was checked by means

1) Dr. W. J. Cherewick, Plant Pathologist, C.D.A. Res. Branch, Winnipeg.

of chlamyospore germination tests prior to each series of inoculations.

Moore and Munnekes' jet-nozzle method (19) was used in making inoculations of U. nuda. An aqueous solution of spores was directed, under pressure, through a small jet, into the individual florets. Each spike was inoculated at two different times; 24 and 48 hours following anthesis of the earliest florets.

Taylor (14) noted that kernel development was reduced when U. nuda chlamyospores were introduced into florets prior to anthesis. The writer has observed that the heaviest U. nuda infections can usually be expected from inoculated spikes that show some degree of sterility in the lower florets following inoculation. It is assumed that, at the time of inoculation, the majority of florets on spikes exhibiting this type of sterility were probably at a stage of development most favorable for infection. Throughout these investigations U. nuda inoculations were made in sufficient quantity to permit the selection of spikes showing this characteristic.

U. nuda inoculations were made in the field and in the greenhouse. Before planting, all the seed was treated with a 1:1 mixture of Ceresan and talc. to minimize the possibility of infection by the seedling infecting smuts and to give protection against root-rot organisms.

Seed to be inoculated with the seedling infecting smuts was dehulled by peeling the lemma back from the germ end of the seed in order to expose the embryo. Inoculation was carried out by

vigorously shaking the dehulled seed in a test-tube with a small quantity of finely sieved chlamydo-spores. Inoculated seed was planted almost immediately.

The method of seeding the material inoculated with the seedling infecting smuts was designed to provide optimum conditions for infection. The inoculated seeds were space-planted in drill-rows that had been made in well-moistened, sandy soil in greenhouse benches. The drill-rows were approximately 30" in length, 1.5" in depth and .5" in width and were spaced at intervals of 4" along the benches. The seed was left uncovered for a period of 18 hours following planting. During that time the temperature within the greenhouse compartments was maintained at 60° F. and the relative humidity at 65 - 70 percent. At the end of the 18 hour period the seed was covered with dry soil. The soil temperature was maintained at 60° F. until after the seedlings had emerged.

#### Hybrid Populations

Hybrid populations were obtained from the crosses of Plush x Jet and Vantage x Jet made at Brandon during the summer of 1956.

Hybrid material was tested for reaction to the seedling infecting smuts in the F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> generations and for reaction to U. nuda in the F<sub>2</sub> and F<sub>3</sub> generations. The parents were inoculated and tested simultaneously with the progeny of the crosses.

The F<sub>1</sub> generation of the cross Vantage x Jet was tested for reaction to U. hordei and U. nigra for the purpose of establishing

the dominance-recessiveness relationships of the genes governing the Jet resistance to the two seedling infecting smuts.

Limited tests were performed on the  $F_2$  generation. The  $F_2$  generation does not permit a satisfactory genetical analysis since an excess of non-infected plants may result from lethal effects of infection (15) or from disease escapes of genetically susceptible plants (13,35). The  $F_2$  data were used mainly to provide an estimate of the percentage of smut expected on segregating  $F_3$  lines. This is based on the fact that when the parents of a cross differ by a single factor pair, the segregations for  $F_3$  lines and  $F_2$  populations are genetically alike. The percentage of smut in the  $F_2$  populations should therefore be approximately equivalent to the percentage in the segregating  $F_3$  lines. The  $F_2$  generations were tested for reaction to U. nuda by inoculating flowers of  $F_1$  plants and growing out the resulting seeds.  $F_2$  reaction to the seedling infecting smuts was tested by inoculating  $F_2$  seeds with U. hordei and U. nigra and growing out the  $F_2$  populations.

The classification of the  $F_2$  plants for smut reaction was based on the behavior of  $F_3$  lines grown from inoculated seed of  $F_2$  plants. The  $F_2$  plants were classified on this basis for reaction to the three smut species. This classification provided the basis for the genetical interpretations of the genes conditioning resistance to the three smut species and also provided a means for determining the interrelationships of these resistance genes.



### Pedigree Methods

Approximately 40 crossed seeds from each of the hybrids Vantage x Jet and Plush x Jet were sown in the field in 1957. Several spikes on a number of the resulting F<sub>1</sub> plants were inoculated with U. nuda. The inoculated seed of these spikes was used to test the F<sub>2</sub> generations for reaction to U. nuda.

The remainder of the F<sub>1</sub> plants, grown in the field in 1957 and not inoculated with U. nuda, were harvested and threshed individually. An F<sub>2</sub> population of each of the crosses was grown in the field in 1958 from seed of several of these F<sub>1</sub> plants.

On each of approximately 350 F<sub>2</sub> plants, 3 to 5 spikes were inoculated with U. nuda in the field in 1958. All of the spikes on these 350 F<sub>2</sub> plants were harvested and the inoculated and uninoculated groups threshed separately. The uninoculated lot of F<sub>3</sub> seed was divided into two portions; one portion inoculated with U. nigra and one with U. hordei. The three lots of F<sub>3</sub> seed, each lot inoculated with a different smut species, were sown as F<sub>3</sub> lines derived from individual F<sub>2</sub> plants. Thirty U. nuda-inoculated F<sub>3</sub> seeds and 20 U. nigra and U. hordei-inoculated F<sub>3</sub> seeds were the minima allowed for F<sub>3</sub> tests. As a result of restricting the number of classifiable F<sub>3</sub> lines to those with over 20 or 30 plants, only a limited number of the 350 F<sub>2</sub> plants that were originally inoculated with U. nuda were classified for reaction to the three smut species. The numbers of F<sub>2</sub> plants originating from individual F<sub>1</sub>'s were reduced in several instances

to less than ten plants. Because of this reduction, it was considered of little value to maintain the pedigree of the classified F<sub>2</sub> plants; rather they were treated as random plants from a large F<sub>2</sub> population.

The F<sub>1</sub> generation of the cross Vantage x Jet was tested for reaction to the seedling infecting smuts by inoculating a limited number of crossed seeds with U. hordei and U. nigra. Reaction of the F<sub>2</sub> generation of the cross was tested by inoculating F<sub>1</sub> seed.

The F<sub>3</sub> tests to the seedling infecting smuts were conducted in duplicate.

All tests were grown in the greenhouses at Brandon.

#### Plant Examination

After the plants had grown to maturity they were pulled to determine the number of smutted and non-smutted plants in each row or line. In all tests, plants with one or more smutted heads were classified as susceptible. In the F<sub>1</sub> and F<sub>2</sub> generations classifications were based on individual plants, whereas in the F<sub>3</sub> generation they were considered on a line basis. The percentage of smutted plants in each row was calculated from the totals obtained.

#### Mode of Inheritance and Association of Resistance Genes

Data provided by the F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> generation tests were used to establish the mode of inheritance of the resistance genes possessed by the variety Jet to each of the three smut species.

Data from the F<sub>3</sub> generation tests were used to establish the genotype for reaction to U. hordei, U. nigra and U. nuda for each of the

individual  $F_2$  plants of the two hybrid populations. An attempt was then made to determine the interrelationships of the genes conditioning resistance to the individual smut species.

Tests of "goodness of fit" and "independence" were made by means of chi-square (8). A probability level less than .05 was considered to indicate significant deviations from fit or independence, as the case may be.

Recombination percentages were computed by the Product Method described by Immer and Henderson (11).

EXPERIMENTAL RESULTS AND DISCUSSION

1. Inheritance of Resistance to U. nuda, U. nigra and U. hordei in the Cross Vantage x Jet.

The reactions of the parents and F<sub>1</sub> and F<sub>2</sub> generations of the hybrid Vantage x Jet to U. nuda, U. nigra and U. hordei are presented in Table 2. The distributions of the parental rows, F<sub>2</sub> rows and F<sub>3</sub> progenies by five-percent infection-class intervals are presented in Table 3.

The population size among the F<sub>3</sub> progenies ranged from 20 to 42 plants, with an average of 27 plants. The parental rows varied from 13 to 39 with an average of 22 plants for the susceptible parent and from 11 to 37 with an average of 27 plants for the resistant parent.

a. Inheritance of Resistance to U. nuda.

The progeny of the 6 inoculated heads of Jet, which contained 136 plants, showed no smut (Tables 2 and 3). This substantiated previous observations by the writer and established, for this investigation, the immunity of Jet to culture Un 49-68 of U. nuda.

The progeny of the seven inoculated heads of Vantage, consisting of 162 plants, showed an average of 79.0 percent smut. This percent infection showed that Vantage was susceptible to culture Un 49-68 of U. nuda. A range of infection from 56 to 95 percent in the individual rows indicated that the method used in making inoculations was effective.

When a single dominant gene is responsible for resistance, twenty-five percent of the F<sub>2</sub> plants from a cross between resistant

Table 2. Percentage of infected plants of parents, F<sub>1</sub> and F<sub>2</sub> of the cross Vantage x Jet inoculated with cultures Un 49-68 of U. nuda, Ung 49-6-2 of U. nigra and UH 47-64-4 of U. hordei.

Treatment	Material	Total Plants	Number Healthy	Number Infected	Percent Infected
Inoculated	F <sub>2</sub>	211	163	48	22.7
to	Vantage	162	34	128	79.0
<u>U. nuda</u>	Jet	136	136	0	0.0
Inoculated	F <sub>1</sub>	16	14	2	14.3
to	F <sub>2</sub>	112	45	67	59.8
<u>U. nigra</u>	Vantage	121	25	96	79.3
	Jet	174	174	0	0.0
Inoculated	F <sub>1</sub>	11	10	1	10.0
to	F <sub>2</sub>	93	55	38	40.8
<u>U. hordei</u>	Vantage	126	36	90	71.4
	Jet	190	190	0	0.0

and susceptible varieties are expected to be susceptible on the average. Inoculated seeds from 7 F<sub>1</sub> plants were grown and 48 of the 163 F<sub>2</sub> plants observed, or 22.7 percent, were smutted, (Table 2). The actual percentage of smutted plants obtained in F<sub>2</sub> approached that expected on the assumption of a single dominant gene for resistance.

The distribution of the 103 U. nuda-inoculated F<sub>3</sub> lines on a percentage infection basis is shown in Table 3. On the assumption that lines showing no smut were homozygous for the resistance of Jet and that those that showed any degree of smut were susceptible or segregating for susceptibility, the F<sub>3</sub> lines may be divided into two groups: 36 resistant and 67 segregating and

Table 3. Distributions of parental rows and F<sub>2</sub> and F<sub>3</sub> progenies of the cross Vantage x Jet inoculated with cultures Un 49-68 of *U. nuda*, Ung 49-6-2 of *U. nigra* and Uh 47-64-4 of *U. hordei* and presented in 5 percent infection class intervals.

Material	0	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	Total Rows
Inoculated to <i>U. nuda</i>																						
F <sub>2</sub>	-	-	0	2	2	0	1	2	0	-	-	-	-	-	-	-	-	-	-	-	-	7
F <sub>3</sub>	36	11	15	6	5	5	2	2	5	0	3	1	1	0	1	2	2	0	3	1	2	103
Vantage	-	-	-	-	-	-	-	-	-	-	-	0	1	0	2	0	1	2	0	1	0	7
Jet	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
Inoculated to <i>U. nigra</i>																						
F <sub>2</sub>	-	-	-	-	-	-	-	0	1	0	1	0	0	5	0	2	0	-	-	-	-	9
F <sub>3</sub>	20	7	13	16	5	9	3	7	5	0	5	4	1	1	2	1	3	0	2	0	1	105
Vantage	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	2	2	2	0	-	-	6
Jet	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
Inoculated to <i>U. hordei</i>																						
F <sub>2</sub>	-	-	-	-	-	-	0	2	0	1	1	0	2	1	1	0	-	-	-	-	-	8
F <sub>3</sub>	33	9	14	16	14	5	6	3	2	0	2	1	0	-	-	-	-	-	-	-	-	105
Vantage	-	-	-	-	-	-	-	-	-	-	0	1	1	1	0	1	0	2	0	-	-	6
Jet	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6

susceptible. Since none of the F<sub>2</sub> rows contained more than 35 percent smut the division between segregating and susceptible F<sub>3</sub> lines was made at that point. The number of F<sub>3</sub> lines assigned to the three classes resistant, segregating and susceptible were 36:46:21.

Two comparisons between the theoretically expected and actual numbers are made possible by the division of the F<sub>3</sub> lines into three classes. The results of the chi-square tests for mode of inheritance of reaction to U. nuda are summarized in Table 4.

Table 4. Summary of chi-square tests for mode of inheritance of reaction to U. nuda in the cross Vantage x Jet.

Character and Cross	Ratio	Chi-Square	P Value
Vantage x Jet (n = 103)			
res.& seg.: susc.lines	3:1	1.1682	.50 - .30
res.: seg.: susc.lines	1:2:1	5.5437	.10 - .05

Both of the probability values (Table 4) were in agreement with the single factor hypothesis. The evidence indicated that the resistance of Jet to culture Un 49-68 was conditioned by a single gene pair.

While no F<sub>1</sub> plants were grown from inoculated seed, the low percentage of infection in F<sub>2</sub> indicated that the gene was dominant in effect.

b. Inheritance of Resistance to U. nigra.

The six rows of inoculated seed of Jet (Table 3), which contained 174 plants (Table 2), showed no smut. This was in agreement with previous results obtained by the writer and showed that Jet was

resistant to Ung 49-6-2 of U. nigra.

The six rows of inoculated seed of Vantage, containing 121 plants, showed an average of 79.3 percent smut. This percentage infection indicated that Vantage was susceptible to culture Ung 49-6-2 of U. nigra. The range of infection in the individual rows, from 75 to 85 percent, indicated the effectiveness of the methods of inoculation.

If resistance was conditioned by a dominant gene or genes, no infection would be expected in the F<sub>1</sub> generation. Two of the F<sub>1</sub> plants, or 14.3 percent of the 16 crossed seeds that were inoculated to U. nigra, were infected with smut. Infection in this generation suggested that resistance to U. nigra was conditioned by a recessive gene or genes.

Sixty-seven plants, or 59.8 percent of the 112 F<sub>2</sub> plants that were grown (Table 2), were infected with U. nigra. The range of infection within the F<sub>2</sub> rows was from 36 to 75 percent. Infection in the F<sub>2</sub> was too high to indicate dominance of the gene or genes responsible for resistance. This confirmed the F<sub>1</sub> results.

The distribution of the 105 F<sub>3</sub> lines on a percentage basis is presented in Table 3. On the assumption that the lines that showed no smut were homozygous for the resistance of Jet and that those showing smut were segregating or susceptible, the F<sub>3</sub> lines were divided into two groups; 20 homozygous for resistance and 85 either segregating for resistance and susceptibility or completely susceptible. In view of the possibility of over-lapping of the segregating



and susceptible classes, which would be expected to occur if resistance were controlled by a recessive gene or genes, no attempt was made to separate the segregating from the susceptible  $F_3$  lines.

A single comparison between the theoretically expected and actual numbers was made possible by the division of the  $F_3$  lines into two classes. The actual number of  $F_3$  lines in the two classes (res. & seg. and susc.), fit the expected 1:3 ratio with a chi-square value of 1.9841 and a P value of between .20 - .10.

The evidence indicated that the resistance of Jet to culture Ung 49-6-2 of U. nigra was conditioned by a single recessive gene.

o. Inheritance of Resistance to U. hordei.

The infection percentages of the six rows of each of Vantage and Jet that were inoculated to culture Uh 47-64-4 of U. hordei were 71.4 and 0.0 respectively, (Tables 2 and 3). These data confirmed previous results obtained by the writer and showed that Vantage was susceptible and Jet resistant to the smut culture used.

One  $F_1$  plant or 10.0 percent of the eleven crossed seeds inoculated to U. hordei was infected with smut. This suggested that the Jet resistance to U. hordei was conditioned by a recessive gene or genes. These results were confirmed by data from the  $F_2$  generation. Infection in the  $F_2$ , (Table 3), ranged between 30.0 and 75.0 percent, with an average of 40.8 percent (Table 2).

The distribution of the 105  $F_3$  lines on a percentage basis is presented in Table 3. The  $F_3$  lines were divided into two groups on the assumption that the homozygous resistant lines were not infected

and the segregating or susceptible lines showed various degrees of infection. Thirty-three lines were classified as resistant and 72 as segregating or susceptible. No attempt was made to further divide the segregating or susceptible group.

The number of  $F_3$  lines in the two classes (res.:seg. and susc.), fitted a 1:3 ratio with a chi-square value of 2.3140 which corresponds to a P value of between .20 - .10.

On the basis of the evidence presented it was concluded that the resistance of Jet to culture Uh 47-64-4 of U. hordei was conditioned by a single recessive gene.

Examination of the distribution of the  $F_3$  lines inoculated to U. hordei (Table 3), reveals that there was an excess of  $F_3$  lines showing no smut. The  $F_3$  distribution was also skewed toward the resistant classes. This suggests that there was a low level of U. hordei infection throughout the  $F_3$  tests. The averages of infection<sup>1</sup> for the  $F_3$  lines inoculated to U. hordei, U. nigra and U. nuda confirmed this assumption. The readings were 11.6, 23.4 and 21.2 percent infection respectively.

Several hypotheses have been advanced to account for low percentages of infection in U. hordei inoculated lines. Johnston (12), Wells (47), and Shands (38), presented evidence to the effect that higher mortality in U. hordei infected seedlings, compared to those not infected, decreased the percentage of smut in  $F_3$  lines

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1) The averages of infection for the  $F_3$  lines inoculated to the three smut species are not presented in the Tables.

segregating for resistance. Infection escape has also been suggested (12,47) as an explanation for low infection in  $F_3$  lines inoculated to U. hordei. Both of these factors may have been operating to account for the results obtained here.

## 2. Inheritance of Resistance to U. nuda, U. nigra and U. hordei in the cross Plush x Jet.

The population size among the  $F_3$  progenies of the cross Plush x Jet ranged from 20 to 32 plants, with an average of 23 plants. The parental rows averaged 22 plants for the susceptible parent and 17 plants for the variety Jet.

$F_1$  and  $F_2$  plants of the cross Plush x Jet were not tested for reaction to U. hordei or U. nigra.  $F_3$  lines from random  $F_2$  plants of the hybrid were tested specifically to determine the genotypes of the  $F_2$  plants for reaction to the three smut species. The data were compared with those obtained from the cross Vantage x Jet and the similarities and differences in the mode of inheritance of the resistances to the three smut species were noted.

The reactions of the parents and  $F_2$  generations of the hybrid to U. nuda and of the parents to U. nigra and U. hordei are presented in Table 5. The distributions by five-percent infection-class intervals, of the parental rows,  $F_2$  rows and  $F_3$  progenies inoculated to U. nuda and the parental rows and  $F_3$  progenies inoculated to U. nigra and U. hordei are presented in Table 6.

Table 5. Percentage of infected plants of parents and F<sub>2</sub> of the cross Plush x Jet inoculated to culture Un 49-68 of U. nuda and of the parents inoculated to culture Ung 49-6-2 of U. nigra and Uh 47-64-4 of U. hordei.

Treatment	Material	Total Plants	Number Healthy	Number Infected	Percent Infected
Inoculated	F <sub>2</sub>	204	170	34	16.7
to	Plush	121	41	80	66.2
<u>U. nuda</u>	Jet	97	97	0	0.0
Inoculated	Plush	142	45	97	68.3
to	Jet	136	136	0	0.0
<u>U. nigra</u>					
Inoculated	Plush	122	62	60	49.2
to	Jet	114	114	0	0.0
<u>U. hordei</u>					

a. Inheritance of Resistance to U. nuda.

The infection percentages of the parent varieties presented in Tables 5 and 6 indicate that Plush was susceptible and Jet resistant to culture Un 49-68 of U. nuda. The average infections for the seven rows of Jet and the six rows of Plush were 0.0 and 66.2 percent respectively.

Inoculated seed from 8 F<sub>1</sub> plants produced 204 F<sub>2</sub> plants. Thirty-four were infected with U. nuda. The range of infection within the F<sub>2</sub> rows was from 6 to 27 percent. Although the 16.7 percent average infection suggested that resistance was dominant, it was too low for an accurate interpretation of the number of genes involved. However, the fact that the F<sub>2</sub> infections within the individual rows ranged as high as 27 percent, supported the single gene hypothesis.

Table 6. Distributions of parental rows, F<sub>2</sub> rows, and F<sub>3</sub> progenies of the cross Plush x Jet inoculated to culture Un 49-68 of *U. nuda* and of the parental rows and F<sub>3</sub> progenies inoculated to cultures Ung 49-6-2 of *U. nigra* and Uh 47-64-4 of *U. hordei* and presented in 5 percent infection class intervals.

Material	0	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	Total Rows
Inoculated to <i>U. nuda</i>																						
F <sub>2</sub>	-	0	1	3	1	2	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	8
F <sub>3</sub>	39	3	19	5	8	6	2	3	0	1	1	1	0	2	1	1	3	1	1	0	1	99
Plush	-	-	-	-	-	-	-	-	-	-	0	1	1	1	1	1	1	0	-	-	-	6
Jet	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
Inoculated to <i>U. nigra</i>																						
F <sub>3</sub>	29	10	11	12	9	5	5	4	4	2	2	2	3	0	1	1	1	0	0	0	0	104
Plush	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	3	2	1	0	-	-	6
Jet	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
Inoculated to <i>U. hordei</i>																						
F <sub>3</sub>	38	7	18	14	14	3	2	2	1	0	2	0	0	0	2	0	1	0	0	0	0	104
Plush	-	-	-	-	-	-	-	-	0	1	1	1	0	1	1	0	1	0	-	-	-	6
Jet	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6

The distribution of the 99 F<sub>3</sub> lines on a percentage basis is presented in Table 6. The F<sub>3</sub> lines were divided into two groups; 39 showing no smut and assumed to be homozygous resistant and 60 showing smut and assumed to be susceptible or segregating for susceptibility. Since none of the F<sub>2</sub> rows showed more than 27 percent smut the division between susceptible and segregating lines was made at that point. The number of F<sub>3</sub> lines in the three classes were; 39 resistant, 43 segregating and 17 susceptible.

The results of the chi-square tests of the mode of inheritance of reaction to U. nuda are summarized in Table 7.

Table 7. Summary of chi-square tests for mode of inheritance of reaction to U. nuda culture Un 49-68 in the cross Plush x Jet.

Character and Cross	Ratio	Chi-Square	P Value
Plush x Jet (n = 99)			
res. & seg.: susceptible lines	3:1	3.2356	.10 - .05
res.: seg.: susc. lines	1:2:1	9.7224	less than .01*

The probability value for the 1:2:1 ratio was less than P = .05 which was the minimum regarded as indicative of a satisfactory fit. Examination of the distribution of the F<sub>3</sub> lines inoculated to U. nuda in Table 6 shows an excess of apparently resistant lines. As the F<sub>2</sub> data, (Tables 5 and 6), showed a low percentage of infection, it is apparent that larger numbers of plants than those available in some of the F<sub>3</sub> lines would be required to distinguish segregating

\* significant chi-square value

from resistant ones.

The P value for the 3:1 ratio was in agreement with the single factor hypothesis; also the F<sub>2</sub> percentage infection was too low for resistance to be conditioned by recessive genes. This was considered sufficient evidence to confirm the hypothesis established in the cross Vantage x Jet, that the resistance of Jet to culture Un 49-68 of U. nuda was conditioned by a single dominant gene.

b. Inheritance of Resistance to U. nigra.

The reactions of the parent varieties and F<sub>3</sub> lines to culture Un 49-6-2 of U. nigra presented in Tables 5 and 6, agreed with the results presented from the cross Vantage x Jet. The 104 F<sub>3</sub> lines were divided into two groups on the assumption that the homozygous resistant lines were not infected and the segregating and susceptible lines showed some infection. Twenty-nine lines were classified as resistant and 74 as segregating and susceptible. The chi-square value of 0.4615 which corresponded to a P value between .50 - .30 was in excellent agreement with the single recessive gene hypothesis established for the cross Vantage x Jet.

c. Inheritance of Resistance to U. hordei.

The distribution of the U. hordei inoculated F<sub>3</sub> lines of the cross Plush x Jet is presented in Table 6. The reaction of the parents to U. hordei is shown in Table 5. No plants were smutted in the Jet rows. Inoculated Plush averaged 49.2 percent infection with the range from 41 to 80 percent.

Of the 104 F<sub>3</sub> lines, the 38 in the zero infection class were assumed to be homozygous resistant; the remaining 66 were classed as segregating or susceptible. The chi-square test for goodness of fit of the data to a 1:3 ratio was negative, (chi-square value 7.3610; P = less than .01.)

Examination of the F<sub>3</sub> distribution (Table 6), reveals a skewness toward the resistant classes and an excess of lines in the zero infection class. The same reasons that were advanced to account for the low percentages of infection in the U. hordei inoculated lines in the cross Vantage x Jet are suggested to account for these results. No genetic interpretations were derived from this chi-square determination. However, the results do not necessarily disprove the single recessive gene hypothesis developed to explain the Jet resistance to U. hordei and established from the cross Vantage x Jet.

### 3. Interrelationships of the Genes in the Variety Jet that Condition Resistance to U. nuda, U. nigra and U. hordei.

The genotypes for reaction to U. nuda, U. nigra and U. hordei of the F<sub>2</sub> plants from the crosses Vantage x Jet and Plush x Jet were established through tests of the F<sub>3</sub> families to each of the three smut species. The F<sub>2</sub> plants were classified into four reaction classes based on the evidence for single gene pairs conditioning resistance to each of two species. The following factor pair combinations were considered: factors conditioning reaction to U. nigra vs. reaction to U. nuda; reaction to U. hordei vs. reaction to U. nuda; and reaction to U. nigra vs. reaction to U. hordei.



The chi-square treatment outlined by Mather (16) was applied to each set of F<sub>2</sub> data in an attempt to determine the existence of associations between the factor pairs under consideration.

The data for each of the various factor combinations will be presented separately.

a. Association of the Factors Conditioning Reaction to U. nigra vs. Reaction to U. nuda.

The factorial constitutions of the susceptible and resistant parents in the two crosses being investigated for reaction to U. nigra and U. nuda were un6 un6, Ung Ung and Un6 Un6<sup>1</sup>, ung ung<sup>2</sup>.

The distribution of the F<sub>2</sub> plants in the reaction classes Un6 Ung, Un6 ung, un6 Ung, un6 ung were as follows:

- for Vantage x Jet - 65:15:13:6, where n = 99.
- and Plush x Jet - 57:13:25:4, where n = 99.

The chi-square values derived from separating the segregation of the two factor pairs into components are presented in Table 8.

The data presented in Table 8 confirmed the monofactorial hypotheses that were previously established to explain the inheritance of the Jet genes for resistance to U. nuda and U. nigra. The relatively large probability values for both the 9:3:3:1 segregation and linkage components in both of the crosses indicated complete independence of the Jet genes conditioning resistance to U. nigra and U. nuda.

- 
- 1) Symbol for the dominant gene conditioning resistance to the Trebi attacking "races" of U. nuda (28).
  - 2) Tentative symbol assigned by the writer to the recessive Jet gene conditioning resistance to culture Ung 49-6-2 of U. nigra.

Table 8. Chi-square values for the components of the segregation of the two factor pairs conditioning reaction to U. nigra vs. U. nuda in the crosses Vantage x Jet and Plush x Jet.

Cross	Component	Chi-square	D.F.	P Value
Vantage x Jet	Seg. for <u>Ung ung</u>	1.7811	1	.20 - .10
	Seg. for <u>Un6 un6</u>	0.7575	1	.50 - .30
	Seg. for linkage	1.3748	1	.30 - .20
	9:3:3:1 seg.	3.9134	3	.30 - .20
Plush x Jet	Seg. for <u>Ung ung</u>	0.9730	1	.50 - .30
	Seg. for <u>Un6 un6</u>	3.2356	1	.10 - .05
	Seg. for linkage	0.4949	1	.50 - .30
	9:3:3:1 seg.	4.7035	3	.20 - .10

b. Association of the Factors Conditioning Reaction to U. hordei vs. Reaction to U. nuda.

The factorial constitutions of the susceptible and resistant parents investigated for reaction to U. hordei and U. nuda were un6 un6, Uhl Uhl and Un6 Un6, uhl uhl<sup>1</sup> respectively. The F<sub>2</sub> segregations for the factor pairs Uhl uhl Un6 un6 in the two crosses under consideration are as follows:

- for Vantage x Jet - 55:15:25:6, where n = 101.
- and Plush x Jet - 49:13:33:4, where n = 99.

The results of the chi-square tests applied to these data are given in Table 9.

The probability values for the single factor segregations (Table 9), confirmed the monofactorial hypotheses established previously to explain the inheritance of the Jet genes for resistance to U. hordei and U. nuda.

1) Symbols for the recessive Jet gene conditioning resistance to "race" 6 of U. hordei. (47).

Table 9. Chi-square values for the components of the segregation of the two factor pairs conditioning reaction to U. hordei vs. U. nuda in the crosses Vantage x Jet and Plush x Jet.

Cross	Component	Chi-square	D.F.	P Value
Vantage x Jet	Seg. for <u>Uh<sub>1</sub> uh<sub>1</sub></u>	1.7458	1	.20 - .10
	Seg. for <u>Un<sub>6</sub> un<sub>6</sub></u>	0.9633	1	.50 - .30
	Seg. for linkage	0.1331	1	.80 - .70
	9:3:3:1 segregation	2.8422	3	.50 - .30
Plush x Jet	Seg. for <u>Uh<sub>1</sub> uh<sub>1</sub></u>	8.0841	1	less than .01*
	Seg. for <u>Un<sub>6</sub> un<sub>6</sub></u>	3.2356	1	.10 - .05
	Seg. for linkage	3.1526	1	.10 - .05
	9:3:3:1 segregation	14.4723	3	less than .01*

Lack of agreement of the F<sub>2</sub> data of the cross Plush x Jet with a 9:3:3:1 ratio can be attributed largely to the poor fit of the Uh<sub>1</sub> uh<sub>1</sub> factor segregation to a 1:3 ratio. Reasons have been presented previously to explain this situation.

The probability values for the linkage components are in agreement with a hypothesis that the genes in Jet that condition resistance to U. hordei and U. nuda are completely independent.

c. Association of the Factors Conditioning Reaction to U. hordei vs. Reaction to U. nigra.

The constitutions of the susceptible and resistant parents for the factor pairs conditioning reaction to U. nigra and U. hordei were Ung Ung, Uh<sub>1</sub> Uh<sub>1</sub> and ung ung, uh<sub>1</sub> uh<sub>1</sub> respectively.

The F<sub>2</sub> segregations for the factor pairs under consideration were as follows:

- for Vantage x Jet - 68 Ung Uhl, 4 Ung uhl, 17 ung Uhl,  
 16 ung uhl, where n = 105.  
 and Plush x Jet - 61 Ung Uhl, 5 Ung uhl, 14 ung Uhl,  
 24 ung uhl, where n = 104.

The chi-square values derived from separating the segregation of the factor pairs Ung ung and Uhl uhl into components are presented in Table 10.

Table 10. Chi-square values for the components of the segregation of the two factor pairs conditioning reaction to U. hordei vs. U. nigra.

Cross	Component	Chi-square	D.F.	P value
Vantage x Jet	Seg. for <u>Uhl uhl</u>	2.3142	1	.20 - .10
	Seg. for <u>Ung ung</u>	1.9841	1	.20 - .10
	Seg. for linkage	23.4931	1	less than .01*
	9:3:3:1 segregation	27.4931	3	less than .01*
Plush x Jet	Seg. for <u>Uhl uhl</u>	7.3846	1	less than .01*
	Seg. for <u>Ung ung</u>	0.4615	1	.90 - .80
	Seg. for linkage	51.7094	1	less than .01*
		59.5555	3	less than .01*

Chi-square tests for the linkage components of segregation (Table 10), gave probability values exceeding the .01 level on the data from both crosses. This was interpreted as an indication that the factors in Jet that condition resistance to U. hordei and U. nigra are not inherited independently.

Recombination percentages for the two factor pairs were determined by the Product Method described by Immer and Henderson (11). These values are presented separately for the two crosses.

The four segregating classes in F<sub>2</sub>, referred to previously, were designated a, b, c and d for the purpose of determining the recombination

values. The ratio of products in the cross Vantage x Jet was  $bc/ad = .06250$ ; where  $a = 68$ ,  $b = 4$ ,  $c = 17$  and  $d = 16$  (previously presented). The recombination fraction for the ratio of products value, as determined by Immer and Henderson's Tables, was  $18 \frac{1}{2} 4.236$  percent. The ratio of products for the cross Plush x Jet was  $.047814$ ; which gave a corresponding recombination fraction of  $16 \frac{1}{2} 3.984$  percent.

The evidence presented above appeared to be overwhelmingly in favor of a hypothesis that single, distinct, but closely linked recessive genes in the variety Jet condition resistance to U. hordei and U. nigra. However, in view of the low level of infection of the U. hordei inoculated  $F_3$  lines, some doubt might exist as to the validity of the recombination values. Examination of the U. hordei and U. nigra infection percentage values for the individual  $F_3$  lines revealed that lines infected with U. hordei were generally infected with U. nigra. The reverse did not hold true however; many U. nigra infected lines, especially those in the lower infection classes, were free of U. hordei infection. This suggested that infection escape rather than segregation could account for the differences in the reactions of the individual  $F_3$  lines to U. hordei and U. nigra. The possibility that a single gene pair in the variety Jet conditioned the reaction to both seedling infecting smuts can not be entirely eliminated.

SECTION TWO

A STUDY OF THE INHERITANCE AND INTERRELATIONSHIPS OF DIFFERENT  
VARIETAL SOURCES OF RESISTANCE TO USTILAGO NUDA

MATERIALS AND METHODS

The general procedures and the materials used in conducting the investigation being presented in this second section of the Thesis were similar to those outlined under Materials and Methods of Section 1. The information to be presented here involves the varieties used in the investigation and the handling of the hybrid populations.

Varieties

One susceptible, one moderately-resistant and eight resistant barley varieties were used in this study. Four of the varieties investigated, Kitchin (C.I.1296-1), Bifarb (C.I.3951-3), C.I.5798 and Jet were reported by Tapke (143), to be immune to 4 physiologic "races" of U. nuda. Moseman and Reid (20), reported that the same four varieties and the Brandon hybrids Br. 5479-680 and Br. 5479-754 were immune in tests to "a composite of, or individual cultures of, Tapke's races" of U. nuda and to virulent culture, P.35<sup>1</sup> from Cloninger and Poehlman (5). Table 11 shows the smut reactions of the parental varieties and the susceptible variety Vantage inoculated to three Trebi-attacking cultures of U. nuda. Inoculations of cultures

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- 1) Trebi-attacking culture of U. nuda obtained from Dr. J. Moseman,  
U.S.D.A., Beltsville, Maryland.

Un 49-68<sup>1</sup> and "Race" C<sup>2</sup> were made in the field at Brandon in 1955, 1956 and 1957. The reactions to the two cultures were obtained from classifiable plants grown in the field from 100 inoculated seeds. Data on reaction to culture P.35 were supplied by W. J. Cherewick (pers. comm.).

Table 11. Smut reactions of 11 barley varieties artificially inoculated with 3 Trebi-attacking cultures of U. nuda.

Variety	C.I.or C.A.N. Number	Percent Infection								Culture P.35 % inf.
		Culture Un 49-68				"Race" Un C.				
		1956	1957	1958	Ave.	1956	1957	1958	Ave.	
Vantage	C.A.N.1162	48.0	75.0	92.0	71.6	59.0	67.0	89.0	71.6	67.0
Newal	C.A.N.1089	70.0	82.0	89.0	80.3	84.0	81.0	86.0	83.6	--
Brachytic-119	---	23.0	47.0	47.0	39.0	59.0	19.0	35.0	37.7	--
Jet	C.I.967	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Br-680	---	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Br-754	---	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Valkie-trd.	---	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nigrinudum	---	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kitchin	C.I.1296-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bifarb	C.I.3951-3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
----	C.I.5798	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

The origins and some varietal characteristics of the varieties used in this study are as follows:

Vantage and Jet were described in Section 1. of this Thesis.

Newal is a six-rowed variety of commercial importance in Alberta.

It originated from the cross Manchuria x Lion, 2 x O.A.C.21.

The varieties Br.5479-680 and Br.5479-754 are six-rowed loose-

- 1) the culture of U. nuda described in Section 1.
- 2) Trebi-attacking culture of U. nuda obtained from Dr. L.P.V. Johnson, University of Alberta, Edmonton.

smut-resistant selections developed at the C.D.A. Research Branch, Experimental Farm, Brandon, from the cross Vantage x Jet, 2 x Vantmore.

Brachytic-119 is a mutant from the cross Himalaya x Persicum. It is homozygous for the factor pair brbr which conditions brachytic growth habit.

Valkie-trd. is a selection from the variety Valkie (C.I.5748), made by Dr. C. F. Konzak, at Cornell University, Ithica, N.Y. It is homozygous for the recessive third-outer-glume character pair trd trd. The original variety Valkie came from Vavilov's South Russian Collection.

Nigrinudum is a selection known as Hordeum distichon nigrinudum 1, made by Robertson (26), from an original strain of H. dist. nigrinudum which was introduced by H. V. Harlan from Abyssinia in 1918. Nigrinudum is heterozygous for the green vs. white seedling character pair An an.

Kitchin is of hybrid origin, coming from the cross Moravian x Deficiens and made by H. V. Harlan in 1914 at St. Paul, Minnesota.

Bifarb is an introduction from Abyssinia. Seed of the variety was presented to H. V. Harlan in 1924 by the Ministry of Agriculture of Giza, Egypt.

C.I.5798 was introduced by Vavilov into Russia from Abyssinia. It was introduced into the United States from Vavilov's collection.

The varieties Jet, Valkie-trd., Nigrinudum, Kitchin, Bifarb and C.I.5798 are two-rowed types.

#### Smuts Culture

The U. nuda culture Un 49-68, which has been described previously,



was used in this study.

Hybrid Populations

The crosses used and the generations in which the hybrid populations were investigated for reaction to U. nuda are indicated in Table 12.

Crosses were made at Brandon in 1956 and 1957.

Table 12. Crosses studied and generations in which the hybrid populations were investigated.

Cross	Generations Investigated
Nigrinudum x Newal	F <sub>2</sub>
C.I.5798 x Newal	F <sub>2</sub>
Bifarb x Newal	F <sub>2</sub> , F <sub>3</sub> .
Kitchin x Newal	F <sub>2</sub> , F <sub>3</sub> .
Jet x Newal	F <sub>2</sub> , F <sub>3</sub> .
Br.5479-680 x Bifarb*	F <sub>3</sub> , F <sub>4</sub> .
Br.5479-754 x Kitchin*	F <sub>3</sub> , F <sub>4</sub> .
Kitchin x Bifarb*	F <sub>3</sub> , F <sub>4</sub> .
Br.5479-754 x C.I.5798	F <sub>3</sub>
Br.5479-680 x C.I.5798	F <sub>3</sub>
Jet x C.I.5798	F <sub>3</sub>
Kitchin x C.I.5798	F <sub>3</sub>
Bifarb x C.I.5798	F <sub>3</sub>
Jet x Nigrinudum	F <sub>3</sub>
Valkie-trd. x Jet	F <sub>3</sub>
Brachytic-119 x Jet	F <sub>3</sub>

Pedigree Methods

Hybrids of the crosses listed in Table 12, involving the loose-smut-susceptible variety Newal and the resistant varieties Nigrinudum, C.I.5798, Kitchin, Bifarb, and Jet, were investigated for the purpose of studying the mode of inheritance of the genes conditioning the immune type of

\*Studied in F<sub>4</sub>

loose smut reaction of the resistant varieties to culture Un 49-68. The remaining crosses, (Table 12), were investigated for the purpose of determining the interrelationships of these various resistance genes with one another and with the gene or genes in the varieties Valkie-trd. and Brachytic-119 conditioning resistance to the same loose smut culture.

The method of handling the hybrid populations were similar to those outlined previously.

Crossed seed of each of the hybrids were sown in the field in 1957. Several spikes on a number of the resulting  $F_1$  plants were inoculated with U. nuda and the seed used to test the  $F_2$  generation. The  $F_3$  lines were tested by growing out U. nuda inoculated  $F_3$  seed from random plants of  $F_2$  populations. The inoculated  $F_3$  seed of each  $F_2$  plant was divided into two seed lots in order to permit duplicate testing of the  $F_3$  lines. One replication of the  $F_3$  lines was grown in the fall of 1958 and one in the spring of 1959. The total number of plants from the two tests were used in the determination of the infection percentages of the  $F_3$  lines.

An attempt was made to check the reaction of a number of  $F_3$  lines of the crosses in Table 12 marked with an asterisk, by growing out U. nuda inoculated  $F_4$  seed of approximately twelve plants of each of the  $F_3$  lines investigated.

All data reported in this Section, with the exception of the data from the  $F_4$  lines, were from material grown in the greenhouses. The  $F_4$  tests were grown in the field at Brandon in 1959.

## EXPERIMENTAL RESULTS AND DISCUSSION

### 1. The Mode of Inheritance of the Genes Conditioning the Immune Type of Loose-Smut Resistance in the Varieties Jet, Kitchin, Bifarb, C.I.5798 and Nigrinudum.

The reactions of the parents and F<sub>2</sub> generations of the crosses involving Newal to culture Un 49-68 of U. nuda are presented in Table 13. The distributions of the parental rows, F<sub>2</sub> rows and F<sub>3</sub> progenies by five percent infection class intervals are shown in Table 14.

The size of the F<sub>3</sub> progenies varied from 20 to 36 plants with an average of 24.0 plants. The number of plants in the parental rows varied from 11 to 21 with an average of 16.1. The average number of plants in the F<sub>2</sub> rows was 14.9.

Loose smut infections for the variety Newal were high, ranging from 69.9 to 82.6 percent (Table 13). The average infection for the variety throughout the tests was 76.9 percent. The reactions of Jet, Kitchin, Bifarb, C.I.5798 and Nigrinudum were consistent with previous results (Table 11) and demonstrated the immunity of this series of varieties to culture Un 49-68.

The F<sub>2</sub> generations of the five crosses being investigated showed approximately the same loose smut reactions. The average infection of the five populations was 22.4 percent. This value and the averages of infection for the individual F<sub>2</sub> populations, presented in Table 13, were in reasonably close agreement with the values expected, (infection of Newal 76.9 percent), when a single dominant gene is responsible for resistance.

Table 13. Percentage of infected plants in the parents and F<sub>2</sub> of the crosses inoculated with culture Un 49-68 of U. nuda and grown in the greenhouse.

Material	Total Plants	Number Healthy	Number Infected	Percent Infected
Jet x Newal F <sub>2</sub>	156	125	31	19.8
Jet	84	84	0	0.0
Newal	103	31	72	69.9
Kitchin x Newal F <sub>2</sub>	98	75	23	23.5
Kitchin	91	91	0	0.0
Newal	100	24	76	76.0
Bifarb x Newal F <sub>2</sub>	133	97	36	27.0
Bifarb	119	119	0	0.0
Newal	(see cross Kitchin x Newal)			
C.I.5798 x Newal F <sub>2</sub>	145	115	30	20.7
C.I.5798	187	187	0	0.0
Newal	149	26	123	82.6
Nigrinudum x Newal F <sub>2</sub>	142	111	31	21.8
Nigrinudum	216	216	0	0.0
Newal	(see cross Kitchin x Newal)			
Average Infection-F <sub>2</sub>	674	523	151	22.4
-Newal	352	81	271	76.9

Infection percentages of 58.3 and 52.1 were obtained in single F<sub>2</sub> rows of the crosses Kitchin x Newal and Bifarb x Newal respectively (Table 14). A single smut-free F<sub>2</sub> row was also noted in the cross C.I.5798 x Newal. These extreme infection values were considered abnormal for this material in view of the relatively normal distribution of the remaining 42 F<sub>2</sub> rows. Infection in these remaining rows ranged from 5 to 38.0 percent. These extreme values were not unexpected however, in view of the limited numbers of plants being grown in the individual F<sub>2</sub> rows.

Table 14. Distribution of parental rows, F<sub>2</sub> rows, and F<sub>3</sub> progenies, in 5 percent infection class intervals, of crosses inoculated with culture Un 49-68 of *U. nuda*.

Material	0	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	Total Rows	
Jet x Newal F <sub>2</sub>	-	0	1	3	2	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10
Jet x Newal F <sub>3</sub>	30	12	8	15	10	3	6	2	4	2	1	1	2	2	4	1	3	1	2	0	-	-	109
Jet	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
Newal	-	-	-	-	-	-	-	-	-	-	-	0	1	2	0	1	1	1	0	-	-	-	6
Kitchin x Newal F <sub>2</sub>	-	-	0	1	0	2	1	1	0	0	0	0	1	0	-	-	-	-	-	-	-	-	6
Kitchin x Newal F <sub>3</sub>	19	2	3	7	3	7	5	5	0	0	1	1	1	3	2	2	2	0	2	1	0	-	66
Kitchin	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
Newal 1)	-	-	-	-	-	-	-	-	-	-	-	-	0	1	1	0	1	1	2	0	-	-	6
Bifarb x Newal F <sub>2</sub>	-	-	1	0	1	2	1	2	0	1	0	1	-	-	-	-	-	-	-	-	-	-	9
Bifarb x Newal F <sub>3</sub>	27	2	3	10	10	7	3	3	2	0	2	1	3	0	4	2	1	0	3	1	1	-	85
Bifarb	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
Newal 1)	-	-	-	-	-	-	-	-	-	-	-	-	0	1	1	0	1	1	2	0	-	-	6
C.I.5798 x Newal F <sub>2</sub>	1	1	1	1	2	2	1	0	1	0	-	-	-	-	-	-	-	-	-	-	-	-	10
C.I.5798	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Newal	-	-	-	-	-	-	-	-	-	-	0	1	0	1	0	3	2	1	2	0	0	-	10
Nigrinudum x Newal F <sub>2</sub>	0	0	0	2	2	2	2	1	0	0	1	-	-	-	-	-	-	-	-	-	-	-	10
Nigrinudum	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
Newal 1)	-	-	-	-	-	-	-	-	-	-	-	-	0	1	1	0	1	1	2	0	-	-	6

1) Infection distributions for the variety Newal obtained from a single test.

The F<sub>3</sub> lines of the crosses Jet x Newal, Kitchin x Newal and Bifarb x Newal (Table 14), were assigned to the genetic classes resistant, segregating and susceptible on the bases of their loose smut reactions. Lines that were free of smut were considered to be homozygous for resistance; those in which the infection percentages were within the range of infection of the corresponding F<sub>2</sub> populations were assigned to the segregating class and the remainder were considered to be susceptible.

The number of F<sub>3</sub> lines assigned to the three genetic classes were as follows: Jet x Newal, 30:56:23; Kitchin x Newal, 19:35:12; Bifarb x Newal, 27:43:16.

Two comparisons between the theoretically expected and actual numbers were made possible by the division of the F<sub>3</sub> lines into three classes. The results of the chi-square tests for goodness of fit for the inheritance of reaction to U. nuda are presented in Table 15.

Table 15. A summary of chi-square tests for inheritance of reaction to culture Un 49-68 of U. nuda in the crosses Jet x Newal, Bifarb x Newal, and Kitchin x Newal.

Character and Cross	Ratio	Chi-square	P value
Jet x Newal (n = 109)			
res. & seg. vs. sus. lines	3:1	1.4801	.30 - .20
res:seg:sus. lines	1:2:1	1.7155	.50 - .30
Kitchin x Newal (n = 66)			
res. & seg. vs. sus. lines	3:1	1.6363	.30 - .20
res:seg:sus. lines	1:2:1	1.4934	.50 - .30
Bifarb x Newal (n = 85)			
res. & seg. vs. sus. lines	3:1	1.8759	.20 - .10
res:seg:sus: lines	1:2:1	2.8139	.30 - .20

All of the probability values in Table 15 were in agreement with single factor hypotheses. The low percentages of infection in the  $F_2$  populations (Table 13), and the large numbers of  $F_3$  lines in the low infection classes (Table 14), indicated that the resistance genes were each dominant in effect. Although the  $F_3$  generations of the crosses Nigrinudum x Newal and C.I.5798 x Newal were not investigated, the similarity of the reactions of the  $F_2$  populations of these two crosses with those involving Newal crossed with Jet, Bifarb and Kitchin, was considered sufficient evidence to warrant the suggestion that Nigrinudum and C.I.5798 also possess single dominant genes conditioning resistance to culture Un 49-68.

2. Interrelationships of the Genes Conditioning Resistance to Culture Un 49-68 of U. nuda in the Varieties Jet, Kitchin, Bifarb, C.I. 5798 and Nigrinudum.

The distribution of loose-smut infection by percentage classes for the parental rows and  $F_3$  progenies of crosses designed to bring together, in various combinations, the loose smut resistance genes of the varieties Jet, Bifarb, Kitchin, Nigrinudum and C.I.5798, are presented in Table 16. The infection percentages of the twenty-two U. nuda inoculated heads of the variety Newal, previously presented in Tables 13 and 14, were included here to represent the infection distribution of a loose-smut susceptible variety.

Included in the  $F_3$  distributions presented in Table 16 were several from hybrids involving the two selections Br.5479-754 and Br.5479-680 crossed to members of the group of loose smut resistant varieties (Table 12). Since both of the selections derived their loose smut resistance factors from Jet, it was assumed that the smut reaction of Jet was represented in crosses involving these selections.

Table 16. Distribution of loose-smut infection by percentage classes for the parental rows and F<sub>3</sub> progenies of crosses involving Jet and Jet-derivatives, Bifarb, Kitchin, Nigrinudum and C.I.5798.

Material	Class Marks of % Infection Classes											Total No. of lines
	0	5	15	25	35	45	55	65	75	85	95	
Newal	-	-	-	-	-	0	2	5	8	5	2	22
C.I.5798	17	-	-	-	-	-	-	-	-	-	-	17
Jet	6	-	-	-	-	-	-	-	-	-	-	6
Br.5479-754	8	-	-	-	-	-	-	-	-	-	-	8
Br.5479-680	8	-	-	-	-	-	-	-	-	-	-	8
Kitchin	5	-	-	-	-	-	-	-	-	-	-	5
Bifarb	4	-	-	-	-	-	-	-	-	-	-	4
F <sub>3</sub> progenies												
Jet x C.I.5798	127	-	-	-	-	-	-	-	-	-	-	127
Br-754 x C.I.5798	120	-	-	-	-	-	-	-	-	-	-	120
Br-680 x C.I.5798	154	-	-	-	-	-	-	-	-	-	-	154
Bifarb x C.I.5798	131	-	-	-	-	-	-	-	-	-	-	131
Kitchin x C.I.5798	120	-	-	-	-	-	-	-	-	-	-	120
										F <sub>3</sub> Total		652
Br-754 x Kitchin	374	-	-	1	-	-	-	-	-	-	-	375
Br-680 x Bifarb	362	-	-	-	-	-	-	-	-	-	-	362
Kitchin x Bifarb	337	-	-	-	-	-	-	-	-	-	-	337
										F <sub>3</sub> Total		1073
Jet x Nigrinudum	290	-	-	-	-	-	-	-	-	-	-	290
F <sub>3</sub> Totals	2015	-	-	1	-	-	-	-	-	-	-	2016

Data presented in Table 16 supported the evidence presented previously (Tables 11, 13, 14), on the reaction of the resistant and susceptible parental varieties to culture Un 49-68 of U. nuda.

Examination of the data from the F<sub>3</sub> lines of the five F<sub>3</sub> distributions of the crosses involving C.I.5798 revealed that no loose smut infection occurred among the 652 F<sub>3</sub> lines. This type



of reaction would be expected to occur if the genes conditioning resistance were either closely linked or occupied the same gene locus. Evidence derived from these five crosses tended to support the latter hypothesis since segregation for reaction to U. nuda apparently did not take place within the progeny of these crosses. An extremely close linkage would be required to result in complete lack of segregation.

A single  $F_3$  line of the cross Br.5479-754 x Kitchin showed 22.3 percent smut infection (Table 16). Two hypotheses could be advanced to account for this situation. Either the infected plants of this line were the result of an admixture of seed of an inoculated susceptible variety and the  $F_3$  seed used to grow this line, or they resulted from the segregation, within an  $F_2$  plant, of closely linked loose smut resistance factors.

In order to check the smut infection classifications of the  $F_3$  lines, a number were reinoculated with U. nuda. An average of 8.4 plants in 93 of the 1073  $F_3$  lines from the crosses Br.5479-754 x Kitchin, Br.5479-680 x Bifarb and Kitchin x Bifarb were inoculated with U. nuda and grown as  $F_4$  lines in 1959. Included in this material were six  $F_4$  progeny plants of the smutted line from cross Br.5479-754 x Kitchin (Table 16). No smut was observed among this group of 778  $F_4$  lines inoculated to U. nuda. The fact that none of the  $F_4$  plants derived from the one infected  $F_3$  line was contaminated with U. nuda suggested that the line was not segregating for loose smut reaction. It was assumed therefore that the infected plants in this line were the result of a seed admixture.

No smutted plants were observed in the F<sub>3</sub> lines of the crosses Br.5479-680 x Bifarb, Kitchin x Bifarb or Jet x Nigrinudum (Table 16).

Although the possibility of closely linked genes could not be entirely eliminated, the evidence presented appeared to be strongly in favor of a hypothesis that the resistance of the varieties Jet, Bifarb, Kitchin, C.I.5798 and Nigrinudum to culture Un 49-68 of U. nuda was conditioned by a single dominant gene at the same locus in each of the varieties.

The similarity of the F<sub>3</sub> distributions of the crosses involving Jet x C.I.5798 and the hybrids Br.5479-754 and Br.5479-680 crossed with C.I.5798 was taken as evidence that the hybrid selections possessed the Jet gene for U. nuda immunity and that the gene had not been affected by the transfer to the Br.5479 hybrid series.

3. The Interrelationships of the Genes that Condition Resistance to Culture Un 49-68 of U. nuda in the Varieties Valkie-trd. and Jet.

The distribution of loose smut infection in the parental rows and F<sub>3</sub> progenies of the cross Valkie-trd. x Jet is shown in Table 17.

Table 17. Distribution of loose smut infection by percentage classes for the parental rows and F<sub>3</sub> progenies of the cross Valkie-trd. x Jet.

Parent or Cross	Class Mark of % Infection Classes											Total No. of Lines
	0	5	15	25	35	45	55	65	75	85	95	
Jet	10	-	-	-	-	-	-	-	-	-	-	10 (206 pl.)
Valkie-trd.	10	-	-	-	-	-	-	-	-	-	-	10 (204 pl.)
Newal	-	-	-	-	-	0	2	2	4	2	0	10 (271 pl.)
F <sub>3</sub> -Valkie-trd. x Jet	221	1	2	6	4	1	2	1	1	1	0	240

With the exception of the 90 - 100 percent infection class, the 240 F<sub>3</sub> progenies (Table 17), covered the whole infection range. The actual proportion of F<sub>3</sub> lines showing smut was extremely small however; only 19 lines exhibited infection.

The 10 rows of each of the varieties Valkie-trd. and Jet (Table 17), were free of smut. Infection of Newal ranged from 50 to 90 percent with an average infection<sup>1</sup> of 72.4 percent.

The division point between the genetically segregating and susceptible classes was placed at the 50 percent infection level; the bases of this division being that this was the low point of the infection distribution of the susceptible variety Newal. Five F<sub>3</sub> lines were classed in the susceptible category. The genetically segregating class was assumed to range from the 50 percent infection point to the zero infection class. Fourteen lines were within this range. The remaining 221 lines were free of smut and were assumed to be homozygous for resistance.

The fact that segregation for smut reaction occurred was considered satisfactory evidence that the genes conditioning resistance in the two varieties were different. Since no readily discernible ratio could be considered for testing, this appeared to be the only conclusive point that could be established on the basis of the evidence provided by the F<sub>3</sub> data.

Two theories will be presented in an attempt to interpret the F<sub>3</sub> distribution of this cross; however, because of the limited

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1) average infection of Newal was not presented in the Tables.

information on the inheritance of the Valkie resistance, neither can be considered conclusive.

When two genes are present, a ratio of 15 resistant and segregating to one susceptible  $F_3$  line is expected as a rule. In the cross under consideration only 5 of the 240  $F_3$  lines could be classified as susceptible and 14 as segregating (Table 17). The low proportion of segregating and susceptible  $F_3$  lines suggested a possible linkage between the Jet gene for resistance and the gene or genes conditioning resistance in the variety Valkie-trd. Since the resistance genes entered the cross in the repulsion phase, susceptible lines would result only from the union of cross-over gametes, and the lines with intermediate infection would result from the union of cross-over gametes with non-cross-overs. Consequently a deficiency of these lines, as shown in Table 17, would be expected, if the resistance genes were located on the same linkage group.

It is also conceivable that the  $F_3$  distribution for the cross Jet x Valkie-trd. could be accounted for on the basis of the interaction of 3 independent dominant genes. Konzak (13) has shown that the resistance of Valkie to two of Tapke's U. nuda "races" was conditioned by "either of two dominant and independent genes". Evidence presented in this Thesis has indicated that Jet possesses a single dominant gene conditioning resistance to culture Un 49-68. If it is assumed that three dominant, independent genes interacted in this cross, then 27 of 64  $F_3$  lines would be expected to show smut infection; eight would segregate 63:1, twelve - 15:1, six - 3:1, and a single line would

be susceptible on the average. In view of the limited numbers of plants in the F<sub>3</sub> lines, it is possible that only those lines segregating 3:1 could be identified. If this had occurred, the ratio of resistant to segregating and susceptible lines would have been 57:7. The 221 resistant to 19 segregating and resistant F<sub>3</sub> lines presented in Table 17 fitted this ratio with a chi-square value of 2.2482. This chi-square value corresponded to a P value between .20 and .10.

4. The Interrelationships of the Genes Conditioning Resistance to Culture Un 49-68 of U. nuda in the Varieties Brachytic-119 and Jet.

The distribution of loose smut infection of the parental rows and F<sub>3</sub> progenies of the cross Brachytic-119 x Jet is presented in Table 18.

Table 18. The distribution of loose-smut infection by percentage classes for the parental rows and F<sub>3</sub> progenies of the cross Brachytic-119 x Jet.

Material	Class Mark of % Infection Classes											Total No. of lines
	0	5	15	25	35	45	55	65	75	85	95	
Jet	6	-	-	-	-	-	-	-	-	-	-	6 (160 pl.)
Brachytic-119	-	0	1	3	2	0	-	-	-	-	-	6 (180 pl.)
Newal	-	-	-	-	-	0	2	2	4	2	0	10 (271 pl.)
F <sub>3</sub> -Brachytic-119 x Jet	125	33	21	9	9	3	2	1	1	1	0	205

The progeny of the 10 inoculated heads of Newal, presented previously in Table 17, were used here to represent the distribution of smutted plants of a susceptible variety.

Jet continued to maintain its immune reaction to culture Un 49-68.

Based on the percentage infection of the susceptible variety Newal, Brachytic-119 exhibited a partial type of resistance to culture Un 49-68. The percentage infection of the variety ranged from 16 to 40 percent with an average infection of 29.4 percent. In view of the smut reaction of the parent varieties the skewness in the distribution of the  $F_3$  lines toward the resistant classes and excess of lines in the zero infection classes were not unexpected.

A complete genetic interpretation of the  $F_3$  distribution of this cross inoculated to U. nuda was not attempted in view of the lack of information on the inheritance of the Brachytic-119 resistance to culture Un 49-68. However, on the basis of the reaction of the parents, (Jet giving immunity to U. nuda and Brachytic-119 showing a partial type of resistance), it seemed logical to assume that the genes conditioning resistance to culture Un 49-68 were different in the two varieties. The evidence provided by the distribution of the  $F_3$  lines (Table 18), indicated that the resistance genes were located at different loci in the two varieties.

The percentages of infection of 5 of the  $F_3$  lines (Table 18), were within the range of infection of the susceptible variety Newal. This evidence of transgressive segregation toward greater susceptibility than either parent substantiated the hypotheses established above.

SECTION THREE

A STUDY OF POSSIBLE LINKAGE RELATIONSHIPS OF THE SMUT RESISTANCE GENES OF JET WITH THOSE RESPONSIBLE FOR OTHER SPECIFIC CHARACTERISTICS OF BARLEY

MATERIALS AND METHODS

Varieties

Investigations of the linkage relationships of the Jet genes conditioning resistance to the smuts of barley with those governing other specific characteristics of barley was conducted by studying hybrids between Jet and tester-stocks involving six of the seven barley linkage groups.

The varietal characteristics of the tester-stocks used in the study are briefly described as follows:

Colsess V is a hooded, six-rowed variety that was selected from Colsess (C.I.2792). It is heterozygous for the chlorina seedling factor pair Fc fc. The seedling is lime-green in color and develops to maturity.

Colsess I is a six-rowed, hooded variety selected out of Colsess. It is homozygous for the hooded character pair KK.

Orange lemma is from the United States Department of Agriculture genetic stock 121. The orange lemma character of the variety is conditioned by the factor pair oo.

Glossy-seedling 2B is a variety that is homozygous for the glossy seedling factor pair gl<sub>2</sub> gl<sub>2</sub>. It is of hybrid origin.

Triple-awned-lemma (C.I.6630), is a two-rowed variety with a white triple awn on the lemma which is conditioned by the factor pair tr tr.

The varieties Plush and Vantage have been described in Sections 1 and 2 of this study. Plush was chosen because it carries the smooth-awn character pair rr and Vantage because it has resistance to Puccinia graminis tritici Eriks. and Henn. conditioned by the factor pair Tt.

The variety Jet has been described previously.

With the exception of Vantage and Plush, seed of the tester-stocks used in this phase of the study was obtained from Dr. D. W. Robertson<sup>1</sup>.

Table 19 shows the loose smut reactions of the tester-stock varieties that were inoculated with culture Un 49-68 of U. nuda.

Table 19. Loose smut reactions of 8 barley varieties artificially inoculated with culture Un 49-68 of U. nuda.

Variety	Percentage Infection			Average
	1956	1957	1958	
Vantage	49.4	75.4	92.0	72.3
Plush	62.9	77.4	89.0	76.4
Glossy-seedling 2B.	48.7	67.5	66.6	60.9
Orange-lemma	47.3	82.3	64.5	64.7
Triple-awned-lemma	61.9	51.1	60.0	57.7
Colsess I	60.6	50.0	100.0	70.2
Colsess V	62.0	59.0	89.7	70.2
Jet	0.0	0.0	0.0	0.0

1) Formerly the Chief Agronomist, Dept. of Agronomy, Colorado State University, Fort Collins, Colorado, U.S.A.



The smut inoculations were made in the field at Brandon in 1955, 1956 and 1957. The reactions to the smuts were obtained from classifiable plants grown from a hundred seeds sown in the field at Brandon in 1956, 1957 and 1958.

#### Pathogen Cultures

Smut culture Un 49-68 was used throughout this phase of the investigations. Urediospores of P. graminis tritici Race 56 were used to test the F<sub>3</sub> lines of the hybrid involving Vantage for reaction to stem rust (linkage-marker Tt).

#### Hybrid Populations

Hybrid populations were obtained from the following crosses which were made at Brandon during the summers of 1955 and 1956.

Plush x Jet  
Vantage x Jet  
Colsess I x Jet  
Colsess V x Jet  
Orange-lemma x Jet  
Glossy-seedling 2B. x Jet  
Triple-awned-lemma x Jet

The F<sub>2</sub> genotypic classifications for reaction to U. nuda, U. nigra and U. hordei of the hybrid populations of the crosses Plush x Jet and Vantage x Jet were presented in Section 1 of these investigations. The same hybrid populations were used to test the associations of the Jet genes conditioning resistance to the various smut species with the marker genes possessed by the two susceptible varieties Plush and Vantage. Approximately 175 random F<sub>2</sub> plants of each of the remaining crosses were classified as to genotype for reaction to U. nuda only; the methods employed

have been described previously. The specific genes possessed by these linkage marker-stocks were then tested for association with the Jet gene pair conditioning reaction to U. nuda.

A summary of the characters studied in hybrids between Jet and the various tester-stocks is presented in Table 20.

Table 20. Marker characters studied in hybrids with Jet.

Linkage Group	Character	Gene Symbol	Hybrid
I	Single vs. triple-awned-lemma	<u>Trtr</u>	Triple-awned-lemma x Jet
I	2 - vs. 6 - rowed	<u>Vv</u>	Vantage x Jet
II	Black vs. white lemma and pericarp	<u>Bb</u>	Vantage x Jet
III	Hulled vs. naked seed	<u>Nn</u>	Vantage x Jet
IV	Hoods vs. awns	<u>Kk</u>	Colsess I x Jet
IV	Normal vs. glossy-seedling	<u>Gl<sub>2</sub>gl<sub>2</sub></u>	Glossy-seedling x Jet
V	Rough vs. smooth awn	<u>Rr</u>	Plush x Jet
VIIA <sup>1</sup>	White vs. orange lemma	<u>Oo</u>	Orange lemma x Jet
VII	Normal vs. chlorina-seedling	<u>Fofc</u>	Colsess V x Jet
VII	Resistance vs. susceptibility to stem rust	<u>Tt</u>	Vantage x Jet

The classifications of the F<sub>2</sub> plants for the specific marker characters indicated in Table 20 were based on character expression within the individual F<sub>3</sub> lines. The genotype for the specific marker characters under investigation in each cross and for reaction to U. nuda were determined simultaneously for the individual F<sub>2</sub> plants. In the crosses Plush x Jet and Vantage x Jet the same F<sub>2</sub> plants were also classified as to genotype for reaction to U. nigra and U. hordei.

1) Linkage group VIIA now known to be located on barley chromosome #6, (see Appendix).

Four class dihybrid groupings were made based on the genotypic analysis of F<sub>2</sub> plants for smut reaction and each of the linkage markers used. The chi-square treatment outlined by Mather (16) was applied to each set of F<sub>2</sub> data. Chi-square values from F<sub>2</sub> populations of less than 100 plants were corrected for continuity by the method described by Goulden (8). Information obtained from the chi-square tests was used in an attempt to verify the reported mode of inheritance of the various marker characters in the varieties studied, and to determine possible associations between the genes conditioning the marker characters and those conditioning reaction to the smut species.

EXPERIMENTAL RESULTS AND DISCUSSION

Vantage x Jet

The parents of the cross Vantage x Jet differed in marker characteristics of 4 of the 7 barley linkage groups and also in their reactions to U. nuda, U. nigra and U. hordei. Vantage has white lemma and pericarp, covered kernel, six-rowed spike and is resistant to P.graminis tritici and susceptible to the three smut species. Jet has a black lemma and pericarp, is naked, two-rowed, resistant to the smuts and susceptible to P.graminis tritici. The four marker-characters have been reported conditioned by single factor pairs (27,40). The resistance of Jet to each of the three smut species was shown in Section 1 to be conditioned by single factor pairs.

A summary of chi-square tests for the mode of inheritance of the genes conditioning the marker characters and the interrelationship of these genes with those conditioning resistance to the three smut species is presented in Table 21.

Table 21. Chi-square tests of the mode of inheritance and relationships of characters in the cross Vantage x Jet.

Character Pairs	n	Component	Chi-sq.	D.F.	P Value
Reaction to <u>U. nuda</u> , ( <u>Un6un6</u> ), vs. reaction to <u>P.gram.tritici</u> , ( <u>Tt</u> ). where a = 99, b = 26, c = 22, d = 9	156	<u>Un6un6-3:1</u>	2.1880	1	.20 - .10
		<u>Tt - 3:1</u>	.5470	1	.50 - .30
		Linkage	.8233	1	.50 - .30
		<u>9:3:3:1</u>	1.6583	3	.70 - .50
Reaction to <u>U. nuda</u> , ( <u>Un6un6</u> ), vs. hull condition ( <u>Nn</u> ). where a = 99, b = 26, c = 23, d = 10	148	<u>Un6un6-3:1</u>	1.4261	1	.30 - .20
		<u>Nn - 3:1</u>	.4135	1	.70 - .50
		Linkage	.2278	1	.70 - .50
		<u>9:3:3:1</u>	2.0674	3	.70 - .50

Table 21 continued

Character Pairs	n	Component	Chi-sq.	D.F.	P Value
Reaction to <u>U.nuda</u> , ( <u>Un6un6</u> ), vs. lemma color, ( <u>Bb</u> ). where a = 94, b = 30, c = 28, d = 5.	157	<u>Un6un6-3=1</u>	1.3269	1	.30 - .20
		<u>Bb - 3=1</u>	.6135	1	.50 - .30
		Linkage	.8669	1	.80 - .70
		<u>9=3=3=1</u>	2.8073	3	.50 - .30
Reaction to <u>U.nuda</u> , ( <u>Un6un6</u> ), vs. 2-or6-rowed, ( <u>Vv</u> ). where a = 85, b = 29, c = 23, d = 6.	143	<u>Un6un6-3=1</u>	1.6993	1	.20
		<u>Vv - 3=1</u>	.0209	1	.90 - .80
		Linkage	.1522	1	.90
		<u>9=3=3=1</u>	1.8724	3	.70 - .50
Reaction to <u>U.nigra</u> , ( <u>Ung ung</u> ), vs. reaction to <u>P.gram.tritici</u> , ( <u>Tt</u> ). where a = 48, b = 7, c = 11, d = 2.	68	<u>Ung ung-1=3</u>	0.9607	1	.50 - .30
		<u>Tt - 3=1</u>	4.4117	1	.05 - .02*
		Linkage	0.1633	1	.70 - .50
		<u>9=3=3=1</u>	5.5357	3	.20 - .10
Reaction to <u>U.nigra</u> , ( <u>Ung ung</u> ), vs. hull condition, ( <u>Nn</u> ). where a = 66, b = 18, c = 14, d = 5.	103	<u>Ung ung-1=3</u>	2.3592	1	.20 - .10
		<u>Nn - 3=1</u>	2.0226	1	.20 - .10
		Linkage	.2427	1	.70 - .50
		<u>9=3=3=1</u>	4.6245	3	.20
Reaction to <u>U.nigra</u> , ( <u>Ung ung</u> ), vs. lemma color, ( <u>Bb</u> ). where a = 62, b = 21, c = 14, d = 6.	103	<u>Ung ung-1=3</u>	1.3564	1	.30 - .20
		<u>Bb - 3=1</u>	.3915	1	.70 - .50
		Linkage	.1305	1	.80 - .70
		<u>9=3=3=1</u>	1.8784	3	.70 - .50
Reaction to <u>U.nigra</u> , ( <u>ung ung</u> ), vs. 2- or 6-rowed, ( <u>Vv</u> ). where a = 50, b = 19, c = 13, d = 5.	87	<u>Ung ung-3=1</u>	0.6475	1	.50 - .30
		<u>Vv - 3=1</u>	0.1877	1	.70 - .50
		Linkage	0.0012	1	.98 - .95
		<u>9=3=3=1</u>	0.8364	3	.90 - .80
Reaction to <u>U.hordei</u> , ( <u>Uh<sub>1</sub>uh<sub>1</sub></u> ), vs. reaction to <u>P.gram.tritici</u> , ( <u>Tt</u> ). where a = 42, b = 6, c = 18, d = 3.	69	<u>Uh<sub>1</sub>uh<sub>1</sub>-1=3</u>	0.8164	1	.50 - .30
		<u>Tt - 3=1</u>	4.6425	1	.05 - .02*
		Linkage	0.0144	1	.95 - .90
		<u>9=3=3=1</u>	5.4733	3	.10 - .05
Reaction to <u>U.hordei</u> , ( <u>Uh<sub>1</sub>uh<sub>1</sub></u> ), vs. hull condition, ( <u>Nn</u> ). where a = 57, b = 15, c = 23, d = 9.	104	<u>Uh<sub>1</sub>uh<sub>1</sub>-1=3</u>	1.8461	1	.20 - .10
		<u>Nn - 3=1</u>	.2051	1	.70 - .50
		Linkage	.6153	1	.50 - .30
		<u>9=3=3=1</u>	2.6665	3	.50 - .30
Reaction to <u>U.hordei</u> , ( <u>Uh<sub>1</sub>uh<sub>1</sub></u> ), vs. lemma color, ( <u>Bb</u> ). where a = 52, b = 19, c = 24, d = 9.	104	<u>Uh<sub>1</sub>uh<sub>1</sub>-3=1</u>	2.5128	1	.20 - .10
		<u>Bb - 3=1</u>	.2051	1	.70 - .50
		Linkage	.0170	1	.90
		<u>9=3=3=1</u>	2.7349	3	.50 - .30

Table 21 continued

Character Pairs	n	Component	Chi-sq.	D.F.	P Value
Reaction to <u>U. hordei</u> , ( <u>Uh<sub>4</sub>uh<sub>4</sub></u> ), vs. 2- or 6-rowed, ( <u>Vv</u> ). where a = 44, b = 12, c = 19, d = 11.	86	<u>Uh<sub>4</sub>uh<sub>4</sub></u> -1:3	3.9689	1	.05 - .02*
		<u>Vv</u> - 3:1	0.0620	1	.90 - .80
		Linkage	2.9767	1	.10 - .05
		9:3:3:1	7.0076	3	.10 - .05

Examination of the data presented in Table 21 revealed that the marker characters hull-condition (Nn), lemma color (Bb), and spike-row number (Vv), were each conditioned by single factor pairs. The P values for the Tt components, when this factor pair was considered in combination with the factor pairs conditioning reaction to U. hordei and U. nigra, were below the .05 limit; in spite of the fact that the correction for continuity had been applied to the corresponding chi-square values. It was assumed that in these two cases the size of the F<sub>2</sub> populations were too small for an accurate interpretation to have been made of the segregation for the Tt factor pair. When considered with the factor pair Un<sub>6</sub> un<sub>6</sub>, in which 156 F<sub>2</sub> plants were classified, segregation for the factor pair conditioning reaction to P. graminis tritici was in good agreement with the monofactorial ratio.

The P values for the goodness of fit tests of the data to the 9:3:3:1 ratios indicated that the factors conditioning reaction to U. nuda, U. nigra and U. hordei were independent of those conditioning the marker characters. These results were confirmed by the results from the linkage tests, as no deviations from independence were detected between the marker characters and the smut reaction factors.

Plush x Jet

In the cross Plush x Jet, chi-square tests for segregation and linkage were conducted involving the factor pairs conditioning reaction to U. nuda, U. nigra and U. hordei and the factor pair conditioning rough vs. smooth awns, (Rr), on linkage group V. The character rough vs. smooth awns has been reported to be controlled by a single gene pair (27). A summary of these tests is presented in Table 22.

Table 22. Chi-square tests of the mode of inheritance of the factor pair Rr, conditioning reaction to rough awn, and the interrelationship of this factor pair with the Jet smut resistance genes.

Character Pair	n	Component	Chi-sq.	D.F.	P value
Reaction to <u>U.nuda</u> , ( <u>Un<sub>6</sub>un<sub>6</sub></u> ), vs. awn condition, ( <u>Rr</u> ). where a = 93, b = 16, c = 26, d = 11.	147	<u>Rr</u> - 3:1	0.0204	1	.90 - .80
		<u>Un<sub>6</sub>un<sub>6</sub></u> -3:1	1.0975	1	.50 - .30
		Linkage	3.0000	1	.10 - .05
		9:3:3:1	4.1179	3	.30 - .20
Reaction to <u>U.hordei</u> , ( <u>Uh<sub>1</sub>uh<sub>1</sub></u> ), vs. awn condition, ( <u>Rr</u> ). where a = 33, b = 32, c = 12, d = 5.	82	<u>Rr</u> - 3:1	0.5853	1	.50 - .30
		<u>Uh<sub>1</sub>uh<sub>1</sub></u> -1:3	16.6504	1	less than .01
		Linkage	3.6639	1	.20 - .10*
		9:3:3:1	20.8996	3	less than .01*
Reaction to <u>U.nigra</u> , ( <u>Ung ung</u> ), vs. awn condition, ( <u>Rr</u> ). where a = 47, b = 19, c = 15, d = 3.	84	<u>Rr</u> - 3:1	0.3968	1	.70 - .50
		<u>Ung ung</u> 1:3	0.0158	1	.95 - .90
		Linkage	0.8941	1	.50 - .30
		9:3:3:1	1.3067	3	.80 - .70

According to the data presented in Table 22, awn condition, reaction to U. nuda and reaction to U. nigra were each controlled by a single gene pair. However, a poor fit to a 1:3 ratio was obtained for the segregation of Uh<sub>1</sub> uh<sub>1</sub>. In view of the poor fit to a 1:3 ratio obtained previously, (Table 7), this result was not unexpected. The failure of

the Uh<sub>4</sub> uh<sub>4</sub> component to fit a 1:3 ratio was attributed, in Section 1, to the low percentage of infection in the F<sub>3</sub> lines inoculated with U. hordei. Since the same hybrid population was used in both tests the deviation noted here could be explained on the same basis. This same reason is also suggested to account for the apparent linkage between the Uh<sub>4</sub> uh<sub>4</sub> and Rr factor pairs, (Table 22).

The P values for the goodness of fit tests to the 9:3:3:1 ratios and for the linkage tests (Table 22), indicated that there was no association between the factors conditioning reaction to U. nuda or U. nigra and those controlling awn condition.

#### Colsess I x Jet

The cross Colsess I x Jet involved the genes conditioning hoods vs. awns, (Kk), a marker character on linkage group IV, and the Jet gene pair conditioning reaction to U. nuda, (Un<sub>6</sub> un<sub>6</sub>). Both of the character pairs have been shown to be conditioned by single gene pairs (27,29). The factorial constitutions of Colsess I and Jet are un<sub>6</sub> un<sub>6</sub>, KK and Un<sub>6</sub> Un<sub>6</sub>, kk respectively.

The range of infection of 100 F<sub>2</sub> plants of the cross Colsess I x Jet, grown as F<sub>3</sub> rows of 20 plants each, was between 17 and 29 percent. Based on these infection percentages the genetic classes for reaction to U. nuda were established as follows: F<sub>3</sub> lines with no infection were classed as Un<sub>6</sub> Un<sub>6</sub>; those with up to 29 percent infection were classed as Un<sub>6</sub> un<sub>6</sub> and those with more than 29 percent infection were classed as un<sub>6</sub> un<sub>6</sub>.

The chi-square values for the action of the two factor pairs, Un<sub>6</sub> un<sub>6</sub> and Kk are presented in Table 23.



Table 23. Chi-square values for inheritance of the factor pair conditioning reaction to U. nuda and hood-awn condition, (Kk), in the cross Colseess I x Jet.

Reaction Classes	Component	Chi-square	D.F.	P Value
n = 178	Seg. for <u>Un<sub>6</sub>un<sub>6</sub></u>	1.2659	1	.30 - .20
113:27:27:11	Seg. for <u>Kk</u>	1.2659	1	.30 - .20
	Seg. for Linkage	1.5605	1	.30 - .20
	9:3:3:1 seg.	4.0923	3	.30 - .20

The chi-square values and corresponding P values indicated normal 3:1 segregations for both the Un<sub>6</sub>un<sub>6</sub> and Kk gene pairs. The non-significant chi-square for the linkage component indicated that there was no association between the factor pair conditioning reaction to U. nuda and the Kk gene pair located on linkage group IV.

#### Triple-awned-lemma x Jet

The cross was made for the purpose of determining possible linkage relationships between the genes conditioning the marker character normal vs. triple-awned-lemma, (Tr tr), located on linkage group I, and the gene pair Un<sub>6</sub>un<sub>6</sub>. The marker character Tr tr has been shown to be conditioned by a single gene pair (28).

The range of infection of 105 F<sub>2</sub> plants of the cross Triple-awned-lemma x Jet grown as F<sub>3</sub> rows, was between 11 and 24 percent. Based on these infection percentages the genetic classes for reaction to U. nuda were established as follows: F<sub>3</sub> lines with no infection were classed as Un<sub>6</sub>Un<sub>6</sub>; those with up to 24 percent infection were classed as Un<sub>6</sub>un<sub>6</sub> and those with more than 24 percent infection were classed as un<sub>6</sub>un<sub>6</sub>.

The chi-square values for the action of the two factor pairs Un<sub>6</sub> un<sub>6</sub> and Tr tr are presented in Table 24.

Table 24. Chi-square values for inheritance of the factor pair conditioning reaction to U. nuda and those conditioning lemma-awn condition, (Tr tr), in the cross Triple-awn-lemma x Jet.

Reaction Classes	Component	Chi-square	D.F.	P Value
n = 141 90:23:22:6	Seg. for <u>Un<sub>6</sub>un<sub>6</sub></u>	1.4775	1	.30 - .20
	Seg. for <u>Tr tr</u>	1.9881	1	.20 - .10
	Seg. for <u>Linkage</u>	0.0638	1	.80
	9:3:3:1 seg.	3.5294	3	.50 - .30

The chi-square values and corresponding P values indicated normal 3:1 segregations for both the Un<sub>6</sub> un<sub>6</sub> and Tr tr factor pairs. The P values for the goodness of fit test to the 9:3:3:1 ratio and for the test of linkage indicated no association between the factor pair conditioning reaction to U. nuda and the factor pair Tr tr.

Orange lemma x Jet

The variety Orange lemma possesses the factor pair bb, the colorless allele of BB for black lemma possessed by Jet. However, this character is not evident in the presence of the factor for orange lemma. Buckley (1) reported evidence of a loose linkage between orange lemma and rachilla hair, placing the character orange lemma in linkage group V. Orange lemma has recently been assigned to linkage group IIIA, (Robertson, D.W. pers. comm.); which is now known as barley chromosome #6, (see Appendix).

Plants were classified for orange lemma before the melanin pigment developed in plants possessing the Jet gene for black lemma and pericarp.

The range of infection of 123 F<sub>2</sub> plants of the cross Orange lemma x Jet grown as F<sub>3</sub> rows was between 9.0 and 27.0 percent. Based on these infection percentages the genetic classes for reaction to U. nuda were established as follows: F<sub>3</sub> lines with no infection were classed as Un<sub>6</sub> Un<sub>6</sub>; those with up to 27 percent infection were classed as Un<sub>6</sub> un<sub>6</sub> and those with more than 27 percent infection were classed as un<sub>6</sub> un<sub>6</sub>.

The chi-square values for the action of the two factor pairs, Un<sub>6</sub> un<sub>6</sub> and Oo are presented in Table 25.

Table 25. Chi-square values for inheritance of the factor pair conditioning reaction to U. nuda and those conditioning orange lemma, Oo, in the cross Orange lemma x Jet.

Reaction Classes	Component	Chi-square	D.F.	P Value
n = 173 110:26:29:8	Seg. for <u>Un<sub>6</sub>un<sub>6</sub></u>	2.6377	1	.20 - .10
	Seg. for <u>Oo</u>	1.2042	1	.30 - .20
	Seg. for Linkage	0.1853	1	.70 - .50
		4.0272	3	.30 - .20

The chi-square values and corresponding P values indicated normal 3:1 segregations for both the Un<sub>6</sub> un<sub>6</sub> and Oo factor pairs. The data from Table 25 also indicated complete lack of association between the two factor pairs.

#### Glossy-seedling 2B x Jet

The cross Glossy-seedling 2B x Jet involved the factor pair

glossy vs. normal seedling, (a marker on linkage group IV), and the factor pair Un<sub>6</sub> un<sub>6</sub>, conditioning reaction to U. nuda. The character glossy-seedling has been shown to be conditioned by a single gene pair designated G<sub>12</sub> g<sub>12</sub> (27).

Compared to phenotypically normal plants, F<sub>2</sub> plants of the genotype g<sub>12</sub> g<sub>12</sub> were weak throughout all stages of their growth. Sterility in U. nuda inoculated heads of these plants made the task of obtaining inoculated F<sub>3</sub> seed extremely difficult. Less than 10 of the 155 F<sub>2</sub> plants classified were of the genetic constitution g<sub>12</sub> g<sub>12</sub>. This number was not considered a true indication of the segregation for this character. Data from this genotypic class were therefore not included in the tests of association. The inheritance and linkage relationships of the factor pairs under consideration were determined by comparing the numbers of F<sub>2</sub> plants in the genotypic classes, (excluding the three classes containing the recessive g<sub>12</sub> g<sub>12</sub> gene pair), with the numbers expected based on independent segregation of the two factor pairs.

The range of infection of F<sub>2</sub> plants of the cross Glossy-seedling 2B x Jet was between 18.0 and 31.0 percent. Based on these infection percentages the genetic classes for reaction to U. nuda were established as follows: F<sub>3</sub> lines with no infection were classed as Un<sub>6</sub> Un<sub>6</sub>; those with up to 31.0 percent infection were classed as Un<sub>6</sub> un<sub>6</sub> and those with more than 31.0 percentage infection were classified as un<sub>6</sub> un<sub>6</sub>.

The numbers of plants observed in the F<sub>2</sub> genotypic classes and the numbers expected based on independent assortment of the two factor pairs, are presented in Table 26.

Table 26. Observed and expected plants in 6 F<sub>2</sub> genotypic classes of the cross Glossy-seedling 2B x Jet.

Number of F <sub>2</sub> plants	$\frac{Un_6G1_2}{Un_6G1_2}$	$\frac{Un_6G1_2}{Un_6g1_2}$	$\frac{Un_6G1_2}{un_6G1_2}$	$\frac{Un_6G1_2}{un_6g1_2}$	$\frac{un_6G1_2}{un_6G1_2}$	$\frac{un_6G1_2}{un_6g1_2}$
Observed	17 1	31 2	20 2	40 4	11 1	21 2
Expected	11.33	22.66	22.66	45.32	11.33	22.66

Since the factors Un<sub>6</sub> Un<sub>6</sub> and G1<sub>2</sub> G1<sub>2</sub> entered the cross in the coupling phase, linkage would tend to keep them together. This would result in an increased number of F<sub>2</sub> plants in the Un<sub>6</sub> G1<sub>2</sub>/Un<sub>6</sub> G1<sub>2</sub> and Un<sub>6</sub> G1<sub>2</sub>/un<sub>6</sub> g1<sub>2</sub> genotypic classes and a corresponding decrease in the numbers of plants in the remaining classes. The data in Table 26 reveal only a slight excess in numbers in the two classes in which the Un<sub>6</sub> Un<sub>6</sub> gene pair was in the homozygous dominant condition and a reasonably close fit to the expected in the remaining classes. Disease escape is suggested to account for the increased number of F<sub>2</sub> plants in the smut resistant classes.

The numbers of F<sub>2</sub> plants classified as homozygous and heterozygous for the factor pair G1<sub>2</sub> g1<sub>2</sub> were 48 and 92 respectively. These totals fitted a 1:2 ratio with a chi-square value of 0.0056 and a corresponding P value between .95 and .90. These data indicate a normal monofactorial segregation for the G1<sub>2</sub> g1<sub>2</sub> factor pair.

The observed data in Table 26 fitted a 1:2:2:4:1:2 ratio with a chi-square value of 6.9840. The corresponding value of P for 5 degrees of freedom was within the .30 - .20 range. This was considered satisfactory evidence that the factor pairs G1<sub>2</sub> g1<sub>2</sub>

and Un<sub>6</sub> un<sub>6</sub> were independently inherited.

Colsess V x Jet

The parents of the cross Colsess V x Jet differed in the genes conditioning normal vs. chlorina seedling, (a marker character on linkage group VII), and in their reaction to U. nuda. The character chlorina-seedling has been shown to be conditioned by a single gene pair designated Fc fc (25).

The difficulties encountered in obtaining U. nuda inoculated F<sub>3</sub> seed from genotypically recessive F<sub>2</sub> plants in the previous cross, Glossy-seedling 2B x Jet, were also encountered in this cross. Only a single F<sub>2</sub> plant of the 199 classified for the factors Un<sub>6</sub> un<sub>6</sub> and Fc fc was of the constitution fc fc. This genotypic class was subsequently eliminated from the F<sub>2</sub> data.

The inheritance and linkage relationships of the two factors under consideration were determined by methods described for the previous cross. The range of infection of F<sub>2</sub> plants of the cross Colsess V x Jet was between 9 and 25 percent. Based on these infection percentages the genetic classes for reaction to U. nuda were established as follows: F<sub>3</sub> lines with no infection were classed as Un<sub>6</sub> Un<sub>6</sub>; those with up to 25 percent infection were classed as Un<sub>6</sub> un<sub>6</sub> and those with more than 25 percent infection were classed as un<sub>6</sub> un<sub>6</sub>.

The numbers of observed plants in the F<sub>2</sub> genotypic classes and the numbers expected based on independent segregation of the two factor pairs are presented in Table 27.

Table 27. Observed and expected plants in 6 F<sub>2</sub> genotypic classes of the cross Colseess V x Jet.

Numbers of F <sub>2</sub> Plants	$\frac{Un_6Fc}{Un_6Fc}$	$\frac{Un_6Fc}{Un_6fc}$	$\frac{Un_6Fc}{un_6Fc}$	$\frac{Un_6Fc}{un_6fc}$	$\frac{un_6Fc}{un_6Fc}$	$\frac{un_6Fc}{un_6fc}$
Observed	21 1	51 2	28 2	49 4	15 1	34 2
Expected	16.5	33	33	66.0	16.5	33

The numbers of F<sub>2</sub> plants classified as heterozygous and homozygous for the factor pair Fc fc were 64 and 134 respectively. The chi-square test for goodness of fit of these data to a 1:2 ratio gave a value of 0.0958 and a corresponding P value between .80 and .70. This was considered satisfactory evidence of a monofactorial ratio for the Fc fc factor pair.

The chi-square value for the fit of the observed data presented in Table 27 to a 1:2:2:1:1:2 ratio was 11.0724. For 5 degrees of freedom this value corresponded to a P value of .05. Based on this evidence it was concluded that there was no association between the factor pair conditioning reaction to U. nuda and the factor pair on linkage group VII conditioning reaction to chlorina-seedling.

### GENERAL DISCUSSION

Throughout the investigations inoculation and seeding methods were designed to provide optimum conditions for smut infection. Although no actual determinations were made concerning the effect of environment on infection, there were some inconsistencies in the results from inoculations with the seedling-infecting smuts which could be explained on the basis of environmental influences.

Infections with U. hordei and U. nigra appeared to be readily affected by slight changes in light intensity and temperature, both at the time of germination and throughout the growth of the host. Material seeded in the greenhouses in midwinter invariably showed heavier infection than that sown in the early fall or early spring seasons. Amount of infection on material grown within certain areas in the greenhouses varied depending on the immediate environment. This effect was often reversed, depending upon the season in which the tests were being conducted. This influence was reflected in the results obtained from tests of the F<sub>1</sub> and F<sub>2</sub> generations of the cross Vantage x Jet inoculated to U. hordei and U. nigra. Plants grown from inoculated F<sub>1</sub> seeds that had been sown in the early fall of 1958 were poorly infected; whereas tests of the F<sub>2</sub>, sown in mid-December, were heavily infected. While allowances were made for these inconsistencies of infection in the interpretation of certain phases of the results, their effects were not considered of sufficient influence to have affected the over-all interpretations derived from this phase of the study.



It has been suggested (15,35), that reduced U. nuda infections in the F<sub>2</sub> generations of crosses between resistant and susceptible varieties and in progeny lines from plants heterozygous for U. nuda reaction, resulted from interference with fungal penetration by the resistant maternal tissues surrounding the embryo. However, it is reasonable to assume that reduction in the germination of the smut infected seeds, selective mortality of infected plants or selectivity in the mortality of flowers following inoculations could also be responsible. Schaller (35) noted a definite reduction in plant numbers in susceptible and segregating F<sub>3</sub> rows compared to resistant rows in a cross of Newal x Trebi; he also found that the total mortality of inoculated flowers was fairly great. Konzak (13) has shown that seed viability following inoculation with U. nuda and "inherent reaction" to U. nuda are separate phenomena. No associations were detected between the factors conditioning the two phenomena in three crosses, (two of them involving Jet), inoculated with two loose smut cultures. He also suggested that the variety Jet probably possesses a "dominant trait" which apparently conditions survival ability following inoculation with U. nuda. This suggestion was confirmed by the results obtained in the present investigation. U. nuda infections in the F<sub>2</sub> and F<sub>3</sub> generations of the crosses involving Jet were high for material of this type. An equally high degree of infection was observed in the F<sub>2</sub> generations of crosses between Newal and the U. nuda immune varieties Bifarb, Kitchin, C.I.5798 and Nigrinudum (Table 13). These results were

interpreted as an indication that, not only Jet but also the loose smut immune varieties of Abyssinian origin, and the variety Kitchin, possessed the "trait" contributing to survival ability. Since a gene common to each of these varieties was found to condition reaction to culture Un 49 - 68 of U. nuda this interpretation suggested that an association existed between the factors conditioning the two phenomena in the immune varieties tested.

In the investigation involving the associations between the factors in Jet conditioning resistance to the three smut species, the interpretations of the distributions of the  $F_3$  lines of the two crosses Vantage x Jet and Plush x Jet, inoculated to U. nuda, indicated a single gene was responsible for resistance to culture Un 49-68. The relatively low infection percentages in the  $F_2$  generations and the large number of  $F_3$  lines with low infection percentages suggested that the gene was dominant in effect. These results were in agreement with those presented by Schaller (35), Skoropad and Johnson (39), Stefansson (41) and Konzak (13) in studies of the inheritance of resistance of the Jet type of smut reaction to virulent Trebi-attacking cultures of U. nuda. The recessive monogenic hypothesis proposed for the inheritance of the Jet gene conditioning reaction to culture Uh 47-64-4 of U. hordei was in agreement with the results presented by Wells (47) in studies of the inheritance of reaction of the Jet gene for resistance to "race" 6 of U. hordei. The discovery that the Jet resistance to culture Ung 49-6-2 of U. nigra was conditioned by a recessive gene represents, to the writer's

knowledge, the first successful attempt at determining the mode of inheritance of resistance to U. nigra. Since no symbols have as yet been assigned to the genes conferring reaction to U. nigra the symbol Ung ung is suggested for this factor pair. The Jet gene for U. nigra resistance to culture Ung 49-6-2 would therefore be designated ung.

The fact that resistance to each of the three smut species is simply inherited demonstrates the desirability of the variety Jet as a source of smut resistance since simply inherited resistances are generally more readily utilized than those of a more complex nature.

Because of the low level of infection of the  $F_3$  lines inoculated to U. hordei, some doubt might possibly exist as to the validity of the interrelationships established for the factor pair combinations Uh<sub>1</sub> uh<sub>1</sub> vs. Un<sub>6</sub> un<sub>6</sub>, Uh<sub>1</sub> uh<sub>1</sub> vs. Ung ung and Ung ung vs. Un<sub>6</sub> un<sub>6</sub>. However, the evidence presented in Tables 9 and 10 appear to be strongly in favor of the hypotheses established; that a strong linkage exists between the recessive factor pairs in Jet conditioning reaction to the seedling-infecting smuts, and that the two recessive factor pairs are independent of the dominant factor in Jet conditioning reaction to U. nuda. The following evidence, although not obtained from the present investigations, is being presented in support of the above linkage hypotheses. Certain specific advanced generation lines from Jet hybrids developed at Brandon have shown resistance to individual smut species while others

have shown resistance to combinations of the three smut species that attack barley. In limited tests to several cultures of both U. nigra and U. hordei the hybrid Br.5479-754 has shown the Jet type of resistance to U. hordei but susceptibility to U. nigra. A sister selection Br.5479-680 has proven to be susceptible to both of the seedling-infecting smuts. Both selections are resistant to the Trebi-attacking cultures of U. nuda (Table 11). Segregation for the three resistance genes has obviously resulted in complete separation of the U. hordei and U. nigra resistance factors in the case of hybrid Br.5479-754; the gene conditioning resistance to U. hordei having been combined with the U. nuda resistance gene. From the practical point of view a less fortunate segregation has occurred in the case of hybrid Br.5479-680 with only a single resistance gene having been retained from the variety Jet.

The fact that Jet, Nigrinudum, Kitchin, Bifarb and C.I.5798 have a gene pair in common conditioning U. nuda resistance whereas the resistances of Valkie-trd. and Brachytic-119 were shown to differ from the Jet type will no doubt prove of value to plant breeders interested in using one or more of these varieties as breeding stocks. In cases where the Jet-type gene is required, breeders now have a choice of breeding material. The comparative value of the five varieties as breeding stocks will no doubt be influenced by variety preference for such features as disease reaction and other agronomic qualities.

It was demonstrated that Valkie-trd. and Brachytic-119 have potential value as sources of smut resistance genes supplementary

to the Jet gene. These two varieties will be particularly useful as sources of resistance genes in areas where the prevalent U. nuda cultures are similar in virulence to Un 49-68.

The fact that the four varieties Jet, Nigrinudum, C.I.5798 and Bifarb, all of Abyssinian origin, possess loose smut resistance factors in common is of interest also from an historical standpoint. It is probable that the deficiens-type variety used by Dr. H. V. Harlan at Minnesota in 1914 to produce Kitchin, (see "Varieties", Section 2), was also of Abyssinian origin since several Abyssinian barley stocks had been brought to the United States by Harlan prior to that date.

The similarity of the genetics of U. nuda resistance in the varieties Jet and Nigrinudum, two morphologically identical barley types, suggests that the two are one variety. Dr. D. W. Robertson has pointed out to the writer, (pers. comm.), that Jet originated from two barley seeds which were selected by Harlan from a mixed lot of barley obtained from Abyssinia. These two seeds probably originated from the Abyssinian stock of the variety Hordeum distichon nigrinudum, from which Nigrinudum was eventually selected (26).

The monohybrid ratios that were established for the segregation of the marker characters of the barley linkage group tester-stocks were in agreement with previously published results (27,28,29,40). The relationships between the Jet genes conditioning resistance to U. nuda and U. hordei and those conditioning the various marker characters were also in fairly close agreement with previous findings.

Of particular interest from the marker-gene linkage study was

the phase concerned with the linkage relationships between the Jet factor pair conditioning reaction to U. nuda and the factor pair conditioning reaction to P.graminis tritici. Shands (37) reported a linkage between the genes conditioning the Trebi type of loose smut resistance and stem rust susceptibility in a cross involving Chevron. The factor pairs were located on linkage group VII (28). The present investigation indicated lack of association between the factor pairs Un<sub>6</sub> un<sub>6</sub> and Tt, (Table 21). These results suggest that the Trebi and Jet factor pairs conditioning reaction to U. nuda are independent and that the Jet gene pair is either independent of linkage group VII or is located at too great a distance from the marker gene for the association to have been readily detected. Lack of association between the Un<sub>6</sub> un<sub>6</sub> factor pair and the Fc fc marker gene pair on linkage group VII, (Table 27), also indicated independence of the Un<sub>6</sub> un<sub>6</sub> factor pair from linkage group VII.

Mohajir et. al (17) obtained what they referred to as "a suggestion" of an association between loose smut reaction and spike row number in crosses in which Jet was involved. The results from the present investigation failed to confirm this suggestion. In the cross Vantage x Jet the factor pairs Vv and Un<sub>6</sub> un<sub>6</sub> were found to be completely independent. In the same cross the factor pairs Kk and Un<sub>6</sub> un<sub>6</sub> were also found to be independent. Thus the suggestion by Poehlman (22) of an association between hooded character and U. nuda resistance was also not confirmed by the results presented here.

The lack of association between the factor pair conditioning reaction to U. nuda and the factor pairs conditioning lemma color, (Bb), awn condition, (Rr) and hull condition, (Nn) were in agreement with previous results (28,29). The relationships between the factor pair conditioning reaction to U. nuda and the factor pairs conditioning glossy seedling, (Gl<sub>2</sub> gl<sub>2</sub>), orange lemma (Oo), and triple-awned lemma, (Tr tr), had not been investigated previously.

Wells (47) was unable to detect associations between the Jet factor pair Un<sub>1</sub> un<sub>1</sub> conditioning reaction to "Race 4" of U. hordei and the factor pairs conditioning spike row-number, Vv, and lemma color, Bb. His results were confirmed by the findings of this study. The present investigation also indicated complete independence of the Uh<sub>1</sub> uh<sub>1</sub> factor pair and the factor pairs conditioning reaction to Puccinia graminis tritici, (Tt) and hull condition, (Nn). These relationships had not been studied previously.

The lack of association between the Jet factor pair conditioning reaction to U. nigra and the factor pairs conditioning the marker characters Tt, Vv, Bb, and Nn were not unexpected in view of the close association detected between the factor pairs conditioning reaction to U. hordei and U. nigra. These relationships were also being investigated for the first time.

With regard to the conduct of future investigations of the type presented here the following suggestions are offered.

Considerable care should be exercised in the selection of varieties for future investigations. It is anticipated, in view of the results obtained from these studies, that additional resistance factors could

probably be expected from varieties of diverse origin. While it would probably be of interest from an historical point of view to study the resistance genes of related varieties, the value of such investigations in breeding for resistance would be rather limited.

It would probably be of advantage to study fewer crosses in future investigations. Those studied could be explored more thoroughly however. Experience from the present investigation has indicated that hybrid populations could probably have been tested to more than a single culture of each smut species since only a relatively small proportion of the spikes and seed produced, by the plants tested, were utilized. This approach would increase the scope of the investigations with little additional effort.

It is apparent from the present investigations that where combinations of disease reaction factors are involved, such as occurred in the present investigation when the factors conditioning reaction to the smuts were combined with those conditioning reaction to stem rust, a relatively large number of  $F_3$  lines is required in order to interpret accurately the combined factor segregation. A minimum of one hundred and fifty  $F_3$  lines is suggested.



SUMMARY

The mode of inheritance of the resistance of the variety Jet to cultures Un 49-68 of U. nuda, Ung 49-6-2 of U. nigra and Uh 47-64-4 of U. hordei, and the interrelationships of the genes conditioning resistance to the three smut species, were studied in hybrids between Jet and the varieties Vantage and Plush. In the inheritance investigations the hybrid material was tested for reaction to the seedling-infecting smuts in the F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> generations. Genetic interpretations were based mainly on the genotype of the F<sub>2</sub> plants when grown as F<sub>3</sub> lines. The genotypes for reaction to U. nuda, U. nigra and U. hordei were established on random F<sub>2</sub> plants from the two crosses. Interrelationships of the genes conditioning resistance to the three smut species were based on distributions of the F<sub>2</sub> plants in reaction classes established by combining, in pairs, the data from reactions to the individual smut species.

The distributions of the F<sub>3</sub> lines of both crosses indicated that the Jet reaction to the individual smut species was conditioned in each case by single factor pairs. Resistance to U. nuda was found to be dominant in effect while resistance to U. nigra and U. hordei was found to be recessive. The Jet gene conditioning resistance to U. nigra was assigned the symbol ung.

Test of association indicated that the gene pairs conditioning reaction to U. nigra and U. hordei were linked. Recombination values of 18  $\frac{1}{2}$  4.236 and 16  $\frac{1}{2}$  3.984 percent were obtained from the crosses

Vantage x Jet and Plush x Jet respectively. Linkage intensity was calculated on the basis of F<sub>2</sub> genotypic data. No associations were detected between the gene pair conditioning reaction to U. nuda and those conditioning reaction to U. hordei and U. nigra.

Hybrids involving the loose-smut-susceptible variety Newal and the resistant varieties Jet, Kitchin, Bifarb, Nigrinudum and C.I.5798 were investigated to determine the mode of inheritance of the genes conditioning the immune type of loose smut reaction of the resistant varieties. The genes conditioning the resistances of the five varieties were brought together in various combinations for the purpose of investigating their interrelationships. In addition, the interrelationships between the U. nuda resistance factor in Jet and those of the varieties Brachytic-119 and Valkie-trd. were investigated.

The distribution of the F<sub>3</sub> progenies of the hybrids Jet x Newal, Kitchin x Newal and Bifarb x Newal demonstrated the existence of a single gene for resistance to culture Un 49-68 of U. nuda in each of the varieties Kitchin, Bifarb and Jet. Evidence provided from the F<sub>2</sub> populations of these three crosses indicated that the genes were each dominant in effect. The similarity of the reactions of the F<sub>2</sub> populations of the crosses C.I.5798 x Newal and Nigrinudum x Newal with those involving Newal and the varieties Jet, Bifarb and Kitchin suggested that C.I.5798 and Nigrinudum also possessed single dominant genes conditioning reaction to culture Un 49-68 of U. nuda. Evidence provided from the resistant x resistant crosses favored the hypothesis

that the single dominant genes conditioning U. nuda reaction were at the same locus in each of the varieties Jet, Nigrinudum, Bifarb, Kitchin and C.I.5798.

The distribution of the F<sub>3</sub> progenies of the hybrids Jet x Brachytic-119 and Jet x Valkie-trd. suggested that the Jet resistance gene differed from the gene or genes conditioning resistance to culture Un 49-68 of U. nuda in Brachytic-119 and in Valkie-trd.

Evidence from investigations on the linkage relationships of the Jet genes conditioning resistance to the smuts of barley with those responsible for the inheritance of specific marker characteristics of barley demonstrated the following: complete independence of the genes conditioning resistance to cultures Un 49-68 of U. nuda, Uh 47-64-4 of U. hordei and Ung 49-6-2 of U. nigra with the genes for the following factors: spike-row number, (Vv), lemma and pericarp color (Bb), hull condition, (Nn), and inheritance of stem rust reaction, (Tt). In addition, U. nuda was found to be independent of the genes responsible for inheritance of triple-awned-lemma, (Tr tr), hooded condition, (Kk), glossy seedling, (Gl<sub>2</sub> gl<sub>2</sub>), rough awn, (Rr), orange lemma, (Oo), and chlorina seedling, (Fc fc).

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APPENDIX

A summary of the suggested designations for the barley chromosomes, presented at the Fourth American Barley Research Workers Conference at Fargo, North Dakota, U.S.A. in February 1960, is given in Table 1.

Table 1. Suggested designations for the barley chromosomes, (February, 1960)

New Chromosome designation	Previous Chrom. designation	Linkage-group	Identifying marker-gene
1. (longest-chromosome)	b	III / VII, (IIIa)	<u>Nn</u>
2.	f	I	<u>Vv</u>
3.	c	VI	<u>Uz uz</u>
4.	e	IV	<u>Kk</u>
5.	a	II	<u>Bb</u>
6. (longest-satelite)	g	VII a	<u>Oo</u>
7. (satelite)	d	V	<u>Rr</u>