THE INHERITANCE OF RESISTANCE TO USTILAGO NUDA (JENS.) K. AND S., RACE I, IN BARLEY

By

Moustapha Ibrahim Zeidan

A THESIS

Submitted to the School of Graduate Studies of Michigan
State College of Agriculture and Applied Science
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Botany and Plant Pathology

1953

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Approved ____________________

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ABSTRACT

Barley has been known for centuries as a cultivated plant used for making bread and as feed for animals. This crop is attacked by many diseases which become important factors in decreasing yields. Loose smut caused by Ustilago nuda (Jens.) K. and S. is one of these diseases.

Its control by the hot water treatment, modified hot water treatment and by organic compounds is unsatisfactory and hazardous. Consequently the use of resistant varieties is the effective method.

The present investigation was concerned with the inheritance of resistance to Ustilago nuda (Jens.) K. and S., race I, the genetic constitution of the parental varieties and the relationship between factors for resistance and those for morphological characteristics.

Four non-commercial varieties (Jet, Anoidium, Harlan, Ogalitsu) resistant to loose smut disease were crossed into all possible combinations: Jet x Harlan, Jet x Anoidium, Jet x Ogalitsu, Harlan x Ogalitsu, Harlan x Anoidium, and Ogalitsu x Anoidium. Jet has a two-rowed head, naked seeds, rough awns, a black lemma and pericarp. The others have six-rowed head, covered seeds, white lemma and pericarp. Harlan and Otalitsu have semi-smooth awns, while the awns of Anoidium are smooth.

The florets of one or two heads of F_2 plants were inoculated. One or two drops of fresh spore suspension were introduced into each floret by means of the "needle" method. The classification of F_3 families which represented the F_2 plants, into resistant, segregating and susceptible groups was made according to the percentages of infection.

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The inheritance of resistance to Ustilago nuda (Jens.) K. and S., race I, in the crosses Jet x Harlan, Harlan x Ogalitsu, Ogalitsu x Anoidium, is explained by two gene pairs acting in duplicate dominant epistatic condition. The two genes were found to be different and independently inherited. Thus, each parent possesses one dominant gene pair for resistance. One gene difference was found between two-rowed vs. six-rowed head, covered vs. naked seeds, black vs. white lemma and pericarp in the hybrids of Jet x Harlan. Also, no linkage was found to exist between factors for resistance and those for the above mentioned morphological characteristics. The inheritance of resistance in the cross Jet x Anoidium and Jet x Ogalitsu was not studied, because of the inadequate number of F_3 families. In the cross Harlan x Anoidium, the resistance was interpreted in terms of two gene pairs exhibiting dominant and recessive epistasis. The genes also were different and independently inherited. The expected ratio was 15:1 but the observed ratio was 13:3. However, the excess of susceptible F_3 families could be interpreted by the occurrence of fluctuation in some genotypes, which might be due to a change in the expression of the resistance and the susceptibility. This change might be influenced by the environment. Thus, each parent also possessed one dominant gene.

Four genes were found to govern the resistance in the four varieties used in this investigation. These genes were found to be different and to be independently inherited. There was no evidence of linkage between resistance and morphological characters.

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INTRODUCTION

The barley crop has been known for centuries as a cultivated plant for making bread and as a feed for animals. In addition, it is also used today in manufacturing items for human consumption: breakfast food, flour and spiritous liquors. Barley is grown under a wide range of environmental conditions in many countries of Asia, Europe, as well as in the United States of America.

In the United States, barley production is concentrated in the mid-west states: North Dakota, Minnesota, South Dakota, Wisconsin, Michigan, Iowa, Illinois, and in the far west in California. It was reported that California was the leading barley producer in 1951. Michigan during the same year produced 3,876,000 bushels of barley grain having a revenue of $4,692,000 which amount gives barley fourth rank after corn, wheat, and oats in crop income (1, 10, 39).

It is true that barley does not occupy first place among the small grains but it is an important crop, especially for animal consumption. Barley can compete with oats for this purpose, and in many places in the United States barley is more profitable and produces more bushels per acre than oats. Besides these benefits, barley is used for breaking new soil (23). Its early maturation allows it to be cut before many other species which have mature seed. It is also used for old lands which have become too poor for producing good crops of wheat or corn.

Barley is affected by many diseases which decrease its production quantitatively and qualitatively. Important among these barley diseases are the smut diseases (loose, semi-loose and covered).

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Of the smut diseases, loose smut caused by <u>Ustilago nuda</u> (Jens.) K. and S. is discussed in this paper. It is known (53) that within the species there are various biological forms, but the present study is confined to race I. Loose smut is not normally a dangerous disease, but it becomes an important factor in reducing the yield in those years during which the environmental conditions are favorable for the growth and the spreading of the causal fungus which occurs often in humid and subhumid areas.

It has been stated (2, 3, 9, 13, 26) that the organism hibernates within the seeds in its vegetative form. Semeniuk (62) reported that the barley yield decreases approximately in direct proportion to the percentage of smutted plants. Consequently, the control of the loose smut organism consists in destroying the dormant mycelium within the seed without damaging the viability of the embryo. It was found that the use of hot water treatment, modified hot water treatment, and of many mercuric compounds for controlling the loose smut disease (29, 32, 34, 54, 55, 57, 71) were unsatisfactory and hazardous. For these reasons, the ideal method for preventing loose smut infection would be breeding for resistance. But to be able to obtain a good stock of resistant varieties, it is important to know about the inheritance of the resistance.

Therefore, the object of this thesis is the study of the inheritance of resistance in the progenies of four varieties of barley which proved to be resistant (Table 1) to loose smut infection, determination of the genetic constitution of the parental varieties, and the relationship between the factor or factors for resistance and those for some important morphological characters.

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REVIEW OF LITERATURE

A. History of Loose Smut Organism
Ustilago nuda (Jens.) K. and S. race I

Smut history is discussed here according to Jensen (29), Kellerman and Swingle (32), Stakman (65), and Reed (48). Plimus (44) in his Naturalis Historiae discussed the effect of weather and location on smut of cereals. Dodens (15) reported that smut was found on oats and wheat. He described them an unfruitful herbs, blackened or blighted. Lobelius (46) gave two names for barley smut: Ustilago pulystichi and Ustilago hordei distychi. Persoon (43) placed the smuts among the fungi.

In the eighteenth century knowledge of the smut fungi increased among scientists, but they did not know the real difference between loose and covered smuts. Prevost, 1807 (47), found that the spores which had been considered abnormal cells of the host were able to germinate. Afterward much became known about spore structure, development of mycelium from the spore, methods of infection, and development of spores.

Dittmar (14) names the loose smut organism Ustilago segetum, while Tulasne (69, 70) named it Ustilago carbo.

The knowledge of fungi in general increased as investigators started to search for something new which would shed more light on the field of fungi. Many phenomena had been observed between the fungus and the host among which was the discovery of physiological races of well-defined morphological species of parasitic fungi, a discovery which was one of the important developments in plant pathology of that time. This distinction between these races was based upon the ability of the fungus to attack

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one host plant and not another. The first investigator to call attention to that phenomenon was Schroeter (60, 61) who, in studying spore germination of the smuts, observed an abundant production of poridia in the oat smut and covered smut of barley and who names the barley smut: Ustilago hordei. He also reported that the smut of oats was incapable of infecting the barley.

Jensen (29) gave loose smut the name Ustilago segetum var. hordei nuda; and covered the name Ustilago segetum var. hordei tecta, on the basis of difference in color, size and character of the spore mass.

Kellerman and Swingle (32) studying the germination phenomena of spores which were obtained from various loose smuts, were able to separate them into four species:

1. Loose smut of wheat - Ustilago tritici.
2. Loose smut of barley - Ustilago nuda.
3. Loose smut of oats - Ustilago avenae.
4. Covered smut of barley - Ustilago hordei.

Meanwhile, investigations on physiologic specialization advanced. Various terms had been found to apply to these races which were distinguished only by their physiological behavior in the choice of the hosts. Schroeter (60) gave the races the names of "sister species" (species sorores) and Hitchcock and Carleton (26) names them: physiological species.

Maddox (37) and Brefled (7) were the first to indicate that the infection in young ovaries of wheat and barley by Ustilago tritici and Ustilago nuda occurred at flowering time.

Rodenhiser (52, 58) reported that physiological specialization did occur with the species Ustilago nuda and Ustilago tritici, and he found more than one form in Ustilago nuda.

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Ruttle-Nebel (56) discovered abundant mycelium in the pericarp, in the crushed nucellus, in the aleruone and in the endosperm of the seed and in the scutellum and hypotocyl of the embryo. She also observed that penetration of hyphae of Ustilago nuda occurred at various points along the ovary wall.

B. Inheritance of Resistance to Ustilago nuda (Jens.) K. and S. in Hybrids

The problem of inheritance of resistance is very important for breeders and pathologists today. The first to study the inheritance of resistance and susceptibility to yellow rust (Puccinia glumarum) in the progenies was Biffen, 1905 (4) who crossed two varieties of wheat: Michigan Bronze with Rivet. The first variety was very susceptible, but the second was somewhat "immune" to the disease. From his results he concluded that the resistant character was governed by one gene and that susceptibility was dominant over "immunity".

Nahmmacher (41) crossing many resistant with susceptible varieties of barley failed to provide an exact analysis of the factors governing the reaction in the F_3 progenies.

Zeiner (74) making genetical studies of eight crosses between resistant and susceptible varieties of barley found that "immunity" or slight susceptibility to loose smut was consistently inherited according to the Mendelian ratio. In a cross between a moderately susceptible variety (Heil's Franken) and highly susceptible variety (Australian Early), he found a transgressive segregation in the direction of greater susceptibility, and he also discovered resistance was governed by one Mendelian

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factor except in one cross (Heil' Franken x Walpersi) in which resistance was found to be governed by two factors. Resistance appeared to be dominant although the evidence was not conclusive.

Livingston (35) studied the inheritance of resistance in the hybrid progenies and in subsequent generations. He adopted the partial vacuum method of inoculation described by Moore (40) throughout the investigation, and made several crosses and reciprocal crosses between susceptible and resistant varieties. He used Colsess and Missouri Early Beardless as susceptible varieties; and Trebi and Hordeum deficiens as the resistant varieties. According to the figures obtained, Trebi and H. deficiens possessed a dominant factor for resistance. When he crossed Missouri Early Beardless with either variety, Trebi or H. deficiens, a similar reaction was obtained in the F_2 generation. This similarity in reaction indicated that the factors for resistance carried by the two resistant varieties exerted a similar effect. He also found no correlation to exist between factors for resistance to loose smut and those which governed hooded and six-rowed heads.

Schaller (58) also studied the inheritance of resistance to loose smut, Ustilago nuda, in hybrids of several crosses. The varieties used were: Trebi (resistant), Newal (susceptible), Jet (resistant), and Dorsett (resistant). He used the "needle" method of inoculation described by Shands and Schaller (63). The inoculum used was collected originally from a single smutted head occurring naturally in the susceptible variety (Newal). In the cross between Trebi and Newal and their back cross, resistance in Trebi was governed by a single dominant gene. He also found similar results in the hybrids of the cross Jet x Colsess IV. But in the

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cross Dorsett with Selection x 173-10-5-6-1, he found a transgressive segregation toward susceptibility. From this it was concluded that the genes which govern the resistant characters in Dorsett and Selection 173-10-5-6-1 were different from those of Jet and Trebi which were also different from each other. His investigation showed that four gene pairs were found to be responsible for controlling the character of resistance, and that the factor of resistance was dominant over susceptibility.

C. Inheritance of Agronomic Characters

Many of the agronomic characters of barley varieties are important from an economic standpoint. Because of that importance, many investigators have studied the genetical constitution and the behavior in the progenies of crosses made for that purpose. The agronomic characters which are studied in the present paper are: two-rowed versus six-rowed heads; rough versus smooth awns; hulled versus naked seeds and black versus white lemma and pericarp of seeds.

1. Two-rowed vs. six-rowed heads. The genetical constitution of tow characters has been studied by many investigators who have emphasized the fertility of the lateral florets as the basis of their studies. All cultivated varieties of barley, according to Jessen, 1855 (30), belong to one species: *Hordeum sativum*. Buckley (8) classified the species *Hordeum sativum* into four groups on the basis of the lateral florets.

a. *Hordeum sativum vulgare*: Lateral florets completely fertile.

b. *H. sativum intermidium*: Lateral florets partially fertile.

c. *H. sativum distichon*: Lateral florets staminate.

d. *H. sativum deficiens*: Lateral florets sexless.

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Biffen (5) made several crosses between different varities of 2-rowed vs. 6-rowed heads, and in each case found that the 2-rowed differed from 6-rowed by one single factor: the 2-rowed character was dominant over 6-rowed character.

Ubisch (72) studied the segregation of 2-rowed barleys, distichon, and 6-rowed barleys, vulgare. He explained the difference between these two characters on the basis of two factors, but the dominance was not complete.

Harlan and Hayes (22) in crossing 2-rowed with 6-rowed varieties found that in most cases an intermediate form was obtained in the F_1 generation, and that the lateral florets were awned and very low in fertility. In addition, they found that segregation in the F_2 generation could be explained on the basis of a single factor difference. In a cross between Manchuria, a 6-rowed variety in which the lateral florets are fertile and long-awned, and Svanhals, a 2-rowed variety with long-awned fertile central florets and awnless, sterile lateral ones, the results supported the two factors pair hypothesis.

Engledow (16) concluded, according to his own observations which were based upon the fertility of the lateral florets, that H. deficiens, H. distichon and H. vulgare formed an allelomorphic series. The dominance existed in the order of deficiens, distichon and vulgare.

Griffee (21) too, studied the fertility of the lateral florets using H. deficiens stendelii, a 2-row variety in which the lemma and palet of of the lateral florets are slightly or not at all developed. Manchuria is a variety with 6 rows. In the F_1 generation under the field conditions, several F_1 plants showed slight development of the glumes and palets in

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the lateral florets. In the F_2 generation the plants were grouped into three types: deficiens type, intermediate, and 6-rowed in a 1:2:1 ratio. In another cross, however, Svanhals x Lion obtained results confirmed with the results found by Harlan and Hayes (24).

Gillis (19) supported the two factor hypothesis of Ubisch between 2-rowed and 6-rowed, but added a third factor, D, for fertility of the lateral florets.

Neatby (42) Tedin and Tedin (66) stated that there was one single factor difference between 2-rowed and 6-rowed heads. Robertson (49) reported the presence of a one gene difference in one cross, and the presence of a two-factor difference in another cross between 2-rowed and 6-rowed. In the latter, the dominance was incomplete. Daane (13), Livingston (35) and Schaller (58) stated one single gene difference for 2-rowed vs. 6-rowed character. Two-rowed character was dominant.

2. Naked versus covered seeds. The inheritance of the factors for naked and covered seeds has been studied extensively by many investigators who all agreed on the mode of inheritance.

Biffen (5) made several crosses finding that the difference between the hulled and naked was based upon one single factor: the hulled factor was dominant over naked. Hor (28) stated there is one single factor difference between hulled and naked character. Neatby (42) studied the hulled vs. naked conditions in the seed by crossing Guy Mayle with Canadian Thrope. The former was 6-rowed, hulless, early, short; the latter was 2-rowed, hulled, late, tall. In the F_2 generation, he found a 3:1 ratio (three hulled and one naked). He concluded that there existed

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one single factor difference between hulled vs. naked. Tedin and Tedin (66), Hayes and Garber (25), Robertson (49), Buckley (8), Daane (11), and Schaller (58) have all reported the occurrence of one single factor difference between hulled and naked: hulled was dominant over naked.

3. Rough versus smooth awns. Because of the commercial importance of rough and smooth characters their inheritance has been studied by many investigators. Harlan (22) studied the inheritance of rough vs. smooth awns and found the progenies in F_1 generation were rough. The F_2 generation segregated into three rough, one smooth. The rough character was dominant over the smooth character.

Griffee (21) also made a cross between Svanhals and Lion finding that the first had rough awns and the second had smooth awns. He reported the results obtained could be explained on a basis of three rough to one smooth.

Sigfusson (64) crosses Bearer x Lion and Chinese x Lion (Bearer and Chinese were rough awned but Lion was a smooth awned). All the F_1 generation had rough awns. In the F_2 generation, he classified four groups: rough, intermediate rough, intermediate smooth and smooth. He stated roughness in barley was controlled by two complementary factors and designated them: R and S. The rough character was expressed when R and S were together. If R factor was absent, the phenotype produced was intermediate smooth. If S factor was absent, the phenotype produced was intermediate rough. The smooth phenotype was obtained in the absence of both factors R and S.

David (12), Robertson (49), and Schaller (58) found that segregation between rough and smooth awns was based upon one single gene difference: rough character was dominant over smooth.

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4. Black lemma and pericarp versus white lemma and pericarp. The inheritance of the color in the paleae also has been studied extensively by many previous workers. Biffen (5), Griffee (21), Hays and Garber (25), Robertson (49), Buckley (8), Daane (11), Powers (46), Schaller (58) and Woodward (73), stated that black and white color in glumes differed by one single factor pair, and that black was dominant over white. Biffen (5) and Buckely (8) found that the black vs. white color of the seeds and of the palea were governed by the same gene.

D. Linkage Studies

Since the parents used in this investigation differed in several agronomic characters, it was important to study the relationships between these agronomic characters and the resistance or susceptibility. Coffman, 1931 (20) reported there was little or no correlation between lemma color and other agronomic characters, or between the factor for resistance and the factor governing lemma color.

Kilduff (33) studied the relations between the agronomic characters and the resistance to bunt in wheat by crossing Koba variety with Red Bobs variety. Koba variety, which was susceptible to bunt and loose smut, had long awns and weak straw. Red Bobs, on the other hand, resistant to bunt and loose smut, was awnless. According to the data obtained, he found no correlation between the awns factors and those for resistance and susceptibility.

Johnston (31) in the genetic study of two varieties of barley (Glabrus x Trebi) found a slight correlation between factors for smut

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infection and those for height of plants. He found, however, no linkage to exist between factors for covered smut reaction and those either for earliness of heading or barbing of awns. Giney and Tolman (68) in their study on the relationship between kernel color, glume color, and loose smut resistance of varieties of wheat, found no evidence of any relationship between the morphological characters and resistance to loose smut (Ustilago tritici). Schlehuber (59) stated that a possible leak linkage existed between smut-resistance to race I reaction and spike density, as well as between race I reaction and seed color in a cross between different varieties of wheat.

Gfeller (18) reported the lack of linkage between factors of resistance and those of awns in garnet wheat. Livingston (35) studied the relation between factors for resistance to Ustilago nuda and those for hoods or six-rowness in a cross between Missouri Early Beardless x Hordeum deficiens. He stated that there was no linkage between the factors for resistance and those for hoods or six-rowness.

Schaller (58) in his study on the inheritance of resistance to Ustilago nuda in barley, reported that no relation was found between factors for resistance and those for rough and smooth awns, black and white lemma and pericarp, two-rowed and six-rowed heads, hulled and naked seeds.

E. Infection of Hybrid Progeny

The infection of hybrids F_1 and F_2 progeny is not investigated in the present work, and before discussing how the fungal hyphae become established after infection, it would be logical to discuss the penetration of infecting hyphae into the embryo.

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Freeman and Johnson (17) investigated the life history of loose smut (Ustilago tritici) of wheat and that (Ustilago nuda) of barley using a susceptible variety of wheat (Minnesota 188) and a susceptible variety of barley (Minnesota 105). They inoculated the flowers of these varieties at different stages finding that the optimum time for maximum infection was from the time when the stamens were green to the time when the ovary was one third its natural size. After that stage the ovary wall and the aleurone layer would stop the penetration of the germ tube.

Lang. (37) after investigating the penetration of smut hyphae in a susceptible variety of barley, stated two hypotheses through which the fungus might be able to reach the embryo. The first hypothesis was that the fungus reached the embryo by direct penetration through the ovary wall; the second was that the fungus reached the embryo through the stigmatic tissues.

Ruttle (56) made some cytological studies on ovaries of Tennessee Winter barley which was resistant to the Featherston collection of Ustilago nuda. Her examinations showed that hyphae were within the pericarp. The extent of penetration into the embryo was not determined. Livingston (35) and Schaller (58) found no infection occurring in F_1 generation which indicated that the genetic constitution of F_1 embryo tissues was heterozygous for resistance, and that this condition gave the embryo complete protection which enabled it to block the penetration of hyphae.

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MATERIALS AND METHODS

In this investigation, four varieties of spring barley, provided by Dr. K. J. Frey of the Farm Crops Department, Michigan State College, were used.

1. Jet is a 2-rowed variety, with black kernels, of Abyssinian origin, and hulless.

2. Anoidium is a 6-rowed variety, with white kernels and flowering glumes, smooth awns and covered seeds.

3. Harlan is a 6-rowed variety, with white kernels and flowering glumes, semi-smooth and covered seeds.

4. Ogalitsi is also a 6-rowed variety, with white kernels and flowering glumes, semi-smooth and covered seeds.

All these varieties were tested for their reaction to the loose smut organism (Ustilago nuda (Jens.) K. and S., race I). The results are recorded in Table 1. V. F. Tapke, at Beltsville, Maryland, also studied the reaction of Jet, Ogalitsu, Anoidium varieties of barley to Ustilago nuda race I. The results which he obtained (Table 2) were confirmed by the author as shown in Table 1 in this study.

The organism (Ustilago nuda (Jens.) K. and S., race I) was first supplied by Dr. V. F. Tapke* and maintained fresh on susceptible varieties in the green house and in the field.

The four varieties were crossed into the six possible combinations, as follows:

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*Senior Pathologist, U.S.D.A., B.P.I.S.A.E.

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Table 1. Reaction of Parental Varieties and o.A.C. 21 Inoculated Artificially with Ustilago nuda (Jens.) K. and S. race I

Variety	Row no.	Inoculated plants obtained no.	Infected plants no.	Infection pct.	Check: T. plant no.	Check: Infected plants no.	Check: Infection pct.
Jet	6	22	0	0	17	0	0
Anoidium	16	192	0	0	42	0	0
Ogalitsu	16	266	3	1.12	41	0	0
Harlan	5	47	0	0	31	0	0
o.A.C.21	11	31	12	38.70			

Table 2.* Reaction of Some Varieties of Barley to Several Races of U. nuda (Jens.) K. and S. Investigated by V. F. Tapke

U. nuda race	Varieties: Jet infec. pct.	Ogalitsu infec. pct.	Anoidium infec. pct.	Gold foil infec. pct.
1	0	0	0	40
2	0	0	9	64
3	0	0	0	50
4	0	0	10	14
5	0	0	0	88
7	0	0	0	67
8	0	0	0	25

*Unpublished data kindly furnished by Dr. V. F. Tapke.

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1. Jet x Harlan
2. Jet x Anoidium
3. Jet x Ogalitsu
4. Harlan x Ogalitsu
5. Harlan x Anoidium
6. Ogalitsu x Anoidium

Dr. K. J. Frey made these crosses at Michigan State College in 1950. The seeds of the F_1 generation were grown in 12-inch pots in the greenhouse in the fall of 1950.

In 1951, the seeds of the F_2 generation were space planted in rows 16 feet long and one foot apart. At the same time seeds inoculated with *Ustilago nuda* race I were sown in the field to secure fresh inoculum at the time of inoculation. To prevent the infection of the germinated infected seed with *Ustilago nuda* race I by the covered smut organism, the seeds were dusted with Cerasan before being planted.

At blossoming time one or two heads were covered with cellophane bags before they emerged from the boots. This was to prevent the occurrency of any natural infection. Similarly, the smutted heads on the stock plants were covered when they emerged. The preparation of teleutospore suspensions and the inoculation methods which were followed in this investigation were suggested by Poehlman (45): fresh smutted heads were obtained from the smutted plants each day and chopped into small pieces and placed in a small piece of cheesecloth, and the spores were then submerged into a beaker containing a 1 percent dextrose solution in distilled water. When the solution turned a dark brown color, the teleutospore suspensions were filtered through clean cheesecloth to obtain a suspension free from foreign matter.

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For inoculation a hypodermic needle (1 inch, 23 gauge) with a syringe (10 cc. capacity) were used. The lemma of each floret in the head was pierced without injuring the flower parts, and then one or two drops of the suspension were injected into each floret. The inoculations were made in one or two days after the head had broken the boot, because at this stage the majority of the florets of the head have already been pollinated. After the inoculation of each plant, cellophane bags were returned for enclosing the inoculated heads. Then each inoculated head was tagged to be distinguished and kept separately at harvest time. At the end of the season, the labeled heads were harvested and kept separately in marked envelopes. Besides, one or two uninoculated heads of each F_2 plant were harvested for linkage studies. The content of each envelope was threshed separately after the removal of some of the terminal and basal spikelets.

Due to the failure of the pollination of the cross Ogalitsu x Anoidium, more than 200 F_2 seeds, which were obtained from K. J. Frey, were planted in 12-inch pots in the greenhouse in the fall of 1952. The inoculation procedure for this material was the same as already described.

In the spring of 1952 (April 22) the F_3 inoculated seeds were planted in the field at the same time in rows four feet long, one foot apart. Every row containing the F_3 seeds of each envelope represented one F_2 plant. They were designated by F_3 family. Similarly, the F_3 uninoculated seeds which represented the same F_2 plants, were planted also in four foot long rows, one foot apart for studying the morphological characters.

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Table 3. - Distribution of F_3 progenies for loose smut infection grouped into 5 percent classes

Cross	Percentage classes																					Total number of rows
	0	0 5	5 10	10 15	15 20	20 25	25 30	30 35	35 40	40 45	45 50	50 55	55 60	60 65	65 70	70 75	75 80	80 85	85 90	90 95	95 100	
O.A.C.21	4							2			3				2							11
Jet	6																					6
Harlan	5																					5
Jet x Harlan	131	6	17	7	7	8	2	2	2	0	1	-	-	-	-	-	-	1	1	0	1	186
Jet	6																					6
Anoidium	16																					16
Jet x Anoidium	37	1	1	2	1	1																43
Jet	6																					6
Ogalitsu	15	0	0	1																		16
Jet x Ogalitsu	12	0	1																			13
Harlan	5																					5
Ogalitsu	15	0	0	1																		16
Harlan x Ogalitsu	47	7	11	8	4	3	2	1	0	2												85
Harlan	5																					5
Anoidium	16																					16
Harlan x Anoidium	102	9	18	12	18	10	10	8	7	2	7	3	6	4	2	6	3	1	3	1	0	232
Ogalitsu	15	0	0	1																		16
Anoidium	16																					16
Ogalitsu x Anoidium	122	0	4	8	8	6	3	2	0	2	3											158

After germination of the planted seeds, the heavy rows were thinned in such a way that all plants benefitted equally from their environments. Before harvest time readings of the total infected and non-infected plants of each row were taken and recorded separately. If one tiller in a plant was infected, the whole plant was recorded susceptible.

Jet differed from the other varieties in more than one morphological character. Therefore readings of the morphological segregation in each corresponding F_3 row of each cross, which included the Jet variety, were recorded [Tables A, B, C (Appendix)]. Then the percentage of infection of each F_3 row which represented the F_2 plant was computed and recorded. Finally F_3 families were grouped into 5 percent classes (Table 3). Then they were classified as resistant, segregating, and susceptible according to the calculated percentage of each family [Plate I, Tables A, B, C, D, E, F (Appendix)]. These classifications were based upon the behavior of the F_3 families. The inheritance of the important morphological characters and the linkage relations between resistance and the morphological characters were also studied.

Eleven rows of seeds inoculated with <u>Ustilago</u> <u>nuda</u> (Jens.) K. and S., race I, of the susceptible variety O.A.C. 21 were also planted to study the reaction of this variety to the disease. Before harvest time, the total of infected plants and the total of healthy plants was recorded. The percentage of infection for each row was computed as for the F_3 families of the different crosses (Table G, Appendix). Then they were also grouped into 5 percent of infection classes (Table 3).

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To study the characters of the teleutospores of the smutted heads in the F_3 families in comparison with those of the original Ustilago nuda (Jens.) K. and S., race I, samples of smutted heads of the F_3 families were taken in the field and kept separately. The laboratory microcropic studies on the morphology of these teleutospores and those of the original ones were made. Similarly the germinations of the teleutospores of the selected smutted heads as well as those of the original teleutospores of Ustilago nuda (Jens.) K. and S., race I, were also observed and compared.

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EXPERIMENTAL RESULTS

A. Study on the Reaction of the Parental Varieties: Jet, Anoidium, Harlan, Ogalitsu to Loose Smut Infection

The reaction of the parental varieties to loose smut infection was studied in the same field. The method used for planting, inoculating, and recording data were the same as previously explained in the chapter on Materials and Method (page 14). However, according to the data in the Table 1, three parents, Jet, Anoidium and Harlan, showed a high resistance. Ogalitsu variety showed 1.12 percent of infection; it was also resistant.

B. Study on the Inheritance of Resistance in Hybrids

1. Jet x Harlan. The F_3 families were classified as resistant, segregating, or susceptible, and the demarcation line between segregating and susceptible progenies was more or less arbitrary. The reason for the arbitrary decision was the lack of a method of inoculation which gave 100 percent infection, because of the variation of the effectiveness of the inoculation method.

O.A.C. 21, a variety susceptible to *Ustilago nuda*, race I, was used to estimate the percentage of infection which could be obtained. The method of inoculation used in this experiment was the hypodermic needle method which was explained previously. The maximum percentage of infection obtained was 38.70 percent (Table 1) compared to 40 percent (Table 2) in the gold foil variety obtained by V. F. Tapke, and the lowest percentage of infection obtained in a row was 33.33 percent (Table G, Appendix).

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Therefore, the demaraction line chosen to show the classification of the progenies between segregating and susceptible was 30 percent. Even if this percentage were true, the whole conception would still be based upon assumption. Therefore, the progeny in which the percentage of infected individuals was more than 30 percent of infection were arbitrarily classified as susceptible (Table 3). The segregating progeny were those in which the percentage of infected individuals was less than 30 percent. Finally, the resistant progeny were those in which no infected plants were found, (but it must not be forgotten that some segregating progeny might have more than 30 percent and some of the susceptible progeny might show less than 30 percent of the plants infected). Generally speaking, the F_3 families could be distinguished on the basis of the results obtained and indicated in Table B (Appendix) and summarized in Table 4).

Table 4. Infection of F_3 Families Obtained from the F_2 Plants Inoculated with Ustilago nuda, race I

Cross	Planted F_2 progeny no.	Germinated F_3 family no.	Total F_3 plants no.	F_3 infected plants no.	Number of infected F_3 families in percentage classes 0.0	0.01-30	30.01-100
Jet x Harlan	195	186*	2365	150	131	47	8

* Nine F_3 families did not germinate.

The foregoing table (4) shows there were 131 F_3 families with 2215 individual plants which showed no smut disease, whereas 55 F_3 families with 150 individual plants showed infection ranging from 0.01 percent to 100 percent. The distribution of these F_3 families and those of the parents in

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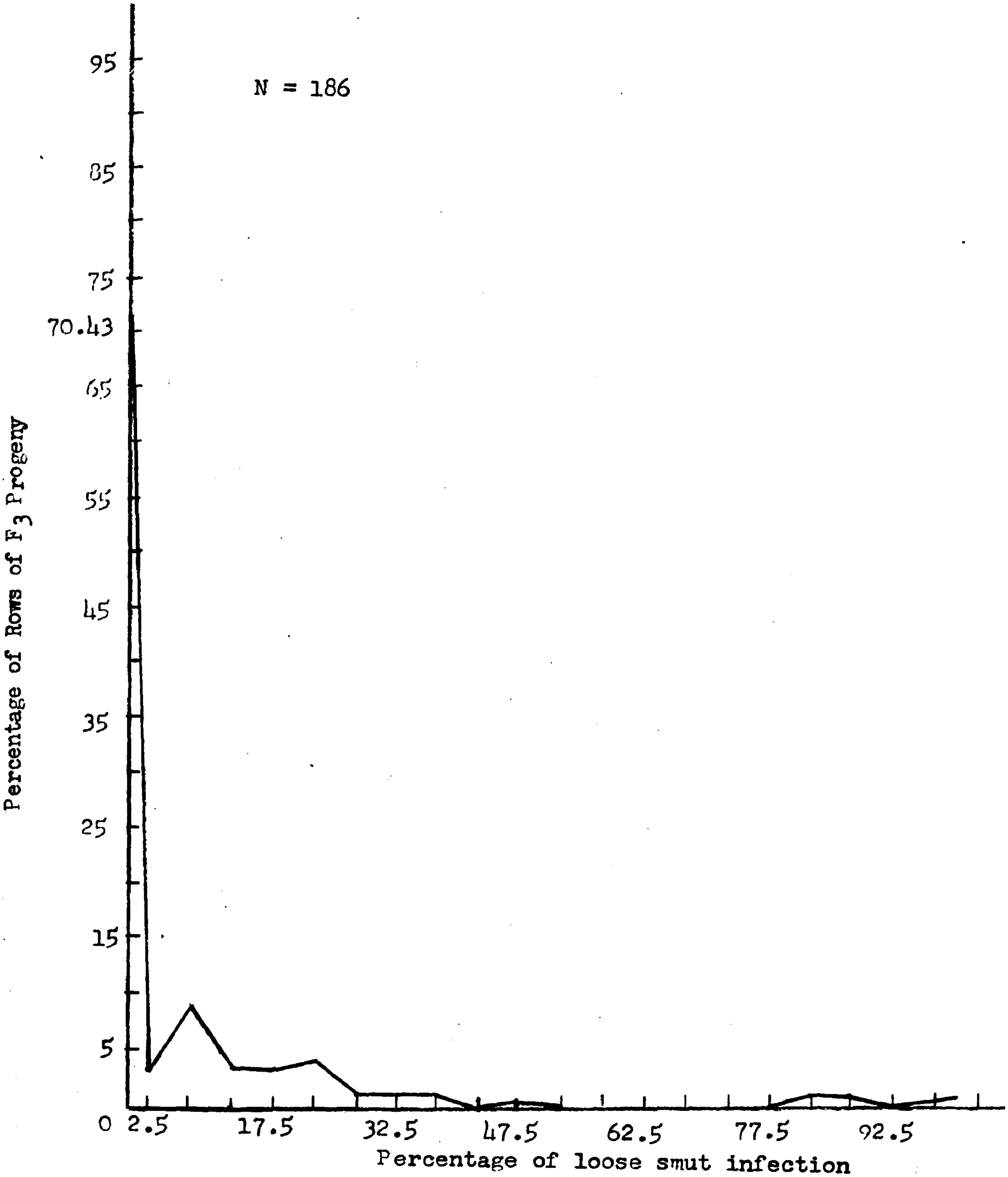

Figure 1. Distribution of F_3 Rows of the Cross Jet x Harlan and the Parents into 5 Percent Infection Classes

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5 percent classes are given in Table 3 and they are shown graphically in Figure 1. According to the arbitrary line which was chosen as a limit between the segregating and susceptible progeny, the F_3 families were divided into two groups. In the first group, a total of 8 F_3 families contained over 30 percent of infection. In the second group, 178 F_3 families contained less than 30 percent of infection. Within those 178 F_3 families there were 47 F_3 families distributed between 0.01 to 30 percent of infection. These 47 F_3 families included the segregating F_3 progeny. Therefore, the 178 F_3 families in the second group were considered to come from resistant F_2 plants and the eight F_3 families, which came from susceptible F_2 plants were considered susceptible. The ratio of the two groups harmonized with the expected ratio 15:1 if the resistant character in the progeny was governed by two genes.

Table 5. Chi-square Test of the F_3 Progeny of the Cross Jet x Harlan, Distributed in 5 Percent Classes

Cross	*Ustilago nuda* race	Character	Observed frequencies no.	Theoretical ratio	Calculated frequencies no.	X^2	Probability range
Jet x Harlan	1	Res.	178		174.3		
		Sus.	8	15:1	11.62	1.129	0.30-0.20

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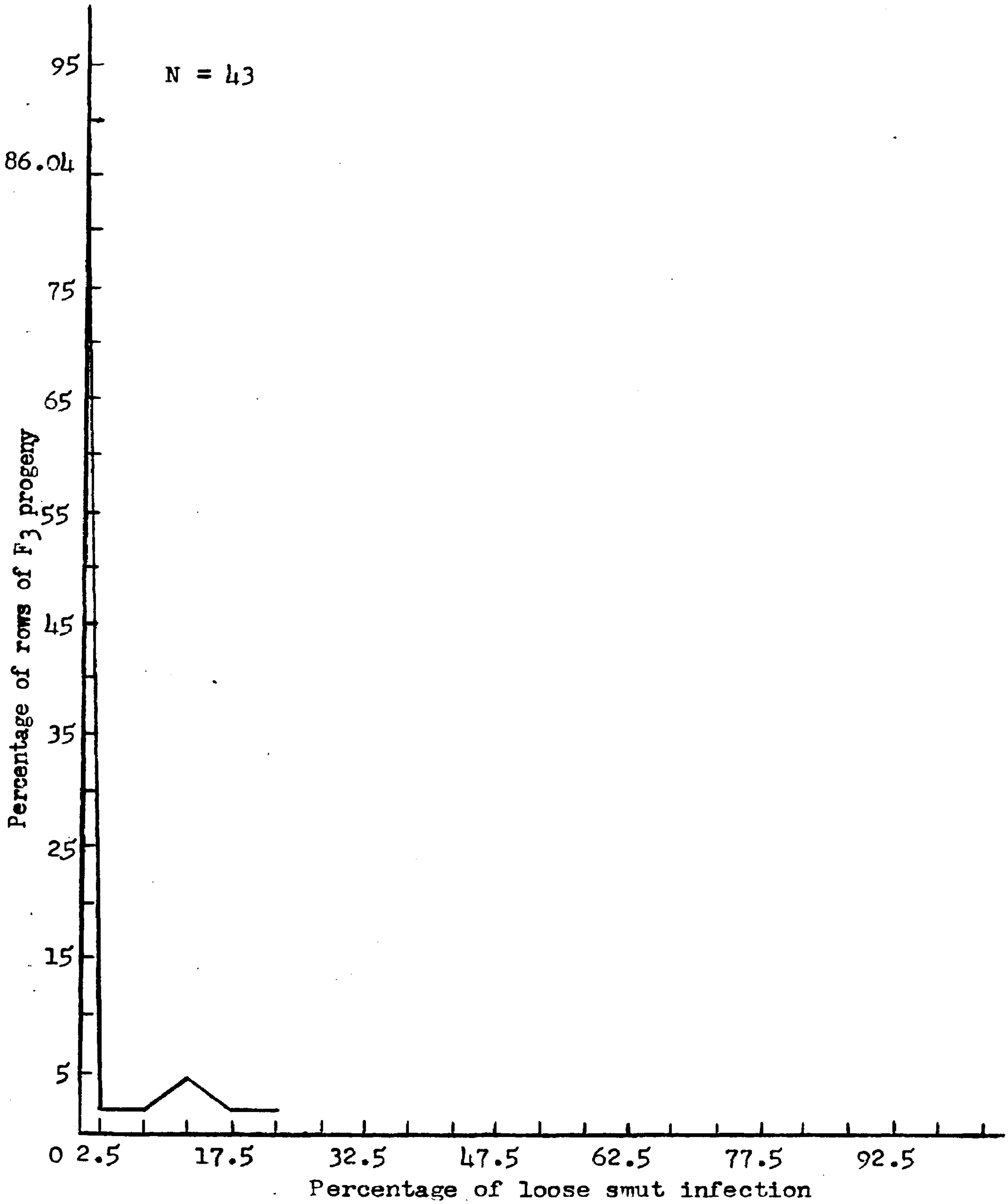

Figure 2. Distribution of F_3 Rows of the Cross Jet x Anoidium and the Parents into 5 Percent Infection Classes

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The chi-square was 1.120 and the probability range was 0.30-0.20. Therefore, the chi-square value (Table 5) indicated that the resistant character in the hybrids of the cross, Jet x Harlan, was controlled by two genes in which they were acting in a duplicate dominant condition of epistasis. These two genes were independent. Since segregation occurred (Table 3) between the two genes, they were different. With two independent genes 1/16 of the total F_2 progeny was completely susceptible. The expected number of F_3 families which should be completely susceptible is 186 x 1/16 = 11.62. But the observed number of the completely susceptible F_2 plants was 8. This number was within the range of the expected susceptible 3 families for independent factor inheritance.

2. Jet x Anoidium. The study of inheritance of resistance to *Ustilago nuda* (Jens.) K. and S., race I, in the hybrids of the cross Jet x Anoidium was accomplished in the same manner and under the same conditions as for the hybrids in the cross Jet x Harlan. In the F_2 generation a total of only 43 F_2 plants were available in this cross. Data were observed and recorded in Table A (Appendix). The distribution of F_3 families into 5 percent infection classes is given in Table 3 and is shown graphically in Figure 2.

Because the number of F_3 families was very small, it was difficult to study the behavior of the resistant factor in the hybrids. The direction of the curve in Figure 2 indicates to a certain extent, however, that if the number of F_3 families was large enough, it would follow the same direction as the curve in Figure 1. The curve in Figure 1 was that of the hybrids which possessed two factor pairs for the resistant character.

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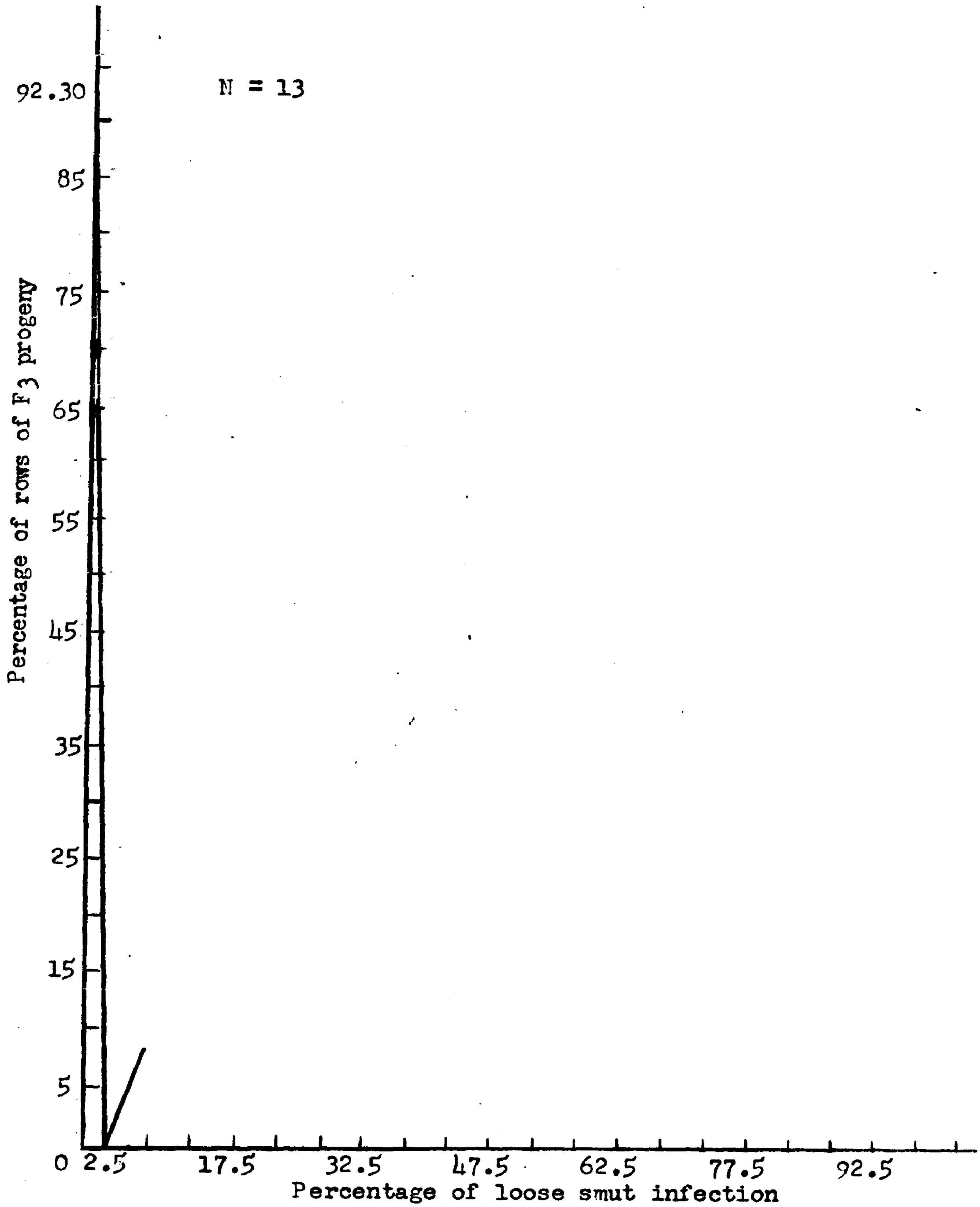

Figure 3. Distribution of F_3 Rows of the Cross Jet x Ogalitsu and the Parent into 5 Percent Infection Classes

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Presumably the hybrids of the cross Jet x Anoidium might possess the resistant character controlled by two factor pairs in the same ratio as that of the hybrids of the cross Jet x Harlan.

3. Jet x Ogalitsu. It has been shown (Table 1) that Jet is highly resistant to *Ustilago nuda*, race I. Similarly, (in the same table) Ogalitsu, which showed 1.12 percent of infection is also resistant to *Ustilago nuda*, race I. The cross was made between the two varieties under the same conditions. The inoculation method, the observations, recording data and the classification into classes, were obtained as previously explained in the other crosses. Data, which were recorded in Table C (Appendix) are given in Table 3 and shown graphically in Figure 3. Because the number of F_3 families was small (13 F_3 families), it was difficult to make an accurate study of the inheritance of resistant factor in the hybrids of the above cross.

4. Harlan x Ogalitsu. The F_3 progeny were used for studying the inheritance of resistance, as was done in the other crosses.

A total of 98 inoculated F_3 families which were obtained from 98 F_2 plants, were grown. The data are listed in Tabld D (Appendix) and are summarized in Table 6.

The distribution of F_3 families in 5 percent infection groups is shown in Table 3 and in Figure 4. There were 47 F_3 families containing 1147 plants which showed no infection. On the other hand, there were 38 F_3 families which included 137 infected plants in which the percentage of infection ranged from 2.43 percent to 44.44 percent. The 30 percent infection was the arbitrary limit chosen for separating the susceptible

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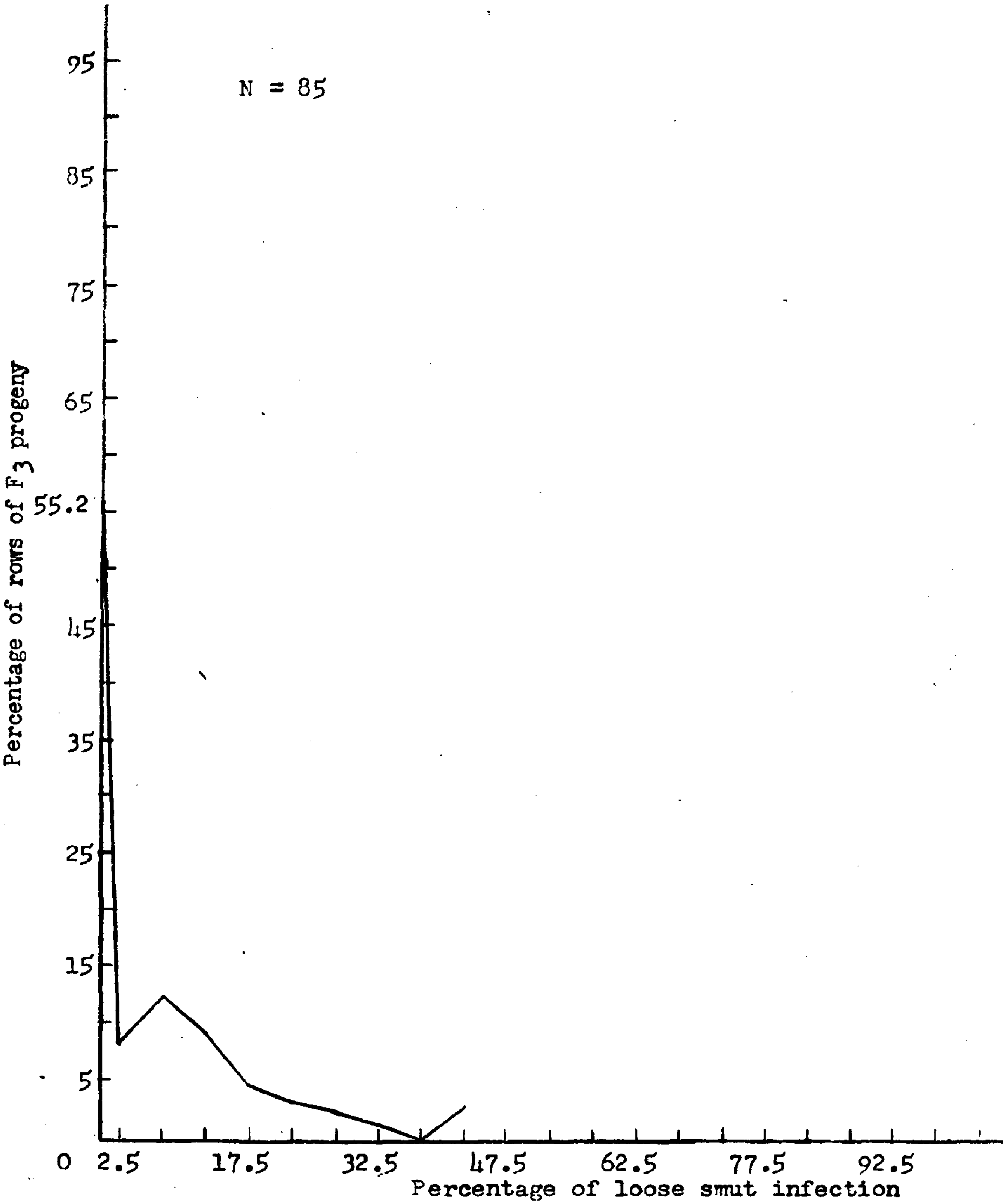

Figure 4. Distribution of F_3 Rows of the Cross Harlan x Ogalitsu and the Parents into 5 Percent Infection Classes

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Table 6. Infection of F_3 Families Which Were Obtained from the Inoculated F_2 Plants with Ustilago nuda, race I

Cross	Planted F_2 progeny no.	Germinated F_3 family no.	Total F_3 plants no.	F_3 infected plants no.	Number of infected F_3 families in percentage classes 0.0	0.01-30	30.01-100
Harlan x Ogalitsu	98	85*	1286	98	47	35	3

* Thirteen F_3 families did not germinate.

families from the segregating ones. The first group consisted of 82 F_3 families. Within these families, there were thirty-five which were distributed between 0.01 percent infection to 30 percent infection. These thirty-five F_3 families were the segregating F_3 progeny. Consequently, this group was considered to have come from F_2 resistant plants. The second group consisted of the 3 remaining families of the total 85. They were distributed between 30.01 percent to 100 percent of infection. They were considered to represent F_2 susceptible plants. The chi-square (Table 7) was 1.069 with a probability range of 0.50-0.30.

Table 7. Chi-square Test of F_3 Progenies of the Cross Harlan x Ogalitsu

Cross	Ustilago nuda race	Char-	Observed frequencies no.	Theoretical ratio	Calculated frequencies no.	X^2	Probability range
Harlan x Ogalitsu	I	Res. Sus.	82 3	15:1	79.65 5.31	1.069	0.50-0.30

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The observed ratio of the two groups agreed with the theoretical one, 15:1, considering the same total of frequencies, but the ratio 15:1 is the expected ratio when two pairs of factors are involved, acting in a duplicate dominant condition of epistasis. Therefore, the resistant character in the hybrids of the cross Harlan x Ogalitsu is apparently controlled by two factor pairs. The occurrence of segregation (Tables 3 and 6) and the chi-square test (Table 7) indicated a difference and an independence of inheritance between the two genes. The observed 3 susceptible F_2 plants were also found to be within the range of the independence.

5. Harlan x Anoidium. To study the inheritance in the hybrids of Harlan x Anoidium, a cross between the two varieties was made. Both varieties showed (Table 1) a high degree of resistance. The general procedure in this study was the same as that in the foregoing crosses. Data and percentages of infection were recorded in Table E (Appendix). The distribution of the F_3 progeny rows was also summarized in Table 8 and shown graphically in Figure 5. Of 232 F_3 families, 179 were resistant. Fifty-three were susceptible.

The observed ratio (Table 9) agreed with the theoretical ratio, 13:3, considering the same total of frequencies. But the ratio 13:3 is the ratio when two factor pairs are involved in the hybrids acting

in dominant and recessive condition of epistasis. Therefore the resistance to Ustilago nuda, race I, in the hybrids if apparently controlled by two genes. And according to the chi-square value, the two genes are independent. The occurrence of segregation (Table 3) indicated that the two genes were different. Detailed discussions are presented later.

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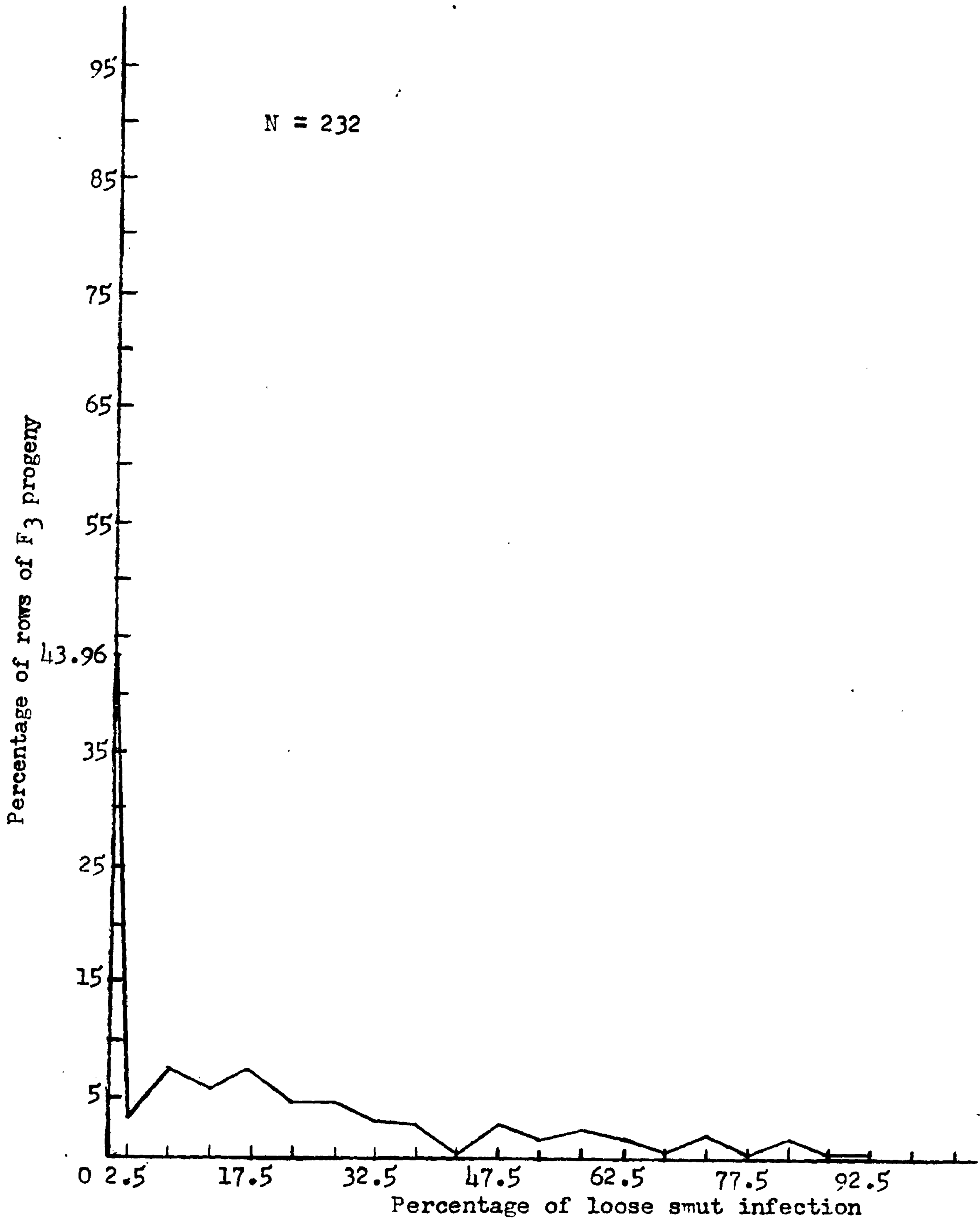

Figure 5. Distribution of F_3 Rows of the Cross Harlan x Anoidium and the Parents into 5 Percent Infection Classes

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Table 8. Infection of F_3 Families Which Were Obtained from the Inoculated F_2 Plants with <u>Ustilago</u> <u>nuda</u>, race I

Cross	Planted F_2 progeny no.	Germinated F_3 family no.	Total plants no.	F_3 infected plants no.	Number of infected F_3 families in percentage classes 0.0	0.01-30	30.01-100
Harlan x Anoidium	234	232*	4666	822	102	77	53

* Nine F_3 families did not germinate.

Table 9. Chi-square of the F_3 Progeny of the Cross Harlan x Anoidium Distributed in 5 Percent Infection Classes

Cross	<u>Ustilago</u> <u>nuda</u> race	Character	Observed frequencies no.	Theoretical ratio	Calculated frequencies no.	X^2	Probability range
Harlan x Anoidium	I	Res.	179		188.5		
		Sus.	53	13:3	43.5	2.552	0.20-0.10

<u>6. Ogalitsu x Anoidium</u>. According to the data in Table 1 Anoidium variety showed 0 percent of infection to <u>Ustilago</u> <u>nuda</u>, race I. Similarly and in the same table, the maximum of infection obtained when Ogalitsu was inoculated with the same organism was 1.12. This classified resistant. The cross between Ogalitsu and Anoidium was made, and the procedures followed

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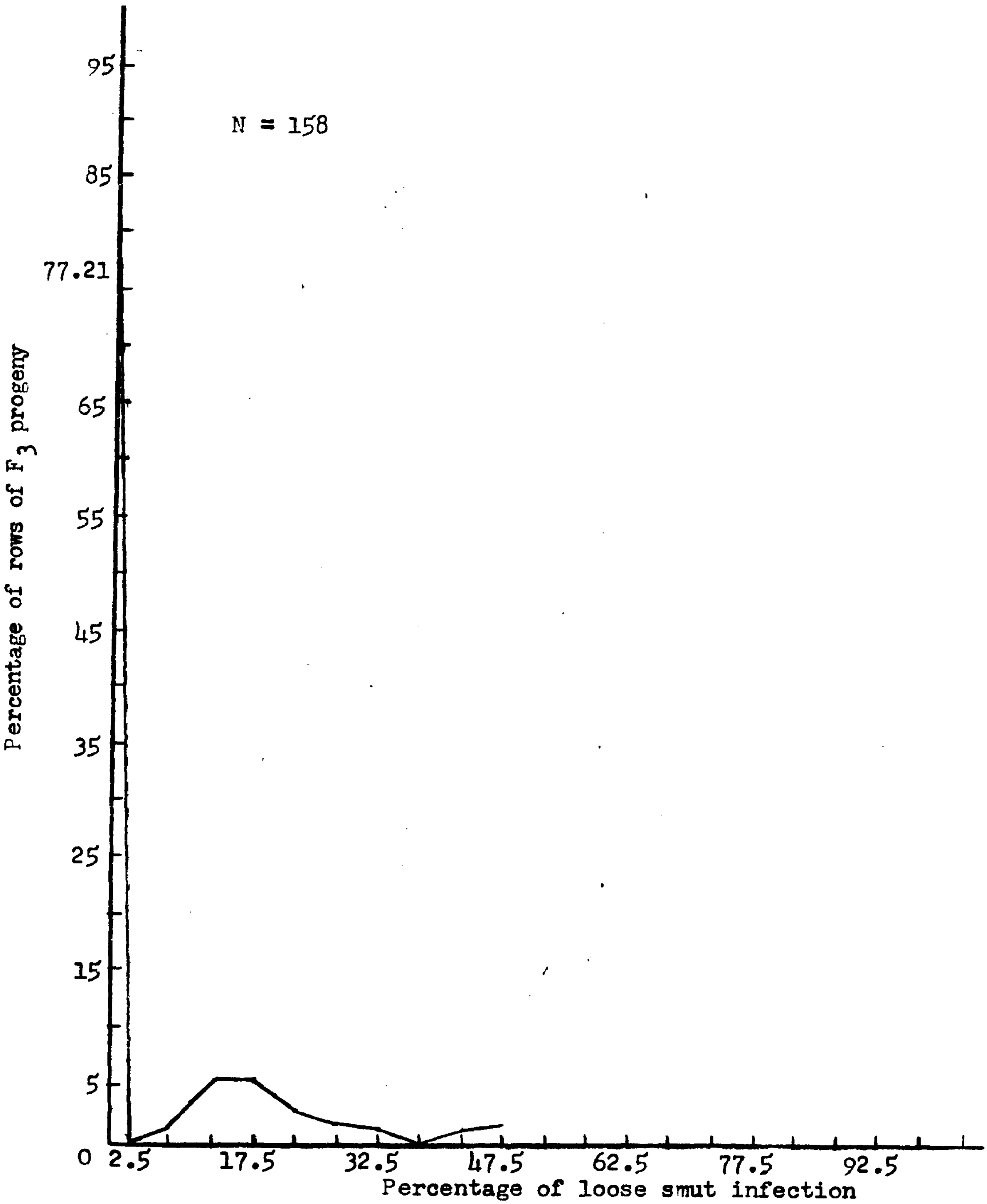

Figure 6. Distribution of F_3 Rows of the Cross Ogalitsu x Anoidium and the Parents into 5 Percent Infection Classes

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in this cross for reading, calculating and classifying the data were the same as in the above crosses (Table F, Appendix). These data were summarized in Table 10 and were represented in Figure 6. Thirty percent of

Table 10. Infection of F_3 Families Which Were Obtained from the Inoculated F_2 Plants with Ustilago nuda, race I

Cross	Planted F_2 progeny no.	Germinated F_2 family no.	Total F_3 plants no.	F_3 infected plants no.	Number of infected F_3 families in percentage classes 0.0	0.01-30	30.01-100
Ogalitsu x Anoidium	166	158	1120	64	122	29	7

infection was also used as an arbitrary limit between segregating F_3 families and susceptible one. The F_3 families which showed less than 30 percent of infection were from resistant F_2 plants and those which showed more than 30 percent were from susceptible F_2 plants. Therefore, the ratio between the resistant and susceptible F_3 families harmonized with 15:1 ratio. The chi-square value 0.893 (Table11) showed a good fit. The probability range was 0.50-0.30. This indicated the presence of two factor pairs acting in duplicate dominant condition of epistasis. These factors were different and independently inherited. The seven susceptible F_3 families also were within the range for the independence.

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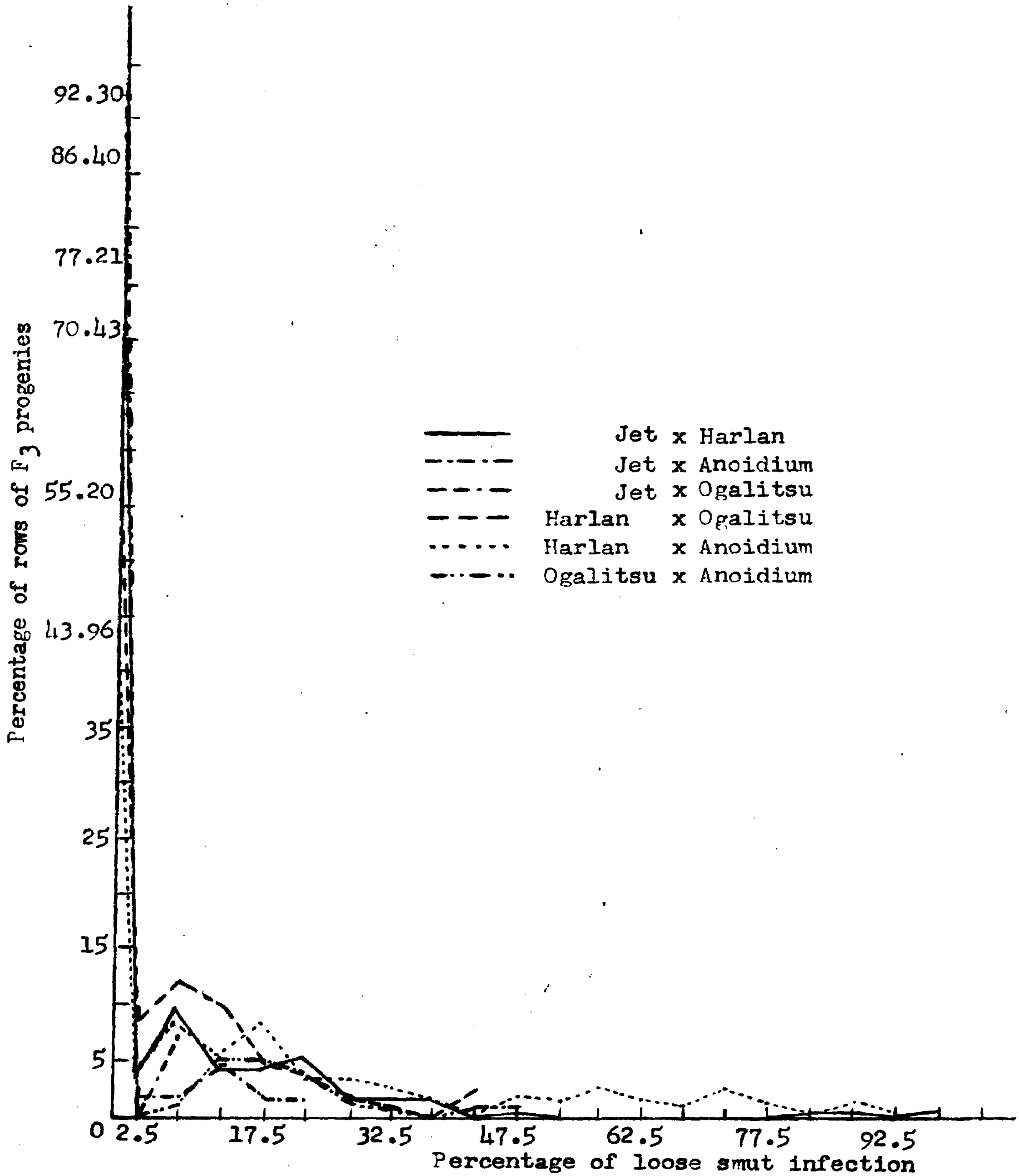

Figure 7. Distribution of F_3 Rows of the Six Crosses into 5 Percent Infection Classes

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Table 11. Chi-square of the F_3 Progenies of the Cross Ogalitsu x Anoidium, Distributed in 5 Percent Classes

Cross	Ustilago nuda race	Character	Observed frequencies no.	Theoretical ratio	Calculated frequencies no.	X^2	Probability range
Ogalitsu x Anoidium	I	Res.	151		148.05		
		Sus.	7	15:1	9.89	0.893	0.50-0.30

C. Study of the Inheritance of Agronomic Characters

The review of literature showed that many studies have been made on the inheritance of many agronomic characters in the progeny of several crosses. In this particular investigation the parental varieties used differed in one or more morphological characters. Therefore, it was desirable to study the inheritance of these characters in the segregating progeny.

1. Two-rowed versus six-rowed heads. According to Robertson (49), Daane (11) and Griffee (20) the characters two-rowed versus six-rowed segregated in a Mendelian ratio in which two-rowed is dominant over six-rowed heads. This segregation was confirmed in this investigation. Data of the segregations in the F_2 generation were taken from the F_2 plants which were grouped on the basis of the behavior of the F_3 families in the cross of Jet x Harlan. All plants of F_1 generation were two-rowed heads. This

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information indicated that the two-rowed character is dominant over the six-rowed character. In the F_2 generation, 186 F_2 plants were observed and the data were recorded and anlyzed in Table 12. One hundred and forty-six

Table 12. F_2 Segregation of Two-rowed vs. Six-rowed Heads in Barley Hybrids of the Cross Jet x Harlan

	2-row no.	6-row no.	X^2	P
Observed	146	40		
Theoretical 3:1	139.5	46.5	1.20	0.30-0.20

of the 186 F_2 plants were classified as two-rowed head, and 40 as six-rowed heads. The ratio obtained agreed with the expected ratio 3:1. Chi-square was 1.20. The probability range was 0.30-0.20. This information indicated that the segregation was controlled by one factor pair and that the two-rowed character was dominant.

In the cross Jet x Anoidium all the plants of F_1 generation were also two-rowed heads. The segregations in F_2 generation are analyzed in Table 13. Of 43 F_2 plants twenty-six plants were classified as two-rowed heads and 17 as six-rowed heads. The ratio observed agreed with the expected ratio 3:1. The chi-square was 4.84. The probability range was 0.05-0.02. These data indicated that the segregation was controlled by one factor pair and that the two-row character was dominant.

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Table 13. F_2 Segregation of Two-rowed Heads vs. Six-rowed Heads in Barley Hybrids of the Cross Jet x Anoidium

	2-row no.	6-row no.	X^2	P
Observed	26	17		
Theoretical 3:1	32.25	10.75	4.84	0.05-0.02

In the cross Jet x Ogalitsu all the F_1 plants were two-rowed heads. The analysis of data in F_2 generation (Table 14) showed that of 13 F_2 plants 10 plants were two-rowed heads and 3 plants were six-rowed heads.

Table 14. F_2 Segregation of Two-rowed Heads vs. Six-rowed Heads in Barley Hybrids of the Cross Jet x Ogalitsu

	2-row no.	6-row no.	X^2	P
Observed	10	3		
Theoretical 3:1	9.75	3.25	0.025	0.90-0.80

The ratio observed agreed with the expected ratio 3:1. The chi-square was 0.025. The probability range was 0.90-0.80. These figures indicated that this segregation was controlled by one factor pair, and that the two-row character was dominant.

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2. Hulled versus naked seeds. According to Daane (11), Robertson (49) and Biffen (5) the difference between the characters hulled and naked were based upon a single factor pair: hulled being dominant over naked. The results of the present investigation agree.

In the cross Jet x Harlan all plants of F_1 generation had hulled seeds. The data of the segregations in F_2 generation were analyzed (Table 15). One hundred and twenty-seven of the 186 F_2 plants were

Table 15. F_2 Segregation of Hulled vs. Naked Seeds in Barley Hybrids of the Cross Jet x Harlan

	Hulled no.	Naked no.	X^2	P
Observed	127	51		
Theoretical 3:1	137.25	45.25	3.061	0.10-0.05

classified hulled seeds and 51 plants were classified naked seeds. The ratio observed agreed with the expected ratio 3:1. The chi-square was 3.061. The probability range was 0.10-0.05. This information indicates that there is one gene difference between the two characters: the hulled character was dominant.

Similar results obtained when Jet was crossed with Anoidium. All plants of F_1 generation had hulled seeds, indication that the hulled character was dominant over naked character. The analysis of the data (Table 16) showed that of the 41 F_2 plants, 27 plants were classified as hulled seeds and 14 as naked seeds. The ratio observed harmonized with the expected

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Table 16. F_2 Segregation of Hulled Seeds vs. Naked Seeds in Barley Hybrids of the Cross Jet x Anoidium

	Hulled no.	Naked no.	X^2	P
Observed	27	14		
Theoretical 3:1	30.75	10.25	1.828	0.20-0.10

ratio 3:1. The chi-square was 1.828. The probability range was 0.2-0.1, indicating that the segregation was governed by a single gene.

In the cross Jet x Ogalitsu, the results shown in Table 17 indicated that the segregation was controlled by a single gene: hulled character was dominant.

Table 17. F_2 Segregation of Hulled Seeds vs. Naked Seeds in Barley Hybrids of the Cross Jet x Ogalitsu

	Hulled no.	Naked no.	X^2	P
Observed	12	1		
Theoretical 3:1	9.75	3.25	2.07	0.20-0.10

3. Rough awns versus smooth awns. Griffee (21), Robertson (29), and others found the difference between rough awn character and smooth awn character was based upon a single factor pair, and that the character rough was dominant over smooth. In the cross Jet x Anoidium all plants of

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F_1 generation had rough awns. Data of the segregation in F_2 generation are analyzed in Table 18. Twenty-eight F_2 plants were classified as rough

Table 18. F_2 Segregation of Rough Awns vs. Smooth Awns in Barley Hybrids of the Cross Jet x Anoidium

	Rough awns no.	Smooth awns no.	X^2	P
Observed	28	14		
Theoretical 3:1	31.5	10.5	1.578	0.30-0.20

awns and 14 as smooth awns. The observed ratio agreed with the expected ratio 3:1. The chi-square was 1.578. The probability range was 0.30-0.20, indicating that the segregation was controlled by one factor pair: rough character was dominant.

In the cross Jet x Ogalitsu, all F_1 plants had rough awns. The chi-square value 0.640 (Table 19) which gave a probability 0.50-0.30, showed a good fit for one single gene governing the awn character. Rough character was dominant.

Table 19. F_2 Segregation of Rough Awns vs. Smooth Awns in Barley Hybrids of the Cross Jet x Ogalitsu

	Rough awns no.	Smooth awns no.	X^2	P
Observed	11	2		
Theoretical 3:1	9.75	3.25	0.640	0.50-0.30

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4. Black lemma and pericarp vs. white lemma and pericarp. Biffen (5), Robertson (49), and Schaller (58) found one single gene difference occurred between black and white lemma. Biffen (5) and Woodward (73) found also that the black and white color of lemma was associated with the black and white pericarp. The results of this investigation agreed. In the cross Jet x Harlan all F_1 plants possessed black lemma and pericarp. The segregations in F_2 generation were observed and recorded (Table B, Appendix). Data were analyzed in Table 20.

Table 20. F_2 Segregation of Black and White Color of Lemma and Pericarp in Barley Hybrids of the Cross Jet x Harlan

	Black lemma and pericarp no.	White lemma and pericarp no.	X^2	P
Observed	144	41		
Theoretical 3:1	138.74	46.25	0.793	0.50-0.30

Of 185 F_2 plants there were 144 plants which were classified as black lemma and pericarp and 41 plants as white lemma and pericarp. The observed ratio agreed with the expected 3:1 ratio. The chi-square was 0.793, and the probability range was 0.50-0.30. The segregation was apparently controlled by one factor pair, and the black character was dominant.

In the cross Jet x Anoidium the F_1 plants were all black lemma and pericarp. The segregations in F_2 generation were analyzed in Table 21.

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Table 21. F_2 Segregation of Black Lemma and Pericarp vs. White Lemma and Pericarp in Barley Hybrids of the Cross Jet x Anoidium

	Black lemma and pericarp no	White lemma and pericarp no.	X^2	P
Observed	34	9		
Theoretical 3:1	32.25	10.75	0.378	0.70–0.50

Thirty-four of the 43 F_2 plants were classified as black lemma and pericarp, and 9 as white lemma and pericarp. The chi-square was 0.378. The probability range was 0.70-0.50. The results indicate that segregation was controlled by one factor pair, and that black character was dominant.

Similar results in the F_1 generation and F_2 generation were found in the cross Jet x Ogalitsu. The data of the segregations in F_2 generation were analyzed (Table 22).

Table 22. F_2 Segregation of Black Lemma and Pericarp vs. White Lemma and Pericarp in Barley Hybrids of the Cross Jet x Ogalitsu

	Black lemma and pericarp no.	White lemma and pericarp no.	X^2	P
Observed	11	2		
Theoretical 3:1	9.75	3.25	0.640	0.50–0.30

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The chi-square was 0.640. The probability range was 0.50-0.30, indicating that one single factor pair was involved. Black character was dominant.

D. Study of the Linkage Relations

Since one of the parents (Jet) was different from the other in more than one morphological character, it was desirable to study the relation between the resistance and these morphological characters. The hybrids of the cross Jet x Harlan were used for the study.

1. Resistance vs. susceptibility with two-row vs. six-row heads. According to the results obtained in this paper (page 22) the resistance character in hybrids of the cross Jet x Harlan was controlled by two factor pairs acting in duplicate dominant condition of epistasis. It has been shown (Table 12) that the character two-row vs. six-row was controlled by one gene. Therefore, the data for the segregation of these characters were recorded and analyzed in Table 23.

Table 23. F_2 Segregation of Resistant vs. Susceptible with Two-row vs. Six-row

	Resistant		Susceptible	
	Two-row no.	Six-row no.	Two-row no.	Six-row no.
Observed	139	39	6	1
Theoretical (15:1)(3:1)	130	43.35	8.67	2.89

Chi-square = 6.64

Probability range = 0.10-0.05

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From this classification, the goodness of fit for independence was computed by the chi-square method. The chi-square was 6.64, and the probability range was 0.10-0.05. The chi-square value indicated a good fit for independence. Therefore, according to the data collected in this study, there was no linkage between the factors controlling the resistance or the susceptibility and those controlling two-row and six-row heads.

2. Resistance vs. susceptibility with hulled vs. naked seeds. The segregations for the above mentioned characters in F_2 generation were analyzed in Table 24.

Table 24. F_2 Segregation of Resistance vs. Susceptibility with Hulled vs. Naked Seeds

	Resistant		Susceptible	
	Hulled no.	Naked no.	Hulled no.	Naked no.
Observed	122	54	6	1
Theoretical (15:1)(3:1)	128.25	42.75	8.55	2.85

Chi-square = 5.224

Probability range = 0.20-0.10

This classification consisted of 122 F_2 plants hulled resistant; 54 F_2 plants, naked, resistant; six F_2 plants, hulled, susceptible; and one F_2 plant, naked, susceptible. The chi-square was 5.224. The probability range was 0.20-0.10, indicating a good fit for independence. Therefore, resistance, susceptibility, hulled and naked character of seeds were independently inherited.

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3. Resistance vs. susceptibility with black lemma and pericarp vs. white lemma and pericarp. The data on the segregations of the above mentioned characters were recorded and analyzed in Table 25.

Table 25. F_2 Segregation of Resistance vs. Susceptibility with Black Lemma and Pericarp vs. White Lemma and Pericarp

	Resistant		Susceptible	
	Black lemma and pericarp no.	White lemma and pericarp no.	Black lemma and pericarp no.	White lemma and pericarp no.
Observed	140	38	4	3
Theoretical (15:1)(3:1)	130.05	43.35	8.67	2.89

Chi-square = 3.945

Probability range = 0.30-0.20

The classification consisted of 140 F_2 plants, resistant, black lemma and pericarp; 38 F_2 plants, resistant, white lemma and pericarp; 4 plants, susceptible, black lemma and pericarp; 3 F_2 plants, susceptible, white lemma and pericarp. The chi-square was 3.945 and the probability range was 0.30-0.20. This value indicated that there was no linkage between the factors controlling the resistance or the susceptibility and those controlling black and white lemma and pericarp.

The following table (26) contains the summary of the results of the chi-square tests of all characters which were included in the hybrids of the crosses used in the present study.

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Table 26. Summary of X^2 Tests for Mode of Inheritance and Linkage Relations of Characters in the Various Crosses Studied in this Paper

Crosses and Characters	Ratio	Chi-square	D.F.	Probability	Observations
Jet x Harlan (N = 186)					
2-row vs. 6-row heads (Vv)	3:1	1.20	1	0.30-0.20	2-row dominant
Hulled vs. naked seeds (Nn)	3:1	3.061	1	0.10-0.05	Hulled dominant
Black vs. white lemma and pericarp (Bb)	3:1	0.723	1	0.50-0.30	Black dominant
Resistant vs. susceptible in relation to:					
2-row vs. 6-row	15:1 3:1	3.111	3	0.50-0.30	Independent
Hulled vs. naked	15:1 3:1	5.224	3	0.20-0.10	Independent
Black vs. white lemma and pericarp	15:1 3:1	3.945	3	0.30-0.20	Independent
Jet x Anoidium (N = 43)					
2-row vs. 6-row heads	3:1	4.84	1	0.05-0.02	2-row dominant
Hulled vs. naked seeds	3:1	1.828	1	0.20-0.10	Hulled dominant
Rough vs. smooth awns	3:1	1.578	1	0.30-0.20	Rough dominant
Black vs. white lemma and pericarp	3:1	0.378	1	0.70-0.50	Black dominant
Jet x Ogalitsu (N = 13)					
2-row vs. 6-row heads	3:1	0.025	1	0.90-0.80	2-row dominant
Hulled vs. naked seeds	3:1	2.07	1	0.20-0.10	Hulled dominant
Rough vs. smooth awns	3:1	0.640	1	0.50-0.30	Rough dominant
Black vs. white lemma and pericarp	3:1	0.640	1	0.50-0.30	Black dominant

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SELECTION

Because the hybrids possessed a very valuable character (resistant to loose smut disease), a selection program was taken into consideration. The F_3 family rows which did not show any infection were selected to be used for further research work.

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DISCUSSION

The study of the inheritance of resistance is complicated because of several important factors. For instance, the lack of an inoculation method to give one hundred percent infection does not allow the researcher in this field to make a definite separation between segregating and susceptible progenies. A demarcation line must be based upon an assumption. Another complicating factor is the presence of many physiologic forms of *Ustilago nuda* within the species and the occurrence of continual hybridization between these forms and between different species, providing new forms which may be present in the natural inoculum. New form, however, were eliminated by using a specific race I. The microscopic study of the morphology of teleutospores, which were collected from the F_3 progenies and that of their germination manner, in comparison to those of the original race I showed a great similarity.

In this thesis the study of the genetic constitution of the F_2 population of six crosses of barley was based upon the classifications of the F_3 families. In the cross Jet x Harlan the observed ratio indicated the presence of two genes controlling the resistant characters. The occurrence of eight susceptible F_3 families in this cross indicated that these genes for resistance in Jet and Harlan were different. Moreover, the chi-square value showed they were inherited independently. The number of F_3 rows planted was 195, and the number of germinated F_3 rows was 186 with nine F_3 families failing to emerge. Several factors could cause this failure. One, already mentioned by Thren (67), was due to the invasion of the embryo

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tissues by the fungus. If J represented the factor for resistance in Jet and H that of Harlan, the genetic constitution of the parental varieties would be JJhh for Jet and HHjj for Harlan.

In the crosses Jet x Anoidium and Jet x Ogalitsu, the number of F_3 families was inadequate to allow any accurate genetical studies. In comparing the graphs of the cross Jet x Anoidium with that of Jet x Harlan (Fig. 7) it seems that if the curve of the former cross was more extended, it would follow the same direction as that of the latter cross. In other words, the data might show two factors governing the resistance in the progeny. The data on the cross Harlan x Ogalitsu explained satisfactorily the fit for two factor pairs controlling the resistance in the progenies. These factors which acted in a duplicate dominant epistatic condition were different and independent. Each factor pair was obtained from one parent. If O represented the factor for resistance in Ogalitsu, the genetic constitution of the latter would be OOhh. The segregation of F_3 families in the cross Harlan x Anoidium agreed with the ratio when two different factor pairs were involved. Moreover, the chi-square value also indicated their independence. This observed ratio harmonized with the theoretical ratio 13:3 which indicated the occurrence of two genes acting in dominant and recessive condition of epistasis. According to Tables 2 and 26 the characters for resistance in Harlan and Anoidium were controlled by one dominant gene. The expected ratio, therefore, between resistance and susceptibility in the progeny of the discussed cross should be 15:1. The presence of three susceptible F_3 families might be interpreted by the presence of fluctuation in some of the nine following genotypes of F_2 progeny: HHAA, HHAa, HHaa, HhAA, HhAa, Hhaa, hhAA, hhAa, hhaa. The genotypes HHAA, HHAa, HHaa, HhAa, hhAA were resistant. The probable

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occurrence of fluctuation was suggested to be in the genotypes Hhaa; hhAa, in which one gene for resistance was in the heterozygous condition while the other was in the recessive condition. The cause of this fluctuation is not known, but it may be due to a change of the expression of the resistance and susceptible which might be influenced by the environments.

In Table 9, the total of F_3 families planted was 234, of which only 232 F_3 families germinated. The failure of germination of these F_3 families could be attributed to the same reason which was discussed above. The genetical study in the cross Ogalitsu x Anoidium indicated the occurrence of two factor pairs in the progenies acting in duplicate dominant epistatic condition. The genetic constitution of the parental varieties was then: OOaa for Lgalitsu; AAoo for Anoidium. These genes were different and independent in their inheritance. The failure of germination of the eight families (Table 10) may be explained as in the case of the cross Jet x Harlan.

Livingston (35) found the same dominant gene controlling the resistance in Trebi and <u>Hordium deficiens</u>. Schaller (58) reported four different dominant genes for the resistance in the resistant varieties he used. In this study four dominant genes were also found to be located in the resistant varieties. These genes were different and independently inherited. Three of them were not reported. Robertson, Wiebe and Shand (50) and Robertson, Wiebe, and Immer (51) recommended the use of the following symbols for three different dominant genes. They recommended Un_3 for the gene in Jet; Un_4 for that in Dorsett; Un_5 for the gene in the selection X173-10-15-61. It may be suggested the symbols Un_6, Un_7, Un_8 for the genes respectively in Harlan, Anoidium and Ogalitsu.

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Because Jet differed from the other varieties in more than one agronomical character, the study of the inheritance of these agronomical characters in the progeny of the cross in which Jet was involved was desirable. In the cross Jet x Harlan, Jet x Anoidium, and Jet x Ogalitsu, one gene difference was found between: two-rowed vs. six-rowed heads, hulled vs. naked seeds, rough vs. smooth awns, black vs. white lemma and pericarp. The factors pairs for two-rowed, hulled and black lemma and pericarp were dominant over those for six-rowed, naked and white lemma and pericarp. These results confirmed those stated by previous investigators (5, 11, 21, 49, 58, 73).

In the cross Jet x Anoidium, the chi-square for two-rowed vs. six-rowed heads was 4.84. This value showed a fair fit for the occurrence of one gene difference between these characters. The reason might be due to the inadequate number of F_3 progenies in the rows in F_3 generation, which did not allow a complete segregation.

The study of the relations between resistance and morphological characters of the parental varieites was accomplished in the cross Jet x Harlan. The results reported in Tables 23, 24 and 25 showed that there was no linkage occurring between factors for resistance and those for two-rowed vs. six-rowed heads, for hulled vs. naked seeds, for black vs. white lemma and pericarp.

The resistant varieties Jet, Anoidium, Harlan and Ogalitsu are not recommended for commercial use. Also the commercial varieties are known to be susceptible to loose smut infection. Therefore, further breeding work would be valuable for introducing the factors for resistance into the desired varieties in a specific region. On the other hand, the lack of a

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method by which it is possible to obtain one hundred percent infection allows the segregating progenies to occur among the homozygous ones for resistance. For this reason, the continuation of varietal reaction tests to Ustilago nuda (Jens.) K. and S., race I, for several generations will be necessary to secure the homozygous progenies for resistance. Another point which appears to be important is that Schaller (58) and the author found different genes controlling the resistance in different varieties. Furthermore, these genes are located on different chromosomes. It would be more desirable to have progenies whose genetic constitution is made up of different factor pairs from different sources for resistance. When these characteristics are obtained in the progenies, a breeding program between the resistant progenies and the commercial varieites will be very valuable.

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SUMMARY

1. *Ustilago nuda* (Jens.) K. and S., race I, was the causal organism of loose smut disease in this study. The varieties of barley which were used as parents were Jet, Anoidium, Harlan, Ogalitsu. The infection reaction of these varieties showed that they were highly resistant to the disease.

2. The F_3 families which represented the F_2 plants were classified according to their percentages of infection, resistant, segregating and susceptible. The demarcation line between the segregating and susceptible F_3 families was abritrarily assumed, possibly attributable to failure to use a method which gives one hundred percent infection.

3. In the crosses Jet x Harlan, Harlan x Anoidium, Harlan x Ogalitsu, and Ogalitsu x Anoidium, the resistant character appeared to be controlled by two factor pairs acting in a duplicate dominant condition of epistasis. The chi-square test showed that these factors were independently inherited, and their segregation in the F_2 generation proved that they were different. Consequently, it is possible to say that resistant character in each parental variety was controlled by one dominant gene; but the four genes, however, were different.

4. The genes for resistance in Anoidium, Harlan, Ogalitsu were not reported before. The use of the following symbols: Un_6, Un_7, Un_8 for the genes respectively in Harlan, Anoidium and Ogalitsu was recommended.

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5. The chi-square test showed that there was one gene difference between the following morphological characters: two-rowed vs. six-rowed heads; hulled vs. naked seeds; rough vs. smooth awns; black vs. white lemma and pericarp, in the crosses Jet x Harlan, Jet x Anoidium, Jet x Ogalitsu.

6. There was no evidence for linkage between the factors for resistance and those for two-rowed vs. six-rowed heads; for hulled vs. naked seeds, and for black vs. white lemma and pericarp.

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APPENDIX

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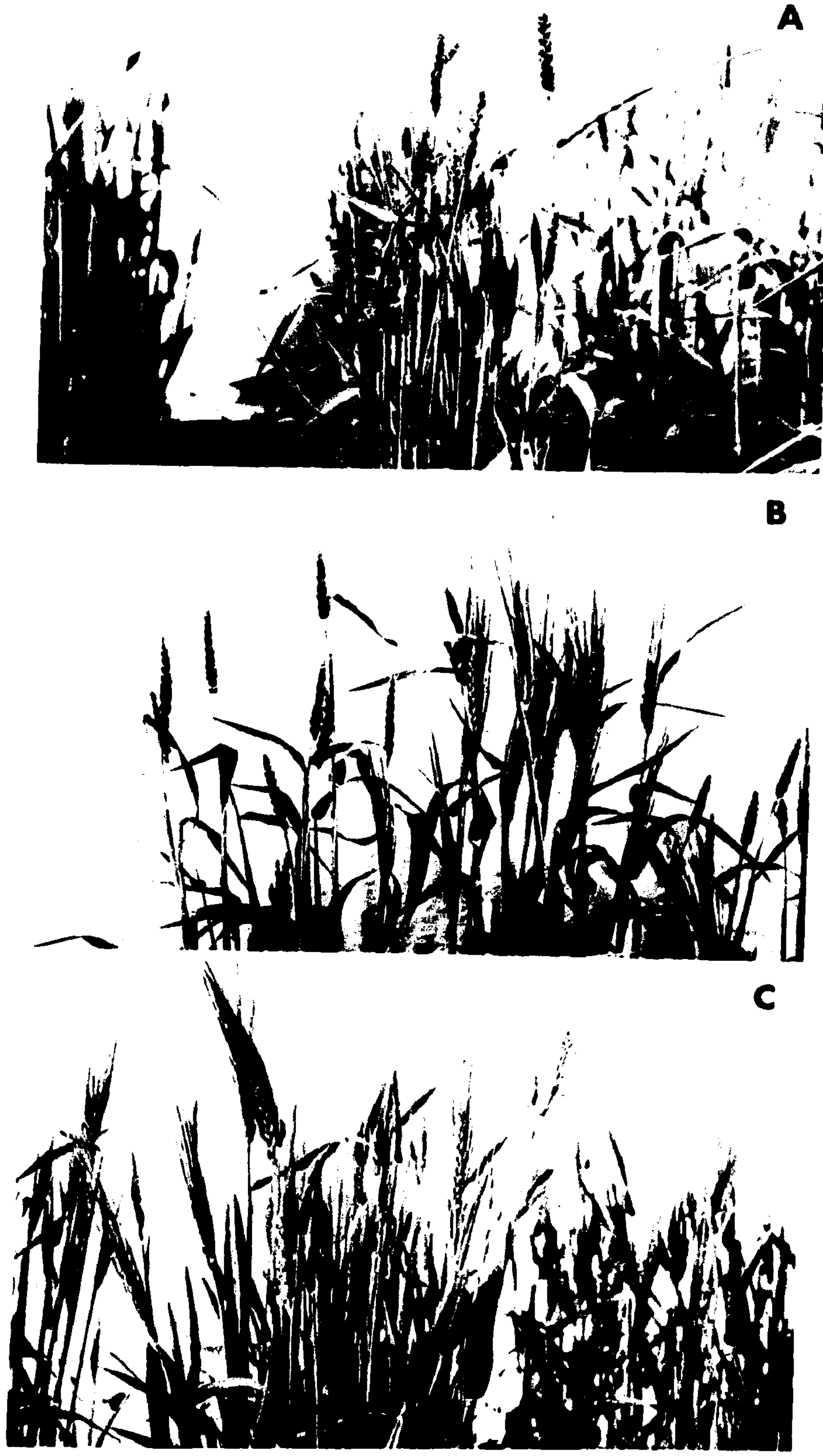

Plate 1. shows typical reaction of hybrid progeny to inoculation with *Ustilago nuda* race I.

A. Susceptible (middle row)
B. Segregating
C. Resistant

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The symbols used in the following tables were suggested by Robertson, Wiebe and Immer (51) to designate the morphological characteristics of the heads of the progeny of each genotype.

Table A. Percentages of Infection of F_3 Families. Morphological Characteristics of F_2 Plants Based upon the Behavior of F_3 Families of the Cross Jet x Anoidium

F_3 rows number	Inoculated plts. obtained: Total number	Inoculated plts. obtained: Infected number	Infection pct.	Head characteristics of F_2 plants: 2-rowed or 6-rowed	Rough or smooth	Covered or naked	Black or white lemma and pericarp
23001	12	0	0	V	Rr	-	b
2	21	0	0	Vv	Rr	N	Bb
3	11	0	0	V	r	Nn	b
4	28	0	0	v	Rr	N	B
5	22	0	0	Vv	r	N	Bb
6	8	0	0	v	Rr	Nn	Bb
7	15	3	20	Vv	Rr	Nn	Bb
8	32	0	0	v	Rr	N	Bb
9	8	2	25	V	R	Nn	Bb
10	18	0	0	V	R	n	Bb
11	22	0	0	Vv	r	N	Bb
12	28	0	0	v	R	n	b
13	12	0	0	Vv	Rr	Nn	B
14	27	0	0	v	R	Nn	b
15	7	0	0	v	Rr	Nn	B
16	10	0	0	V	R	n	B
17	7	0	0	Vv	r	N	B
18	2	0	0	v	r	n	Bb
19	15	0	0	v	R	n	b
20	27	0	0	v	R	n	Bb
21	2	0	0	V	R	n	b
22	8	0	0	V	r	Nn	Bb
23	16	0	0	Vv	Rr	Nn	Bb
24	8	0	0	V	r	Nn	Bb
25	12	0	0	Vv	r	n	b
26	28	0	0	v	R	n	Bb
27	11	0	0	Vv	r	Nn	Bb
28	13	0	0	v	Rr	Nn	b
29	10	0	0	V	r	N	B
30	4	0	0	Vv	R	n	B

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TABLE A. (continued)

F_3 rows number	Inoculated plts. obtained: Total number	Inoculated plts. obtained: Infected number	Infection pct.	Head characteristics of F_2 plants: 2-rowed or 6-rowed	Rough or smooth	Covered or naked	Black or white lemma and pericarp
23031	15	0	0	v	Rr	N	Bb
32	5	0	0	Vv	r	Nn	B
33	6	0	0	V	Rr	Nn	B
34	7	1	14.28	Vv	Rr	n	Bb
35	15	1	6.66	v	Rr	n	Bb
36	8	0	0	Vv	r	N	B
37	12	0	0	v	Rr	N	b
38	3	0	0	Vv	Rr	Nn	Bb
39	15	0	0	v	-	-	Bb
40	20	1	5	v	Rr	n	Bb
41	6	0	0	v	r	n	B
42	7	1	14.28	V	r	N	Bb
43	8	0	0	Vv	Rr	Nn	Bb

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Table B. Percentages of Infection of F_3 Families. Morphological Characteristics of F_2 Plants of the Cross Jet x Harlan

F_3 rows number	Inoculated plts. obtained: Total number	Inoculated plts. obtained: Infected number	Infection pct.	Head characteristics of F_2 plants: 2-rowed or 6-rowed	Rough or smooth	Covered or naked	Black or white lemma and pericarp
23044	13	3	23.07	V	R	N	b
45	30	8	26.66	v	R	Nn	Bb
46	33	0	0	v	-	-	B
47	18	1	5.55	Vv	R	n	b
48	28	0	0	Vv	Rr	Nn	b
49	16	0	0	Vv	R	Nn	Bb
50	24	0	0	Vv	Rr	Nn	Bb
51	24	2	8.33	Vv	Rr	Nn	Bb
52	3	0	0	Vv	r	n	Bb
53	8	0	0	Vv	R	N	B
54	24	1	4.16	Vv	Rr	n	b
55	31	3	9.67	v	R	Nn	Bb
56	20	5	25	V	R	Nn	B
57	32	1	3.12	Vv	Rr	Nn	b
58	9	8	88.88	v	R	N	b
59	29	0	0	Vv	Rr	Nn	Bb
60	33	13	39.39	Vv	Rr	Nn	Bb
61	18	0	0	V	R	Nn	Bb
62	12	2	16.66	Vv	R	Nn	b
63	18	4	22.22	Vv	R	N	B
64	20	5	25	v	R	Nn	Bb
65	5	0	0	V	Rr	Nn	Bb
66	12	1	8.33	Vv	Rr	N	b
67	20	0	0	v	Rr	Nn	Bb
68	21	0	0	v	R	Nn	Bb
69	26	0	0	Vv	R	Nn	Bb
70	20	2	10	Vv	R	N	Bb
71	10	2	20	V	R	n	Bb
72	10	1	10	Vv	R	n	B
73	37	1	2.70	v	R	n	Bb
74	29	0	0	Vv	r	Nn	Bb
75	18	0	0	v	Rr	Nn	Bb
76	6	0	0	V	Rr	Nn	b
77	22	0	0	V	R	N	Bb
78	22	0	0	v	R	n	Bb
79	12	3	25	V	Rr	N	Bb
80	8	0	8	V	R	n	B
81	5	0	0	Vv	R	N	Bb

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Table B. (Continued)

F_3 rows number	Inoculated plts. obtained: Total number	Inoculated plts. obtained: Infected number	Infection pct.	Head characteristics of F_2 plants: 2-rowed or 6-rowed	Rough or smooth	Covered or naked	Black or white lemma and pericar
23082	7	0	0	V	Rr	n	Bb
83	22	0	0	Vv	r	n	b
84	14	2	14.28	v	Rr	N	b
85	15	1	6.66	V	Rr	Nn	b
86	18	0	0	Vv	r	n	Bb
87	15	0	0	Vv	Rr	n	B
88	19	0	0	Vv	R	N	B
89	10	0	0	Vv	R	n	B
90	13	11	84.61	V	Rr	N	Bb
91	9	0	0	Vv	Rr	Nn	Bb
92	9	0	0	V	r	n	Bb
93	16	0	0	Vv	R	N	Bb
94	15	0	0	Vv	R	Nn	Bb
95	19	5	26.31	V	R	Nn	B
96	14	0	0	Vv	Rr	N	Bb
97	30	1	0.03	v	R	Nn	Bb
98	19	3	15.78	Vv	Rr	N	Bb
99	11	2	18.18	Vv	r	Nn	Bb
23100	15	0	0	V	R	Nn	Bb
101	8	1	12.5	Vv	R	Nn	B
102	8	1	12.5	V	R	N	b
103	13	0	0	V	R	Nn	B
104	16	0	0	Vv	Rr	n	Bb
105	4	0	0	Vv	R	n	b
106	7	1	14.28	Vv	r	N	B
107	23	1	4.34	Vv	R	N	b
108	29	2	6.9	v	R	n	b
109	11	0	0	Vv	R	n	Bb
110	16	0	0	v	Rr	Nn	Bb
111	10	0	0	Vv	R	n	B
112	22	0	0	V	R	Nn	Bb
113	15	1	6.66	V	Rr	n	B
114	13	1	7.68	Vv	R	n	Bb
115	19	2	10.52	Vv	R	Nn	Bb
116	29	7	24.13	v	r	Nn	Bb
117	13	0	0	V	r	Nn	B
118	28	5	17.85	Vv	R	Nn	b
119	14	1	7.14	V	R	n	b
120	22	0	0	Vv	Rr	Nn	b
121	16	1	6.25	Vv	R	Nn	Bb
122	22	4	18.18	Vv	R	Nn	b

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F3 rows number	Inoculated plts. obtained Total number	Infected number	Infection pct.	Head characteristics of F2 plants: 2-rowed or 6-rowed	Rough or smooth	Covered or naked	Black or white lemma and pericarp
23123	9	0	0	Vv	R	Nn	b
124	18	0	0	v	R	n	B
125	27	0	0	v	r	Nn	b
126	10	0	0	V	R	N	Bb
127	20	3	15	Vv	R	Nn	b
128	6	0	0	Vv	R	n	Bb
129	12	6	50	V	R	Nn	Bb
130	15	0	0	Vv	R	Nn	b
131	21	1	4.76	Vv	R	Nn	B
132	10	0	0	Vv	r	N	b
133	13	0	0	Vv	R	N	Bb
134	5	0	0	Vv	r	Nn	Bb
135	6	0	0	Vv	R	Nn	Bb
136	7	0	0	V	R	n	B
137	9	0	0	Vv	R	Nn	Bb
138	9	0	0	Vv	R	Nn	b
139	16	0	0	v	R	N	Bb
140	9	0	0	V	R	Nn	B
141	4	1	25	Vv	R	n	B
142	8	1	12.5	V	Rr	Nn	b
143	13	0	0	v	Rr	n	B
144	16	0	0	v	Rr	Nn	Bb
145	6	0	0	Vv	Rr	n	B
146	16	0	0	v	Rr	N	B
147	8	0	0	Vv	r	n	B
148	6	0	0	Vv	R	Nn	b
149	5	0	0	Vv	R	n	Bb
150	8	0	0	Vv	R	Nn	B
151	11	0	0	Vv	Rr	Nn	Bb
152	16	0	0	v	r	Nn	Bb
153	8	0	0	Vv	Rr	Nn	B
154	16	0	0	Vv	Rr	N	Bb
155	13	0	0	V	R	N	Bb
156	14	0	0	Vv	R	Nn	Bb
157	34	0	0	v	r	Nn	B
158	22	0	0	v	r	Nn	b
159	13	0	0	Vv	R	Nn	Bb
160	17	0	0	Vv	Rr	n	B
161	13	0	0	Vv	Rr	Nn	Bb
162	4	0	0	V	R	Nn	Bb
163	1	0	0	v	Rr	Nn	Bb
164	12	1	8.33	Vv	R	Nn	b
165	17	6	35.29	V	R	Nn	b

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F3 rows number	Inoculated plts. obtained: Total number	Inoculated plts. obtained: Infected number	Infection pct.	Head characteristics of F2 plants: 2-rowed or 6-rowed	Rough or smooth	Covered or naked	Black or white lemma and pericarp
23166	16	0	0	Vv	R	n	B
67	9	0	0	Vv	R	Nn	b
68	7	0	0	V	Rr	Nn	b
69	11	1	9.09	V	R	N	B
70	-	-	-	-	-	-	-
71	8	2	25	v	r	n	Bb
72	10	0	0	V	Rr	Nn	B
73	6	0	0	v	R	N	b
74	7	0	0	Vv	Rr	n	Bb
75	3	0	0	Vv	R	n	Bb
76	16	0	0	v	R	Nn	Bb
77	6	2	33.33	V	R	n	B
78	2	0	0	V	Rr	N	B
79	3	0	0	V	Rr	Nn	Bb
80	-	-	-	-	-	-	-
81	-	-	-	-	-	-	-
82	5	0	0	v	r	Nn	b
83	-	-	-	-	-	-	-
84	-	-	-	-	-	-	-
85	6	1	16.66	Vv	Rr	Nn	Bb
86	7	0	0	v	R	n	Bb
87	6	0	0	v	Rr	n	b
88	3	0	0	Vv	R	Nn	Bb
89	18	0	0	Vv	R	n	B
90	4	0	0	Vv	Rr	n	Bb
91	10	0	0	V	Rr	Nn	Bb
92	7	0	0	Vv	R	n	B
93	1	0	0	v	R	Nn	Bb
94	4	0	0	v	R	N	B
95	6	0	0	Vv	r	Nn	B
96	6	0	0	V	R	Nn	b
97	3	0	0	v	R	n	Bb
98	-	-	-	-	-	-	-
99	5	0	0	V	R	n	b
23200	3	0	0	V	R	n	Bb
1	2	0	0	V	r	N	Bb
2	9	0	0	V	Rr	Nn	B
3	7	0	0	Vv	Rr	Nn	Bb
4	11	0	0	Vv	Rr	Nn	B
5	15	0	0	Vv	r	N	Bb
6	18	1	5.55	v	-	-	-
7	11	0	0	v	R	n	Bb
8	-	-	-	-	-	-	-
9	7	0	0	Vv	r	n	B

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F_3 rows number	Inoculated plts. obtained: Total number	Inoculated plts. obtained: Infected number	Infection pct.	Head characteristics of F_2 plants: 2-rowed or 6-rowed	Rough or smooth	Covered or naked	Black or white lemma and pericarp
23210	14	0	0	V	Rr	n	Bb
11	5	0	0	Vv	r	Nn	B
12	8	0	0	Vv	R	Nn	Bb
13	1	0	0	V	R	N	Bb
14	2	0	0	Vv	R	N	B
15	10	1	10	Vv	Rr	Nn	Bb
16	-	-	-	-	-	-	-
17	9	0	0	Vv	R	n	Bb
18	11	0	0	V	R	N	B
19	7	0	0	v	r	N	B
20	8	0	0	V	R	N	B
21	4	0	0	Vv	R	Nn	Bb
22	6	0	0	V	Rr	n	Bb
23	4	0	0	Vv	R	n	B
24	10	1	10	v	Rr	Nn	Bb
25	2	2	100	-	-	-	-
26	8	0	0	Vv	Rr	N	b
27	11	0	0	Vv	Rr	n	Bb
28	4	0	0	V	R	Nn	Bb
29	4	0	0	V	Rr	n	Bb
30	3	1	33.33	Vv	R	N	b
31	8	0	0	Vv	r	N	B
32	13	0	0	v	R	n	b
33	11	0	0	Vv	R	Nn	B
34	7	0	0	V	Rr	Nn	B
35	-	-	-	-	-	-	-
36	8	0	0	v	Rr	Nn	Bb
37	8	0	0	Vv	R	n	B
38	4	0	0	Vv	R	n	B

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Table C. Percentages of Infection of F_3 Families. Morphological Characteristics of F_2 Plants Based upon the Behavior of F_3 Families of the Cross Jet x Ogalitsu

F_3 rows number	Inoculated plts. obtained: Total number	Inoculated plts. obtained: Infected number	Infection pct.	Head characteristics of F_2 plants: 2-rowed or 6-rowed	Rough or smooth	Covered or naked	Black or white lemma and pericarp
23239	12	0	0	V	Rr	N	b
40	11	0	0	V	R	Nn	Bb
41	31	0	0	Vv	r	n	Bb
42	1	0	0	v	R	Nn	Bb
43	14	0	0	Vv	Rr	Nn	Bb
44	18	1	5.55	v	Rr	Nn	Bb
45	9	0	0	Vv	Rr	Nn	Bb
46	8	0	0	Vv	R	Nn	Bb
47	5	0	0	v	R	Nn	b
48	7	0	0	Vv	R	Nn	Bb
49	2	0	0	Vv	Rr	Nn	B
50	7	0	0	V	R	N	Bb
51	4	0	0	Vv	r	N	B

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Table D. Percentages of Infection of F_3 Families of the Cross Harlan x Anoidium

F_3 rows number	Inoculated plts. obtained		Infection pct.
	Total number	Infected number	
23252	28	0	0
53	32	0	0
54	30	0	0
55	26	0	0
56	35	12	34.28
57	28	0	0
58	12	2	16.66
59	25	6	24
60	25	4	16
61	23	0	0
62	30	0	0
63	26	0	0
64	23	0	0
65	26	0	0
66	23	4	17.39
67	27	6	22.22
68	9	0	0
69	30	3	10
70	26	6	23.07
71	23	16	69.56
72	30	0	0
73	13	0	0
74	23	7	30.43
75	16	0	0
76	15	3	20
77	22	0	0
78	10	6	60
79	21	0	0
80	23	17	73.91
81	25	0	0
82	20	3	15
83	12	0	0
84	21	0	0
85	21	0	0
86	25	12	48
87	22	0	0
88	22	4	18.18
89	16	2	12.5
90	17	0	0

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F_3 rows number	Inoculated plts. obtained Total number	Infected number	Infection pct.
23291	21	6	28.57
92	14	3	21.28
93	18	0	0
94	27	2	7.40
95	24	0	0
96	7	0	0
97	26	13	50
98	13	0	0
99	19	3	15.78
300	22	7	31.81
1	16	3	18.75
2	14	4	28.57
3	12	0	0
4	32	1	3.12
5	18	2	11.11
6	17	5	29.41
7	25	4	16
8	6	0	0
9	13	1	7.68
10	21	6	28.52
11	18	0	0
12	16	0	0
13	35	0	0
14	22	0	0
15	31	1	3.22
16	19	0	0
17	20	13	65
18	37	5	13.51
19	11	1	9.09
20	12	3	25
21	-	-	-
22	10	1	10
23	4	0	0
24	17	0	0
25	23	13	56.52
26	37	5	13.51
27	42	0	0
28	22	8	36.36
29	9	0	0
30	34	0	0
31	12	5	41.66
32	19	0	0
33	30	19	63.33
34	22	1	4.54
35	15	2	13.33

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F$_3$ rows number	Inoculated plts. obtained Total number	Infected number	Infection pct.
23336	23	0	0
37	7	0	0
38	30	22	73.33
39	22	0	0
40	16	0	0
41	18	0	0
42	23	0	0
43	21	0	0
44	23	0	0
45	30	19	63.33
46	23	6	26.08
47	20	1	5
48	12	0	0
49	10	0	0
50	19	0	0
51	27	2	7.40
52	19	0	0
53	21	0	0
54	17	0	0
55	25	0	0
56	21	0	0
57	27	0	0
58	21	2	9.52
59	30	0	0
60	32	0	0
61	24	1	4.16
62	32	10	31.25
63	19	15	78.94
64	23	0	0
65	17	0	0
66	20	7	35
67	15	3	20
68	7	0	0
69	17	0	0
70	24	12	50
71	25	1	4
72	23	0	0
73	27	3	11.11
74	19	5	26.31
75	18	7	38.88
76	9	2	22.22
77	21	0	0
78	10	0	0
79	20	15	75
80	25	0	0

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F3 rows number	Inoculated plts. obtained		Infection pct.
	Total number	Infected number	
23381	14	1	7.14
82	12	2	16.66
83	12	0	0
84	1	0	0
85	16	0	0
86	16	8	50
87	18	7	38.88
88	25	13	52
89	22	0	0
90	13	0	0
91	15	5	33.33
92	12	0	0
93	20	0	0
94	32	1	3.12
95	13	0	0
96	8	0	0
97	26	4	15.38
98	18	3	16.66
99	22	7	31.81
400	17	1	5.88
1	24	3	12.50
2	22	19	86.36
3	23	0	0
4	21	8	38.09
5	16	0	0
6	18	1	5.55
7	24	18	75
8	21	18	85.71
9	20	9	45
10	21	2	9.52
11	25	1	4
12	10	1	10
13	15	4	26.66
14	22	0	0
15	24	0	0
16	25	5	20
17	14	0	0
18	14	4	28.57
19	18	14	77.77
20	12	3	25
21	15	4	26.66
22	17	0	0
23	12	0	0
24	14	1	7.14
25	-	-	-

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F_3 rows number	Inoculated plts. obtained		Infection pct.
	Total number	Infected number	
23426	15	7	46.66
27	12	0	0
28	13	11	46.66
29	11	1	9.09
30	5	2	40
31	14	8	57.14
32	20	0	0
33	24	14	58.33
34	25	20	80
35	22	2	9.09
36	28	4	14.28
37	10	0	0
38	22	4	18.18
39	13	0	0
40	22	4	18.18
41	2	0	0
42	25	8	32
43	12	3	25
44	21	0	0
45	18	7	38.88
46	14	0	0
47	20	2	10
48	16	11	68.75
49	11	3	27.27
50	15	0	0
51	18	13	72.22
52	12	0	0
53	11	9	8.81
54	14	5	35.71
55	11	0	0
56	19	12	63.15
57	21	3	14.28
58	17	10	58.82
59	22	5	22.72
60	18	1	5.55
61	12	3	25
62	25	23	92
63	14	8	57.14
64	13	2	15.38
65	12	0	0
66	21	18	85.71
67	7	0	0
68	8	1	12.50
69	2	0	0
70	9	1	11.11

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F_3 rows number	Inoculated plts. obtained Total number	Infected number	Infection pct.
23471	11	6	54.54
72	23	0	0
73	10	1	10
74	31	5	16.12
75	1	0	0
76	17	0	0
77	22	11	50
78	29	0	0
79	32	1	3.12
80	17	0	0
81	16	12	75
82	18	0	0
83	15	8	53.33
84	19	3	15.78
85	35	0	0

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Table E. Percentages of Infection of F_3 Families of the Cross Harlan x Ogalitsu

F_3 rows number	Inoculated plts. obtained		Infection pct.
	Total number	Infected number	
23486	21	1	4.76
87	27	0	0
88	16	1	6.25
89	24	1	4.16
90	34	5	14.70
91	41	1	2.43
92	10	0	0
93	18	2	11.11
94	33	2	6.06
95	24	1	4.16
96	11	0	0
97	22	2	9.09
98	22	3	13.63
99	20	1	5
500	27	0	0
1	38	10	26.31
2	22	2	9.09
3	16	2	12.50
4	18	2	11.11
5	24	4	16.66
6	5	0	0
7	40	0	0
8	27	0	0
9	30	5	16.66
10	7	3	42.85
11	24	0	0
12	7	0	0
13	21	2	9.52
14	10	0	0
15	12	0	0
16	11	0	0
17	22	1	4.54
18	11	1	9.09
19	8	0	0
20	17	0	0
21	13	0	0
22	-	-	-
23	-	-	-
24	3	0	0
25	8	0	0

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F_3 rows number	Inoculated plts. obtained		Infection pct.
	Total number	Infected number	
23526	-	-	-
27	4	0	0
28	40	8	20
29	11	2	18.18
30	15	0	0
31	34	3	8.82
32	8	1	12.5
33	42	3	7.14
34	9	4	44.44
35	15	0	0
36	26	1	3.84
37	21	0	0
38	24	2	8.33
39	2	0	0
40	25	3	12
41	-	-	-
42	14	3	21.42
43	15	0	0
44	16	2	12.50
45	1	0	1
46	-	-	-
47	4	0	0
48	-	-	-
49	5	0	0
50	-	-	-
51	8	0	0
52	1	0	0
53	-	-	-
54	3	0	0
55	1	0	0
56	-	-	-
57	17	0	0
58	8	0	0
59	-	-	-
60	1	0	0
61	-	-	-
62	9	2	22.22
63	1	0	0
64	11	1	9.09
65	9	0	0
66	6	0	0
67	-	-	-
68	2	0	0
69	9	2	22.22
70	11	3	27.27

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F_3 rows number	Inoculated plts. obtained		Infection pct.
	Total number	Infected number	
23571	1	0	0
72	5	0	0
73	14	0	0
74	3	0	0
75	-	-	-
76	19	0	0
77	6	0	0
78	2	0	0
79	7	0	0
80	16	5	31.25
81	18	1	5.55
82	10	0	0
83	13	0	0

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Table F. Percentages of Infection of F_3 Families of the Cross Ogalitsu x Anoidium

F_3 rows number	Inoculated plts. obtained: Total number	Inoculated plts. obtained: Infected number	Infection pct.
23584	4	0	0
85	-	-	-
86	2	1	50
87	5	1	20
88	7	1	14.28
89	1	0	0
90	12	0	0
91	10	0	0
92	6	0	0
93	3	0	0
94	4	0	0
95	8	4	50
96	18	0	0
97	2	0	0
98	4	0	0
99	10	0	0
600	1	0	0
1	9	0	0
2	10	0	0
3	4	0	0
4	20	0	0
5	4	0	0
6	11	0	0
7	11	0	0
8	4	0	0
9	11	1	9.09
10	8	0	0
11	8	2	25
12	8	1	12.50
13	6	0	0
14	2	0	0
15	9	4	44.44
16	10	0	0
17	8	0	0
18	10	0	0
19	3	0	0
20	12	2	16.66
21	11	0	0
22	10	1	10
23	1	0	0

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F_3 rows number	Inoculated plts. obtained Total number	Infected number	Infection pct.
23624	3	1	33.33
25	6	0	0
26	4	0	0
27	14	3	21.42
28	1	0	0
29	3	0	0
30	10	0	0
31	7	0	0
32	11	0	0
33	5	0	0
34	10	2	20
35	17	0	0
36	4	0	0
37	6	0	0
38	15	1	6.66
39	8	2	25
40	8	0	0
41	11	0	0
42	2	0	0
43	2	0	0
44	5	0	0
45	-	-	-
46	4	0	0
47	15	0	0
48	2	0	0
49	6	0	0
50	2	0	0
51	1	0	0
52	1	0	0
53	9	0	0
54	12	0	0
55	6	0	0
56	4	0	0
57	2	0	0
58	1	0	0
59	1	0	0
60	2	0	0
61	11	0	0
62	7	0	0
63	-	-	-
64	9	1	11.11
65	3	0	0
66	5	0	0
67	8	0	0
68	4	1	25

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F_3 rows number	Inoculated plts. obtained: Total number	Inoculated plts. obtained: Infected number	Infection pct.
23669	1	0	0
70	2	0	0
71	14	4	28.57
72	6	1	16.66
73	7	1	14.28
74	7	2	28.57
75	4	0	0
76	5	0	0
77	7	1	14.28
78	7	2	28.57
79	3	1	33.33
80	5	0	0
81	3	0	0
82	3	0	0
83	5	0	0
84	14	0	0
85	-	-	-
86	3	0	0
87	13	0	0
88	3	0	0
89	5	0	0
90	17	0	0
91	5	1	20
92	4	2	50
93	1	0	0
94	6	0	0
95	4	0	0
96	5	0	0
97	2	0	0
98	14	2	14.28
99	7	0	0
700	9	0	0
1	10	0	0
2	5	0	0
3	9	0	0
4	15	2	13.33
5	10	0	0
6	14	3	21.42
7	5	0	0
8	11	2	18.18
9	11	0	0
10	9	1	11.11
11	4	0	0
12	10	0	0
13	12	0	0
14	9	0	0
15	3	0	0
16	7	0	0

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F_3 rows number	Inoculated plts. obtained		Infection pct.
	Total number	Infected number	
23717	9	0	0
18	4	0	0
19	14	0	0
20	16	0	0
21	7	3	42.85
22	2	0	0
23	3	0	0
24	7	0	0
25	7	0	0
26	8	0	0
27	4	0	0
28	20	0	0
29	1	0	0
30	13	0	0
31	9	0	0
32	3	0	0
33	3	0	0
34	6	1	16.66
35	6	0	0
36	3	0	0
37	7	0	0
38	17	3	17.64
39	12	0	0
40	11	1	9.09
41	16	0	0
42	-	-	-
43	-	-	-
44	7	0	0
45	-	-	-
46	3	0	0
47	5	0	0
48	8	2	25
49	-	-	-

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Table G. Percentages of Infection of the Susceptible Variety O.A.C. 21

Row number	Inoculated plts. obtained: Total number	Inoculated plts. obtained: Infected number	Infection pct.
1	4	2	50
2	1	0	0
3	6	2	33.33
4	4	2	50
5	1	0	0
6	3	2	66.66
7	3	1	33.33
8	1	0	0
9	2	0	0
10	3	2	66.66
11	2	1	50

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