THE INHERITANCE OF SEEDLING REACTION TO *PUCCINIA RUBIGO-VERA TRITICI* (ERIKS.) CARLETON RACE 9, AWNEDNESS, AND SEED COLOR IN WHEAT CROSSES INVOLVING AKMANA

By

LEWIS EUGENE BROWDER

Bachelor of Science

Oklahoma Agricultural and Mechanical College

Stillwater, Oklahoma

1954

Submitted to the faculty of the Graduate School of
the Oklahoma Agricultural and Mechanical College
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
August, 1956

THE INHERITANCE OF SEEDLING REACTION TO

PUCCINIA RUBIGO-VERA TRITICI (ERIKS.)

CARLETON RACE 9, AWNEDNESS, AND

SEED COLOR IN WHEAT CROSSES

INVOLVING AKMANA

Thesis Approved:

A. M. Schlehuber
Thesis Adviser

James S Brooks

Barry Young Jr

M L Thorne
Head of Department

Robert MacVicar
Dean of Graduate School

ACKNOWLEDGEMENTS

The author expresses appreciation to his major adviser, Dr. A. M. Schlehuber, for his counsel and inspiration during the period of this study. Appreciation also is expressed to Dr. Harry C. Young, Jr., of the Botany and Plant Pathology Department, for his assistance and cooperation in the technical details of the study, as well as his advice in planning the experiment. Credit is due Dr. James S. Brooks for his advice in planning the study and preparation of this manuscript.

The author is grateful to the Oklahoma Agricultural and Mechanical College for the Research assistantship which made it possible for the writer to carry on his graduate program and for the excellent facilities with which to conduct this experiment.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES (Continued)

INTRODUCTION

A knowledge of the inheritance of the important economic characters is of utmost value to the plant breeder. A "blood bank" of such characters, properly cataloged, can be a valuable asset in emergencies.

Leaf rust resistance is 1 of the chief objectives of the wheat breeding program at the Oklahoma Agricultural Experiment Station, since leaf rust is the most destructive disease of wheat in the state.

In a breeding program for rust resistance, the genetics of the pathogen as well as the genetics of the host plant must be considered. The genetics of the pathogen, however, cannot be controlled. In nature, physiologic races arise within the causal organism. These races are indistinguishable morphologically, but differ in their ability to attack varieties of the host, i.e., a given variety may be resistant to 1 race, but susceptible to others, etc. Races are identified by their reaction on a set of differential host varieties and are merely assigned Arabic numerals.

The interaction of host and pathogen causes changes in the prevalence of the various races making up the total population. When varieties resistant to the prevalent races are released and become widely grown, new or minor races virulent on these varieties will increase. In this manner, a different race or group of races becomes prevalent and rust is again a factor in wheat production. The plant breeder then has a new problem of developing an acceptible resistant variety. Virulence and competition among races are also believed to affect the prevalence of any particular race.

Race 9, the race used in this study, increased to serious proportions on susceptible varieties in previous years, but gave way to other races when the resistant Pawnee variety was released. At the present time, race 9 is of very little importance in Oklahoma. Race 15 is now the major race found; while races 105A and 105B are steadily increasing in importance.

Although race 9 has been replaced as the major race in Oklahoma, all recommended varieties do not carry resistance to it. No variety recommended in Oklahoma carries the high type of resistance found in the variety Akmana P.I. 166711[1/]. For this reason, it was believed desirable to study the inheritance of this reaction so that its potential as a source of resistance might be known. The study reported here was initiated with this objective in mind.

The F_2 and F_3 generations of 2 crosses involving Akmana were tested for seedling resistance to race 9 in the greenhouse. Backcross and outcross material from 1 of the crosses also was available. In addition, F_2 populations were observed for awnedness and seed color. Chi-square tests to determine the association of leaf rust reaction to awnedness and to seed color were computed.

1/ P.I. number refers to a Plant Introduction accession number assigned to foreign introductions.

REVIEW OF LITERATURE

Inheritance of Leaf Rust Reaction

Literature on the inheritance of resistance to wheat leaf rust, *Puccinia rubigo-vera tritici* (Eriks.) Carleton, may be divided into two catagories: the inheritance of mature plant resistance, and the inheritance of seedling resistance.

Studies of the inheritance of seedling resistance in the greenhouse, where rust races and environment can be controlled, are generally considered more reliable than field studies of resistance. For this reason and also because the study reported herein deals with seedling resistance, only papers dealing with the inheritance of seedling resistance will be reviewed here. Several investigators have reported on the inheritance of both mature plant and seedling resistance in the same paper.

In the first report of inherited leaf rust resistance, Mains, Leighty, and Johnston (13)[2] found seedling resistance to 6 different races to be controlled by 1 factor pair in 4 different varieties. Resistance was dominant in some crosses, intermediate in some, and recessive in others. Mains (12) reports seedling resistance to race 3 dependent on 1 gene pair in a Norka X Ceres cross, with resistance

[2] Figures in parentheses refer to "Literature Cited" page 35.

dominant. Schlehuber (18) reported that resistance to race 9 could be explained by a single recessive factor pair in 4 crosses. The inheritance of resistance to 2 other races could not be determined.

In studies of the resistance to race 9 found in the Pawnee variety, Heyne and Johnston (10) found this resistance to be dependent on 1 major gene. They also found this factor to be non-allelic to the factor controlling resistance to race 9 in Timstein. These workers further found that Timstein seedling resistance to 5 races was controlled by 1 major recessive and 1 or more modifying factors.

By monosomic analysis, Heyne and Livers (11) determined the gene for resistance to race 9 in Pawnee to be located on Chromosome X. They further found an interaction of the Pawnee factor and a factor for resistance in the Chinese Spring monosomic lines.

Caldwell and Compton (4) report resistance to 8 different races to be controlled by 1 recessive gene in the Wabash variety. In direct contrast, Martinez, et al (14) found resistance to 6 races, 1, 2, 5, 15, 28, and 128a, to be conditioned by 6 genes, 1 for each race, with susceptibility dominant in each case. In the same study, segregations fitting a 2 factor ratio were observed when races 3, 58, 126, and a bulk of 18 races were used.

Wu and Ausemus (27) found seedling resistance to 2 races, 126 and 5, in a Lee X Mida cross to be controlled by 2 linked factors. One factor was dominant and the other recessive. Although both parents were highly resistant to race 9, these investigators found moderately resistant segregates in the hybrid population. This was explained by the presence of different factors in each parent.

Inheritance of Awnedness

Ausemus, et al (1) cite 30 investigators who found awnedness to be monogenic in inheritance with A as the recommended symbol, while 22 investigators report a digenic mode of inheritance. Three investigators observed trigenic segregation, and 1 reported a tetragenic inheritance of the awned condition. In general, the awnless condition is considered dominant. The F_1 generation of crosses of awned X awnless varieties is usually awnletted or half-awned. As early as 1905, Biffin (2) stated, "The beardless condition is a dominant, the bearded a recessive character."

Quisenberry and Clark (16) report segregation of 5 per cent awned and 13.2 per cent awnless in the F_2 of a cross of 2 awnletted varieties. The authors suggested a 2 major factor difference with the awned condition as recessive. Clark, Florell, and Hooker (6) suggest a 3 factor inheritance in a Hard Federation X Propo cross. They believed 2 major factors and 1 minor factor responsible for the awned condition.

By monosomic analysis, Heyne and Livers (11) have made a comprehensive study of factors affecting awnedness in the Pawnee variety. These workers found the awned condition of Pawnee to be conditioned by no less than 5 genes in the recessive state. The designation Hd, B_2, A_3, A_4, and A_5 are suggested for these factors, which were found on chromosomes VIII, X, XII, XVI, and XXI, respectively. The factors Hd and B_2 are awn inhibitors, while the "A" series are awn producing genes. The "A" series is believed to be non-epistatic, but incompletely dominant over its allelle <u>a</u>. Therefore, any 1 <u>a</u> gene in the homozygous state <u>aa</u> could produce full awns in the absence of the Hd and B_2 factors. The authors state that this theory is proposed as an extension of previous ideas rather than a contradiction of them. They also state detection of the minor factors is possible only by monosomic analysis. Wiggin (25) agrees with their hypothesis on the basis of his monosomic analysis of Kentana 52.

Inheritance of Seed Color

Two seed colors, namely, red and white, are observed in common wheat, Triticum vulgare Vill. Literature dealing with the inheritance of this character shows red color to be dominant over white. According to Percival (15), segregation in the F_2 of a red X white cross depends on the nature of the red parent. In some cases, seed color is reported to be inherited on a monohybrid basis. In most cases, however, 2 and 3 factor inheritance is postulated.

Biffin (2) found seed color to be inherited on a monohybrid basis, as did Clark and Hooker (7), Gaines (8), and Worzella (26). According to Heyne and Livers (11), the Pawnee variety has only 1 factor for red seed.

Stewart (19) reports a 2 factor segregation for seed color in a Ridit X (Federation-Sevier) cross. Stewart and Dalley (22) observed a 15:1 ratio in a Ridit X Utac hybrid. Schlehuber (17) found 2 factors to control the red seed color of Minhardi and Buffum 17 winter wheat varieties.

Percival (15) reports that Nilsson-Ehle discovered a trihybrid ratio in the F_2 generation of certain red X white hybrids. The investigations of Clark, et al (5), Gaines (8), Hayes and Robertson (9), Stewart (19, 20), Stewart and Woodward (23), and Worzella (26) agree with such a hypothesis.

Association of Leaf Rust Reaction and Morphological Characters

Several investigators have tested material for inheritance association of leaf rust reaction and various morphological characters, chiefly awnedness and seed color. All have reported independent inheritance of these characters. Some workers reporting such results are Biffin (3), Heyne and Johnston (10), Martinez, et al (14), Swenson, et al (24), and Wu and Ausemus (27).

MATERIALS AND METHODS

Experimental Materials

The wheat variety Akmana P.I. 166711 is highly resistant to race 9 of wheat leaf rust, Puccinia rubigo-vera tritici (Eriks.) Carleton. Akmana originated in Turkey and was first grown at the Oklahoma Agricultural Experiment Station as a foreign introduction in the crop year 1950-51. It has awnless to awnletted spikes, white seed, white chaff, and appears to be a non-hardy winter type. The agronomic type of Akmana shows little promise, but the strain was retained for its high resistance to leaf rust race 9. It is susceptible to all other races to which it has been tested at this station.

The F_2 and F_3 generations of crosses of Akmana with Klein Aniversario C.I. 12578[3/] and with Westar Selection C.I. 13090, outcrosses of Klein Aniversario X Akmana F_1 to Comanche C.I. 11673, to Triumph C.I. 12132, and to Ponca C.I. 12128, and backcrosses of Klein Aniversario X Akmana F_1 to each of its parents constituted the material used in this study. Actual parental seeds were not available. The crosses, cross numbers, and the number of F_1 plant progenies tested were as follows:

[3/] C.I. numbers are the accession numbers of the Cereal Crops Section, U. S. Department of Agriculture.

Cross	Cross Number	Number F_1 Families Tested
Klein Aniversario X Akmana	'52 X 20b	3
Westar Selection X Akmana	'52 X 18a	3
Comanche X (Klein Aniversario X Akmana F_1)	'52 X 15b	4
Triumph X (Klein Aniversario X Akmana F_1)	'53 X 36b	1
Ponca X (Klein Aniversario X Akmana F_1)	'53 X 1a	2
(Klein Aniversario X Akmana) X Akmana B_1	'53 X 42c	5
(Klein Aniversario X Akmana) X Klein Aniversario B_1	'53 X 44b	6

Klein Aniversario, a foreign introduction from Argentina, South America, is fully awned, white chaffed, red seeded, of spring habit, and resistant to race 9 and most other leaf rust races found in Oklahoma.

Westar Selection is a hard red winter wheat variety resistant to race 9. It is a white chaffed, awned variety. Its chief value is in the resistance it carries to race 105A.

The other varieties used in the crosses are important commercial varieties in Oklahoma. All are white chaffed, red seeded, and fully awned. Comanche and Triumph are completely susceptible to race 9, while Ponca is resistant.

While Klein Aniversario and Ponca are rated as resistant to race 9, their reactions and the reaction of Akmana are distinguishable. Leaf rust pustule types are rated as follows:

0 = Immune
0; = Infection without pustule development
1 = Small resistant pustule
2 = Moderate resistant pustule
3 = Moderate susceptible pustule
4 = Completely susceptible pustule

The reaction of Akmana to race 9 borders on immunity and is rated 0 to 0;. The reaction of Klein Aniversario and Ponca is rated 0; to 1. Westar Selection is rated 0; to 2 and usually can be distinguished from any of the other varieties used.

The leaf rust inoculum used in the experiment was obtained from Dr. Harry C. Young, Jr. of the Botany and Plant Pathology Department. The rust was collected from natural infections and identified to race by its reaction on 6 differential varieties.

Experimental Methods

Leaf rust race 9 was used throughout the study and varietal reactions were all obtained in the seedling stage. Data for the F_2 generation were obtained in the greenhouse in January, 1955 and January, 1956. In 1955, one hundred and ten seed were planted from each of the Klein Aniversario X Akmana F_1 and Westar Selection X Akmana F_1 plants. In the outcrosses, 30 to 50 seeds from each F_1 plant were seeded. Appropriate checks were seeded along with the hybrid material. Seeds were planted in individual 1 3/4 by 1 3/4 inch plant bands inside flats. The F_2 population was seeded in a mixture consisting of approximately 3 parts Kirkland clay loam, 1 part peat moss, 1 part pulverized cow manure, and 1 part sand. When the plants were 10 days old, their leaves were finger-stripped to reduce surface tension and inoculated by brushing with potted plants infected with leaf rust race 9. The inoculated plants were placed in an incubator of approximately 100 per cent relative humidity for 24 hours to insure infection. Leaf rust reaction was recorded 12 days after inoculation. In 1955, both the stands and the per cent of rust infection were low. Difficulty in properly stripping the leaves was believed to be responsible for the low infection. For this reason, another test of the F_2 generation of the Klein Aniversario X Akmana and Westar Selection X Akmana hybrids was made in 1956. Instead of finger-stripping the leaves they were sprayed with a dilute solution of Photo-Flo, a wetting agent, to reduce surface tension. A good infection resulted from this technic.

Approximately 10 plants from each reaction class representing each F_1 family were selected from the F_2 population. These plants were transplanted to the field in March, 1955 to obtain seed for testing F_3 lines in the winter of 1955-56. Classifications for awn condition and for seed color were made on these plants.

In testing the F_3 lines, the seeds were placed 3/4 inch part in $1\frac{1}{2}$ inch rows. A mixture of approximately 3 parts Kirkland clay loam, 1 part peat moss, 1 part pulverized cow manure, and 5 parts sand was used.

Duplicate sets of 17 seeds of each line were tested, except in a few cases where the F_2 plant did not produce sufficient seed for such a test. In these cases, all seeds produced were tested. The F_3 lines were inoculated in the same manner as described for the F_2 generation. The leaves were sprayed with a Photo-Flo solution to reduce surface tension. Very good infection was obtained.

In the leaf rust reaction classification of the F_2 material, plants were classified for their similarity of reaction to the parent varieties. In classifying the F_3 lines, plants with questionable reactions were recorded as such, since intermediates were a possibility. The spikes were classified into awnless, awnletted, and awned types. Seed from each F_2 plant was classified as red, light red, or white. However, the red and light red classes were later combined, when Chi-square values were calculated, because of the difficulty in distinguishing these classes.

On the basis of F_3 progeny, some F_2 plants were evidently misclassified for leaf rust reaction. In the Klein Aniversario X Akmana cross, the misclassifications were the same in each direction and therefore cancelled themselves. However, in the Westar Selection X Akmana cross, it was desirable to adjust the 1955 F_2 reading, since misclassifications were evident only in the Akmana class. The F_3 lines, classified as Akmana type reaction in F_2, but having a preponderance of Westar Selection reaction plants in the F_3, were subtracted from the F_2 Akmana class and added to the intermediates, since there was no evidence that they belonged in the Westar Selection reaction class.

Since approximately equal numbers were selected from each F_2 reaction class, the F_3 lines tested do not represent a random sample of the cross as a whole. In the Klein Aniversario X Akmana and Westar Selection X Akmana crosses, the F_3 breeding behavior expected if the total F_2 population had been tested was calculated from the available F_3 data. To do this, the percentage of true breeding lines found in the F_3 population tested was calculated within each parental reaction class. The number of plants in each F_2 class was then multiplied by its respective per cent value. This calculation resulted in an adjusted figure of the true breeding lines expected had the entire F_2 intermediate or segregating class been tested.

The adjustments outlined above are presented in the discussion of their respective crosses in the Experimental Results and Discussion.

EXPERIMENTAL RESULTS AND DISCUSSION

Inheritance of Leaf Rust Reaction

Klein Aniversario X Akmana

F_2 and F_3 leaf rust reaction data for Klein Aniversario X Akmana, '52 X 20b along with Chi-Square and P values for a 9:7 ratio in the F_2 tests are shown in Table 1. The F_2 data presented are combined counts from 3 F_1 families. Homogeneity tests of these families gave a P value of .50-.70 each year. The P values obtained for a 9:7 ratio indicate a good fit to such a ratio in the 1955 and in the 1956 test.

These data indicate that the Akmana reaction is controlled by the interaction of 2 dominant genes in this cross. However, difficulty in classifying heterozygotes prevent more conclusive proof of such a hypothesis. It should be kept in mind that the classification of intermediates, if any existed, would be extremely difficult in a cross such as the one under study. The reactions of the pure varieties are at times difficult to distinguish, but under some conditions, as many misclassifications probably would be made in 1 direction as the other, and thereby cancel out their effects. This is shown in Table 2, where as many F_2 plants were found to be misclassified into the Akmana class as into the Klein Aniversario class.

If the Akmana reaction is controlled by 2 complementary dominant factors, no intermediates would be expected in the F_3 generation. However, many F_3 plants were classified as questionable in either class.

Table 1. -- Inheritance of leaf rust race 9 reaction in the cross Klein Aniversario X Akmana, '52 X 20b, at Stillwater, Oklahoma, in 1955 and 1956.

Observed or Expected	Leaf Rust Reaction (No. of Plants or Lines) Akmana	Segregating	Kl. Aniv.	Chi-Square	P Value
		F_2 Plants 1955			
Obs.	97		76		
Exp. (9:7)	97.32	---	75.68	.0229	.80-.90
		F_2 Plants 1956			
Obs.	117		78		
Exp. (9:7)	109.68	---	85.32	1.114	.20-.30
		F_3 Lines From Selected F_2 Plants 1956			
Obs.	2	46	2		

Table 2. — Original and adjusted F_2 and F_3 leaf rust race 9 reaction data from the cross, Klein Aniversario X Akmana, '52 X 206, at Stillwater, Oklahoma, in 1955 and 1956.

Reading or Calculation	Leaf Rust Reaction Class: Akmana	Leaf Rust Reaction Class: Intermediate or Segregating	Leaf Rust Reaction Class: Klein Aniversario
Original F_2 Reading (No. of Plants)	97		76
Number F_3 Lines Tested	25		26
Number Plants Found to be Misclassified in F_2	7		7
Per cent of Total F_2 Population Tested as F_3 Lines	25.77		34.21
True Breeding F_3 Lines Observed in 1956			
Number	2		2
Per cent	8		7.69
Number True Breeding F_3 Lines Expected if Total F_2 Population Had Been Tested (Adjusted)	7.76		5.84
Number Intermediate or Segregating F_3 Lines Expected if Total F_2 Population Had Been Tested (Adjusted)		159.40	

Chi-Square value for goodness of fit to 1:14:1 F_3 ratio = 3.51 P = .10-.20

The lines reported as true breeding are lines on which there was no question of the classification of any plant in either test. Other lines had only a very few questionable plants, and could possibly have been true breeding lines.

If it is assumed that the interaction of A and B genes is responsible for Akmana resistance, there is some question as to the breeding behavior of the F_2 genotypes AAbb and aaBB. Under a 9:7 hypothesis, these types would breed true for the Klein Aniversario reaction in the F_3 generation. Sufficient true breeding Klein Aniversario lines were not found to support such a theory. However, it is logical that lines of such genotypes might appear as segregating or intermediate when one considers the difficulty of classification. The lines mentioned as having a few questionable plants may be of the genotypes AAbb or aaBB and, therefore, explain the shortage of true breeding Klein Aniversario lines observed. It is on this assumption that the 9:7 ratio is hypothesized.

The P value of .10-.20 for a 1:14:1 ratio in the F_3 generation indicates a good fit. This is the ratio of true breeding:segregating: true breeding lines expected under a complementary gene hypothesis if the genotypes AAbb and aaBB are assumed to appear as segregating.

Although conclusive proof of a complementary gene mode of inheritance cannot be shown, the data obtained indicate strongly some type of 2 factor inheritance of the Akmana reaction in this cross.

Similar data also were obtained on the second and third generation of backcrosses of Klein Aniversario X Akmana F_1 to both its parents. The backcross to Akmana resulted in no additional information on the inheritance of the Akmana leaf rust reaction. Pollen from susceptible plants was apparently used to produce some of the F_1 families studied. Such plants are known to occur in the Akmana variety. Observations made in this study show the plant type of such susceptible individuals to be very much like other plants in the variety, i.e. they are awnless to awnletted, and are similar in growth habit and maturity. However, there are seed color differences in some of the susceptible offtypes, the offtype being light red in seed color. Since the crosses used in this study were made in the field in past years, there was no opportunity to test the parents for leaf rust reaction before the crosses were made. The results obtained from tests of this material are presented in Table 3.

The pollen used in these backcrosses does not trace to an individual plant, but to the plants in a row. Pollen from highly resistant Akmana plants was evidently used to produce the F_1 plants 5674-3 and 5674-5. The limited data from their progeny support the theory that the Akmana reaction is dominant in this cross. However, no evidence is shown as to the exact mode of inheritance.

Data from the cross (Klein Aniversario X Akmana F_1) X Klein Aniversario are shown in Table 4. Only a few plants of the second generation following the backcross were tested. Such data do not lend any conclusive proof of the hypothesis outlined previously but neither does it disprove such a hypothesis. Some difficulty was experienced in classifying the material in 1955.

One family, 5678-5 segregated heavily toward Akmana, although it did not breed true Akmana. This would be expected under the hypothesis suggested. Considering the small numbers involved, the homozygous dominant ovule crossed to homozygous recessive pollen might explain the existance of such a line.

Table 3. -- Leaf rust race 9 reaction data for the second and third generations of the cross, (Klein Aniversario X Akmana F_1) X Akmana, '53 X 42c, at Stillwater, Oklahoma, in 1955 and 1956.

SECOND GENERATION PLANTS, 1955

F_1 Family No.	Leaf Rust Reaction (No. of Plants) Akmana	Kl. Aniv.	Susc.	Total
5674-1	0	12	4	16
5674-2	0	5	11	16
5674-3	9	3	0	12
5674-5	13	3	0	16
5674-7	4	6	10	20

THIRD GENERATION LINES, 1956

F_1 Family No.	Leaf Rust Reaction (No. of Lines) True Breeding Akmana	True Breeding Kl. Aniv.	Seg.	True Breeding Susc.
5674-1	0	7	1	1
5674-2	0	3	0	5
5674-3	5	2	1	0
5674-5*	9	9	0	0
5674-7	1	6	1	1

*Includes 2 lines from "no test" class in second generation.

Table 4. -- Leaf rust race 9 reaction data from the second and third generations of the cross (Klein Aniversario X Akmana F_1) X Klein Aniversario, '53 X 44b, at Stillwater, Oklahoma, in 1955 and 1956

SECOND GENERATION PLANTS 1955

F_1 Family No.	Leaf Rust Reaction (No. of Plants) Akmana	Kl. Aniv.	Susc.	Total
5678-1	4*	6	0	10
5678-2	1**	6	2	9
5678-3	2**	6	0	8
5678-4	3	1***	0	4
5678-5	5	4	0	9
5678-6	0	0	2	2

THIRD GENERATION LINES 1956

F_1 Family No.	Leaf Rust Reaction (No. of Lines) True Breeding Akmana	True Breeding Kl. Aniv.	Seg.	True Breeding Susc.
5678-1	0	1	7	0
5678-2	0	6	0	0
5678-3	0	2	5	0
5678-4	3	0	1	0
5678-5	2	2	4	0
5678-6	0	0	0	2

*One of these Kl. Aniv. type based on the third generation test.
**Kl. Aniv. type on the basis of reaction in the third generation.
***Akmana type on the basis of reaction in the third generation.

Four susceptible plants were discovered in the second generation material. Two of these, both from the same F_1 family, were tested as F_3 lines and both were true breeding susceptible. The only explanation for the occurrence of such plants is a very infrequent occurrence of susceptible plants in Klein Aniversario. As in the other backcross, the pollen used was from different plants within a row.

Since no data were available on the first generation plants of this backcross, their reaction can be postulated only from data of later generations. On this basis, F_1 plants 5678-1, -2, and -3 had a Klein Aniversario reaction, and 5678-4 had an Akmana reaction. The reaction of 5678-5 is indeterminable; while 5678-6 would probably have been susceptible. A 3 Klein Aniversario:1 Akmana ratio would be expected from a 2 factor inheritance of the Akmana reaction. Again attention is called to the low numbers.

Leaf rust race 9 reaction data from crosses of (Klein Aniversario X Akmana F_1) to Comanche, to Triumph, and to Ponca are shown in Tables 5, 6, and 7 respectively.

The number of plants tested does not permit a complete analysis of the inheritance of the Akmana reaction in these crosses. Rather, this information serves to indicate what might be expected, were it desirable to incorporate the Akmana reaction into these Oklahoma recommended varieties. In the presence of susceptible germ plasm, the Akmana and the Klein Aniversario reactions both appear to act as a recessive character. It is noticed in the cross to Triumph that no plants of Akmana reaction were observed in the F_1 family studied. This is possible under the complementary gene hypothesis previously advanced.

Table 5. -- F_2 and F_3 leaf rust race 9 reaction data for the cross Comanche X (Klein Aniversario X Akmana F_1), '53 X 15b, Stillwater, Oklahoma, in 1955 and 1956.

F_2 Plants

F_1 Family No.	Leaf Rust Reaction (No. of Plants) Akmana	Kl. Aniv.	Comanche	Total
5586-1	1	10	12	23
5586-2	4	5	8	17
5586-3	4	0	3	7
5586-4	4	2	2	8
	13	17	25	55

F_3 Lines from Selected F_2 Plants

F_1 Family No.	No. Lines Tested	Leaf Rust Reaction (No. of Lines) True Breeding Kl. Aniv.	Seg.	True Breeding Comanche
5586-1	15	0	13	2
5586-2	14	1	11	2
5586-3	7	0	5	2
5586-4	8	1	7	0

Table 6. -- F_2 and F_3 leaf rust race 9 reaction data from the cross Triumph X (Klein Aniversario X Akmana F_1), '52 X 36b, at Stillwater, Oklahoma in 1955 and 1956.

F_2 Plants 1955

F_1 Family No.	Leaf Rust Reaction (No. of Plants) Akmana	Kl. Aniv.	Triumph	Total
5592-1	0	5	17	22

F_3 Lines From Selected F_2 Plants 1956

F_1 Family No.	No. Lines Tested	Leaf Rust Reaction (No. of Lines) Seg. Toward Kl. Aniv.	True Breeding Tri.	Seg. Toward Tri.
5592-1	9	5	2	2

Table 7. -- F_2 and F_3 leaf rust race 9 reaction data for the cross Ponca X (Klein Aniversario X Akmana F_1), '52 X 1a, at Stillwater, Oklahoma, in 1955 and 1956.

F_2 Plants 1955

F_1 Family No.	Leaf Rust Reaction (No. of Plants) Akmana	Kl. Aniv. and Ponca
5583-2	5	13
5583-3	3	10
Totals	8	23

F_3 Lines From Selected F_2 Plants 1956

F_1 Family No.	No. Lines Tested	Leaf Rust Reaction (No. of Lines) Segregating	True Breeding Ponca
5583-2	10	9	1
5583-3	9	9	0

The F_2 data closely fit a 3 susceptible:1 resistant ratio in Triumph X (Klein Aniversario X Akmana F_1) cross and a 3 resistant:1 highly resistant ratio in the Ponca X (Klein Aniversario X Akmana F_1) cross. These ratios may or may not be meaningful in the inheritance of leaf rust reaction in these crosses.

Also, it is important to note that, with these small numbers, no true breeding Akmana type F_3 line was recovered in any of these crosses. Following the hypothesis advanced by this study, such a reaction could be stabilized from such hybrids, if sufficient plants were tested.

Westar Selection X Akmana

The results obtained from testing the F_2 and F_3 generations of Westar Selection X Akmana, '52 X 18a, to race 9 are shown in Table 8. The data presented are pooled results from 3 homogeneous F_1 families. On the basis of F_3 segregation, some plants in the F_2 Akmana class were believed to be misclassified. No misclassification was evident in the other F_2 classes. Since the F_2 plants were selected in approximately equal numbers within reaction classes, the F_3 ratio also requires some adjustment to correct it to the breeding behavior expected if all F_3 lines from the F_2 population has been tested. Such adjustments were made and are shown in Table 9. The plants removed from the F_2 Akmana class were added to the intermediate class, since there was no evidence that they should be added to the Westar Selection class.

The inheritance of the Akmana reaction in this cross is not readily determined. At least 2 possibilities can be shown. The first is that the Westar Selection variety is heterozygous for 1 or more factors which control it reaction to race 9. Evidence for this

Table 8. -- F_2 and F_3 leaf rust race 9 reaction data for the cross, Westar Selection X Akmana, '52 X 18a, at Stillwater, Oklahoma, in 1955 and 1956.

	F_2 Plants		
Akmana	Intermediate	Westar Selection	Total
		1955	
44	153	68	265
		1956	
21	135	78	234
	F_3 Lines From Selected F_2 Plants, 1956		
True Breeding Akmana	Segregating	True Breeding Westar Selection	Total
1	86	11	98

Table 9. -- Original and Adjusted leaf rust race 9 reaction data from the cross, Westar Selection X Akmana, '52 X 18a, at Stillwater, Oklahoma, in 1955 and 1956.

Reading or Calculation	Leaf Rust Reaction Class		
	Akmana	Intermediate or Segregating	Westar Sel.
Original F_2 Reading 1955 (No. of Plants)	44	153	68
Number F_3 Lines Tested 1956	30	38	30
Per cent of Total Population Tested as F_3 Lines	68.18	24.84	44.11
Number Plants Found to be Misclassified	11	0	0
Per cent Misclassification	36.67	0	0
Adjusted F_2 Reading 1955 (No. of Plants)	28	169	68
Number F_3 Lines Tested (Adjusted)	19	49	30
Number True Breeding F_3 Lines Observed in 1956	1		11
Per cent True Breeding Lines in F_3 Population Tested	5.21	---	36.67
Number True Breeding F_3 Lines Expected if Total Population Had Been Tested, (Adjusted)	1.46		24.94
Number Intermediate or Segregating F_3 Lines Expected if Total F_2 Population Had Been Tested (Adjusted)		238.60	

possibility is the erratic results obtained in other tests with this variety and the undeterminable inheritance of its reaction in other crosses. The homogeneity of the 3 F_1 families tested would seem to rule out such a hypothesis. The 1955 test, after adjustment, shows a P value of .30-.50 for homogeneity of the F_1 families and the 1956 test yields a P value of .80-.90 for homogeneity. If either variety were heterozygous, different segregations would be observed between F_1 families. The number of F_1 families used is too low, however, to definitely rule out such a hypothesis.

The other possibility is that the Akmana reaction is inherited as a recessive with a relatively large number of factors operating. This is shown in the adjusted data presented in Table 9, in that only 1.46 of 265 F_3 lines are true breeding Akmana. Evidence against such a theory is the fact that the Akmana reaction appeared to be dominant in the cross with Klein Aniversario where the difference between parental reactions was not so great. This might indicate that the Akmana reaction is controlled by a large number of genes, while Klein Aniversario and Akmana differ at only 2 loci. Then, Westar Selection, being less resistant, would differ from Akmana at more loci than is the case with Klein Aniversario.

The data obtained do not permit any definite conclusions as to the inheritance of the Akmana reaction in the Westar Selection X Akmana cross. It does, however, appear to be inherited as a recessive character.

Inheritance of Awnedness

Observations of awnedness in the F_2 generation of Klein Aniversario X Akmana, '52 X 20b, are presented in Table 10. These observations were made on transplanted F_2 plants growing in the field for increase in 1955. They represent the 2 leaf rust reaction classes and, in addition, 25 plants having a "no test" reaction in the F_2 generation. A total of 76 plants were classified. Chi-square and P values for a 3:1 ratio of awnless and awnletted to awned plants are also shown in Table 10.

Table 10. -- Inheritance of awnedness in the F_2 generation of the cross, Klein Aniversario X Akmana, '52 X 20b, at Stillwater, Oklahoma, in 1955.

Observed or Expected	Awnedness (No. of Plants)		Chi-Square	P Value
	Awnless and Awnletted	Awned		
Obs.	60	16		
Exp. (3:1)	57	19	.632	.30-.50

These values indicate a good fit to a 1 factor difference. This agrees with other studies although no F_3 data were available here and some other studies have shown awnedness to have a more complex inheritance.

Awnedness data from the backcross material are presented in Tables 11 and 12. These data support the hypothesis of a 1 factor difference for awn expression in the Klein Aniversario and Akmana varieties. In the (Klein Aniversario X Akmana F_1) X Akmana backcross, a 1 true awnless:1 segregating ratio would be expected in the second generation. As shown in Table 11, only 1 of 5 were true breeding awnless, but the low numbers used may again affect the results.

Table 11. -- Awnedness data for the second generation of the backcross (Klein Aniversario X Akmana F_1) X Akmana, '53 X 42c, at Stillwater, Oklahoma, in 1955.

F_1 Family No.	Awnedness (No. of Plants)		
	Awnless and Awnletted	Awned	Total
5674-1	6	3	9
5674-2	8	2	10
5674-3	8	0	8
5674-5	9	5	14
5674-7	12	1	13

Table 12. -- Awnedness data for the second generation of the backcross (Klein Aniversario X Akmana F_1) X Klein Aniversario, '53 X 44b, at Stillwater, Oklahoma, in 1955.

F_1 Family No.	Awnedness (No. of Plants)		
	Awnless and Awnletted	Awned	Total
5678-1	0	8	8
5678-2	5	1	6
5678-3	0	7	7
5678-4	0	4	4
5678-5	7	1	8
5678-6	2	0	2

The (Klein Aniversario X Akmana F_1) X Klein Aniversario backcross data presented in Table 12, show 3 awned lines and 2 segregating lines, with 1 line having only 2 plants, both awnless. A 1:1 ratio would be expected under a 1 factor hypothesis.

No significant data were obtained on the inheritance of awnedness in the outcrosses studied. All selected F_2 plants were awned. This would indicate that pollen from the F_1 plants used to produce all of the 7 F_1 families studied carried recessive gametes to the recessive ovules of the awned parents. This might also raise a question as to whether or not a cross was effected in all cases. However, leaf rust reaction and seed color segregation indicate that the material was actually hybrid in nature.

Plant counts, Chi-square, and P values of a 3:1 ratio for awnedness in the F_2 generation of the Westar Selection X Akmana cross are presented in Table 13. These data were taken on 98 transplanted F_2 plants in 1955. The P value of .30-.50 indicates a simple 1 factor

Table 13. -- Inheritance of awnedness in the F_2 generation of the cross, Westar Selection X Akmana, '52 X 18a, at Stillwater, Oklahoma, in 1955.

Observed or Expected	Awnedness (No. of Plants)		Chi-Square	P Value
	Awnless and Awnletted	Awned		
Obs.	70	28		
Exp. (3:1)	73.5	24.5	.667	.30-.50

inheritance of awnedness in this cross. This indicates there is only a 1 factor difference, a dominant inhibitor, in the parents, while several genes could be involved in the expression of awnedness. Each variety would be homozygous and alike at all awn expression loci except 1.

Inheritance of Seed Color

Segregation for seed color in the F_2 generation of Klein Aniversario X Akmana, '52 X 20b, is shown in Table 14. These data were taken from the same plants on which awnedness classification was made. Chi-square and P values for a 63 red:1 white ratio are also shown. These values indicate a good fit to a 3 factor hypothesis for the

Table 14. -- Inheritance of seed color in the F_2 generation of the cross Klein Aniversario X Akmana, '52 X 20b, at Stillwater, Oklahoma, in 1955.

Observed or Expected	Seed Color (No. of Plants) Red	White	Chi-Square	P Value
Obs.	75	1		
Exp. (63:1)	74.8	1.2	.003	.80-.90

inheritance of seed color in this cross. This would mean that the Klein Aniversario variety has 3 dominant factors for red seed color. Various degrees of red were observed, but were combined since it was felt they could not be distinguished accurately. Here again, no F_3 data were available.

Since only 2 F_1 families were believed to be actual backcrosses in the (Klein Aniversario X Akmana F_1) X Akmana material, this material is of little value as a test cross of the 3 factor hypothesis of seed color inheritance. All progeny of the (Klein Aniversario X Akmana F_1) X Klein Aniversario backcross were red seeded as might be expected if Klein Aniversario carries 3 dominant factors for red seed color. A very small number of white seeded types would appear in a large segregating population of this type. The numbers observed here would not necessarily show such recessive segregates.

All selected F_2 plants from the outcrosses of Klein Aniversario X Akmana F_1 to Comanche, to Ponca, and to Triumph were red in seed color. Varying degrees of red were observed, indicating segregation for this character. As in the backcross to the Klein Aniversario parent, crosses to these common red seeded varieties should produce results such as those observed. If a 3 factor hypothesis is correct, true breeding types should be recovered in the F_3 generation, but such data were not available.

Data pertaining to F_2 seed color segregation in Westar Selection X Akmana are given in Table 15. Chi-square and P values for a 63 red:1 white ratio were computed from these data. These values indicate a

Table 15. -- Inheritance of seed color in the F_2 generation of the cross Westar Selection X Akmana, '52 X 18a, at Stillwater, Oklahoma, in 1955.

Observed or Expected	Seed Color (No. of Plants) Red	White	Chi-Square	P Value
Obs.	95	3		
Exp. (63:1)	96.7	1.53	1.636	.20-.30

good fit to a 3 factor inheritance of red seed color in this cross. Westar Selection would contain the 3 dominant factors for red seed color since the Akmana variety is white seeded, the recessive condition. Such an hypothesis agrees with the studies of other workers.

Association Studies

Tests for independence of inheritance of awnedness and seed color to leaf rust reaction were calculated from the Klein Aniversario X Akmana and from the Westar Selection X Akmana data. Chi-square and P values were obtained from contingency tables comparing F_2 seed color or awnedness and F_3 leaf rust reaction.

Similar results were obtained from both crosses. A summary of the results are as follows:

Cross and Comparison	Chi-Square	P Value
Klein Aniversario X Akmana Awnedness and Leaf Rust Reaction	1.813	.50-.70
Klein Aniversario X Akmana Seed Color and Leaf Rust Reaction	.074	$>$ .99
Westar Selection X Akmana Awnedness and Leaf Rust Reaction	.148	.98-.99
Westar Selection X Akmana Seed Color and Leaf Rust Reaction	1.504	.50-.70

The P values obtained indicate that leaf rust reaction, seed color, and awnedness are inherited independently in these crosses. Such results agree with those of other investigations.

SUMMARY

The inheritance of leaf rust race 9 reaction, awnedness, and seed color was studied in hybrids of Akmana crossed to Klein Aniversario and to Westar Selection, as well as in backcrosses of the Klein Aniversario X Akmana F_1 to each parent and outcrosses of such an F_1 to the varieties Comanche, susceptible; Triumph, susceptible; and Ponca, resistant.

The Akmana reaction to leaf rust race 9 was found to be controlled by some 2 dominant factor interaction in the Klein Aniversario X Akmana cross. Sufficient backcross data were not available to draw definite conclusions as to the exact inheritance of the Akmana reaction in this cross. The Akmana reaction appeared to be recessive in the outcrosses of the Klein Aniversario X Akmana F_1 to susceptible varieties.

The mode of inheritance of the Akmana reaction could not be determined in the Westar Selection X Akmana cross, but it appeared to behave as a recessive.

The Akmana variety is shown to possess 1 dominant inhibitor which results in its awnless to awnletted condition.

Seed color was inherited on a 3 factor basis in both the Klein Aniversario X Akmana and the Westar Selection X Akmana crosses. This would indicate that Klein Aniversario and Westar Selection each possess 3 dominant factors for red seed color. Akmana is white seeded, the recessive condition.

Association studies indicate independent inheritance of leaf rust race 9 reaction, awnedness and seed color.

LITERATURE CITED

1. Ausemus, E. R., et al. A summary of genetic studies in hexaploid and tetraploid wheats. Jour. Amer. Soc. Agron. 38:1082-1099. 1947.

2. Biffin, R. H. Mendel's Laws of inheritance and wheat breeding. Jour. Agr. Sci. 1:4-48. 1905.

3. ___________. Studies in the inheritance of disease resistance. Jour. Agr. Sci. 2:109-128. 1907.

4. Caldwell, R. M., and Compton, L. E. Correlated inheritance of resistance to eight races of leaf rust powdery mildew, and glume color. (abstract) Phytopath. 37:4. 1947.

5. Clark, J. A., Quisenberry, K. S., and Powers, L. Inheritance of bunt reaction and other characters in Hope wheat crosses. Jour. Agr. Res. 46:413-425. 1933.

6. ___________, Florell, V. H., and Hooker, J. R. Inheritance of awnedness, yield, and quality in crosses of Bobs, Hard Federation, and Propo wheats at Davis, California. U.S.D.A. Tech. Bul. 39. 1928.

7. ___________, and Hooker, J. R. Segregation and correlated inheritance in Marquis and Hard Federation crosses, with factors for yield and quality of spring wheat in Montana. U.S.D.A. Bul. 1403. 1926.

8. Gaines, E. F. Inheritance in wheat, barley, and oat hybrids. Wash. Agr. Exp. Sta. Bul. 135. 1917.

9. Hayes, H. K., and Robertson, D. W. The inheritance of seed color in wheat. Jour. Amer. Soc. Agron. 16:787-790. 1924.

10. Heyne, E. G., and Johnston, C. O. Inheritance of leaf rust reaction and other characters in crosses among Timstein, Pawnee, and Red Chief wheats. Agron. Jour. 46:81-85. 1954.

11. ___________, and Livers, R. W. Monosomic analysis of leaf rust resistance, awnedness, winter injury, and seed color in Pawnee wheats. Agron. Jour. 45:54-58. 1953.

12. Mains, E. B. Inheritance of resistance to powdery mildew in wheat. Phytopath. 24:1257-1261. 1934.

13. __________, Leighty, C. E., and Johnston, C. O. Inheritance of resistance to leaf rust in crosses of common wheat. Jour. Agr. Res. 32:931-972. 1926.

14. Martinez, L. M., Ausemus, E. R., and Burnham, C. R. Inheritance of reaction to leaf rust, and of certain other characters in a wheat cross. Univ. of Minn. Tech. Bul. 205. 1953.

15. Percival, J. The Wheat Plant. Duckworth and Company, London 463 pp. 1921.

16. Quisenberry, K. S., and Clark, J. A. Inheritance of awn development in Sonora wheat crosses. Jour. Amer. Soc. Agron. 25:482-492. 1933.

17. Schlehuber, A. M. Wheat Inheritance: Reaction to four bunt biotypes, spike density, and seed color. Wash. Agr. Exp. Bul. 323. 1935.

18. ______________. Reaction of varieties and inheritance of resistance to races of leaf rust, Puccinia rubigo-vera tritici (Eriks.) Carleton in hard red winter wheat. Zeitschrift f. Pflanzenzüchtung. 29:193-208. 1950.

19. Stewart, G. Correlated inheritance in Kanred-Sevier varieties of wheat. Jour. Agr. Res. 36:873-896. 1928.

20. __________. Inheritance in a wheat cross between Ridit and a segregate of Federation-Sevier (14-85). Jour. Amer. Soc. Agron. 23:964-967. 1931.

21. __________. Miscellaneous genetic data from wheat crosses. Jour. Amer. Soc. Agron. 26:249-250. 1934.

22. __________, and Dalley, C. L. A cumulative transgressive segregation in wheat. Jour. Amer. Soc. Agron. 24:755-764. 1932.

23. __________, and Woodward, R. W. Inheritance in a wheat cross between Hybrid 128 X White Odessa and Kanred. Jour. Agr. Res. 42:507-520. 1931.

24. Swenson, S. P., Buchholtz, W. F., and Grafius, J. E. Complementary genes for leaf rust reaction and awnedness in a spring wheat cross. Jour. Amer. Soc. Agron. 39:739-749. 1942.

25. Wiggin, H. C. Monosomic analysis of stem rust resistance and awn expression in Kentana 52 wheat. Jour. of Hered. 46:239-242. 1955.

26. Worzella, W. W. Inheritance and interrelationship of components of quality, cold resistance, and morphological characters in wheat hybrids. Jour. Agr. Res. 65:501-522. 1942.

27. Wu, C. S., and Ausemus, E. R. Inheritance of leaf rust reaction and other characters in a spring wheat cross. Agron. Jour. 45:42-48. 1953.

VITA

Lewis Eugene Browder

Candidate for the Degree of

Master of Science

Thesis: THE INHERITANCE OF SEEDLING REACTION TO PUCCINIA RUBIGO-VERA TRITICI (ERIKS.) CARLETON RACE 9, AWNEDNESS, AND SEED COLOR IN WHEAT CROSSES INVOLVING AKMANA

Major Field: Agronomy (Field Crops)

Minor Field: Botany and Plant Pathology

Biographical:

Personal data: Born January 29, 1932, at McQueen, Oklahoma.

Education:

Undergraduate Study: Cameron State Agricultural College, 1950-52; Oklahoma Agricultural and Mechanical College, 1952-54.

Graduate Study: Oklahoma Agricultural and Mechanical College, 1954-56.

Professional Experience: Graduate Assistant in Agronomy, Oklahoma Agricultural and Mechanical College, 1954-56.

Member: Alpha Zeta

Date of Final Examination: July, 1956

Thesis Title: THE INHERITANCE OF SEEDLING REACTION TO *PUCCINIA RUBIGO-VERA TRITICI* (ERIKS.) CARLETON RACE 9, AWNEDNESS, AND SEED COLOR IN WHEAT CROSSES INVOLVING AKMANA

Author: LEWIS EUGENE BROWDER

Thesis Adviser: DR. A. M. SCHLEHUBER

The content and form have been checked and approved by the author and thesis adviser. Changes and corrections in the thesis are not made by the Graduate School office or by any committee. The copies are sent to the bindery just as they are approved by the author and faculty adviser.

Typist: ZADA BROWDER