INHERITANCE STUDIES IN THE CROSS PAWNEE X RED CHIEF WINTER WHEAT

by

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INTRODUCTION

An understanding of the general principles of genetics and a familiarity with the specific genetic factors involved in the material being used is necessary for any successful scientific plant breeding program. Many general principles of genetics have been well established, and a thorough understanding of them is basic. However, a plant breeder must know also the specific mode of inheritance of the important characters involved in the material he is using. Variation among individuals is the foundation upon which plant breeders build their programs. Combining of the desirable variations for several characters can be accomplished quickly and efficiently only if a scientific program for causing and retaining these variations is followed. Such a program must include planning and use of both general and specific genetic information. Clark (7) stated, "The importance of genetics in solving the underlying principles of inheritance, thus facilitating more efficient breeding operations, cannot be overemphasized."

The inheritance of many characters in wheat has been investigated and has been found to be simple in some cases and quite complex in others. Ausemus, et al. (4) compiled a list of 236 references concerning genetic studies on wheat and suggested gene symbols for those characters which had been studied. Modes of inheritance have differed widely between varieties. As new varieties are developed which have agronomic characters leading to their possible use in plant breeding programs, it is desirable to obtain some genetic data on them. The genetic study reported here was made on two such new varieties of wheat now being grown in Kansas.

A genetic study may furnish information of both a scientific and a practical nature. Quisenberry and Clark (28), discussing awn inheritance studies, said,

> In addition to determining the mode of inheritance there is a practical side to the problem, as in some sections of the United States increasing length of awns is known to be associated with increased yield.

Many projects are planned in such a manner as to have the development of new superior varieties as the major objective and the gaining of other knowledge as a by-product. Much important and reliable genetic data have been gained in this manner. The cross studied here was made primarily in an attempt to combine the high yield, good quality, disease resistance, and other desirable characteristics of Pawnee with the high test weight and desirable appearance of the grain of Red Chief. Other differing characters of the two parents also afforded an excellent opportunity for a genetic study. The characters studied were date of first heading, plant height, awnedness, glume color, kernel color, a "swayback" character of the grain, grain bleaching, and leaf rust resistance.

REVIEW OF THE LITERATURE

Date of Heading and Plant Height

It has been difficult to set up a definite factorial explanation of quantitative characters such as date of heading, plant height, etc. Freeman (15) did not attempt to assign definite numbers of genes to plant height but thought that there must have been several. Clark (6) found earliness of heading dominant and tallness partially dominant in a cross of two spring wheats. Aamodt (1) decided from a study of crosses between winter and spring wheats that there must be two or more factors for early and late heading in addition to the genes for winter and spring growth habit. In contrast Florell (13) found segregates from a Marquis x Sunset cross grouping into two classes and explained it as due to one factor. In another cross Florell (14) found earliness due to three or more factors with both parents contributing some dominants. Gfeller (18) likewise believed earliness in a cross of Garnet x Red Fife to be controlled by many factors.

Awnedness

Varieties of common wheat are now classified into five distinct awn classes. These classes as outlined by Clark, Florell, and Hooker (8) are awnless, apically awnletted, awnletted, short awned, and awned. Class 1, awnless, includes those types with no development of awnlets as well as types which sometimes may have a few awnlets 1 to 2 mm long at the tip of the spike. Class 2, apically awnletted, has awnlets 1 to 15 mm long at the apex of the spike but rarely occurring in the central or basal portions. Class 3, awnletted, has awnlets from 3 to 40 mm long, the shorter ones occurring at the base of the spike and the length increasing toward the apex. This class may be quite variable and is sometimes divided into classes 3 - and 3+ . Class 4, short awned, has short awns varying throughout the spike from 18 to 50 mm long, but only about half the length of normal awns and frequently incurved or recurved. Class 5, awned, has awns varying from 30 to 100 mm in length.

Biffen (5) was the first investigator to make a genetic study of awnedness in wheat. He concluded that the development of awns was controlled by a single factor and that the beardless condition was dominant. Gaines (16), Hayes and Aamodt (21), Gaines and Singleton (17), Goulden, Neatby, and Welsh (19), Clark and Quisenberry (10), Ausemus (3), and Clark and Smith (12) all presented data verifying these early findings.

Clark (7) cited work of Howard and Howard who were the first to work with a true awnless wheat and reported two factors involved in awn inheritance. Since those very early investigations, many other workers have reported results involving more than one factor. In a cross of Sonora, weakly awnletted, by Quality, strongly awnletted, Quisenberry and Clark (28) recovered progeny ranging through all five awn classes from fully awned to truly awnless. Tingey and Tolman (35) found that in the cross Hope x Dicklow No. 3 one factor could explain the results, but in the cross Hope x Federation two factors segregating independently were necessary. Two factors segregating independently were necessary also to explain results obtained by Stewart and Heywood (33). Love and Craig (25) reported that one factor for awns was very closely linked with the factor for the pubescent node character. Clark (6) concluded that two factors could not completely account for all of the awn variation in a Kota x Hard Federation cross. Stewart (30) explained his results in Federation x Sevier with two factors for awns with linkage and 35 percent crossing over. Clark and Hooker (9) found that two factors, one primary and one secondary, explained their results. Clark, Florell, and Hooker (8) reported, "There are as many as four genetic factors involved in the inheritance of awnedness in wheat." Gfeller (18) concluded from his results of a cross Garnet, awnletted, by Red Fife, apical-awned, that in addition to a gene for awns each parent carried a separate dominant inhibitor for that character. Watkins and Ellerton (37) noted that five established major genes, alone or in combination, led to the production of the major awn classes.

Glume Color

Biffen (5) reported that brown glume color was dominant to white and was inherited on a one factor basis. Studies by Stewart and Bischoff (32), Clark, Quisenberry, and Powers (11), Stewart (31), Platt, Darroch, and Kemp (27), and many others confirmed these statements.

Torrie (36) reported three crosses in which he found segregation for glume color on a two factor basis. He also cited work by Nilsson-Ehle which indicated that there were two factors for brown glumes in common wheat.

Kernel Color

Various workers have reported crosses in which the progeny segregated for kernel color in 3:1, 15:1, or 63:1 ratios. Stewart and Woodward (34) found that the red color in Kanred was due to three independently inherited dominants any one of which could cause the red color. Hayes and Robertson (22) showed in a cross Bobs x Marquis that the Marquis parent carried two factors for red kernel color. When Marquis was crossed with Kanred or Minturki, both red grained varieties, white segregates were recovered on a three factor basis showing that they carried a different gene for red color from the two of Marquis. The report in one case that Kanred had three factors for red kernel color and in the other case that it had one might be accounted for as being due to variation within the variety. Schlehuber (29) found in crosses with Albit that Minhardi and Buffum both carried two factors for red kernel color. Clark and Hooker (9) found that of 12 families with which they worked ten segregated for kernel color on a two factor basis and two on a one factor basis. Worzella (39) found linkage between the genes for protein content and kernel color.

Leaf Rust

Resistance to leaf rust in wheat is an inherited character. Mains, Leighty, and Johnston (26) investigated the mode of inheritance in a number of crosses. Using Kanred as a resistant parent, they found varying results in the field and concluded that several factors probably were involved. A greenhouse experiment using physiologic race 9 on seedlings of a cross of susceptible Kanred x resistant selections of Fulcaster indicated that resistance to that race of the rust organism was due to a single dominant factor. A cross of Malakof, resistant to physiologic race 12, by C. I. 3778, resistant to race 5, produced lines in later generations resistant to both races. The resistance in Malakof was due to a single dominant while that of C. I. 3778 was due to a single recessive. Malakof also carried dominant resistance to races 1 and 3; and Norka, C. I. 3756, carried a dominant for resistance to race 12. They concluded that,

> Resistance to the various physiologic forms of leaf rust is due, therefore, to different factors, or groups of factors inherited as a unit, the different factors or groups being independently inherited.

Wismer (38), using a cross of Oro x Tenmarq, found evidences of transgressive segregation and concluded that the results could best be explained on a multiple factor basis.

Johnston and Melchers (24) found that the leaf rust reaction of some varieties changed with the stages of growth. However, strains resistant at the seedling stage usually retained a higher degree of resistance in all stages than those that were susceptible at the seedling stage and became resistant in the mature plant stage.

MATERIALS AND METHODS

The study reported here was made in the spring and summer of 1946 on the F_3 generation of the cross Pawnee x Red Chief common wheats. Characteristics of Pawnee, C. I. 11669, include a bearded spike, white glumes, light red kernels, a moderately early heading period, and a short straw. It is known to have some resistance to leaf rust. Red Chief, C. I. 12109, is one of the varieties of the Blackhull group of hard red winter wheats. It has dark red kernels, brown glumes striped with black, an awnletted spike, and moderately long straw. One prominent morphological character of Red Chief kernels is a concave curved ridge along the back, referred to by Heyne and Reitz (23) as a "swayback". They state that in plump samples 95 percent of the kernels show this character.

The cross was made in reciprocal at Manhattan, Kansas in the spring of 1942. Three F_1 plants were grown in the greenhouse and seven in the field during the 1942-43 season. The F_1 plants and their F_2 kernels were examined for possible non-crosses or mixtures. The F_2 grain from all ten plants was bulked and a random sample space planted in the fall of 1943. In the spring of 1944 the individual plants were harvested and threshed separately. The grain from each F_2 plant was planted in an individual three foot row three grams to a row in the fall of 1945. Every tenth row was planted with parental checks, rows of Pawnee and Red Chief alternating. Two replications were planted except in those cases where there was enough seed for only one row. The first replication consisted of 666 hybrid rows and 37 rows of each Pawnee and Red Chief. The second replication included 605 hybrid rows, 61 fill-in rows of Pawnee, and 37 check rows of each of the two parents. At harvest time, one of the Pawnee and two of the Red Chief checks were discarded as being not typical of those varieties.

The method of handling the material up to the F_3 generation did not make it possible to trace each row back to the original F_1 seed from which it descended, as it would have been desirable to have done, particularly in the study of kernel color.

Rows were marked as headed when approximately ten percent of the heads were emerged to the extent that the last floret was free from the "boot". As soon as all plants were fully headed and had ceased elongating, notes were taken on leaf rust infection and height. Percentage leaf rust infection was estimated based upon the United States Department of Agriculture rust infection scale for use in the field. Height was measured to the tip, exclusive of awns, of an average group of spikes in the row. Notes on awns and glume color were taken just previous to harvest time. Each row was marked as bearded, awnless, or segregating for awns and was given a classification of brown, white, or segregating for glume color. In addition, all rows in which some of the plants had black pigment on the glumes like the Red Chief parent were noted.

The first replication was harvested in two groups. As soon as approximately one-half of the rows was fully ripe, this group of rows was cut, tied, bagged in bundles of approximately eight rows and stored in a seed house until threshing time. The remainder was ripe and was cut three days later. The second replication was left standing in the field 12 days after all of the first replication had been harvested in order to expose the grain to the weather and thus allow an opportunity for the grain to bleach. The second replication was then cut, tied, bagged, and stored in a seed house until threshing time.

All rows were threshed separately and a weight per unit measure taken. The unit measure weight used was the weight in grams of the aggregate grain from three independently taken vials level full of grain. The vial used was approximately 18 mm in diameter and 57 mm in depth. This method is very similar to that used by Aamodt and Torrie (2) except that they used a smaller vial. They found that the high degree of correlation in relative weights per measured bushel of different wheat samples obtained by the pint and the vial measures indicated that the latter measure was sufficiently reliable to be a useful instrument in determining the weight per bushel of small samples.

Grain notes were taken on the presence of white kernels and kernels exhibiting the swayback character of the Red Chief parent. For this character the samples were classed as "normal" if less than ten percent showed any tendency toward swaying, "swayed minus" if from ten to 90 percent were swayed, and "swayed plus" if 90 percent or more of the kernels showed some swaying. These percentages were only approximate and were used to allow for the unswayed kernels in Red Chief and the apparently swayed kernels in normal populations. The apparent swaying of kernels in normal populations probably was not due to genetic causes but may have been the result of improper development of the kernel, roughening of the bran coat near the brush end, or other unrelated causes.

The grain from the second replication showed a bleaching difference from almost no change in color or roughening of the bran coat in Red Chief to almost complete bleaching of the red color in Pawnee. An arbitrary five unit scale for use in classifying bleaching differences was set up using the Red Chief type as grade 1 and the Pawnee type as grade 5. Grade 2 included those samples having slight to moderate bleaching of the color with no perceptible roughening of the bran coat. Grade 3 consisted of those showing moderate bleaching and slight bran coat roughening. Those samples having either medium bleaching and very rough bran coat or much bleaching of the color and slight or medium roughening of the bran coat made up class 4.

Unevenness of the soil and stand and the fact that the second replication was not complete made it advisable to use only the first replication for a study of quantitative characters. However, the second replication was used for the study of bleaching, as a check on the first, for such characters as awn development, glume color, and swayback kernels, and for the study of black on the glumes and white kernels where the particular character showed in one but not both replications. This occurred in several cases and was due probably to an insufficient number of plants within rows.

An attempt was made to obtain additional data on awns and glume color from an F_4 bulk population of the same Pawnee x Red Chief cross. This population had been carried in bulk in the wheat breeding nursery at Manhattan, Kansas, and had received no intentional selection for awns or glume color. The grain in bulk from F_2 plants had been screened and bunted with only the plump grains being planted in 1944. The bulk grain from F_3 plants received similar treatment in 1945 except that fanning replaced screening. The bulk population of F_4 plants used here was pulled when it was fully ripe; and the individual plants were separated and classified for awns, brown or white glumes, and presence or absence of black on the glumes.

Data on seedling resistance to leaf rust physiologic race 9 were obtained in the greenhouse in the fall of 1946. Samples of 25 kernels from each of the 666 hybrid rows and from 30 of the Pawnee and 30 Red Chief rows were planted in four inch pots. Ten days after planting, at the two leaf stage, they were dusted with spores from a pure culture of leaf rust physiologic race 9. After inoculation they were left 24 hours in a moist chamber under conditions of approximately 100 percent humidity. Ten to 12 days later, readings were made of the leaf rust reaction using the scale for classifying seedling reaction as described by Mains, Leighty, and Johnston (26).

EXPERIMENTAL RESULTS AND DISCUSSION

Date of Heading

Results of the observations of dates of heading are presented in Table 1. The first hybrid row to head did so on April 29, three days earlier than the first Pawnee row; and the latest hybrid row headed May 13, two days later than the latest Red Chief. The day when 50 percent of the rows of each variety and of the hybrid rows had headed could be used as the average heading date for that group. That average date was April 4 for Pawnee, April 5 for the hybrids, and April 7 for Red Chief. This agreed with Clark's (6) findings that earliness of heading was dominant to lateness. Evidences of transgressive segregation indicated that several genetic factors were involved. Both parents probably carried genes for both early and late heading

Table 1. Date of first heading of parental check and F_3 hybrid rows of the cross Pawnee x Red Chief.

Variety	Date -- April and May															Total
	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	
Pawnee																
No. rows				3		15	11		5	1		1				36
Cumulative %				8	8	50	78	78	94	97	97	100				
Red Chief																
No. rows						2	10	1	15	5	1		1			35
Cumulative %						6	34	37	80	94	97	97	100			
F_3 hybrids																
No. rows	1	4	25	59	20	124	148	31	142	32	58	4	14	3	1	666
Cumulative %		1	5	13	16	35	57	57	83	88	97	97	99	100	100	

with Pawnee carrying a preponderance of those for earliness and Red Chief carrying more for lateness. The unevenness of the distribution of the hybrid rows probably was due to environmental rather than genetic factors as the same unevenness was apparent in both parents.

Plant Height

Measurements of plant height were taken on all rows. Results of these measurements are presented in Table 2. The Pawnee checks averaged 40.7 inches tall; Red Chief, 44.1; and the hybrids averaged 42.6 with an approximate normal distribution and a range from one as short as the shortest Pawnee to one taller than the tallest Red Chief. A test for significance between means indicated that all differences were significant. No definite factorial basis could be assigned, but the normal distribution indicated that probably there were several genetic factors operating.

Awnedness

The F_3 hybrid rows could be arranged very well into the following three distinct groups; those awned like the Pawnee parent, awnletted like the Red Chief parent, and segregating for both types. The results as presented in Table 1 show that 145 awnletted, 349 segregating, and 172 awned rows were observed. A chi-square value of 3.727 and resulting probability of .16 indicated that the deviation from a single factor 1:2:1 ratio was well within the bounds of chance variation.

Table 2. Plant height of parental check and F_3 hybrid rows of the cross Pawnee x Red Chief.

Variety	37	38	39	40	41	42	43	44	45	46	47	Total number rows	Mean height
Number or rows													
Pawnee	1		6	11	7	7	4					36	40.7±1.7
Red Chief					1	4	4	10	15	1		35	44.1±1.2
F_3 hybrids	1	4	17	48	98	146	150	127	57	17	1	666	42.6±1.1

Significance of differences between means

	Difference	t value	Probability
Pawnee-Red Chief	3.4	10.95	less than .01
Pawnee-F_3 hybrids	1.9	10.11	less than .01
Red Chief-F_3 hybrids	1.5	7.94	less than .01

Data from the F_4 bulk, also presented in Table 3, did not fit the expected single factor ratio due to an excess of awned plants and corresponding deficit of awnletted and heterozygous ones. Observed numbers of 323 awnletted, 98 heterozygous, and 539 awned plants deviated enough from the expected 420, 120, and 420 numbers to cause a calculated chi-square value of 60.152 and probability of less than .01.

It is suggested that part of the excess in awned plants was the result of a higher yield of grain in previous generations in the awned plants. Quisenberry and Clark (28), Clark, Florell, and Hooker (8), and Hayes (20) have found that increased awn length was associated with increased yield. Hayes made the following statement about some of his material:

> In each of the generations from the F_3 to the F_5 the bearded families gave a higher average yield per plant than the awnless families. These results show that the awn is an important organ. In the 1918 and 1920 seasons, which were favorable years for growing wheat, the bearded families yielded between seven and eight percent more grain than the awnless families. In the unfavorable season of 1919 the bearded wheats yielded nearly 17 percent more grain than the awnless.

Since this population was carried in bulk entirely without intentional artificial selection for awns, any correlation between awns and yield would alter the ratio of awned to awnless plants.

Glume Color

The data relative to glume color from both the F_3 rows and the F_4 plants are recorded in Table 4. The F_3 rows were classed as either brown, white, or segregating; the F_4 plants were class-

Table 3. Segregation for awnedness of F_3 rows and F_4 plants of the cross Pawnee x Red Chief.

Generation	Awnletted	Segregating	Awned	Total
F_3 rows				
Number of rows				
Observed	145	349	172	666
Calculated 1:2:1	166.5	333	166.5	666
Difference	21.5	16	5.5	
Chi-square value	2.776	0.769	0.182	3.727
Probability				.16
F_4 plants				
Number of plants				
Observed	323	98	539	960
Calculated 7:2:7	420	120	420	960
Difference	97	22	119	
Chi-square value	22.402	4.033	33.717	60.152
Probability				less than .01

ified merely as brown or white. In the F_3 rows 170 brown, 328 segregating, and 168 white represented an unusually close fit to a single factor hypothesis. A chi-square value of .016 and a probability of .90 were obtained. There were slight observable differences in the intensity of the brown color indicating that brown might not have been completely dominant as others have reported or that modifying factors might have been present.

An excess of brown glumed plants in the F_4 bulk produced a significant deviation from the expected single factor ratio. The observed numbers of plants were 608 brown and 352 white as compared with 540 brown and 420 white which were expected. A chi-square value of 19.573 and a probability of less than .01 were obtained. No reasonable single genetic theory was known to the author which could explain the results from both sources. The F_3 rows were considered a more reliable source of information than the F_4 plants; therefore the single factor hypothesis was thought to be correct.

The inheritance of black pigment on the glumes was apparently more complex than brown and white glume color. The amount of black varied from an almost undiscernable fringe along the edge of the outer glumes of one or two spikelets to an almost complete covering of the outer glumes and lemmas and a partial covering of the paleas of most of the spikelets of a spike. This indicated that there probably were two or more factors involved. The hypothesis which best explained the results obtained from both the F_3 rows and the F_4 plants, as given in Table 5, was one of two factor pairs, one (Bg,bg) dominant for the presence of

Table 4. Segregation for glume color (brown vs. white) of F_3 rows and F_4 plants of the cross Pawnee x Red Chief.

Generation	Brown	Segregating	White	Total
F_3 rows				
Number of rows				
Observed	170	328	168	666
Calculated 1:2:1	166.5	333	166.5	666
Difference	3.5	5	1.5	
Chi-square value	0.007	0.008	0.001	0.016
Probability				.90
F_4 plants				
Number of plants				
Observed	608		352	960
Calculated 9:7	540		420	960
Difference	68		68	
Chi-square value	8.563		11.010	19.573
Probability				less than .01

black and the other (Bgi,bgi) a partial inhibitor which when present in the homozygous recessive condition prevented the expression of the black character when the plant was heterozygous for the first or black factor. The following genotypes resulted in black on the glumes of the individuals: BgBg BgiBgi, BgBg Bgibgi, BgBg bgibgi, Bgbg BgiBgi, and Bgbg Bgibgi. All other genotypes resulted in an absence of black. The observed 408 F_3 rows showing black and 258 with no black on the glumes represented a close fit to the expected 416 showing black and 250 showing no black as calculated from a 10:6 two factor ratio. Likewise, the 486 F_4 plants showing black and the 474 showing no black approached very closely to the expected numbers of 487.5 and 472.5 respectively. Calculated chi-square values and probabilities were .409 and .53 for the F_3 rows and .010 and .93 for the F_4 plants.

Although the results support the above explanation very well it is intended only as a hypothesis, further experimentation being necessary to prove or disprove it. Further work is also necessary to determine the amount of black shown by individuals with each of the possible genic combinations of the two factors.

Kernel Color

Results of white kernel occurrence are given in Table 6. Of the common one, two, or three factor ratios that other workers have observed in studies of kernel color, these results fit best the three factor explanation. Observed numbers of 659 rows showing all red or both red and white kerneled plants to seven showing only white types compared favorably with expected numbers of 656

Table 5. Segregation for black pigment on the glumes of F_3 and F_4 plants of the cross Pawnee x Red Chief.

Generation	Black on glumes	No black on glumes	Total	P.
F_3 Number of rows				
Observed	408	258	666	
Calculated 10:6	416	250	666	
Difference	8	8		
Chi-square value	0.153	0.256	.409	.53
F_4 Number of plants				
Observed	486	474	960	
Calculated 130:126	487.5	472.5	960	
Difference	1.5	1.5		
Chi-square value	0.005	0.005	.010	.93

and ten respectively and gave a calculated chi-square value of .914 and probability of .35. On this basis 385 rows were expected with only red kerneled plants, 42 with three red to one white, 125 with 15 red to one white, 104 with 63 red to one white, and ten with only white kerneled plants. It was impossible to accurately classify those rows showing white kernels into the 3:1, 15:1, and 63:1 groups; so all rows were classed into the categories all red, segregating, or all white. The observed numbers 442, 216, and seven respectively deviated significantly from the expected and gave a chi-square value of 20.800 and a probability of less than .01.

There were several explanations for part of the deficit of rows segregating for white kerneled plants, and probably more than one cause was responsible for the total. Part of it could be assessed to insufficient numbers of plants to show white kernels in all of the potential 63:1 rows. However, this reason alone could account for only part of the deficit. The most plausible explanation was that either or both of the parents may have been heterogenous for the number of factors for red color. Since the selection which later became Pawnee was made in the F_4 generation and Red Chief probably resulted from a natural hybrid, either parent could easily have been variable for a character not observable at the time of the final selection for the variety. If one or possibly two of the original F_1 seeds had been the result of a cross of two individuals carrying a common gene for red color, no lines showing white grain would have developed from those F_1 seeds. This easily could have accounted for much of the smaller than expected numbers of white grained or segregating lines. Contamination with foreign pollen at the time of the cross would have produced the same result. Had it been possible to trace each row back to the F_1 kernel from which it descended, these last two suggested explanations could have been tested.

Table 6. Segregation for kernel color in F_3 rows of the cross Pawnee x Red Chief.

	All red	Segregating	All white	Total
Number of rows				
Observed	443	216	7	666
Calculated 37:26:1	385	271	10	666
Difference	58	55	3	
Chi-square value	8.738	11.162	0.900	20.800
Probability				less than .01

Swayback

The results of the swayback classification are given in Table 7. A single factor hypothesis was assumed. The observed numbers of 150 normal, 350 swayed minus, and 166 swayed plus are sufficiently close to the expected numbers of 166.5 normal, 333 swayed minus, and 166.5 swayed plus to give a non-significant chi-square value of 2.505 with a probability of .29. The classes as described elsewhere in this paper were set up on an arbitrary percentage of swayback kernels, and there may have been some error in this classification. However, the classes were easily distinguishable so that the error of classifying should not have been sufficient to alter the ratio greatly.

Table 7. Segregation for swayback kernels in the grain from F_3 rows of the cross Pawnee x Red Chief.

	Normal	Swayed minus	Swayed plus	Total
Number of rows				
Observed	150	350	166	666
Calculated 1:2:1	166.5	333	166.5	666
Difference	16.5	17	0.5	
Chi-square value	1.635	0.868	0.002	2.505
Probability				.29

Bleaching

Several interesting facts were brought to light in the study of bleaching of the grain of the second replication. This replication was harvested July 2, 12 days after harvest of the first replication was completed. A study of Table 8 indicates that the presence of beards had a very definite influence upon the amount of bleaching which occurred. In the bearded rows there was a heavy preponderance of rows falling in bleaching grades 3, 4, and 5; whereas the awnless rows tended to fall more in bleaching grades 1, 2, and 3. Of the 154 bearded rows classified for bleaching, 21 were grade 1 or grade 2 while 74 were either grade 4 or grade 5. Of the 131 awnless rows classified, 48 were grades 1 or 2; and only 16 were grade 4 or grade 5. A chi-square test of independence indicated that this trend was definite and due to something other than chance variation.

Another observation which could be made from Table 8 was that other factors, probably genetic, were operating to cause differences in bleaching. Each of the three awn classes included some rows in each of the five bleaching grades.

Table 9 shows the mean weights per unit measure of the grain from the rows, grouped by bleaching grades, of both replications and the mean reductions in weight between the two replications. There was considerable difference in the level of weights of the grain of the first replication and their corresponding reductions between those rows cut on June 17 and those cut on June 20, and therefore the analysis of the data of these two groups was done separately. These differences were probably due to environmental rather than genetic causes as the weights in the second replication are essentially the same for both groups.

Rains of .13 and 1.62 inches occurred on June 18 and 19, respectively. These rains probably accounted for the lower mean weights and accompanying lower reductions between first and second replications in the group in which the first replication was cut June 20. Other rains during the bleaching period were .05 on June 25, .28 on June 29, and .03 on July 1.

The weight of the grain of the second replication was definitely lower than the weight of the grain of the first replication, and this reduction increased with the amount of bleaching that had occurred. The group in which the first replication was cut June 17 had reductions in weight between the two replications of 0.9, 1.2, 1.4, 1.7, and 1.7 grams respectively for the bleaching grades from 1 to 5. The other group had reductions of 0.5, 0.6, 0.8, 1.0, and 1.2, respectively. The reduction in Red Chief was 0.4 while in Pawnee it was 2.4. A test of significance showed that the mean reductions in weight between the two replications was highly or very highly significant in all cases.

Some difficulty was encountered in classifying as the classes were based on relative characters and not all samples conformed to a definite class. This fact in addition to the fact that awnedness and possibly other factors were involved made it seem unwise to assign any definite number of genetic factors to the bleaching character. However, the frequency of recovery of parental types indicated that two or more genetic factors other than the one for awns were concerned.

Calculations of the regression and correlation coefficients as shown in Fig. 1 were based upon data from hybrid rows only although points were indicated for Pawnee and Red Chief also. All correlation and regression coefficients were significant.

Table 8. Segregation within awn classes for bleaching of the grain from F_3 rows of the cross Pawnee x Red Chief.

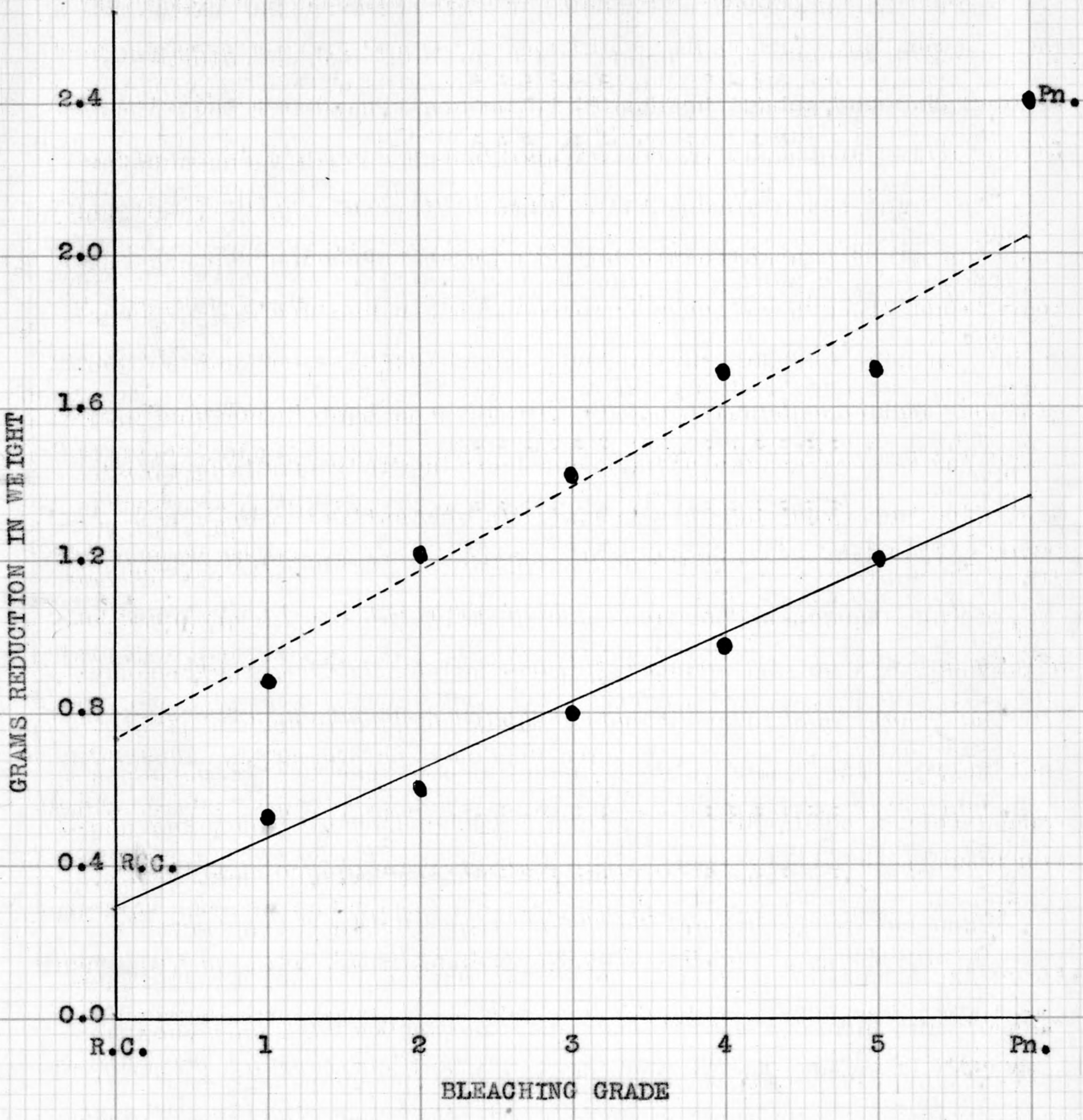
Bleaching grade	Number of rows			
	Bearded	Segregating	Awnless	Total
1	3	19	9	31
2	18	68	39	125
3	59	156	67	282
4	49	59	11	119
5	25	16	5	46
Total	154	318	131	603

Test of independence

Chi-square value----------59.239 Probability--less than .01

Table 9. Mean weights per unit measure of grain from parental check and F_3 rows, grouped by bleaching grades, in the cross Pawnee x Red Chief.

Bleaching grade	Number or rows	Weight of grain in grams		
		First replication	Second replication	Reduction
		First replication cut June 17		
1	8	31.2±0.3	30.4±0.2	0.9±0.4
2	35	31.2±0.5	30.0±0.4	1.2±0.6
3	110	31.1±0.4	29.7±0.4	1.4±0.5
4	61	31.0±0.4	29.3±0.5	1.7±0.5
5	11	30.8±0.5	29.0±0.5	1.7±0.7
Pawnee	22	30.8±0.2	28.3±0.3	2.4±0.4
		First replication cut June 20		
Red Chief	35	31.4±0.2	31.1±0.2	0.4±0.3
1	22	30.9±0.5	30.4±0.4	0.5±0.4
2	87	30.6±0.4	29.9±0.4	0.6±0.4
3	166	30.4±0.4	29.6±0.4	0.8±0.4
4	52	30.3±0.4	29.3±0.4	1.0±0.5
5	30	30.0±0.5	28.7±0.5	1.2±0.4



----------First replication cut June 17
regression coefficient-----2.1
correlation coefficient----0.972
__________First replication cut June 20
regression coefficient-----1.8
correlation coefficient----0.984

Figure 1. Correlation between bleaching grade and mean reduction in grain weight between first and second replications of F_3 rows of the cross Pawnee x Red Chief.

Leaf Rust

Results of leaf rust readings taken on the mature plant basis in the field are given in Table 10. The mean readings were 26.9 percent for Pawnee, 30.9 percent for Red Chief, and 37.9 percent for the hybrids. Since there are usually several physiologic races of leaf rust present in the field, little can be learned about inheritance of resistance from this type of study. Although Pawnee had a somewhat lower mean reading than Red Chief, the difference was not significant. However, the mean of the hybrid rows was significantly higher than either of the parents. This indicated that both parents had some mature plant resistance to one or more of the races present in the field. Races 9 and 126 were known to be present, and several others probably were also. Pawnee was known to have resistance to race 9, but Red Chief was not known to have resistance to any race.

Results of the greenhouse experiment to determine the mode of inheritance of the Pawnee resistance to physiologic race 9 as presented in Table 11 indicated that a single factor was responsible for the differences. The 161 resistant, 325 segregating, and 180 susceptible lines approached very nearly the expected 166.5 resistant, 333 segregating, and 166.5 susceptible. A chi-square value of 1.794 and probability of .42 were obtained. In the segregating lines intermediate or heterozygous types were easily distinguishable thus indicating that dominance was incomplete.

Table 10. Leaf rust reaction (field) of parental check and F_3 rows of the cross Pawnee x Red Chief.

Variety	Percent leaf rust infection																Total number rows	Mean percent infection
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80		
Number of rows																		
Pawnee		3	5	5	8	5	2	4	3	1							36	26.9±11.0
Red Chief			2	2	9	8	8	3	1	2							35	30.9± 6.4
F_3	3	8	25	23	66	116	112	114	58	45	29	41	17	5	1	3	666	37.9±13.0

Significance of differences between means

	Difference	t value	Probability
Pawnee-Red Chief	4.0	1.873	.07
Pawnee-F_3	11.0	4.991	less than .01
Red Chief-F_3	7.0	3.169	less than .01

Pawnee and Red Chief were also tested with pure cultures of rust of races 5, 15, 37, 44, 58, 105, and 126. These races are all commonly found in Kansas. Red Chief proved to be fully susceptible to all races tested. Pawnee was highly resistant to race 37 and showed some resistance, an x or intermediate type reaction, to races 15 and 126.

Table 11. Leaf rust reaction to physiologic race 9 in the cross Pawnee x Red Chief.

Variety	Number of rows			
	Resistant	Segregating	Susceptible	Total
Pawnee	31			31
Red Chief			31	31
Hybrids				
Observed	161	325	180	666
Calculated 1:2:1	166.5	333	166.5	666
Difference	5.5	8	13.5	
Chi-square value	0.183	0.192	1.419	1.794
Probability				.42

General Discussion

Ausemus, et al. (4) suggested the following gene symbols for characters in wheat: awnedness A,a; date of heading Dh,dh; glume color Gc,gc; plant height Hh,hh; greenhouse seedling resistance to leaf rust physiologic race 9 Lr3,lr3; and kernel color R,r. Other characters reported on here but for which no gene symbols had been suggested previously were symbolized as follows: black on glumes Bg,bg; inhibitor of black glume factor Bgi,bgi; and swayback kernels Sb,sb. If these symbols were used, the results reported here indicated that the two parents had the following gene constitutions: Pawnee aa DhDh gcgc hhhh Lr3Lr3 RRrrrr bgbg BgiBgi SbSb or sbsb, Red Chief AA dhdh GcGc HhHh lr3lr3 rrRRRR BgBg bgibgi sbsb or SbSb. It was assumed from the fact that Red Chief had a grain that was darker than that of Pawnee and from their performance in other crosses that Red Chief had two factors for red kernels and Pawnee had only one. It was not known whether the swayback character of the kernels was dominant or recessive.

For the most part the results reported here agreed satisfactorily with results obtained by other investigators working with the same characters. The study furnished data on the inheritance of several characters and the probable gene constitution of the two parents. It furnished a possible explanation of the inheritance of the presence of black on the glumes of some varieties, but more investigation is necessary to establish that explanation as correct. Of the characters studied the bleaching of the grain was probably the most important from a practical plant breeding standpoint. In areas where harvesting is done with a combine, bleaching becomes an important factor. More work is necessary to determine what genetic, as well as other factors, affect it.

SUMMARY

The genetic study reported here was made on two new varieties of wheat now being grown in Kansas. Both have agronomic characters leading to their possible use in plant breeding programs.

The characters studied were date of heading, plant height, awnedness, glume color, kernel color, swayback kernels, bleaching of the grain, and leaf rust resistance.

The study was made in the spring and summer of 1946 on a population of F_3 and parental check rows and the grain harvested from them. An attempt was made to obtain additional data on awns and glume color from an F_4 bulk population of the same Pawnee x Red Chief cross. Data on seedling resistance to leaf rust physiologic race 9 were obtained in the greenhouse in the fall of 1946.

The first hybrid row to head did so three days earlier than the first Pawnee row, and the latest hybrid row headed two days later than the latest Red Chief row. The average heading date was April 4 for Pawnee, April 5 for the hybrids, and April 7 for Red Chief. Indications of transgressive segregation indicated that several genetic factors were involved.

The Pawnee checks averaged 40.7 inches tall; Red Chief, 44.1; and the hybrids averaged 42.6 with an approximate normal distribution and a range from one as short as the shortest Pawnee to one taller than the tallest Red Chief. There probably were several genetic factors operating.

Data from the F_3 hybrid rows indicated that segregation for awns was on a single factor basis. Data from the F_4 bulk did not fit a single factor ratio. The excess in awned plants was probably the result of a higher yield of grain in previous generations in the awned plants.

The data relative to brown and white glume color from the F_3 rows represented an unusually close fit to a single factor hypothesis. The data from the F_4 plants did not fit this explanation. The inheritance of black pigment on the glumes was due to two factors, one a dominant for black pigment and the other a partial inhibitor which when present in the homozygous recessive condition prevented the expression of the black character when the plant was heterozygous for the first or black factor.

Results of white kernel occurrence fit best a three factor explanation although there was a large deficit of rows segregating for white kerneled plants. The most plausible explanation for the deficit of rows segregating for white kerneled plants was that either or both of the parents may have been heterogenous for the number of factors for red color.

The data on swayback kernel occurrence indicated that one factor was responsible for that character.

The presence of beards had a very definite influence upon the amount of bleaching which occurred to the grain of the second replication. Other factors, probably genetic, were also operating to cause differences in bleaching. The weight per unit measure was definitely lower for the rows of the second replication than for the rows of the first replication. This reduction in weight was more for the badly bleached samples than for the slightly bleached ones.

The mean percentage leaf rust reading was significantly higher for the hybrid rows than for the rows of either parent. This indicated that both parents had resistance to some races of leaf rust. In the greenhouse Pawnee was found to have a high level of seedling resistance to races 9 and 37 and moderate resistance to races 15 and 126. The resistance of Pawnee to race 9 was shown to be due to a single factor.

Using suggested gene symbols for the various characters studied, Pawnee had the gene constitution aa DhDh gcgc hhhh Lr3Lr3 RRrrrr bgbg BgiBgi SbSb or sbsb and Red Chief had the Constitution AA dhdh GcGc HhHh lr3lr3 rrRRRR BgBg bgibgi sbsb or SbSb.

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