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Inheritance of Awns in a Cross Between Hard Federation and Kota Wheats

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INHERITANCE OF AWNS IN A CROSS BETWEEN HARD FEDERATION AND KOTA WHEATS

A

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INTRODUCTION

During the past few years there have been numerous studies made of various characters in wheat. Some characters which were thought at first to be simple in inheritance have since been found to be rather complex.

The data in the following pages are the results of an investigation made to study the inheritance of awns in a cross between Hard Federation and Kota varieties of wheat.

REVIEW OF LITERATURE

Until the last few years awn inheritance in wheat has been regarded as extremely simple, that is, as being dependent on a single factor difference. The awns of the F_1 plants have nearly always been intermediate in length between the awns of the two parents with the F_2 ratios 3:1 or 1:2:1, awnlessness usually being regarded as dominant. Recently, however, it has become apparent that the inheritance of awns is much more complex than the original data indicated. Several workers have found two independent factors and one has found two factors segregating in such a fashion as strongly to suggest linkage between these two factors.

The first genetic study on awnedness inheritance in wheat hybrids was reported in 1905 by Biffen(1) who concluded that "the beardless condition is a dominant, the bearded a recessive character". Other early workers, particularly Tschermak(12) and Spillman(8), obtained similar results in the first generation and in the second generation also, when the awnless and awned plants occurred in a simple mendelian ratio of 3:1.

Recent studies by Gaines and Singleton(3) show similar segregation while Percival(4) reported F_2 segregation in numerous crosses to approach a 1:2:1 ratio when intermediates occurred. Saunders(9) questioned the idea that the first generation between an awnless and an awned wheat always is awnless and maintained that the character of awns in the F_1 varied with the wheats used.

Howard and Howard(4) were the first to work with the true awnless wheat. They crossed a fully bearded wheat with one described as being really awnless, a fact they emphasized as important, in as much as many of the so-called awnless varieties really have short tip awns. In the F_2, five awn-classes were obtained, viz., (a) entirely awnless, (b) short tips, (c) long tips, (d) nearly full bearded, and (e) fully bearded. They grouped all awned and tip-awned classes together as awned which in comparison with the awnless gave a 15:1 ratio. These results were explained on a two-factor basis. Four classes bred true, and when the short-tipped plants were crossed, F_2 segregation showed some fully bearded and some awnless plants as well as the intermediate forms. They thus concluded that the awned condition was dominant, which was an opposition to the conclusion of other previous workers.

In similar studies between Kota and Hard Federation, Clark(2) found a somewhat complex condition in the inheritance of awns. He made five classes of awn types in F_2 and he arrived at the conclusion that the awnless condition was dominant, since the F_1(class 2) approached more nearly the awnless than the awned parent and also that two genetic factors could not entirely account for the breeding behavior in the F_2 and F_3 breeding behavior.

Nilsson - Ehle(6) obtained by mutation true-breeding forms of awnless, half-awned, and awned wheats. Awnless forms were partly dominant to half-awned and to awned, and half-awned forms to awned. He explained his results on the basis of multiple allelomorphs for half-awned and fully awned plants arising by complex mutation from the awnless plants.

A parallel case in rice has been recently reported by Jones(5) who found evidence of two independently inherited factors for awnedness. In a cross between a fully awned variety and an awnless one, the F_1 was intermediate. He took his data from the F_2 plants and grew a few F_3 progenies. He concluded that either of the two factors alone produced an intermediate condition and that the two together produced fully developed awns. He was unable to separate his two intermediate classes.

Stewart(10) recently reported a strong indication of linkage between two factors for awnedness in a cross between pure lines of Federation and Sevier wheats. A pure line of each parental variety and three F_2 families were used in the study. In two of the families, kernels from all of the F_2 plants were sown for F_3 progeny rows. In the other case 74 F_3 families were grown, the F_2 plants from which these came being selected at random so far as awns were concerned.

There were four true breeding classes, viz., (a) fully awned similar to the Sevier parent; (b) awnless, similar to the Federation parent, and (c) and (d) two intermediate classes. The true-breeding parental forms were regularly much more numerous than the true-breeding intermediate forms. He explains this data by stating that the F_2 genotypes as classified by the F_3 breeding behavior rather highly substantiates the presence of two factors for awns, both in the same chromosome, with crossing over to the extent of about 35 per cent.

In another paper Stewart(11) found evidence which indicated very strongly that the above theory was at least approximately correct. From these latter studies it is evident that each of the two factors when present separately produces a different, but somewhat equal major effect. The separate effects of the two factors could be identified not only in the true breeding F_3 progenies but also in the segregating ones.

DESCRIPTION OF THE PARENTS

The parents used, as previously stated, were Hard Federation -- a selection from Federation, and Kota -- a wheat introduced from Russia. Both are grown only to a limited extent under irrigation in Utah and as yet neither are very well known in this section.

Hard Federation

Hard Federation is a variety of white spring wheat which has proved very resistant to drouth. It was developed about 1908 by J.T. Pridham, at the Cowra Experiment Station in New South Wales, Australia, by selection from Federation. It was introduced into the United States in 1915 and was first tested at the experiment stations at Mora Oregon and Chico California. From these two stations seed was first distributed to farmers.

Description.- Hard Federation has awnless, oblong spikes; glabrous, brown glumes; and short, hard, white kernels. It is an early spring wheat which has very strong stems and small leaves, which twist or curl. This latter habit decreases transpiration and Clark(2) states that it is undoubtedly heritable.

Adaptation.- Hard Federation has proved to be a high-yielding variety of spring wheat grown under dry-farm conditions at Mora Oregon. It also does well on some soils of California. In the Pacific Coast and intermountain states it often out yields Marquis from 5 to 10 bushels per acre, and is rapidly becoming an important variety in many of the semi-arid sections of the west.

Kota

Kota is a variety of hard red spring wheat which is resistant to black stem rust. The original seed of this variety was obtained in Russia by Professor H.L. Bolley, of the North Dakota Experiment Station, in 1903.

Description.- Kota has awned, fusiform spikes; glabrous, white glumes; and midlong, hard, red kernels. It is a mid tall, midseason, spring wheat which has weak to mid strong stems.

Adaptation.- The acre yields of Kota have averaged considerably higher in North and South Dakota during the past few years than those of Marquis, the standard variety of hard red spring wheat, as reported by Clark(1). Kota has also produced good yields in the northeastern parts of Montana and Wyoming. It has proved somewhat resistant to drouth, as well as distinctly resistant to black stem rust, in the northern Great Plains area. In the more humid sections of the spring wheat region Kota is not well adapted.

METHOD OF PROCEDURE

It is known that wheat belongs to a group of normally self-fertilized plants, natural crossing occurring in very rare cases. In artificial crossing the cross is made at about the time the ovaries are sufficiently mature and before the anthers have broken. All but the outer florets of eight or ten of the central spikelets are removed. The upper and lower spikelets are cut off with shears. The central floret on each spikelet is removed by grasping it near the top by forceps and pulling downward. The forceps are then carefully pushed between the lemma and palea and the flower opened. The three stamens are then removed, care being exercised not to perform this operation sometime before the pollen is mature. When all the stamens are removed, mature pollen from the other parent is secured and shaken on the stigmas in each floret. The pollen should be obtained from anthers that have turned yellow but not broken, but when it is ready to do so. Usually a single anther, that has just dehisced in handling, is placed in each floret, though sometimes one anther is used to pollinate several stigmas. After all the emasculated florets are pollinated, the head is wrapped up with a leaf from the wheat plant and labeled. When the grain is mature the heads are broken off and reserved until the next planting season.

The cross between Hard Federation and Kota was made after the above mentioned manner by Dr. George Stewart, in the spring of 1925 primarily to study the inheritance of awns. Four families were used up to the F_2 generation but at planting time, in 1928, all but two were discarded.

At the time of seeding the F_1 grain was sown in rows two feet apart, with the kernels about a foot and a half apart in the rows. At maturity the heads were broken off and the grain saved for seeding the next season.

The kernels from the F_1 plants were sown the next season in rows one foot apart with plants three or four inches in the row. Data on the awns of each F_2 plant were taken at the time of harvest.

In the beginning the plants were classified into 5 classes according to awns: Awn class 0(awnless); awn class 1(short awn tips); awn class 2 (short-tip awns in lower half of spike and part length awns in upper hals); awnclass 3(nearly fully awned) and awnclass 4(fully awned). A notation was also made as to the color of the grain and color of the glumes. Two heads from each plant were threshed to get grain color, and these same threshed kernels were placed in an envelope which was marked with the pedigree number and plant number and saved until the following year when they were seeded in a F_3 progeny row.

The plants from these F_2 kernels constituted the F_3 progeny rows from which the data for the conclusions were obtained, each progeny being regarded as denoting the true genotype of F_2 plant from which it was descended. The data on the F_3 progeny plants were taken as soon after heading as the awns were fully developed.

The first thing done in collecting the field data on the F_3 progeny rows was to go thru the rows and mark those which appeared to be breeding true for one of the awn types and then go thru very carefully a second or third time, if necessary, to make sure they were true breeding.

After this was done the writer went thru the rows which were segregating and made a count of the number of plants of each type found while a helper tallied these.

This was done by getting astride the row and gathering the heads of each plant in a bunch and calling off the awn class to which it belonged. In places where the plants were very thick and the culms more or less interwoven, it was necessary to begin at the ground grasping all the culms of the plant together and following these up to the spikes.

EXPERIMENTAL RESULTS

It was at first attempted to divide the awns into five classes, in keeping with Clark's(2) suggestions, who thought he found five true-breeding awn classes. Careful checking of F_3 progenies and comparison with the parents showed only four true-breeding classes. Hard Federation ranged from entirely awnless to very short beaks. Progenies with a similar range were classified as belonging to awn class 1.

In family 323 there were 323 F_3 progenies each from a single F_2 plant. The plants of each F_3 family were classified according to awns.

A summary of the data is given below;

No. of F_3 families breeding true for:		No. of F_3 families segregating for:	
Awns 1	18	Awns 1, 2	37
Awns 2	21	Awns 1, 2, 3	48
Awns 3	20	Awns 1, 2, 3, 4	76
Awns 4	19	Awns 2, 3, 4	43
		Awns 3, 4	39

In family 33F an F_3 progeny of every F_2 plant was likewise grown. The plants in each of the 316 rows were classified and the data summarized by families as follows;

No. of F_3 families breeding true for:		No. of F_3 families segregating for:	
Awns 1	21	Awns 1, 2	32
Awns 2	17	Awns 1, 2, 3	32
Awns 3	16	Awns 1, 2, 3, 4	81
Awns 4	23	Awns 2, 3, 4	47
A		Awns 3, 4	48

An examination of the summaries of awn behavior shows that in the F_2 generation of families 32G and 33F there occurred 9 genotypes of plants according to awn-breeding behavior in F_3. Four of these bred true and five segregated each in a distinct manner.

Let us designate full awns such as occur in the Kota parent by AATT(awn class 4); long apical awns but short lateral awns(awn class 3) by AAtt; well developed tip awns(awn class 2) by aaTT; very short tip awns and awnless beaks by aatt(awn class 1). Awn class 1, as here determined, has the same range as the awnless parent, Hard Federation.

The following zygote genotypes as far as awns are concerned are expected:

(1) AATT
(2) AATt
(3) AaTT
(4) AaTt
(5) AAtt
(6) Aatt
(7) aaTt
(8) aaTT
(9) aatt

The expected breeding nature of the 9 zygotypes is indicated here:

(1) Breed true for awns 4
(2) Segregate for awns 3, 4
(3) Segregate for awns 2, 3, 4
(4) 1, 2, 3, 4
(5) Breed true for awns 3
(6) Segregate for awns 1, 2, 3
(7) 1, 2
(8) Breed true for awns 2
(9) 1

Of the 9 sorts of genotypes (1), (5), (8), and (9), are the true-breeding forms for awn classes 4, 3, 2, and 1 respectively. Genotypes (2) and (3) are each homozygous for one dominant factor and heterozygous for the other, (2) being heterozygous for Tt and (3) for Aa. Genotypes (6) and (7) differ only in that (6) is homozygous recessive for tt and heterozygous for Aa, whereas (7) is homozygous recessive for aa and heterozygous for Tt.

On the basis of total F_3 families, the ratios of families that bred true for awns in various ways suggest a two factor difference. A strictly independent segregation would give approximately equal numbers in each of the four classes that bred true. This was found in both families studied. There was found a ratio that approximates a 1:2:2:4:1:2:1:2:1 for independent segregation, or a 9:3:3:1 taking the 9 genotypes which indicates a 2 factor difference. There is a much closer approximation to this in family 32G than family 33F as indicated by the goodness of fit study.

In Table 1 the closeness of fit to the calculated expectancy is given

Table 1. Calculated(C) and observed(O) numbers of F_2 genotypes as determined by the F_3 breeding behavior

(Family 32G; grown in 1928 at Logan, Utah)

Genotype	O	C	O - C	$(O - C)^2$	$\frac{(O - C)^2}{C}$
AATT	19	20.1875	- 1.1875	1.4101	.0698
AATt	39	40.375	- 1.375	1.8806	.0465
AaTT	43	40.375	2.625	6.8906	.1706
AaTt	78	80.75	- 2.75	7.5625	.0937
AAtt	20	20.1875	- .1875	.0352	.0012
Aatt	37	40.375	- 3.375	11.3906	.2821
aaTt	48	40.375	7.625	58.1416	1.4403
aaTT	21	20.1875	.8125	.6602	.0327
aatt	19	20.1875	- 1.1875	1.4101	.0698
Total	323	323	P =	.9714	X^2 = 2.2067

Table 2. Calculated(C) and observed(O) numbers of plants in each awn group of F_2 genotypes as determined by the F_3 breeding behavior

(Family 33F; grown in 1928 at Logan, Utah)

Genotype	O	C	O - C	$(O - C)^2$	$\frac{(O - C)^2}{C}$
AATT	23	19.75	3.25	10.5625	.5348
AATt	48	39.50	8.50	72.2500	1.8291
AaTT	47	39.50	7.50	56.2500	1.4240
AaTt	81	79.00	2.00	4.0000	.0506
AAtt	16	19.75	- 3.75	13.0625	.6669
Aatt	32	39.50	- 7.50	56.2500	1.4240
aaTt	32	39.50	- 7.50	56.2500	1.4240
aaTT	17	19.75	- 2.75	7.5625	.3824
aatt	21	19.75	1.25	1.5625	.0790
Total	316	316	P =	.4526	X^2 = 7.8148

for family 32G. P = .9714 which is an extremely good fit, shows that 97 cases of 100 worse fit might be expected from chance alone. In Table 2, the closeness of fit for family 33F is shown to be .4526 which, tho not nearly so good a fit as found in family 32G, still indicates a good one.

As stated before, both these families approximate a 1:2:2:4:1:2:2:1 ratio, which is what is expected for strictly independent segregation. It may, therefore, be safely concluded that the F_2 genotypes as classified by the F_3 breeding behavior rather highly substantiates the presence of two factors for awns, independently inherited.

SUMMARY

This cross was made to study awn inheritance and to discover the number of factors involved.

The parents used in the cross were Hard Federation, an awnless variety and Kota, a fully awned wheat.

In F_3 the F_2 genotypes were tested by the breeding behavior of F_3 families, each from a single F_2 plant. Four true breeding classes were found and five which segregated each in a distinct manner.

When the observed proportions of each of these 9 genotypes were studied by the closeness-of-fit method, the two P's were 0.97 and 0.45, both good fits. It seems reasonable to conclude that there is a two-factor difference for awns, independently inherited. The classes were clear-cut and definite when determined by the F_3 breeding behavior.

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Inheritance of awns in a Kota x Hard Federation Wheat Cross

Geo Stewart and B. Ira Judd

~~INTRODUCTION~~

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The kernels from the F_1 plants were sown the next season in rows one foot apart with plants three or four inches apart in the row. Data on the awns of each F_2 plant were taken at the time of harvest.

In the beginning the plants were classified into 5 classes according to awns: Awn class 0(awnless); awn class 1(short awn tips); awn class 2(short awns on the upper half of the spike); awn class 3 (short-tip awns in lower half of spike and part length awns in upper half); ~~awnclass 3(nearly fully awned)~~ and awnclass 4(fully awned). A notation was also made as to the color of the grain and color of the glumes. ~~Two~~ a head ~~s~~ from each plant were threshed to get grain color, and the ~~se same~~ threshed kernels were placed in an envelope which was marked with the pedigree number ~~and plant number~~ and saved until the following year when ~~they were~~ when the kernels from each F_2 plant were seeded in a F_3 progeny row. There was, therefore an F_3 progeny of 20 to 40 plants from every F_2 plant, 373 in one case and 316 in the other.

~~The plants~~ grown ~~from these F_2 kernels constituted~~ It was from the F_3 progeny rows ~~from which~~ that the data ~~for the conclusions~~ here reported were obtained, each progeny being regarded as denoting the true genotype of F_2 plant from which it was descended. The data on the F_3 progeny plants were taken as soon after heading as the awns were fully developed.

The first thing done in collecting the field data on the F_3 progeny rows was to go thru the rows and mark those which appeared to be breeding true for one of the awn types and then go thru very carefully a second or third time, if necessary, to make sure they were true-breeding.

After this was done the writer went thru the rows which were segregating and made a count of the number of plants of each type found while a helper tallied these.

This was done by getting astride the row and gathering the heads of each plant in a bunch and calling off the awn class to which it belonged. In places where the plants were very thick and the culms more or less interwoven, it was necessary to begin at the ground grasping all the culms of the plant together and following these up to the spikes.

EXPERIMENTAL RESULTS

It was at first attempted to divide the awns into five classes, in keeping with Clark's(2) suggestions, who thought he found five true-breeding awn classes. Careful checking of F_3 progenies and comparison with the parents showed only four true-breeding classes. Hard Federation ranged from entirely awnless to very short beaks. Progenies with a similar range were classified as belonging to awn class 1.

In family 32G there were 323 F_3 progenies each from a single F_2 plant. The plants of each F_3 family were classified according to awns.

A summary of the data is given below:

No. of F_3 families breeding true for:	No. of F_3 families segregating for:
Awns 1 -------------------- 18	Awns 1, 2 ------------------ 37
Awns 2 -------------------- 21	Awns 1, 2, 3 --------------- 48
Awns 3 -------------------- 20	Awns 1, 2, 3, 4 ------------ 78
Awns 4 -------------------- 19	Awns 2, 3, 4 --------------- 43
	Awns 3, 4 ------------------ 39

In family 33F an F_3 progeny of every F_2 plant was likewise grown. The plants in each of the 316 rows were classified and the data summarized by families as follows:

No. of F_3 families breeding true for:	No. of F_3 families segregating for:
Awns 1 -------------------- 21	Awns 1, 2 ------------------ 32
Awns 2 -------------------- 17	Awns 1, 2, 3 --------------- 32
Awns 3 -------------------- 16	Awns 1, 2, 3, 4 ------------ 81
Awns 4 -------------------- 23	Awns 2, 3, 4 --------------- 47
A	Awns 3, 4 ------------------ 48

An examination of the summaries of awn behavior shows that ~~in the F_2 generation of families 32G and 33F~~ there occurred 9 genotypes of plants according to awn-breeding behavior in F_3. Four of these bred true and five segregated each in a distinct manner.

Let us designate full awns such as occur in the Kota parent by AATT(awn class 4); long apical awns but short lateral awns(awn class 3) by AAtt; well developed tip awns(awn class 2) by aaTT; very short tip awns and awnless beaks by aatt(awn class 1). Awn class 1, as here determined, has the same range as the awnless parent, Hard Federation.

The following zygote genotypes as far as awns are concerned are expected:

(1) AATT	(6) Aatt
(2) AATt	(7) aaTt
(3) AaTT	(8) aaTT
(4) AaTt	(9) aatt
(5) AAtt	

The expected breeding nature of the 9 zygotypes is indicated here:

(1) Breed true for awns 4
(2) Segregate for awns 3, 4
(3) Segregate for awns 2, 3, 4
(4) 1, 2, 3, 4
(5) Breed true for awns 3
(6) Segregate for awns 1, 2, 3
(7) 1, 2
(8) Breed true for awns 2
(9) 1

Of the 9 sorts of genotypes (1), (5), (8), and (9), are the true-breeding forms for awn classes 4, 3, 2, and 1 respectively. Genotypes (2) and (3) are each homozygous for one dominant factor and heterozygous for the other, (2) being heterozygous for Tt and (3) for Aa. Genotypes (6) and (7) differ only in that (6) is homozygous recessive for tt and heterozygous for Aa, whereas (7) is homozygous recessive for aa and heterozygous for Tt.

On the basis of total F_3 families, the ratios of families that bred true for awns in various ways suggest a two factor difference. A strictly independent segregation would give approximately equal numbers in each of the four classes that bred true. This was found in both families studied. There was found a ratio that approximates a 1:2:2:4:1:2:1:2:1 for independent segregation, or a 9:3:3:1 taking the 9 genotypes which indicates a 2 factor difference. There is a much closer approximation to this in family 32G than family 33F as indicated by the goodness of fit study.

In Table 1 the closeness of fit to the calculated expectancy is given for family 32G. P = .9714 which is an extremely good fit, shows that 97 cases of 100 worse fit might be expected ~~from~~ due to chance alone. In Table 2, the closeness of fit for family 33F is shown to be .4526 which, though not nearly so good a fit as found in family 32G, still indicates a good one.

As stated before, both these families approximate a 1:2:2:4:1:2:2:1 ratio, which is what is expected for strictly independent segregation. It may, therefore, be safely concluded that the F_2 genotypes as classified by the F_3 breeding behavior rather highly substantiates the presence of two factors for awns, independently inherited.

SUMMARY

This cross was made to study awn inheritance and to discover the number of factors involved.

The parents used in the cross were Hard Federation, an awnless variety and Kota, a fully awned wheat.

In F_3 the F_2 genotypes were tested by the breeding behavior of F_3 families, each from a single F_2 plant. Four true breeding classes were found and five which segregated each in a distinct manner.

When the observed proportions of each of these 9 genotypes were studied by the closeness-of-fit method, the two P's were 0.97 and 0.45, both good fits. It seems reasonable to conclude that there is a two-factor difference for awns, independently inherited. The classes were clear-cut and definite when determined by the F_3 breeding behavior.

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INHERITANCE OF AWNS IN A KOTA X HARD FEDERATION WHEAT CROSS

George Stewart and B. Ira Judd

Until the last few years awn inheritance in wheat has been regarded as extremely simple, that is, as being dependent on a single factor difference. The awns of the F_1 plants have nearly always been intermediate in length between the awns of the two parents with the F_2 and F_3 ratios most frequently 3:1 or 1:2:1. ~~Awnlessness has usually been regarded as dominant.~~ Recently, however, it has become apparent that the inheritance of awns is much more complex than the original data indicated. Several workers have found two independent factors and one has found two factors segregating in such a fashion as strongly to suggest linkage.

REVIEW OF LITERATURE

The first genetic study on awnedness inheritance in wheat hybrids was reported in 1905 by Biffen(1) who concluded that "the beardless condition is a dominant, the bearded a recessive character". Other early workers, particularly Tschermak(12) and Spillman(8), obtained similar results in the first generation and in the second generation also, when the awnless and awned plants occurred in a simple mendelian ratio of 3:1. Recent studies by Gaines and Singleton(3) show similar segregation while Percival(4) reported F_2 segregation in numerous crosses to approach a 1:2:1 ratio when intermediates occurred. Saunders(9) questioned the idea that the first generation between an awnless and an awned wheat always is awnless and maintained that the character of awns in the F_1 varied with the wheats used.

Howard and Howard(4) were the first to work with the true awnless wheat. They crossed a fully bearded wheat with one described as being really awnless, a fact they emphasized as important, in as much as many of the so-called awnless varieties really have short tip awns. In the F_2, five awn-classes were obtained, viz., (a) entirely awnless, (b) short tips, (c) long tips, (d) nearly full bearded, and (e) fully bearded. They grouped all awned and tip-awned classes together as awned which in comparison with the awnless gave a 15:1 ratio. These results were explained on a two-factor basis. Four classes bred true, and when the two short-tipped ~~plants~~ types were crossed, F_2 segregation showed some fully bearded and some awnless plants as well as the intermediate forms. They thus concluded that the awned condition was dominant, which was in opposition to the conclusion of other previous workers.

In similar studies between Kota and Hard Federation, Clark(2) found a somewhat complex condition in the inheritance of awns. He made five classes of awn types in F_2 and he arrived at the conclusion that the awnless condition was dominant, since the F_1(Class 2) approached more nearly the awnless than the awned parent and also that two genetic factors could not entirely account for the breeding behavior in the F_2 and F_3 breeding behavior.

Nilsson - Ehle(6) obtained by mutation true-breeding forms of awnless, half-awned, and awned wheats. Awnless forms were partly dominant to half-awned and to awned, and half-awned forms to awned. He explained his results on the basis of multiple allelomorphs for half-awned and fully awned plants arising by complex mutation from the awnless plants.

A parallel case in rice has been recently reported by Jones(5) who found evidence of two independently inherited factors for awnedness. In a cross between a fully awned variety and an awnless one, the F_1 was intermediate. He took his data from the F_2 plants and grew some F_3 progenies. He concluded that either of the two factors alone produced an intermediate condition and that the two together produced fully developed awns. He was unable to separate his two intermediate classes.

Stewart(10) reported a strong indication of linkage between two factors for awnedness in a cross between pure lines of Federation and Sevier wheats. A pure line of each parental variety and three F_2 families were used in the study. In two of the families, kernels from all of the F_2 plants were sown for F_3 progeny rows. In the other case 74 F_3 families were grown, the F_2 plants from which these came being selected at random so far as awns were concerned.

There were four true-breeding classes, viz., (a) fully awned similar to the Sevier parent; (b) awnless, similar to the Federation parent, and (c) and (d) two intermediate classes. The true-breeding parental forms were regularly much more numerous than the true-breeding intermediate forms. The F_2 genotypes as classified by the F_3 breeding behavior rather highly substantiated the presence of two factors for awns, both in the same chromosome, with crossing over to the extent of about 35 per cent.

In other crosses Stewart(11) found evidence which indicated that the above theory was at least approximately correct. From these latter studies it is evident that each of the two factors when present separately produces a different, but somewhat equal major effect. The separate effects of the two factors could be identified not only in the true-breeding F_3 progenies but also in the segregating ones.

DESCRIPTION OF THE PARENTS

The parents used, Hard Federation and Kota, are grown only to a limited extent under irrigation in Utah and as yet neither are very well known in this section. Both are however valuable varieties other regions where they are adapted.

Hard Federation

Hard Federation is a variety of white spring wheat which has proved very resistant to drouth. It was developed about 1908 by J.T. Pridham, at Cowra Experiment Station in New South Wales, Australia, by selection from

Federation. It was introduced into the United States in 1915 and was first tested at the experiment stations at Moro, Oregon and Chico, California. From these two stations seed was first distributed to farmers.

~~Description~~.- Hard Federation has awnless, oblong spikes; glabrous, brown glumes; and short, hard, white kernels. It is an early spring wheat with very strong stems and small leaves, which twist or curl. This latter habit is thought to decrease transpiration and Clark(2) states that it is undoubtedly heritable.

~~Adaptation~~ Hard Federation has proved to be a high-yielding variety of spring wheat grown under dry-farm conditions at Moro,Oregon. It also does well on some soils of California. In the Pacific Coast and northern inter-mountain states it often outyields Marquis from 5 to 10 bushels an acre,

Kota

Kota is a variety of hard red spring wheat which is resistant to black stem rust. The original seed of this variety was obtained in Russia by Professor H.L. Bolley, of the North Dakota Experiment Station, in 1903.

~~Description~~- Kota has awned, fusiform spikes; glabrous, white glumes; and midlong, hard, red kernels. It is a mid tall, midseason, spring wheat which has weak to mid strong stems.

~~Adaptation~~. The acre yields of Kota have averaged considerably higher in North and South Dakota during the past few years than those of Marquis, the standard variety of hard red spring wheat, as reported by Clark(2). Kota has also produced good yields in the northeastern parts of Montana and Wyoming. It has proved somewhat resistant to drouth, as well as distinctly resistant to black stem rust, in the northern Great Plains area. In the more humid sections of the spring wheat region Kota is not well adapted.

Methods of Procedure

The cross between Hard Federation and Kota was made in the spring of 1925 primarily to study the inheritance of awns. Four families were used up to the F_2 generation but at planting time, in 1928, all but two were discarded.

The F_1 kernels were sown in rows two feet apart, with the kernels about a foot and a half apart in the rows. At maturity the heads were harvested and the grain saved for seeding the next season.

The kernels from the F_1 plants were sown the next season in rows one foot apart with plants three or four inches apart in the row. Data on the awns of each F_2 plant were taken at the time of harvest.

In the beginning the plants were classified into 5 classes according to awns: Awn class 0(awnless); awn class 1(short awn tips); awn class 2(short awns on the upper half of the spike); awn class 3(short-tip awns in lower half of spike and part length awns in upper half); and awnclass 4(fully awned). A notation was also made as to the color of the grain and color of the glumes. A head from each plant was threshed to get grain color, and the threshed kernels were placed in an envelope which was marked with the pedigree number and saved until the following year when the kernels from each F_2 plant were seeded in a F_3 progeny row. There was, therefore an F_3 progeny of 20 to 40 plants from every F_2 plant, 323 in one family and 316 in the other.

It was from the F_3 progeny rows that the data here reported were obtained, each progeny being regarded as denoting the true genotype of F_2 plant from which it was descended. The data on the F_3 progeny plants were taken as soon after heading as the awns were fully developed.

The first thing done in collecting the field data on the F_3 progeny rows was to go through the rows and mark those which appeared to be breeding true for one of the awn types and then go thru very carefully a second or third time, if necessary, to make sure they were true-breeding. After this was done the writers went through the rows which were segregating and made a count of the number of plants of each type found while a helper tallied these.

This was done by getting astride the row and gathering the heads of each plant in a bunch and calling off the awn class to which it belonged. In places where the plants were very thick and the culms more or less interwoven, it was necessary to begin at the ground grasping all the culms of the plant together and following these up to the spikes.

EXPERIMENTAL RESULTS

It was at first attempted to divide the awns into five classes, in keeping with Clark's(2) suggestions, who thought he found five true-breeding awn classes. Careful checking of F_3 progenies and comparison with the parents showed only four true-breeding classes. Hard Federation ranged from entirely awnless to very short beaks. Progenies with a similar range were classified as belonging to awn class 1.

In family 32G there were 323 F_3 progenies each from a single F_2 plant. The plants of each F_3 family were classified according to awns.

A summary of the data is given below:

No. of F_3 families breeding true for		No. of F_3 families segregating for:	
Awns 1	18	Awns 1, 2	37
Awns 2	21	Awns 1, 2, 3	48
Awns 3	20	Awns 1, 2, 3, 4	78
Awns 4	19	Awns 2, 3, 4	43
		Awns 3, 4	39

In family 33F an F_3 progeny of every F_2 plant was likewise grown. The plants in each of the 316 rows were classified and the data summarized by families as follows:

No. of F_3 families breeding true for	No. of F_3 families segregating for:
Awns 1 ---------------------- 21	Awns 1, 2 ------------------ 32
Awns 2 ---------------------- 17	Awns 1, 2, 3 --------------- 32
Awns 3 ---------------------- 16	Awns 1, 2, 3, 4 ------------ 81
Awns 4 ---------------------- 23	Awns 2, 3, 4 --------------- 47
	Awns 3, 4 ------------------ 48

An examination of the summaries of awn behavior shows that there occurred 9 genotypes of plants according to awn-breeding behavior in F_3. Four of these bred true and five segregated each in a distinct manner.

Let us designate full awns such as occur in the Kota parent by AATT (awn class 4); long apical awns but short lateral awns(awn class 3) by AAtt; well developed tip awns(awn class 2) by aaTT; very short tip awns and awnless beaks by aatt(awn class 1). Awn class 1, as here determined, has the same range as the awnless parent, Hard Federation.

The following zygote genotypes as far as awns are concerned are expected:

(1) AATT	(6) Aatt
(2) AATt	(7) aaTt
(3) AaTT	(8) aaTT
(4) AaTt	(9) aatt
(5) AAtt	

The expected breeding nature of the 9 zygotypes is indicated here:

(1) Breed true for awns 4
(2) Segregate for awns 3, 4
(3) Segregate for awns 2, 3, 4
(4) 1, 2, 3, 4
(5) Breed true for awns 3
(6) Segregate for awns 1, 2, 3
(7) 1, 2
(8) Breed true for awns 2
(9) 1

Of the 9 sorts of genotypes (1), (5), (8), and (9), are the true-breeding forms for awn classes 4, 3, 2, and 1 respectively. Genotypes (2) and (3) are each homozygous for one dominant factor and heterozygous for the other, (2) being heterozygous for Tt and (3) for Aa. Genotypes (6) and (7) differ only in that (6) is homozygous recessive for tt and heterozygous for Aa, whereas (7) is homozygous recessive for aa and heterozygous for Tt.

On the basis of total F_3 families, the ratios of families that bred true for awns in various ways suggest a two factor difference. A strictly independent segregation would give approximately equal numbers in each of the four classes that bred true. This was found in both families studied. There was found a ratio that approximates a 1:2:2:4:1:2:1:2:1 for independent segregation, or a 9:3:3:1 taking the 9 genotypes which indicates a 2 factor difference. While there is a much closer approximation to this in family 32G than family 33F as indicated by the goodness of fit study, both values are such [illegible] be highly corroborative of the two-factor hypothesis.

In Table 1 the closeness of fit to the calculated expectancy is given for family 32G. P = .9714 which is an extremely good fit, and shows that in 97 cases of 100 worse fit might be expected due to chance alone. In Table 2, the closeness of fit for family 33F is shown to be .4526 which, though not nearly so good a fit as found in family 32G, still indicates a good one.

As stated before, both these families approximate a 1:2:2:4:1:2:2:1 ratio, which is what is expected for strictly independent segregation. It may, therefore, be safely concluded that the F_2 genotypes as classified by the F_3 breeding behavior rather highly substantiates the presence of two factors for awns, independently inherited. ¶ One worker who [illegible] used these varieties questioned that there were really true-breeding rows of the [illegible]

SUMMARY

This cross was made to study awn inheritance and to discover possible the number of factors involved.

The parents used in the cross were Hard Federation, an awnless variety and Kota, a fully awned wheat.

In F_3, all the F_2 genotypes were tested by the breeding behavior of F_3 families, each from a single F_2 plant. Four true-breeding classes were found

Table 1. Calculated(C) and observed(O) numbers of F_2 genotypes as determined by the F_3 breeding behavior

(Family 32G; grown in 1928 at Logan, Utah)

Genotype	O	C	O - C	$(O - C)^2$	$\frac{(O - C)^2}{C}$
AATT	19	20.1875	- 1.1875	1.4101	.0698
AATt	39	40.375	- 1.375	1.8806	.0465
AaTT	43	40.375	2.625	6.8906	.1706
AaTt	78	80.75	- 2.75	7.5625	.0937
AAtt	20	20.1875	- .1875	.0352	.0012
Aatt	37	40.375	- 3.375	11.3906	.2821
aaTt	48	40.375	7.625	58.1416	1.4403
aaTT	21	20.1875	.8125	.6602	.0327
aatt	19	20.1875	- 1.1875	1.4101	.0698
Total	323	323	P =	.9714	X^2 = 2.2067

Table 2. Calculated(C) and observed(O) numbers of plants in each awn group of F_2 genotypes as determined by the F_3 breeding behavior

(Family 33F; grown in 1928 at Logan, Utah)

Genotype	O	C	O - C	$(O - C)^2$	$\frac{(O - C)^2}{C}$
AATT	23	19.75	3.25	10.5625	.5348
AATt	48	39.50	8.50	72.2500	1.8291
AaTT	47	39.50	7.50	56.2500	1.4240
AaTt	81	79.00	2.00	4.0000	.0506
AAtt	16	19.75	- 3.75	13.0625	.6669
Aatt	32	39.50	- 7.50	56.2500	1.4240
aaTt	32	39.50	- 7.50	56.2500	1.4240
aaTT	17	19.75	- 2.75	7.5525	.3824
aatt	21	19.75	1.25	1.5625	.0790
Total	316	316	P =	.4526	X^2 = 7.8148

and five which segregated each in a distinct manner.

When the observed proportions of eachnof these 9 genotypes were studied by the closeness-of-fit method, the two P's were 0.97 and 0.45, both good fits. It seems reasonable to conclude that there is a two-factor difference for awns, independently inherited. The classes were clear-cut and definite when determined by the F_3 breeding behavior, and as carefully checked in the F_4 and the F_5 generations.

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