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

B. Ira Judd

Follow this and additional works at: https://digitalcommons.usu.edu/etd
Part of the Agronomy and Crop Sciences Commons

## Recommended Citation

Judd, B. Ira, "Inheritance of Awns in a Cross Between Hard Federation and Kota Wheats" (1928). All Graduate Theses and Dissertations. 3937.
https://digitalcommons.usu.edu/etd/3937

This Thesis is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.

#   

A<br>Thesis<br>Subaitted to the Departitent of Agranory Utian Agr lowifural follege

In Partind Pulfialment of the Regufremonts for the Degree of Naster of Salonge by
B. TBA JTDD

Angust 1928
Pege
I. Introduction ..... 2
II. Review of Literstuce ..... 1
III. Description of Parents ..... 4

1. Hard Federation ..... 4
A. Desoription ..... 4
B. Adaptation ..... 4
IV. Itethod of Irocedure ..... 5
V. Experinantal Resulte ..... 7
VI. Sumaxy ..... 12
VII. IIterature Oited ..... 28

## IWXHODUCTIOE

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

The data in the following pages are the rosulto of an investigation made to stuay the inheritance of awns in a oross between Hard Pederation and Kota varieties of wheat.

## BgYTEM OF LITEARATURE

Tht11 the laat few yearm awn inheritance in wheat has been rem garded as extremely simple, that is, as being dependent on a single factor difference. The awns of the $F_{1}$ plants have nearly alwaye been intermediate in length between the avms of the two parents with the $\mathbb{F}_{2}$ ratioa 3 zl or $1 ; 2,1$, amiesmess usualiy being regarded as dominant. Recently, however, it has become apparent that the inheritence of ams is much more complex than the original data indicated. Several woricers have found two Independent factors and one has foun two factors segregating in avah a Pashion as strongly to suggest linkage between these two factors.

The first genetic study on amneiness inheritance in wheat hybrids was reperted in 1905 by Biffen(1) who concluded that "the beardiees condition is a dominant, the bearded a recessive character". Other early woricers, partioularly Tscharmak(12) and Spiliman(b), obtained aimilar results in the Pirst generation and in the second generation also, when the ambless and amed plants occurred in a simple mendelian ratio of $3: 2$.

Recent studies by Gaines and Singleton(3) show similar segregation wile Percival(4) reported $\mathrm{I}_{2}$ egrregation in numerous arosses to approach a 1:2:1 ratio when intermediates ocourred. Saunders(9) questioned the Ides that the first genarstion between an awnless and an awned weat always is amilees and maintained that the charsoter of awns in the $F_{2}$ varied with the wheate used.

Howard and Howard(4) were the Pirst to work with the true amleas wheat. They orossed a Pully bearded wheat with one cesoribed as being really ammess, a fact they emphasized as importart, in as much as many of the so-galled ampess varieties really have short tip awns. In the ${ }^{2}{ }_{2}$, five awn-alasses were obtained, vise, (a) ontirely amless, (b) short tips, (o) long tips, (d) nearly full bearded, and (e) fully beardod. They grouped all avmed and tip-ammed clasees together as amed wioh in comparison with the amless geve a 25,1 ratio. These results were explained on a two-factor bsais. Four alasses bred true, and when the short-tipped. plants were arossed, $\mathcal{F}_{2}$ segregation showed some fully bearded and some ammess plants as well as the intermediate forma. They thus conoluded that the ammed condition was dominant, which was an opposition to the conolusion of other previous voricers.

In Bimilar etudies between Kota and Hard Federation, Olark(2) found a somewhat complex condition in the Inheritance of amns. He made Pive classes of am types in $\mathbb{Z}_{2}$ and he arrived at the conelusion that the amles condition was dominant, since the $\mathcal{Z}_{2}$ (olass 2) approached more nearly the aunlese than the amed parent and also that two genotie factors could not ontirely account for the breeding behavior in the $\bar{P}_{2}$ and $\bar{P}_{8}$ breeding behavior.

Hilason - Ehle(6) obtained by matation true-breeding forms of avmless, half-amed, and avmed wheats. Avmless forms were partly dominant
to half-awned and to awned, and half-avmed forms to amed. He explained his results on the basis of multiple allelonorphs for half-awned and fully ammed pleats arising by complex matation from the awnless plants. A parallel case in rice has been recently reported by Jones(B) who Pound evidence of two independently inherited factor: for annedness. In a cross between a fully awned variety and an awnless one, the $P_{1}$ was Intermediate. He took his data from the $\mathcal{F}_{2}$ plants and grew a few $\mathbb{F}_{3}$ proseniew. He concluded thst either of the two factors alone produced an Intermediate condition and that the two together produced fully developed amm. He was unable to separate his two intermediate olasses.

Stewart(20) recently reported a strong indication of 1 inkage between two factors for amedness in a cross between pure 1 ines of Federation and Sevier wheats. A pure line of oach parental variety and three $\mathrm{F}_{2}$ families were used in the study. In two of the fanilies, kernels from all of the $\bar{F}_{2}$ plente were sown for $\bar{F}_{3}$ progeny rows. In the other case $74 \mathrm{~F}_{3}$ fanilies were grow, the $\mathrm{F}_{2}$ plants from which these come being seleated at random so far as awns were concerned.

There were four true breeding classes, viso, (a) fully amed similar to the Sevier parent; (b) awless, similar to the Federation parent, and (a) and (d) two internediate classes. The true-breeding parental forms were regulariy nuch more nwnerous than the true-breeding intermediate forms. He explains this data by stating that the $F_{2}$ genotypes as claseified by the $\mathrm{I}_{3}$ breeding behavior rather highly substantiates the presence of two factors for awns, both in the same chromosome, with oroasing over to the exteat of about 35 per cent.

In another paper Stewart(21) found ovidence which indicated very strongly that the above theory was at laast approximately correct. From these latter atudiee it is evident that each of the two factors when preeent
separately produces a different, but somewhat equal major offect. the soparate effects of the two factors could be 1 dentified not only in the true breading ${ }^{P} 3$ progenies but alse in the segregating ones.

## 

The parents used, as previously stated, were Hard Fedoration a selection from Federation, and Kota -- a wheat introduced from Russia, 3oth are grown only to a limited oxtent under irrigation in Utah and as yet neither are very well known in this section.

## Bard Eederation

Hard Pederation is a variety of white equing wheat whoh has proved very resistant to drouth. It was developed about 2900 by J. $\mathrm{T}_{\mathrm{o}}$ Fridham, at the Cowna zxperiment Station in Hew South Wales, Australis, by aeleation froa Poceration. It was introduced into the Onited states In 2915 and was first testod at the experiment stations at ware oregon and Chico Galifornia. From these two stations seed was first distributed to Parmers.

Descriptiono- Hard Federation has amiess, oblons apices; glabrous, browa slwaes; and short, hasd, white kernels. It is am early spring wheat which has very strong stems and small leaves, whioh twist on ourl. This latter habit deoreases transpiration and Clark(2) states thst it is undoubtedly heritable.

Adeptation, Flard Federation has proved to be a hisheyielding variety of spring wheat grow under dry-farm conditions at Mora Oregon. It also does well on some soils of California. In the pacific Goest and Intermountain states it often out yielde darquie from 5 to 10 bushels per aore, and is rapidiy becoming an laportant variety in many of the semi-arid
sections of the west.

## Kota

Kota is a variety of hard red epring wheat widch is resistant to black stem rust. 贯he originsi seed of this varioty was obtained in Aussia by Frofessor Hol. Bolley, of the North Dakota Experimont Station, in 1903.

Desoription. Kota has amned, fusiform spikes; glabrous, wite glunes; and midiong, hard, red kernele. It is a nid tall, midseason, spring wheat which has weak to mid atrong stems.

Adsptation- The arre yiolds of gote have averaged cons iderebly higher in Worth and South Dakota during the past few years than those of harguis, the standard variety of hard red spring wheat, as reported by Glaric(1). Kota has also produced good yields in the northeastern perts of Montana and Wyoming. It has proved somewhet resistant to drouth, as well as distinctly resistant to black stem rust, in the northern Great Rlains ares. In the more humid sections of the spring whest region Kota is not well adapted.

## MBTHOD OF HROGBURS

It Is fonow that wheat belongs to a sroup of normally self-fortilised plants, natural crossing oacursing in very rare cases. In artificial orossIng the cross is made at about the tima the ovaries are sufficiently matute and before the anthers have broken. 412 but the outer plorets of eight or tan of the contral spikelels are removed. The upper and lower spikelets are out off with shoars. The contral eloret on each spicelet is removed by grasping it near the top by forceps and pulling downward. The forceps are then aarefully pushod between the lemas and pales and the flower opened. The three ataraens are then renoved, aare being exeraised not to perform this operation sometime before the polien is mature. When all the stamens
are removed, mature polien from the other parent is seoured and shaken on the stigmas in each ploret. The pollen should be obtained from anthera that have turned yellow but not broiken, but when it is ready to do so. Ueually a single anther, that hee just dehisced in handing; is placed in each floret, though sometimes one anther is used to pollinate several stignas. After all the omasculated florete 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 oross between Hard Federation and Kota was made aftor the above mentioned nanner by Dr. Ceorge Stewart, in the epring of 2925 primarily to study the inheritance of awns. Four families were used up to the $\mathrm{F}_{2}$ Generation but at plantins time, in 1926, all but two were discarded.

At the timo of seeding the ${ }_{1}$ grain was sow 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 ${ }_{1}$ plante were som the next season in rows one foot upart with plants three or four inches in the row. Data on the awns of each ${ }_{2}$ plant vere taken at the time of harvest,

In the bogiming the plants were claseifled into 5 classes according to amm: Am cless o(amlese); am olass 1(short amn tips); awn elsss 2 (short-tip awns in lower half of spice and part length awns in upper hals); awnolass 3(noarly fully awned) and awnelass 4(fully smed). A notation wes also made as to the color of the Grain and color of the glumes. Two hesds from each plant were threshed to get gra in 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 deeded in a $F_{3}$ progeny row.

The plants from these $\mathcal{F}_{2}$ kernels conetituted the $\mathcal{F}_{3}$ progeny rows from fitch the dats for the conclusions were obtained, each progeny being regarded as cenoting the true genotype of $\mathrm{F}_{2}$ plant from which it was demeonded. The data on the $\mathbb{F}_{3}$ progeny plants were teken as soon after hoading as the avme were fully developed.

The firat thing done in colleating the Pleld data on the $\mathrm{F}_{3}$ progeny rowe was to go thru the rows and mark those which appeared to be breeding true for one of the aim types and then go thru very carefully a second or third time, if necessary, to make sure they were true breeding.

After this was dona the writer went thru the rowe which were segregeting and nade a oount 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 heade of esch plant in a bungh and calling off the asm class to whioh it belonged. In places where the plants were very thick and the aulms more or less interwoven, It was necessary to bogin at tho ground grasping all the oulms of the plant together and following these up to the spikes.

## EXPER IIGNTRAL FESULPS

It was at first attempted to divide the awns into $f$ ive olasses, in koeping with Glark' ${ }^{2}$ (2) sugsestions, who thought he found five true-breeding awn classes. Caraful oheoicing of $\bar{Z}$ grogenias and comparison with the parants showod only four true-breeding classes. Hard Federation ranged from ontirely amaless to very short beaks. Progenies with a aimilar range wore claselfied as belonsing to amn class 1.

In family 32 a there wore 323 F3 progenies each from a single ${ }_{2}$ plant. Tho plants of each $B_{3}$ family ware alassified sagording to amme.

A sumary of the data is esiven belows


In family 33 an $\overline{3}_{3}$ progeny of every $P_{2}$ plant was likawise grom. The plants in each of the 316 rows were alassified and the data summsised by facallies as follows:


An examination of the summaries of avn behavior shows that in the $\mathbb{F}_{2}$ generation of families 323 and 33 there oecurred 9 senotypes of plants according to avn-breeding behavior in $\mathbb{F}_{3}$. Four of theee bred true and five secregated each in a distinct mannor.

Let va ceaignsto pril awn such as oceuz in the Rota paront by AATY(am olats 4); long apical awns but short latoral awnafam class 3) by AAtt; well Covoloped tip aunsfam olass 2) by aamis very short tip ams and amless beaks by astt (am class 1). Awn class 1 , as hore determined, has the seme renge as the amless parent, Hard Federation.

The following zygote genotypes as far as awns are ooncerned are expeoted:


The expected breeding nature of the 9 sygotypes is indieated here:
(1) Broed true for awne 4
(2) Segregate for awns 3, 4
(3) Secregate for awns $2,3,4$
(4) $t$ 1, 2, 3, 4
(5) Breed true for amms
(6) Segragate for awns $1,2,5$
(7) 2,2
(8) Bresd true for awna 2
(9)
of the 9 sorts of genotypes (1), (5), (0), and (2), are the truebreeding form for avm clasaes $4,3,2$, and 1 respectively. Genotypes (2) and (3) are each homozygous for one doninant factor and heterozygous for the other, (2) being heteroaygous for 24 and (5) for Aa. Oonotypes (8) and (7) diffor only in that (6) is homozygous recessive for tt and heterosygous for $A a_{\text {, }}$, whereas (7) is homozygous recessive for as and hoteroaygous for $2 t$.

On the basis of total ${ }_{z}$ femilises, the rutios of fanilies that bred true for awn in verious ways augeest a two factor difference. A strictly independent segregation would give approximately equal numbers In each of the four olasees that bred true. Thie was found in both fanslies atudied. Thore was found e ratio that approxinates a $2: 2: 2: 4: 1,2: 1: 2: 1$ for indopendent segregation, or a $9,8: 5: 2$ taking the 9 genotypes wich indieates a 2 factor ifference. There is a auoh closer approxfastion to this in fanily 320 than fanily 33 es indicated by the goodness of fit study.

In "able 2 the closeness of fit to the onlculated expectancy is given

Table 1. Galculated(a) and observed(0) numbers of ${ }^{2}$ g senotypes as determined by the $\mathbb{F}_{3}$ bseeding behavior


| Gonotype | 3 | 0 | $i$ | $g$ | 8 | $0-0$ | 1 | $(0-c)^{2}$ | 1 | $\frac{(0-c)^{2}}{c}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 3 |  | 1 |  | ! |  | 3 |  | 4 |  |
| AATET | $t$ | 19 | 1 | 20.1075 | 1 | - 1.1878 | : | 1.4101 | 1 | . 0698 |
| Mat | \% | 39 | ! | 40.375 | : | - 1.375 | $\geq$ | 1.8806 | ? | . 0465 |
|  | 8 | 20 | : | 40.375 | \% | - 2.30 | \% | 2.0006 | : |  |
| Aall | : | 43 | : | 40.575 | : | 2.685 | : | 6.8906 | 1 | . 1706 |
|  | 1 |  | 1 |  | ! |  | 2 |  | 1 |  |
| Aalt | 4 | 76 | 8 | 80.75 | 1 | -2.75 | 1 | 7.5625 | $t$ | . 0937 |
|  | ; |  | $\stackrel{1}{2}$ |  | ! |  | 8 |  | \% |  |
| Aatt | : | 20 | 1 | 20.1075 | 1 | -. 1875 | : | .0358 | 1 | . 0012 |
| Astt | 8 |  | ! |  | \% |  | 8 |  |  |  |
| Aatt | \% | 37 | 4 | 40.375 | ! | - 3.375 | 1 | 21.3906 | ! | . 2821 |
| aalt | 8 | 48 | 5 | 40.875 | : | 7.625 | 1 | 50.1416 | \% | 1.4403 |
|  | $\pm$ |  | 1 |  | : |  | 3 |  | : |  |
| 3839 | 1 | 21 | 1 | 20.1875 | $:$ | .3125 | 3 | . 6602 | 8 | .0327 |
| aatt | 1 | 19 | $t$ | 20.1875 | ! | - 2.18185 | ? | 1.4102 | 2 | 0698 |
|  | 1 |  |  |  | : |  | 2 |  |  |  |
| Total | 1 | 383 | 1 | 385 | 8 | Po | $\frac{1}{4}$ | . 9714 |  | $2=2.2067$ |

Table 2. Galoulated( 0 ) and obsarved( 0 ) numbers of plants in each awn sroup of $\mathbb{F}_{2}$ genotypes as deternined by the $\mathbb{Z}_{3}$ breeding behavior
(Family 35\%; erovn in 1928 at Logan, Wtah)

for framily 326. P $=.9714$ which is an extremely good ift, shows that 97 cases of 100 worse fit might be expected from chance alone. In Table 2, the oloseness of fit for family S5i is shown to be .4586 which, tho not nearly so good a fitt as found in fanily 320 , still indiastes a good one.

As stated before, both these fanilies approxinate a $1: 2: 2: 4,2: 2: 2: 1$ ratio, which is what is expeoted for striotly independent segregation. It may, thereiore, be safely coneluded that the $\Sigma_{2}$ genotypos as elessified by the $\mathrm{F}_{3}$ breeding behavior rather highly subatantiates the presence of two factore for ams, indopendently inherited.

## SWIMARY

This aross was made to atudy awn inheritance and to discovor the number of factors involved.

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

In $F_{3}$ the $\mathrm{F}_{2}$ cenotypes were tested by the breed ing behavior of ${ }^{7}{ }_{3}$ families, each from a aingle $\mathrm{F}_{2}$ plant. Zous true breeding clasess were found and five wich segregated each in a. distinct manner.

When the observed proportions of each of these 9 genotypes were stualed by the sloseness-of-fit method, the two pla were 0.97 and 0.45 , both good fits. It seens reasonable to condiude that there is a twofactor difference for avms, independently inhorited. The elasses were clear-aut and Cefinite nhon Cotormined by the $\mathrm{F}_{3}$ braoding behavior.
(2) BiPfen, RoH.

Mendel's Law of Inheritance and Whest Breeding, Jour. Agr. Sci. is 4-48
(2) Olark, J. $A_{0}$ 1924

Segregation and Correlated Inheritance in Grosses between rota and Hapd Federation Theata for Rusta and Drouthe, Jour, Agr, Rech. 39: 1-47
(3) Gaines, BoFo, and Singleton, HoP.

1926 Genetios of IFarquis $x$ Turkey Wheat in Reppent to Bunt Resistence, 带Inter Habit and Amlessmess. Jour. AgK. Rech. 32: 165-183
(4) Howard, A., and Howard, GoLeC.

1912-15 on the Inhoritance of Some Charasters in Wheat. Nen. Dept. Agr. Indis, Bot. Sor. E1 1-47, 2912; 7: 873-285, 2915
(5) Jones, J.w.

1987 Inheritance of Amedness in lice. Jour. Amer. Sod. Agron. 20: 803-839
(6) Willsen - Ehle

1920 itultiple Allelomorphies und Kimpleanutetionets Dien wisen Hereditas. 2: 277-311
(7) Percival, Jo

1912 The Wheat Plant; A Yonographe 853 pe , London
(8) Saunders, C.E. $^{\text {B }}$

1907 The Inheritance of Amms in Thest. Apt. Internat. Gonf. Genetios(1306) 3, 370-572
(9) Spillman, H.J.

1902
Huceptions to Kondol's Law. Salonce(n.se) 26; 792-794
(20) Stemart, Geo.

1926 Correlatud Inheritance in Theat. Jour. Agr. Rsch. 35; 1163-1192
(12)

1927 Inheritande of Auns in Crosses Involving Eevier and Feleration heets. Jour. Aner. Soc. Agron. 201 $160-170$
(12) Trahermak, E. Von

1901 Veber Juah2ung newer Getreldorassen Juttelet Kunstlisoher Kreusung. Zeschr. Landw. Vorsuahev Oesterr 4: 2029-1060

## IHMODUOLOM

During the past few years there have been $\Lambda$ morose 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 awn in a cross between Hard Federation and Iota varieties of wheat.


Until the last few years awn inheritance in wheat has been resanded as extremely simple, that is, as veins dependent on a single factor difference. The awns of the $F_{1}$ plants have nearly always been intermediate in length between the arms of the two parents with the $F_{2}{ }^{4} d \mathcal{H}_{3}$ viedifrque try les ratios $3: 1$ or $1: 2: 1$, qumlessness $\Lambda^{\text {usually befits regarded as dominant. }}$ Recently, however, it has become apparent that the inheritance of awns is much more complex then the original data indicated. Several workers have found two independent factors and one has found two factors segregeting in such a fashion as strongly to suggest I inkace, between these two sectors. Review of Atestive
The first genetic study on amedness 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 Spillinan(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 end Singleton(3) show Similar segregation while Percival(4) reported $\mathbb{F}_{2}$ segregation in numerous crosses to approach a 1:2:1 ratio when intermediates ocourred. Samders(9) questioned the idea that the first generation between an awnless and an awned vineet always is awnless and maintained that the charsater 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 $\mathbb{F}_{2}$, five awn-classes were obtained, viz., (a) ontirely avmless, (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 wioh in comparison with the amless gave a $15: 1$ vatio. These results were explained on a two-factor basis. Four clesses ored true, and when the short-tipped plants were crossed, $\mathrm{F}_{2}$ aegregation showed some fully bearded and some ammess plents as well as the intermediate forms. They thus concluded that the amed condition was dominant, which was opposition to the conclusion of other previous worlcers.

In similar studies between Kota and Hard Federation, Olark(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 amless condition was dominent, since the $\mathbb{P}_{2}$ (class 2) approached more nearly the awless than the awned parent and also that two genetic factors could not entirely account for the breeding behavior in the $\mathbb{F}_{2}$ and $\mathbb{F}_{3}$ breeding behavior.

Nilsson - Bhle(6) obtained by matation true-breeding forms of awnless, halp-awned, and awned wheats. Awnless forms were partly dominent
to half-awned and to awned, and half-awmed forms to swned. He explained his results on the basie of multiple allelomorphs for helf-awmed and. fully avmed plants arising by complex mutation from the amless 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 grev a $F_{3}$ progenies. He concluded that either of the two factors alone produced an intermediate condition and that the two together produced fully developed swns. Hie 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 sow for $F_{3}$ progeny rows. In the other asse $74 \mathrm{~F}_{3}$ families were grown, the $\mathrm{F}_{2}$ plants from which these came being selected at random so far as avms were concerned.

There were four true-breeding classes, viz., (a) fully awned similar to the Seviar 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 then the true-breeding intermediate forms. He expleine tiriv tater-by-eterting that The $\mathrm{F}_{2}$ senotypes 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 wother evecect Stewert(11) found evidence which indicated
anchit that the above theory was at least approximately correct. From these latter studies $i t$ is evicent 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 ldentifled not only in the true - breeding $F_{3}$ progenies but also in the segregating ones.

## DESCRIPTION OR THE PARENMS

The parents used, previousiy stated, were Hard Federation and tate, a. seleetion from Federation, and Kota - - a wheat introdmed fron Fivesiar Fow are grown only to a limited extent under irrisation in Utah and as jet neither are very well known in this section.

## Hard Federation

Hard Federation is a variety of white spring wheat wich has proved very resistant to drouth. It was developed about 1908 by J.T. Pridham, at the Cowfa 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 Mori, oregon and Chico, dalifornia. From these two stations seed was first distributed to farmers.

Desoription.- Hard Federation has amless, oblons spikes; glatorous, brown glumes; and short, hard, white kernels. It is an early spring wheat with
which very strong stems and small leaves, which twist on curl. This latter habif decreasef transpiration and Clark(2) states that it is undoubtediy heritable.

Adaptation.- Herd Federation has proved to be a high-yieldinc variety of spring wheat frown under ory-farm conditions at $1 \mathrm{Hor} \&$ oregon. It also does well on some soils of California. In the Pacific coast and therm
$n^{\text {intermountain }}$ states it often out yields liarquis from 5 to 10 bushels acre, and io rapitiz booming an-important variety-in-meny of the sominante

Kota is a variety of hard red sprine wheat which is resistent to black stem rust. The orisinal seed of this veriety was obtained in Russie by Professor H.L. Bolley, of the North Dakota Experiment Station, in 1903. Description.- Kota has amed, fusiform spikes; Elabrous, white flumes; and midiong, hard, red kernels. It is a mid tall, midseason, sprins Wheat which has weak to mid strong stems.

Adaptation.- The acre yields of Kota have averaged considerably hisher 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 Clarik(1). Kota has also produced good yields in the northeastern parts of Montana and Tyoming. It has proved somewhat resistant to drouth, as well as distinctly resistant to black stem rust, in the northern Greut Plains area. In the more hunid sections of the spring wheat region Kota is not well adapted.

## MGTHOD OF PHOCSDURE

It is knovm that wheat belongs to a group of normally self-fertilized plants, netural orossing ocourring in very rare cases. In articiciel crossing the cross is made at whout the time the ovaries are sufficientiy matube and before the anthers have broken. All but the outer florets of eight or toh of the central epirelets are ranoved. The upper and lower spikelets dre out off with shears. The central floret on each spikelet is removed by graspins it near the top by forceps and pulling dowmerd. The forcoes are then aarefully pushed between the lempa and palea and the flower ppened. The three stamens are then removed, care being exercised yat to perform this operation/sometime before the pollem is meture. Then eil the stamens
are removed, mature pollen from the other parent is secured and shaken on the stigmas in each floret. The pollen should be potained from anthers that have turned yellow but not broken, but when it is ready to do so. Usually s single anther, that has just dehisced in handing, is placed in each floret, though sometimes one antler is used to pollinate several stigmas, After all the emasculated florets are pollinated, the head is wrapped/ up with a leaf from the wheat glent and labeled. Then the grain is mature the heads are broken off and reserved until the next planting season.

The cross between Hard Federation and Rota was made aetew the eve mentioned manner by De. George Steweath, in the spring of 1925 primarily to study the inheritance of awns. Four families were used up to the $\boldsymbol{F}_{2}$ generation out at planting time, in 1928, all but two were discarded. With the kernels about a foot and a half apart in the rows. At maturity harvester the heads were preikn off and the grain saved for seeding the next season.

The kernels from the $P_{1}$ plants were sown the next seas on in rows one coot apart with plants three or four inches an the row. Data on the awns of each $\vec{F}_{2}$ plant were taken at the time of harvest.

In the beginning the plants were classified into 5 classes according
to awns: Awn class o(smless); awn, class 1 (short, am tips); awn class a ( Lh ant annie wu the sufpevereffotte peke); (short-tip awns in lower half of spike avid part length awns in upper half);
awnolasa 3 (remriy-fully awed and anoles $4(f u l l y$ swed). A notation was also made as to the color of the grain and color of the glumes. \#u heads from each plant were threshed to set grain color, and the ad same threshed kernels were placed in an envelope which was marked with the
 progeny of 20 to 40 plate than every

The plants firm thee- I2 kernels constituted the $\mathbb{F}_{3}$ progeny rows tron. - the data regarded as denoting the true genotype of $F_{2} p l a n t$ from which it was descended. The data on the $\mathrm{F}_{3}$ 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 there the rows and mark those which appeared to be breeding true for one of the am 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 wile e 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 ales to which it belonged. In places where the plants were very thick and the culms more or lees interwoven, it was necessary to begin at the ground grasping all the culms of the plant together and following these up to the spikes.

## EXPRR I MMTAL RESULTS

It was at first attempted to divide the aws into five classes, in keeping with Clark's(2) suggestions, who thought he Pound five true-breeding awn classes. Careful checking of $P_{3}$ 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 alass 1.

In family $32 G$ there were $323 \sum_{3}$ progenies each from a single $\sum_{2}$
plant. The plants of each F3 family were classified according to awns.


In family $33 F^{2}$ an $\mathbb{F}_{3}$ progeny of every $\mathbb{F}_{2}$ plant was likewise grown. The plants in each of the 316 rows were classified and the data sumarized by families as follows:


An examination of the sumnaries of awm behavior shows that in the ${ }^{3}$ _ gention-of fomilies-3RG ent- 30 there ocourred 9 genotypes of plants according to am-breeding behavior in B3. Four of these bred true and five secregated each in a distinct manner.

Let us designate full awns such as oocur in the Kota parent by AATM(avm class 4); long apical awns but short lateral swns(awn class 3) by AAtt; well developed tip avms(avm class 2) by aaMT; very short tip awns and awnless beaks by autt(awn class 1). Avm 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) AAMT | (6) Aatt |
| :--- | :--- |
| (2) AAMt | (7) aaMt |
| (3) AaMT | (8) aaMT |
| (4) AaMt | (9) satt |
| (5) AAtt |  |

The expeoted breeding nature of the 9 zygotypes is indicated here:
(1) Breed true for $a \mathrm{wms} 4$
(2) Secregate for ewns 3, 4
(3) Segregate for amm 2, 3, 4
(4) $1,2,3,4$
(5) Breed true for awns 3
(6) Segregate for avms 1, 2, 3
(7) 1,2
(B) Breed true for avns 2
(9) 1

Of the 9 sorts of genotypes $(1),(5),(8)$, and (9), are the truebreeding forms for awm classes 4, 3, 2, and 1 respectively. Genotypes (2) and (3) are each homozygous for one dominant factor and heterozygous for the other, (2) beins heterozycous for it and (3) for Aa. Geriotypes (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 heterozysous for Tt.

On the basis of total F $F_{3}$ families, the ratios of families that bred true for awns in various ways sugcest 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 $9: 5: 3: 1$ taking the 9 genotypes which indicates a. 2 factor difference. There is a much closer approximation to this in family 326 than family $33 F$ as indicated by the goodness of fit study.

In Table I the closeness of fit to the calculated expectancy is given
for family $32 G$. $I=.9714$ which is an extremely good fit, shows that 97 cases of 100 worse fit might be expected Aneto chance alone. In Table 2, the closeness of fit for family 33 is show to be . 4.526 which, th 5 Hot 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 med wheat.

In $\mathbb{F}_{3}$ the $\mathbb{F}_{2}$ 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 oloseness-of-fit method, the two $\mathrm{P}^{\prime}$ s were 0.97 and 0.45 , both good fits. It seems reasonable to conclude that there is a twofactor difference for awns, independently inherited. The classes were clear-cut and definite when determined by the $F_{3}$ breeding behavior,

## LITERATURG CITED

(1) Biffen, R.H.

1905 Hendel's Law of Inheritance and Theat Breeding, Jour. Asr. Sci. 1: 4-48
(2) Clark, J.A. 1924

Segregation and Correlated Inheritance in Crosses between Kota and Hard Federation Wheats for Rusts and Drouths. Jour, AsF. Risch. 39: 1-47
(3) Gaines, E.F., and Singleton, H.P.

1926 Genetics of Marquis $x$ Thrkey Wheat in Reppect to Bunt Resistance, Winter Habit and Amlessness. Jour. Agr. Rsch. 52: 165-183
(4) Howard, A., and Howard, G.L.C.

1912-15 On the Inkeritance of Some Characters in wheat. Mem. Dept. ASt. India, Bot. Ser. 5: 1-47, 1912; 7: 273-285, 1915
(5) Jones, J.W. 1927 Inheritance of Amedness in Aice. Jour. Amer. Soc. Agron. 20: 803-839
(6) Willson - Bhle

1920 Nultiple Allelomorphies und Kimplexmutetioneu bien weizen Hereditas. 1: 277-311
(7) Percival, J.

1912 The Wheat Plant; A Honograph. $\$ 63 \mathrm{p}$, London
(8) Saunders, C.E.

1907 The Inheritance of Awns in theat. Rpt. Internat. Conf. Genetics(1906) 3: 370-372
(9) Spillman, V.J.

1902 Exceptions to ILendel's Law. Science(n.s.) 16: 792-794
(10) Stewart, Geo. 1926

Correlated Inheritance in Wheat. Jour. Agr, Rsch. 33: 1163-1192
(11) 1927 Inheritance of Awns in Orosses Involving Sevier and Federation Whasts. Jour. Aner. Soo, Asron. 20: 160-170
(12) Mschermak, B. Von
1901

Ueber Zuchlung neuer Getreiderassen Nuttelst Kunstlicher Kreuzung. Zeschr. Landw. Versuchsw Oesterr 4: 1029-1060

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 $\mathrm{F}_{2}$ and $\mathrm{F}_{3}$ ratios most frequently 3:1 or $1: 2: 1$ Awnleseness has usually been regandec 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 IITERATURE

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 Techermak(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 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 $\mathbb{F}_{2}$, 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 wich 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, $\mathrm{F}_{2}$ 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) obteined by mutation true-breeding forms of awnless, half-awned, and awned wheats. Awnless forms were partly dominant to halfawned 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 plents 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.
Stevart(l0) reported a strong indication of linkage between two factors for awnedness in a cross between pure lines of Pederation 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 $P_{3}$ progeny rows. In the other case $74 \mathrm{~F}_{3}$ families were grown, the $\mathbb{F}_{2}$ plents from which these came being selected at random so far as awns were concerned. $A$

There were four true-breeding classes, viz., ( $\varepsilon$ ) 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


Hard Pederation 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.

AeAcrustibA.- 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.

Hadedtedear 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 intermountain 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 HaI. Bolley, of the North Dakota Experiment Station, in 1903.

Hescelythed 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.

Whetratkanth The acre yields of Kota have averaged considerably higher in North and South Dakota during the past few years than those of Marquis, the stendard 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 somewhial 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 whett region Kotpis not well adapted.

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 $\mathrm{F}_{2}$ 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 $\mathrm{F}_{2}$ plant were taken at the time of harvest.

In the beginning the plants were classified into 5 classes according to awns: Awn class O(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 helf 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 plent was threshed to get grain color, and the threshed kernels were placed in en envelope which was marked with the pedigree number and saved until the following year when the kernels from each $\mathrm{F}_{2}$ plant were seeded in a $F_{3}$ progeny row. There was, therefore an $F_{3}$ progeny of 20 to 40


It was from the $F_{3}$ progeny rows that the data here reported were obtained, each progeny being regarded as denoting the true कenotype of $\mathrm{F}_{2}$ 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. 7

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.

## EXPERIMENPAL RESUITS

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 elass 1 .

In family $32 G$ there were $323 F_{3}$ progenies each from a single $\mathbb{F}_{2}$ plant. The plants of each $F_{3}$ family were classified according to awns. A sumary of the data is given below:


In family $33 F$ 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 sumarized by families as follows:


An examination of the sumaries of awm behavior shows that there occurred 9 genotypes of plants according to awn-breeding behavior in $\mathrm{F}_{3}$. 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 AATY (awn class 4); long apical awns but short lateral awns(awn class 3) by AAtt; well developed tip awns(awn class 2) by aaTP; very short tip awns and awnless beaks by aatt(awn class 1). Awn elass 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) AATMI
(6) Aatt
(2) AATt
(7) aaTt
(3) AaTT
(8) $a \mathfrak{T T}$
(4) AaTt
(9) aatt
(5) AAtt

The expected breeding ne ture 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 $1,2,3$
(8) Breed true for awns 2
(9)

Of the 9 sorts of genotypes $(1),(5),(8)$, and $(9)$, are the truebreeding 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 A\&. Genotypes (6)
and (7) differ only in that (6) is homozygous recessive for th and heterozygous for $A a$, whereas (7) is homozygous recessive for aa and heterozygous for Th.

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 while difference. there is a much closer approximation to this in family $32 G$ than family $33 F$ as indicated by the goodness of fit study,

In Table I the closeness of fit to the calculated expectancy is given for family 32G. $P=.9714$ which is on extremely good fit, shows that in 97 cases of 100 worse ft might be expected due to chance alone. In Table 2, the closeness of fit for family 33 F 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
 weed these uannelyee questioned that the were


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. al
In $\mathbb{F}_{3}$, the $\mathrm{F}_{2}$ genotypes were tested by the breeding behavior of $\mathrm{F}_{3}$ families, each from a single $F_{2}$ plant. Four true-breeding classes were found

Table 1. Calculated( 0 ) and observed( 0 ) numbers of $\mathrm{F}_{2}$ genotypes as determined by the $\mathbb{F}_{3}$ breeding behavior
(Family 32G; grow in 1928 at Logan, Utah)


Table 2. Calculated( $C$ ) and observed $(0)$ numbers of plants in each awn group of $F_{2}$ genotypes as determined by the $P_{3}$ breeding behavior
(Family 33F; Erown in 1928 at Logen, Uteh)

and five wich 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 $\mathrm{P}^{\boldsymbol{\prime}}$ 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, alucked ru

(1) Biffen, R.H.

1905 Mendel's Law of Inheritance and Wheat Breeding, Jour, Agr. Sci. 1: 4-48
(2) Clark, J.A.

1924 Segregation and Correlated Inheritance in Crosses between Kota and Hard Federation Wheats for Rusts and Drouths. Jour. Agr. Ksch. 39: 1-47
(3) Gaines, E.F., and Singleton, H.P. 1926 Genetics and Msrquis $x$ Turkey Wheat in Respect to Bunt Resistance, Winter Habit and Awnlessness. Jour. Agr. Rsch. 32: 165-183
(4) Howard, A., and Howard, G.L.C. 1912-15 On the Inheritance of Some Characters in Wheat. Mem. Dept. Agr. Indie, Bot. Ser. 5: 1-47, 1912; 7: 273-285, 1915
(5) Jones, J.W.

1927 Inheritance of Awnedness in Rice. Jour. Amer. Soc. Agron. 20: 803-839
(6) Nillson - Ehle

1920 Multiple Allelomorphies and Kimplexmutationeu bien weizen Hereditas. 1: 277-311
(7) Percival, J.

1912 The Wheat Plant; A Monograph. 463 p., London
(8) Saunders, C.E.

1907 The Inheritance of Awns in Wheat. Rpt. Internat. Conf. Genetics(1906) 3: 370-372
(9) Spillman, W.J.

1902 Exceptions to Mendel's Law. Science(n.s.) 16: 792-794
(10) Stewart, Geo.

1926 Correlated Inheritance in Wheat. Jour. Agr. Rsch. 33: 1163-1192
(11) Stewart, Geo.

1927 Inheritance of Awns in Crosses Involving Sevier and Federation Wheats. Jour. Amer. Soc. Agron. 20: 160-170
(12) Tschermak, E. Von 1901

Ueber Zuchlung neuer Getreiderassen Nuttelst Kunstlicher Kreuzung. Zeschr. Landw. Versuchsw Oesterr 4: 1029-1060

