A study of the inheritance of awnedness, aleurone color, growth habit, and spike density in barley
by John M Green

A THESIS Submitted to the Graduate Committee in partial fulfillment of the requirement for the degree of Master of Science in Agronomy
Montana State University
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Abstract:
The objective of this study was to determine the mode of inheritance and linkage relationships of four characters in barley. The mode of inheritance was determined by observing the F1 generation plants and by studying segregation in the F2 and F3 generations. Linkage intensities were calculated by the product method using the combined F2 and F3 data.

The inheritance of awnedness and growth habit ms studied in crosses of Arlington Aimless, C. I. 702, with the two Atrada varieties, C. I. 6641 and C. I. 5638. In addition the inheritance of aleurone color and spike density was studied in the cross with Atrada, C. I. 6638.

Although a two-factor difference for awnedness was observed in each cross, a total of three different factor pairs affecting awnedness were present in the two crosses studied. A factor pair for normal versus reduced lateral awns, which affected length of central awns also, was carried in the dominant condition in each Atrada variety and in the recessive condition in Arlington Awnless. Two factor pairs for awn length were carried in the dominant condition in Arlington Awnless; one was dominant in Atrada, C. I. 5638, and recessive in Atrada, C. I. 5641; and the other was recessive in Atrada, C. I. 5638, and dominant in Atrada, C. I. 5641.

Normal lateral awns were partially dominant over reduced and long awns were apparently completely dominant over short. Growth habit, aleurone color, and spike density were each inherited on a single-factor basis, although additional modifying factors not detected in this study may have affected growth habit in the cross Arlington Awnless x Atrada, C. I. 5638. Blue aleurone color was dominant over white and xenia was observed in the inheritance of this character. Erect growth habit was dominant over decumbent , and lax spikes were dominant over dense.

In Arlington Awnless x Atrada, C. I, 5641, the two factors for awnedness were inherited independently of each other and independently of growth habit. In Arlington Awnless x Atrada, C. I. 5658, long versus short awns were linked with lax versus dense spikes with 24.18±6.30 percent crossing over. The linkage relationships of growth habit in this cross were not determined because the ratio observed for this character did not fit a monohybrid ratio, although segregation in the Fg generation indicated a single factor difference. All other characters segregated independently of each other.

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JOHN M. GREEN

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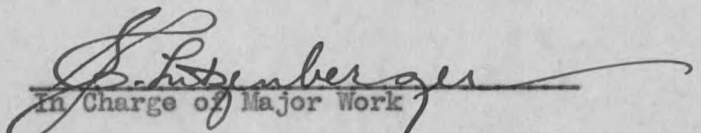
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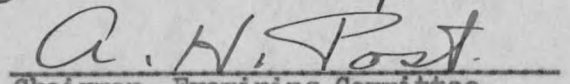
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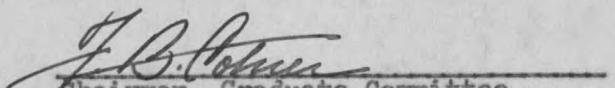
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INTRODUCTION

One of the first genetic studies in barley, the results of which were published in 1901, was conducted in Austria by von Tschermak. Since that time the possibilities afforded by barley for such studies have attracted the attention of many students of genetics and plant breeding. At the present time, genetic studies with several different barley crosses are being conducted at the Montana Agricultural Experiment Station. The results of one of these studies, a study of the inheritance of awnedness, aleurone color, growth habit, and spike density in two crosses, are presented in this paper.

REVIEW OF LITERATURE

Awn Length

The inheritance of awn length in the progeny of numerous crosses was studied by von Ubisch (20)1/. He concluded that awn length was controlled by three factor pairs which he designated Aa, Uu, and Vv. The genotype A-U-vv gave rise to awns of extreme length; A-uuvv, A-uuV-, and aaU-V-, long awns; aaU-vv, aauuV-, and aauuvv, short awns. Density of

1/ Figures in parenthesis refer to "Literature cited and consulted", page 48.

spike was closely associated with awn length in the crosses studied.

Miyake and Imai (12) also found three factor pairs involved in the inheritance of awn length in some crosses studied. In other crosses a single-factor difference between long and short awns was observed. Long versus short awns was found to be linked with hulled versus naked seed with 5 percent crossing over and with awned versus awnless lateral florets. In crosses in which three factor pairs for awn length were involved, awn length was linked with two row versus six row, awned versus awnless lateral florets, normal versus curled (a dwarf character), and probably linked with purple versus white seed.

Ikeno (9) reported a two-factor difference for awn length in Kinukawa, a long awned variety, crossed with Nogenhasi, a variety which is generally awnless, but sometimes has short central awns. In four different crosses Myler (14) also found a two-factor difference for awnedness when awnless and awned types were crossed. In three of these crosses long awned varieties were crossed with Awnless, C. I. 5631,[2/] an awnless variety. All were six-rowed barleys. The two awn factors for which segregation was observed were designated Lk and Lk_1 by Myler. Segregates carrying both factors in the dominant condition were long-awned; those carrying only Lk in the dominant condition were short awned; those carrying only Lk_1 in the dominant condition were "awnletted"; and those recessive for both factor pairs were awnless. The "awnletted" type had awns on the central spikelets

2/ C. I. number refers to the accession number of Division of Cereal Crops and Diseases.

only. In the fourth cross, Redrachis, C. I. 5649, x Awnless, a 15:1 ratio for awned to awnless was observed. Redrachis is a two-rowed, awned variety.

A single-factor difference between long and short awns in a cross of Atrada, C. I. 5638 x Trebi-Velvet was reported by Sturm (19). He found the factor pair for awn length (Lk_4lk_4) to be inherited independently of rough versus smooth awns (Rr) and to be linked with lax versus dense spikes (L_6l_6) with 23 percent crossing over.

Glinyany (6) found a single factor pair affecting awn length in Nudihaxtoni, a variety with normal central awns but no lateral awns, when crossed with a hooded variety. The factor pair (Nn) for long versus short awns was hypostatic to a factor pair present which controlled the development of lateral awns (Aa).

Normal versus Reduced Lateral Awns

Ikeno (9) observed a 1:2:1 ratio for absence of lateral awns, intermediate lateral awns, and fully developed lateral awns in the F_2 progeny of a cross of Kinukawa x Nogenhasi. Kinukawa is a fully awned variety while Nogenhasi is generally awnless but sometimes has short central awns. He concluded that the factor responsible was a partially dominant inhibitor factor. Similar segregation was observed by Glinyany (6) in a cross of Nudihaxtoni times a hooded variety. He also concluded that the factor responsible was an inhibitor and found that it was epistatic to a factor for awn length present in the cross.

A single-factor difference was also reported by Engeldow (3), Miyake and Imai (12), and Leonard (11). Engeldow studied a cross of Haxtoni, a

variety similar to Nudihaxtoni, with a long awned variety. Miyake and Imai studied several crosses of normal awned varieties on varieties having no awns on the lateral spikelets. They found the factor for normal versus reduced lateral awns to be linked with normal versus curled (dwarf), and probably linked with purple versus white seed. They placed the factor pair for normal versus reduced lateral awns in linkage group II.

Leonard studied crosses of Nudihaxtoni on three hooded varieties, Colsess IV, Colsess V, and Antrum. He designated the factor pair controlling lateral awn development as Lrlr, and found it linked with green versus orange seedling color (Oror) with 38.58 ± 1.20 percent crossing over. The factor pair Lrlr was inherited independently of black versus white floral bracts (Bb), covered versus naked seed (Nn), hoods versus awns (Kk), long- versus short-haired rachilla (Ss), green versus xantha seedling color (X_cx_c), and green versus chlorina seedlings (F_cf_c). Leonard concluded that the factor pair Lrlr was in linkage group I.

Blue versus White Aleurone Color

Harlan (7) reported that colors in barley are caused by two pigments: anthocyanin and a melanin-like compound. The anthocyanin is violet in its acid condition and blue in its alkaline condition, and the melanin-like compound is black. These pigments may occur in the pericarp, hulls, aleurone layer, and occasionally in the endosperm. The presence of anthocyanin in the pericarp gives a violet color; in the aleurone, blue color; and if present in both the pericarp and aleurone, a purple color results. In the absence of the pigment in both the pericarp and aleurone

the kernel is white.

The results of two different studies of the same material were published jointly by Miyazawa, and So and Imai (13). The earlier study was made by Miyazawa, who concluded that the blue color was inherited as a mosaic in a cross of Sekitori, a Japanese blue variety, times Goldenmelon, an Australian variety with pale yellow kernels. He observed varying ratios of blue kernels to white on individual F_1 heads but when he counted the kernels on all heads he found 1009 blue and 1019 pale yellow, approximately a 1:1 ratio. So and Imai studied Miyazawa's material and concluded that the color was not a mosaic but an endosperm character carried in the aleurone layer. From their classification of the F_2 population they obtained a 3:1 ratio for blue to white kernels. They concluded that the character showed xenia and was inherited as a single-factor difference.

Similar results were reported by Buckley (2), who did not list the crosses studied, and by Robertson, Deming, and Koonce (17), who studied a cross of Colsess IV x Minnesota 72-8. Buckley found aleurone color to be independent of black versus white glumes, two row versus six row, long versus short rachilla hairs, hulled versus naked caryopsis, and probably independent of straight versus curved peduncle and purple versus white lemma. He found aleurone color linked with hooded versus awned with 41 percent crossing over and placed the factor pair for blue versus white in linkage group III. Robertson, Deming, and Koonce also found aleurone color to be inherited independently of long versus short rachilla hairs and linked with hooded versus awned. They found 22.58± 0.82 percent crossing over.

Myler and Stanford (15) found a single-factor difference for blue versus white aleurone in crosses of Kwan (blue) x Nepal (white), Algerian (blue) x Nepal, and Awnless (blue) x Nepal, but they found that the color was actually dependent on two complementary factors. In a cross of two white varieties, Goldfoil x Nepal, they observed a 9:7 ratio for blue to white in the F_2 generation. They concluded that in crosses where only a single-factor difference is observed the blue parent has the factors $B1B1B1_1B1_1$ and that the white parent has either $B1B1b1_1b1_1$ or $b1b1B1_1B1_1$. The factor pair B1b1 was found to be linked with hooded versus awned with 24.72 ± 1.73 percent crossing over. Myler and Stanford concluded that this was the same factor studied by Buckley (2) and Robertson, Deming, and Koonce (17), and that it was located in linkage group IV. The factor pair $B1_1b1_1$ was found to be linked with hulled versus naked (Nn) with 9.88 ± 0.44 percent crossing over and was placed in linkage group III.

Spring versus Winter Habit of Growth

Gaines (5) observed winter habit plants in the segregating generations of two crosses, Rice x Beardless and Rice x Excelsior, all spring varieties. He observed a ratio of 13 spring to 3 winter plants in the F_2 generation and concluded that two factors, one an inhibitor, controlled habit of growth.

The occurrence of winter habit segregates in the progeny of a cross of two spring varieties was also reported by Neatby (16). He concluded that three factor pairs controlled growth habit in Guy Mayle x Canadian Thorpe and that in the winter-habit segregates all three factor pairs

were homozygous recessive.

Lax versus Dense Spikes

Biffen (1) observed a single-factor difference for density of spike with lax dominant over dense in three crosses studied. Similar results were reported by Sturm (19), who found that lax versus dense was inherited independently of rough versus smooth awns (Rr) and was linked with long versus short awns (Lk_4lk_4) with approximately 23 percent crossing over. In two different crosses, Miyake and Imai (12) observed a single-factor difference for lax versus dense spikes. In one cross the density factor (L_1l_1) was linked with covered versus naked seed with 13 percent crossing over, and in the other cross the density factor (L_2l_2) was linked with covered versus naked with 23 percent crossing over.

Neatby (16) reported that a single factor pair with minor modifying factors controlled density in a cross of Guy Mayle x Canadian Thorpe. Spike density was inherited independently of earliness in this cross, but both density and earliness were linked with lateral floret fertility.

A two-factor difference for density was reported by Wexelsen (21). He designated the factor pairs L_1l_1 and L_2l_2 and found that the factor pair L_2l_2 was linked with rough versus smooth awn (Rr) with 10 percent crossing over. In a later paper, Wexelsen (22) reported single-factor and two-factor differences in some crosses studied. One of the factor pairs for density (L_4l_4) in Asplund x Smooth awn, C. I. 4152, was linked with the factor for fertility (Zz) with 40 percent crossing over.

Von Ubisch (20) concluded that three factor pairs controlled density

in crosses that he studied. He found the lax condition dominant over dense, with the length of spike directly proportional to the number of dominant factors present. Density was found to be closely associated with awn length.

In studies by Hayes and Harlan (8) single-factor differences were observed with complete dominance of dense over lax in some cases and incomplete dominance in others. In other crosses studied, they observed a three-factor difference. Minor modifying factors were present in some crosses.

Linkage Groups in Barley

Seven linkage groups have been established for cultivated barley. The literature for these groups has been reviewed by Robertson, Wiebe, and Immer (18), and factor pairs previously reported were located in linkage groups whenever possible. The character pairs included in this study and the linkage groups in which they were placed are given below:

Linkage Group:	Character Pair	Symbol
I	Long versus short awns	Lklk
	Normal versus reduced lateral spikelet appendages	Lrlr
	Dense versus lax spikes	Ll
	Dense versus lax spikes	L_4l_4
III	Dense versus lax spikes	Ll
	Dense versus lax spikes	L_1l_1
	Dense versus lax spikes	L_al_a
	Dense versus lax spikes	L_2l_2
	Long versus short awns	Lklk
IV	Dense versus lax spikes	Ll
	Blue versus white aleurone	Blbl

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MATERIALS AND METHODS

Description of Parents and Characters Studied

The three varieties used as parents in the crosses studied were Arlington Awnless, C. I. 702, Atrada, C. I. 5641, and Atrada, C. I. 5638. A description of these varieties follows.

Arlington Awnless is characterized by a decumbent type of growth in the seedling stage, blue aleurone, lax spikes, occasional awn points on usually awnless lateral spikelets, and short awns on the central spikelets. The modal class for length of central awns is 35.0 mm. to 39.9 mm.

Atrada, C. I. 5641, has an erect type of growth in the seedling stage, blue aleurone, lax spikes, and short central and lateral awns. The modal class for length of central awns is 50.0 mm. to 54.9 mm., and for length of lateral awns is 30.0 mm. to 34.9 mm.

Atrada, C. I. 5638, has an erect type of growth in the seedling stage, white aleurone, dense spikes, and short central and lateral awns. The modal class for length of central awns is 50.0 mm. to 54.9 mm., and for the length of lateral awns is 30.0 mm. to 34.9 mm.

The decumbent type of growth made in the seedling stage by the Arlington Awnless variety is similar to that produced by most winter varieties of cereal crops. The erect type of growth as observed in the Atrada varieties is similar to the type observed in spring cereal crops. Although it is not known whether the type of growth in the seedling stage is entirely associated with spring and winter habit, for the purpose of this study it will be assumed that such is the case. Therefore, throughout this paper erect versus decumbent habit of growth will be referred to as

spring versus winter habit.

Arlington Awnless was crossed with each of the Atrada varieties in 1939 at the Montana Agricultural Experiment Station, Bozeman, Montana. The contrasting characters studied in each cross are listed below:

Arlington Awnless x Atrada, C. I. 5641

Long versus short awns

Normal versus reduced lateral awns

Spring versus winter habit

Arlington Awnless x Atrada, C. I. 5638

Long versus short awns

Normal versus reduced lateral awns

Blue versus white aleurone

Spring versus winter habit

Lax versus dense spikes

Method of Growing the Filial Generations

The F_1 generation was grown during the winter of 1939-40 in the greenhouse in Washington, D. C., by Dr. G. A. Wiebe of the Division of Cereal Crops and Diseases. The F_2 and F_3 generations were grown at the Montana Agricultural Experiment Station as a part of the barley improvement program.

The F_2 generation was seeded in 1940 in space planted rows with the seed spaced three inches apart to allow for plant separation. The decumbent plants were marked in the field during the third week following emergence. The plants were pulled just before ripening to be stored

in the laboratory for classification of other characters. The erect and decumbent plants were kept separate when pulled.

The F_3 generation was grown in 1941; it was repeated in 1942 because the families grown in 1941 were so badly weathered that color could not be determined. The 1941 planting was made with seed from a random sample of heads from each F_2 plant. The seed planted in 1942 was from the F_2 heads not used for seeding in 1941. The seed from each F_2 plant was space planted in an eighteen-foot row which gave an F_3 family. The F_3 families were pulled just before ripening and were stored for classification.

The F_2 and F_3 generations were seeded in the spring. Both spring and winter segregates headed and matured when seeded in the spring.

Methods of Classification

The F_1 plants of each cross were classified for the characters being studied. A description of the F_1 type in each cross follows:

Arlington Awnless x Atrada, C. I. 5641

Central spikelets approximately two-thirds fully awned

Lateral spikelets bearing awns approximately one-half as long as the central awns

Aleurone blue

Plants erect in the seedling stage

Spikes lax

Arlington Awnless x Atrada, C. I. 5638

Central spikelets approximately two-thirds fully awned

Lateral spikelets bearing awns approximately one-half as long as the central awns

Blue and white aleurone on the same spikes, blue predominating

Plants erect in the seedling stage

Spikes lax

A preliminary classification of the F_2 generation plants was made on the basis of their phenotypes; this classification was corrected and the F_2 genotypes were determined by checking the breeding behavior of each F_2 plant in the F_3 generation.

Classification for growth habit was made in the field on the basis of type of growth exhibited by the plants during the second or third week following emergence. It was considered that the segregates making an erect type of growth were spring habit plants, and the segregates that made a decumbent type of growth were winter habit plants.

Classification for awnedness, aleurone color, and density of spike was made in the laboratory. In order to establish phenotypic awn classes it was necessary to study variation in awn length. It was evident that such a study was necessary from variations observed in the F_1 generation and from observed variations within the Arlington Awnless variety. Ten plants of the Arlington Awnless parental variety were selected at random from a group of seventy grown in a space planted row in 1941. Ten heads were taken from each plant for awn measurement. The fourth spikelet from the base of the head, counting spikelets on only one side of the rachis, was arbitrarily chosen as the one on which to measure the central awn.

The mean length of central awns on each plant and the standard error of each mean was determined. Fisher's analysis of variance method and the F and t tests were used to determine whether or not differences between the means were significant. The length of the longest lateral awn point in the central portion of each head was recorded in order to determine the frequency of occurrence.

On the basis of information obtained regarding variability of awn length and frequency of occurrence of awn points and on the basis of the F_2 and F_3 segregation, the segregates were divided into six phenotypic awn classes as described below:

Class No.	Description	Lateral Awns	Central Awns
1	Awnless	None	None or points
2	Arlington Awnless type	None or points	Modal class for length 35.0 mm. -39.9 mm.
3	Reduced Atrada type	Modal class for length 5.0 mm.- 9.9 mm.	Modal class for length 25.0 mm. -29.9 mm.
4	Atrada type	Modal class for length 30.0 mm.- 34.9 mm.	Modal class for length 45.0 mm. -54.9 mm.
5	F_1 type-- Central awns twice as long as laterals	Modal length approximately 40 mm.	Modal length approximately 80 mm.
6	Fully awned	Modal length approximately 110 mm.	Modal length approximately 115 mm.

Heads of barley representative of these awn classes are shown in plate II.

The segregates were grouped into two phenotypic classes for aleurone color. The homozygous blue and heterozygous plants were included in the blue class and the homozygous white plants comprised the white class.

Two phenotypic classes for density of spike were observed. The segregates were classified as lax or dense on a visual basis.

Symbols for Genetic Characters

All genetic symbols except the one for spring versus winter habit were taken from the list of symbols recommended by Robertson, Wiebe, and Immer (18). The subscript numbers used in most cases indicate that these factor pairs are not necessarily the same ones reported by previous workers. The factor pairs for awn length and lax versus dense spikes in the cross Arlington Awnless x Atrada, C. I. 5638, were found to be the same ones reported by Sturm (19) and were assigned the same subscript numbers used by him.

The genetic symbols used are listed below:

Character Pair:	Symbols Used:
Long versus short awns	Lk_4lk_4, Lk_5lk_5
Normal versus reduced lateral awns	Lr_1lr_1
Blue versus white aleurone color	Bl_2bl_2
Spring versus winter habit	Ee
Lax versus dense spikes	L_6l_6

Analysis of Data

All phenotypic ratios observed in the F_2 generation and all genotypic ratios as determined by the F_3 segregation were compared to calculated theoretical ratios. The observed ratio in each case was tested for goodness of fit to the calculated ratio by use of the Chi-square test.

All P values were taken from the table of Chi-square prepared by Fisher (4).

To test for linkage between the various characters studied, the observed genotypic ratio for each character was combined in a dihybrid ratio with the observed genotypic ratio for every other character studied. Each of these dihybrid ratios was compared with a calculated 1:2:2:4:1:2:1:2:1 ratio by use of the Chi-square test. When the observed ratio fit the calculated ratio closely, the factor pairs being tested were considered independent of each other. If a poor fit to the calculated ratio was obtained, the factor pairs were assumed to be linked.

Crossover values were determined by the product method. To facilitate calculation, the tables prepared by Immer (10) were used. The observed ratio was compared with the ratio expected with the calculated percentage of crossing over by use of the Chi-square test for goodness of fit.

EXPERIMENTAL RESULTS

Variation in Awn Length

Variation in awn length was studied as a preliminary step in establishing phenotypic awn classes. The data obtained on the plants selected for study from the Arlington Awnless parent appear in table I. Some of the differences between mean lengths of central awns were found to be significant, indicating that environmental factors definitely affected awn development. Awn points on lateral spikelets were observed on as many as six of the ten heads taken from some of the plants. Tolerance within awn classes is based on the results of this study.

Inheritance of Awnedness

Since it was necessary to summarize the results obtained in both crosses before the mode of inheritance could be explained satisfactorily, the results obtained with both crosses will be presented first and will be followed by an explanation of the mode of inheritance.

Arlington Awnless x Atrada, C. I. 5641.- The F_1 progeny of this cross had longer awns than either parent, indicating that each parent carried dominant or partially dominant genes for the development of awns not carried by the other. The central awns were approximately two-thirds fully awned, and the lateral awns were approximately one-half as long as the central awns (Plate I).

Transgressive segregation for awnedness was observed in the F_2 generation, the segregates ranging from awnless to fully awned (Plate II). The observed and calculated F_2 phenotypic ratios are given in table II.

Table I Measurements recorded and the analysis of variance calculated on central awn lengths as a part of the study of variation in awn length within the Arlington Awnless variety

Plant number	Head number 1	2	3	4	5	6	7	8	9	10	Mean S.E.
	Length of lateral awn points in millimeters										
1	0	0	0	15	0	0	0	0	0	0	
2	0	0	0	5	0	0	0	0	0	0	
3	7	0	0	0	0	0	0	5	7	10	
4	0	0	0	0	0	0	0	5	0	0	
5	5	0	0	0	0	0	5	10	5	15	
6	5	0	7	7	0	0	7	0	0	0	
7	0	0	0	5	7	10	0	15	15	8	
8	20	0	15	7	5	0	0	0	0	12	
9	5	0	0	0	5	10	0	5	0	0	
10	0	10	15	15	0	12	7	0	5	0	
	Length of central awns in millimeters										
1	25	45	30	40	45	40	7	35	15	20	30.2±4.15
2	40	25	25	35	30	25	40	35	25	40	32.0±2.13
3	45	25	25	30	40	40	35	50	40	40	37.0±2.60
4	25	35	35	50	20	30	25	25	25	5	27.5±3.67
5	30	20	40	45	40	60	30	35	40	35	37.5±3.35
6	25	45	20	25	25	15	20	40	30	35	28.0±3.00
7	35	25	45	40	50	50	40	40	50	40	41.5±2.48
8	50	65	45	50	30	35	25	35	50	35	42.0±5.06
9	45	50	40	35	25	20	25	25	30	10	30.5±3.83
10	50	45	55	35	55	45	35	55	45	40	46.0±2.45

Analysis of variance on length of central awns

Variation due to:	D/F	Sum of squares	Mean square	Variance F
Plants	9	3759.56	417.73	4.07**
Heads	9	1052.56	116.95	1.14
Interaction	81	8317.04	102.68	10.13
Total	99	13129.16		

**F value significant at the 1% point

$S.E._{\bar{x}} = 3.38$ $S.E._{diff.} = 4.77$ Level of Significance (5%) = 9.35
t = 1.95996

The calculated 3:6:1:2:3:1 ratio for the awn types 6,5,4,3,2, and 1 is the ratio expected with awnedness inherited as a two-factor difference with complete dominance in one factor pair and incomplete dominance in the other. When the observed and calculated ratios were compared, a P value of 0.66 was obtained indicating that the observed ratio fit the calculated ratio closely.

Table II Observed and calculated F_2 phenotypic ratios for awn types in Arlington Awnless x Atrada, C. I. 5641

	Number of indicated phenotype								
Item	Fully awned (6)	F_1 type (5)	Atrada type (4)	Reduced Atrada type(3)	Arlington Awnless type(2)	Awnless (1)	Totals	X^2	P
Observed counts	19	42	5	13	15	3	97		
Calculated 3:6:1:2:3:1 ratio	18.19	36.38	6.06	12.12	18.19	6.06	97.00	3.258	0.66

The observed F_2 genotypic ratio as determined by the F_3 segregation and the calculated genotypic ratio are given in table III. The calculated 1:2:2:4:1:2:1:2:1 genotypic ratio for awnedness is the ratio expected with inheritance on a two-factor basis with independent assortment of the two factor pairs. The observed ratio fit the calculated ratio closely, a P value of 0.71 being obtained.

Table III Observed and calculated F_2 genotypic ratios for awnedness as determined by the F_3 segregation in Arlington Awnless x Atrada, C. I. 5641

Genotypes	Numerical awn class	Observed counts	Calculated 1:2:2:4:1:2:1:2:1 ratio	X^2	P value
$Lr_1Lr_1Lk_5Lk_5$	6	6	6.0625		
$Lr_1Lr_1Lk_5lk_5$	6	13	12.1250		
$Lr_1lr_1Lk_5Lk_5$	5	11	12.1250		
$Lr_1lr_1Lk_5lk_5$	5	31	24.2500		
$Lr_1Lr_1lk_5lk_5$	4	5	6.0625		
$Lr_1lr_1lk_5lk_5$	3	13	12.1250		
$lr_1lr_1Lk_5Lk_5$	2	7	6.0625		
$lr_1lr_1Lk_5lk_5$	2	8	12.1250		
$lr_1lr_1lk_5lk_5$	1	3	6.0625		
Totals		97	97.0000	5.392	0.71

Arlington Awnless x Atrada, C. I. 5638.- The F_1 progeny of this cross had longer awns than either parent indicating that in this cross also each parent carried dominant or partially dominant genes for the development of awns not carried by the other. The central spikelets were approximately two-thirds fully awned, and the lateral awns were approximately one-half as long as the central awns (Plate I).

The awn types observed in the F_2 generation were 2,3,4,5, and 6 (Plate II). The observed and calculated phenotypic ratios are given in

table IV. When the observed ratio was compared with a calculated 3:6:1:2:4 ratio for the awn types 6,5,4,3, and 2, a P value of 0.83 was obtained, indicating that the observed ratio fit the calculated ratio closely. The calculated 3:6:1:2:4 ratio is the ratio expected if awnedness is inherited as a two-factor difference with complete dominance in one factor pair and incomplete dominance in the other with the lr_1Lk_4 and lr_1lk_4 phenotypes indistinguishable.

Table IV Observed and calculated F_2 phenotypic ratios for awnedness in Arlington Awnless x Atrada, C. I. 5638

	Number of indicated phenotype							
Item	Fully awned (6)	F_1 type (5)	Atrada type (4)	Reduced Atrada type (3)	Arlington Awnless type (2)	Totals	X^2	P
Observed counts	15	34	6	9	17	81		
Calculated 3:6:1:2:4 ratio	15.19	30.38	5.06	10.12	20.25	81.00	1.484	0.83

The F_2 genotypic ratio as determined by the F_3 segregation and the calculated genotypic ratio are given in table V. The calculated 1:2:2:4:1:2:4 ratio for awnedness is the ratio expected with awnedness inherited as a two-factor difference with the two factor pairs independently assorted when the $lr_1lr_1Lk_4Lk_4$, $lr_1lr_1Lk_4lk_4$, and $lr_1lr_1lk_4lk_4$ genotypes cannot be satisfactorily differentiated. When the observed and calculated ratios were compared a P value of 0.52 was obtained. This agreement between the observed and theoretical ratios indicates that the assumption of a two-factor difference for awnedness is probably correct.

Table V Observed and calculated F_2 genotypic ratios for awnedness as determined by the F_3 segregation in Arlington Awnless x Atrada, C. I. 5638

Genotype	Awn class	Observed counts	Calculated 1:2:2:4:1:2:4 ratio	X^2	P value
$Lr_1Lr_1Lk_4Lk_4$	6	3	5.0625		
$Lr_1Lr_1Lk_4lk_4$	6	12	10.1250		
$Lr_1lr_1Lk_4Lk_4$	5	7	10.1250		
$Lr_1lr_1Lk_4lk_4$	5	27	20.2500		
$Lr_1Lr_1lk_4lk_4$	4	6	5.0625		
$Lr_1lr_1lk_4lk_4$	3	9	10.1250		
$lr_1lr_1Lk_4Lk_4$	2				
$lr_1lr_1Lk_4lk_4$	2	17	20.2500		
$lr_1lr_1lk_4lk_4$	2				
Totals		81	81.0000	5.193	0.52

An attempt was made to separate the three genotypes, $lr_1lr_1Lk_4Lk_4$, $lr_1lr_1Lk_4lk_4$, and $lr_1lr_1lk_4lk_4$, that were grouped into the phenotypic awn class 2. The central awns of fifteen F_3 families grown from F_2 plants included in this group were measured. The lengths recorded were grouped into classes of 10.0 mm. and the frequency distribution of each family was compared to the distribution of awn lengths in the Arlington Awnless parent variety. The frequency distribution of central awn lengths in these F_3 families and in Arlington Awnless are presented in table VI. From these distributions it is evident that most of these families were different from Arlington Awnless, but it would be necessary to grow an additional generation to determine whether or not the genotypes could be distinguished.

Table VI Frequency distribution of central awn lengths in F_3 families grown from fifteen F_2 plants classified as having the Arlington Awnless, or 2, awn type

Family number	Length in millimeters					
	0.0-9.9	10.0-19.9	20.0-29.9	30.0-39.9	40.0-49.9	50.0-59.9
57	3	8	0	0	0	0
7	17	5	8	6	0	1
8	11	24	12	2	1	0
14	1	26	15	7	0	0
72	0	16	10	10	4	1
73	6	12	11	7	5	0
71	12	16	18	13	5	0
4	5	11	20	8	6	0
9	4	11	13	6	2	0
5	1	6	7	10	2	0
28	4	6	7	10	3	0
2	0	6	9	20	8	1
75	0	0	2	16	13	7
3	1	5	4	2	8	1
74	0	0	0	6	26	6
Arlington Awnless	0	1	0	5	2	2

The results indicate that in each cross awnedness was inherited as a two-factor difference with complete dominance in one factor pair and incomplete dominance in the other. In each parent in the two crosses one of the factor pairs was in the dominant and the other in the recessive condition. On the basis of segregation observed, it was concluded that in each cross one factor pair affected lateral awn development primarily and the other factor pair affected awn length only.

The factor pair for normal versus reduced lateral awns was designated Lr_1lr_1. Since the Arlington Awnless parent had no lateral awns, it was assumed that it carried the factor pair for lateral awn development in the recessive condition (lr_1lr_1).

Although the awns of the two Atrada parents are similar, these varieties carry different dominant factors for awn length[3]. The factor for awn length carried in the recessive condition in Atrada, C. I. 5638, was reported by Sturm (18), who designated it Lk_4lk_4. This variety carried one factor for awn length in the dominant condition, which is designated Lk_5lk_5 in this study. On the basis of these facts and on the assumption that Arlington Awnless carries Lr_1 in the recessive condition, the genotypes of the Atrada parents would be: Atrada, C. I. 5641, $Lr_1Lr_1Lk_4Lk_4$ lk_5lk_5, and Atrada, C. I. 5638, $Lr_1Lr_1lk_4lk_4Lk_5Lk_5$. Since the results indicated a two-factor difference in each cross, the genotype of Arlington Awnless was assumed to be $lr_1lr_1Lk_4Lk_4Lk_5Lk_5$. Hypothetical genotypes of the F_2 generation segregates were based on these parental genotypes. These F_2 genotypes and the segregation observed in the F_3 generation are given in table VII.

The closeness of fit of the phenotypic and genotypic ratios observed in the two crosses to the ratios expected on the basis of the hypothesis formulated indicate that this hypothesis is probably correct.

The presence of the dominant awn length factor Lk_4Lk_4 in the awnless segregates from the cross Arlington Awnless x Atrada, C. I. 5641, can be satisfactorily explained if it is assumed that this factor pair (Lk_4) is dependent on the presence of Lr_1 in the dominant condition in order to produce any effect. Conversely, the absence of any awnless segregates in

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3/ Unpublished data on awn inheritance studies by S. C. Litzenberger, Montana Agricultural Experiment Station, Bozeman, Montana.

Table VII Hypothetical genotypes and observed breeding behavior of the F_2 generation segregates in Arlington Awmless x Atrada, C. I. 5641, and Arlington Awmless x Atrada, C. I. 5638

Genotypic ratio	F_2 genotype	Numerical awn class	Phenotypic ratio	Segregation observed in the F_3 generation
Arlington Awmless x Atrada, C. I. 5641				
1	$Lr_1Lr_1Lk_4Lk_4Lk_5Lk_5$	6	3	True breeding.
2	$Lr_1Lr_1Lk_4Lk_4Lk_5lk_5$	6		Segregating for classes 4 and 6.
2	$Lr_1lr_1Lk_4Lk_4Lk_5Lk_5$	5	6	Segregating for classes 2,5 and 6.
4	$Lr_1lr_1Lk_4Lk_4Lk_5lk_5$	5		Segregating for all classes, 1 to 6.
1	$Lr_1Lr_1Lk_4Lk_4lk_5lk_5$	4	1	True breeding (Atrada type)
2	$Lr_1lr_1Lk_4Lk_4lk_5lk_5$	3	2	Segregating for classes 1,3, and 4.
1	$lr_1lr_1Lk_4Lk_4Lk_5Lk_5$	2	3	True breeding (Arlington Awmless type).
2	$lr_1lr_1Lk_4Lk_4Lk_5lk_5$	2		Segregating for classes 1 and 2.
1	$lr_1lr_1Lk_4Lk_4lk_5lk_5$	1	1	True breeding.
Arlington Awmless x Atrada, C. I. 5638				
1	$Lr_1Lr_1Lk_4Lk_4Lk_5Lk_5$	6	3	True breeding.
2	$Lr_1Lr_1Lk_4lk_4Lk_5Lk_5$	6		Segregating for classes 4 and 6.
2	$Lr_1lr_1Lk_4Lk_4Lk_5Lk_5$	5	6	Segregating for classes 2,5, and 6.
4	$Lr_1lr_1Lk_4lk_4Lk_5Lk_5$	5		Segregating for classes 2 to 6.
1	$Lr_1Lr_1lk_4lk_4Lk_5Lk_5$	4	1	True breeding (Atrada type).
2	$Lr_1lr_1lk_4lk_4Lk_5Lk_5$	3	2	Segregating for classes 2,3, and 4.
	$lr_1lr_1Lk_4Lk_4Lk_5Lk_5$	2		True breeding (Arlington Awmless type).
4	$lr_1lr_1Lk_4lk_4Lk_5Lk_5$	2	4	Apparently true breeding.
	$lr_1lr_1lk_4lk_4Lk_5Lk_5$	2		True breeding.

the progeny of Arlington Awnless x Atrada, C. I. 5638, can be explained by the presence of the length factor Lk_5Lk_5 in the dominant condition if this factor is assumed to be independent of Lr_1 in its expression.

From inspection of the genotypes listed it can be seen that normal lateral awns was partially dominant over reduced since the segregates carrying Lr_1lr_1 in the heterozygous condition were less awned than those carrying this factor pair in the homozygous dominant condition. It can also be seen by comparing the segregates in classes 2, 5, and 6, which carried lr_1lr_1, Lr_1lr_1, and Lr_1Lr_1 respectively that this factor pair affected length of central awns with long awns partially dominant over short. The central awns in class 2 were short, in class 5, intermediate, and in class 6, long.

In each of the factor pairs affecting awn length only (Lk_4lk_4 and Lk_5lk_5)long was apparently completely dominant over short. The segregates that carried the length factor (Lk_4 or Lk_5) in the homozygous dominant condition could not be distinguished on a visual basis from those that were heterozygous for the same factor pair.

Inheritance of Aleurone Color in Arlington Awnless x Atrada, C. I. 5638

Segregation for blue and white aleurone was observed on the F_1 heads, but no attempt was made to analyze this segregation in this generation. Ratios were determined on the plant basis in the F_2 generation and were corrected after checking segregation in the F_3 generation. Of the 80 F_2 plants classified, 60 were classified as blue and 20 as white. The observed

ratio fit a calculated 3:1 ratio exactly, indicating a single-factor difference.

The breeding behavior of 77 of the F_2 plants was observed in the F_3 generation. The observed and calculated F_2 genotypic ratios as determined by the F_3 segregation are given in table VIII. A P value of 0.72 was obtained, indicating that the observed ratio fit the calculated 1:2:1 ratio closely. This closeness of fit to a monohybrid ratio indicates that aleurone color was inherited as a single-factor difference.

Table VIII Observed and calculated F_2 genotypic ratios for blue versus white aleurone as determined by the F_3 segregation of Arlington Awnless x Atrada, C.I. 5638

	Number of indicated genotype					
	Bl_2Bl_2	Bl_2bl_2	bl_2bl_2	Totals	X^2	P
Observed counts	17	42	18	77		
Calculated 1:2:1 ratio	19.25	38.50	19.25	77.00	0.662	0.72

Inheritance of Growth Habit in
Arlington Awnless x Atrada, C. I. 5641

The plants of the F_1 generation made an erect type of growth, indicating that spring habit of growth was dominant over winter.

The F_2 phenotypic and genotypic ratios as determined by the F_3 segregation are given in tables IX and X respectively. The phenotypic ratio fit a calculated 3:1 ratio closely, a P value of 0.50 being obtained. The genotypic ratio fit a calculated 1:2:1 ratio closely since a P value of 0.61 was obtained.

It was concluded that growth habit was inherited as a single-factor difference in this cross. Spring habit of growth was apparently completely dominant over winter.

Table IX Observed F_2 phenotypic ratios for spring versus winter growth habit in Arlington Awnless x Atrada, C. I. 5638, and in Arlington Awnless x Atrada, C. I. 5641

Cross	Number of indicated phenotype a/				
	Spring	Winter	Totals	X^2	P
Arlington Awnless x Atrada, C. I. 5641	76	21	97	0.581	0.50
Arlington Awnless x Atrada, C. I. 5638	66	15	81	1.815	0.18

a/ Compared with a calculated 3:1 ratio.

Inheritance of Growth Habit in
Arlington Awnless x Atrada, C. I. 5638

The F_1 plants of this cross also made an erect type of growth, indicating that spring habit was dominant over winter.

The observed and calculated F_2 phenotypic ratios are given in table IX. Of the 81 F_2 plants classified, 66 were of the erect type and 15 were decumbent. A P value of 0.18 was obtained when the observed ratio was compared with a calculated 3:1 ratio. Although this is a relatively poor fit, the segregation observed in the F_3 generation indicated that the inheritance of growth habit was on a major single-factor basis.

The observed and calculated F_2 genotypic ratios as determined by the F_3 segregation are given in table X. Of the phenotypically spring habit plants 29 bred true and 37 segregated for spring and winter habit,

and the 15 winter habit plants bred true. When this observed ratio was compared with a calculated 1:2:1 ratio, a P value of 0.07 was obtained. On the basis of the breeding behavior of the F_2 plants it was concluded that this character was inherited as a single-major-factor difference. The poor fit to a monohybrid ratio may have been caused by other factors not detected in this study. Additional work with this cross would be necessary to determine whether or not this is true.

Table X Observed F_2 genotypic ratios for spring versus winter growth habit as determined by the F_3 segregation in Arlington Awnless x Atrada, C. I. 5638 and in Arlington Awnless x Atrada, C. I. 5641

Item	Number of indicated genotype a/			Totals	X^2	P
	Spring	Heterozygous	Winter			
Arlington Awnless x Atrada 5641	28	48	21	97	1.021	0.61
Arlington Awnless x Atrada 5638	29	37	15	81	5.445	0.07

a/ Compared with a calculated 1:2:1 ratio.

Inheritance of Density of Spike in Arlington Awnless x Atrada, C. I. 5638

The spikes of the F_1 plants were lax, indicating that lax was dominant over dense.

The observed and calculated F_2 phenotypic ratios are presented in table XI. Of the 81 F_2 plants grown, 65 were classified as lax and 16 as dense. When this observed ratio was compared with a calculated 3:1

ratio, a P value of 0.30 was obtained, indicating that the observed ratio fit a monohybrid ratio fairly well.

Table XI Observed and calculated F_2 phenotypic ratios for lax versus dense spike in Arlington Awnless x Atrada, C. I. 5638

Item	Number of indicated phenotype: Lax	Dense	Totals	X^2	P
Observed counts	65	16	81		
Calculated 3:1 ratio	60.75	20.25	81.00	1.189	0.30

The observed and calculated F_2 genotypic ratios as determined by the F_3 segregation are presented in table XII. When the observed ratio of 24 homozygous lax, 41 heterozygous, and 16 homozygous dense was compared with a calculated 1:2:1 ratio, a P value of 0.46 was obtained.

Table XII Observed and calculated F_2 genotypic ratios for lax versus dense spike as determined by the F_3 segregation in Arlington Awnless x Atrada, C. I. 5638

Item	Number of indicated genotype: Lax L_6L_6	Heterozygous L_6l_6	Dense l_6l_6	Totals	X^2	P
Observed counts	24	41	16	81		
Calculated 1:2:1 ratio	20.25	40.50	20.25	81.00	1.593	0.46

It was concluded that a single factor pair controlled the inheritance of spike density in this cross and that the lax condition was dominant over dense.

Linkage Relationships in Arlington Awnless x Atrada, C. I. 5641

Characters inherited independently.- The observed and calculated genotypic ratios for the characters inherited independently in this cross are given in table XIII. The calculated dihybrid genotypic ratio expected with independent assortment is 1:2:2:4:1:2:1:2:1. The observed segregation between character pairs was compared with this theoretical ratio.

The three characters studied in this cross, normal versus reduced lateral awns, long versus short awns, and growth habit, were all inherited independently of each other. The ratio for normal versus reduced lateral awns and long versus short awns ($Lr_1lr_1Lk_5lk_5$) fit the calculated ratio closely, a P value of 0.71 being obtained. When the ratio for each of these characters was combined in a dihybrid ratio with spring versus winter habit, good fits to independent ratios were obtained, the P value in both cases being 0.90.

No linkages were observed in this cross.

Linkage Relationships in Arlington Awnless x Atrada, C. I. 5638

No attempt was made to determine the linkage relationships of spring versus winter habit in this cross. Although this character appeared to be inherited as a single-major-factor difference, the observed ratio in the F_2 generation did not fit a monohybrid ratio closely enough to justify its use in linkage determinations.

Characters inherited independently.- The observed and calculated F_2 genotypic ratios for the characters inherited independently in this cross

Table XIII Observed and calculated F_2 genotypic ratios for spring versus winter habit of growth and two factors for awnedness as determined by the F_3 segregation of Arlington Awnless x Atrada, C. I. 5641

Genotype studied	Number of indicated genotype									Totals	X^2	P
	AABB	AABb	AaBB	AaBb	AAbb	Aabb	aaBB	aaBb	aabb			
Observed counts												
$Lr_1lr_1Lk_5lk_5$	6	13	11	31	5	13	7	8	3	97	5.392	0.71
Lr_1lr_1E e	6	13	16	27	5	11	6	8	5	97	3.495	0.90
Lk_5lk_5E e	6	11	15	28	7	9	7	9	5	97	3.454	0.90
Calculated ratio	6.06	12.13	12.13	24.24	6.06	12.13	6.06	12.13	6.06	97.00		

Table XIV Observed and calculated F_2 genotypic ratios as determined by the F_3 segregation for characters inherited independently in Arlington Awnless x Atrada, C. I. 5638

Genotype studied	Number of indicated genotype									Totals	X^2	P
	AABB	AABb	AaBB	AaBb	AAbb	Aabb	aaBB	aaBb	aabb			
Observed counts												
$Lr_1lr_1Lk_4lk_4$	3	12	7	27	6	9	--	17	--	81	5.193	0.52
$Lr_1lr_1L_6\ l_6$	5	12	11	21	4	11	8	8	1	81	6.842	0.56
Calculated ratio	5.06	10.13	10.13	20.24	5.06	10.13	5.06	10.13	5.06	81.00		
Observed counts												
$Lr_1lr_1Bl_2bl_2$	6	11	9	23	4	9	2	8	5	77	3.430	0.90
$L_6l_6Bl_2bl_2$	3	12	10	23	8	6	4	7	4	77	6.612	0.58
Calculated ratio	4.81	9.63	9.63	19.24	4.81	9.63	4.81	9.63	4.81	77.00		
Observed counts												
$Lk_4lk_4Bl_2bl_2$	8	10	5	16	4	6	2	8	5	64	7.375	0.50
Calculated ratio	4	8	8	16	4	8	4	8	4	64		

are given in table XIV. All of the observed ratios except one were compared with calculated 1:2:2:4:1:2:1:2:1 genotypic ratios. The observed ratio for normal versus reduced lateral awns and long versus short awns ($Lr_1lr_1Lk_4lk_4$) was compared with a calculated 1:2:2:4:1:2:4 ratio, since the three genotypes $lr_1lr_1Lk_4Lk_4$, $lr_1lr_1Lk_4lk_4$, and $lr_1lr_1lk_4lk_4$ could not be distinguished.

When the observed and calculated ratios for the genotype $Lr_1lr_1Lk_4lk_4$ were compared, a P value of 0.52 was obtained, indicating that these two characters were inherited independently. Lax versus dense spikes (L_6l_6) and blue versus white aleurone (Bl_2bl_2) were also inherited independently of normal versus reduced lateral awns. The P values obtained for these comparisons were 0.56 for $Lr_1lr_1L_6l_6$ and 0.90 for $Lr_1lr_1Bl_2bl_2$.

The observed ratio for spike density and aleurone color ($L_6l_6Bl_2bl_2$) gave a P value of 0.58 when compared with the calculated ratio which indicated that these characters were inherited independently. Aleurone color was found to be inherited independently of the factor pair for awn length (Lk_4lk_4)also, as indicated by the P value of 0.50. In this observed ratio only 64 individuals of the F_2 population were used. It was necessary to omit the 17 plants grouped in awn class 2 because the genotypes included in this group contained the three combinations of the factor pair for awn length, Lk_4Lk_4, Lk_4lk_4, and lk_4lk_4.

Characters linked in inheritance.- The observed and calculated F_2 genotypic ratios for long versus short awns and lax versus dense spikes are given in table XV. When the observed and calculated ratios were compared,

a P value of 0.06 was obtained. This would indicate that these characters were probably linked. The percentage of crossing over calculated by the product method was 24.18 ± 6.30 percent. The observed phenotypic ratio and the calculated ratios with independent assortment and with 24.18 percent crossing over are given in table XVI. The observed ratio fit the calculated 9:3:3:1 ratio poorly, the P value being between 0.01 and 0.02. A close fit to the ratio expected with 24.18 percent crossing over was obtained. The P value for this comparison was 0.95, indicating that these characters were linked.

Table XV Observed and calculated F_2 genotypic ratios as determined by the F_3 segregation for long versus short awns and lax versus dense spikes in Arlington Awnless x Atrada, C. I. 5638

F_2 genotype	Observed counts	Calculated 1:2:2:4:1:2:1:2:1 ratio	X^2	P value
$Lk_4Lk_4L_6L_6$	6	4		
$Lk_4Lk_4L_6l_6$	6	8		
$Lk_4lk_4L_6L_6$	10	8		
$Lk_4lk_4L_6l_6$	21	16		
$Lk_4Lk_4l_6l_6$	0	4		
$Lk_4lk_4l_6l_6$	7	8		
$lk_4lk_4L_6L_6$	1	4		
$lk_4lk_4L_6l_6$	5	8		
$lk_4lk_4l_6l_6$	8	4		
Totals	64	64	15.043	0.06

Table XVI Observed and calculated F_2 phenotypic ratios for long versus short awns and lax versus dense spikes in Arlington Awnless x Atrada, C. I. 5638

	Number of indicated phenotype						
	Long awns		Short awns				
	Lax	Dense	Lax	Dense	Totals	X^2	P
Observed counts	43	7	6	8	64		
Calculated 9:3:3:1 ratio	36	12	12	4	64	10.444	.01-.02
Calculated ratio with 24.18 per cent crossing over	41.2	6.8	6.8	9.2	64.0	0.335	0.95

DISCUSSION

In each of the two crosses studied, awnedness was inherited as a two-factor difference. In Arlington Awnless x Atrada, C. I. 5638, the segregates ranged from long-awned to the Arlington Awnless type, and in Arlington Awnless x Atrada, C. I. 5641, the segregates ranged from long-awned to awnless. A two-factor difference between long-awned and awnless was reported by Myler (14). In crosses of long-awned varieties on an awnless one, he observed intermediate true breeding types that were very similar in awnedness to the Atrada and Arlington Awnless varieties. However, Myler did not report either factor as primarily affecting lateral awn development. Whether or not he observed the effects of the same factors operating in Arlington Awnless x Atrada, C. I. 5641, can be determined only by further study.

A single-factor difference for normal versus reduced lateral awns with normal partially dominant over reduced was observed in each cross in this study. This factor, which was designated Lr_1, also affected the length of central awns. Ikeno (9), Glinyany (6), Engeldow (3), Miyake and Imai (12), and Leonard (11) reported a single factor difference for this character with partial dominance, but none of these workers reported any effect of this factor on central awn length. Two of these workers, (9) and (6), concluded that the factor operated as an inhibitor and was dominant when lateral awns were reduced.

Although segregation for only two factor pairs was observed in each of the two crosses, it was concluded that three factor pairs for awnedness were present in each of the parental varieties. In addition to the factor

pair for lateral awn development, Lr_1, two factor pairs affecting awn length only, Lk_4 and Lk_5, were present. The awn length factor, Lk_4, for which segregation was observed in Arlington Awnless x Atrada, C. I. 5638, was apparently the same factor reported by Sturm (19). He observed a single-factor difference between long and short awns in Atrada, C. I. 5638, x Trebi-Velvet. A single-factor difference between long and short awns has also been reported by Glinyany (6) and Miyake and Imai (12). A total of three factor pairs affecting awnedness has been reported by von Ubisch (20), Miyake and Imai (12), and Ikeno (9).

The inheritance of blue versus white aleurone on a single-factor basis, as observed in Arlington Awnless x Atrada, C. I. 5638, has been previously reported by Miyazawa, So, and Imai (13), Buckley (2), Robertson, Deming, and Koonce (17), and Myler and Stanford (15). Myler and Stanford also reported a 9:7 ratio for blue to white in a cross of two white varieties. Xenia was observed in this study and was also reported by all of these workers.

Spring versus winter habit was apparently inherited on a major single-factor basis in both crosses studied, but difficulty in classification and the poor fit of the observed ratio to a monohybrid ratio in Arlington Awnless x Atrada, C. I. 5638, indicated that other factors may have affected this character in this cross. Spring versus winter habit was previously reported to be inherited as a two-factor difference by Gaines (5) and as a three-factor difference by Neatby (16).

The inheritance of lax versus dense spikes on a single-factor basis with lax dominant over dense, as observed in Arlington Awnless x Atrada,

C. I. 5638, is in agreement with results reported by Biffen (1), Sturm (19), Miyake and Imai (12), and Wexelsen (21). Wexelsen (22) observed a two-factor difference in some crosses studied. Neatby (16) reported a single-factor difference with minor modifying factors present, and von Ubisch (20) reported a three-factor difference. Hayes and Harlan (8) found dense dominant over lax in crosses that they studied.

The data obtained are not sufficient to place the factor pairs in linkage groups because none of the characters studied were controlled by known factors of known location. Those characters shown to be inherited independently can be considered to be in different linkage groups or over 50 crossover units apart on the same chromosome. Those characters found to be linked are in the same linkage group.

Because of the difficulty of classification and the resultant skewed monohybrid ratio for spring versus winter habit in Arlington Awnless x Atrada, C. I. 5638, no attempt was made to determine the linkage relationships of this character in this cross.

The only characters that were shown to be linked were lax versus dense spikes and long versus short awns. These characters were linked in the coupling phase with 24.18±6.30 percent crossing over in Arlington Awnless x Atrada, C. I. 5638. Sturm (19) observed this same linkage with approximately 23 percent crossing over in Atrada, C. I. 5638 x Trebi-Velvet. Since the Atrada parent occurred in both crosses and since the crossover percentages were not significantly different, it was concluded that the same factor pairs probably controlled these characters in both crosses.

The linkage relationships of the characters studied in the two crosses are summarized below.

Arlington Awnless x Atrada, C. I. 5641

Long versus short awns inherited independently of

Normal versus reduced lateral awns

Spring versus winter habit

Normal versus reduced lateral awns inherited independently of

Spring versus winter habit

Arlington Awnless x Atrada, C. I. 5638

Long versus short awns inherited independently of

Normal versus reduced lateral awns

Blue versus white aleurone

Normal versus reduced lateral awns inherited independently of

Blue versus white aleurone

Lax versus dense spikes

Lax versus dense spikes inherited independently of

Blue versus white aleurone

Long versus short awns linked in inheritance with

Lax versus dense spikes with 24.18 ± 6.30 percent crossing over

Spring versus winter habit

Linkage relationships were not determined for this character in this cross

SUMMARY

The inheritance of awnedness and growth habit in Arlington Awnless x Atrada, C. I. 5641, and the inheritance of awnedness, growth habit, aleurone color, and spike density in Arlington Awnless x Atrada, C. I. 5638, were studied.

Three different factors for awnedness were found in the two crosses studied. Awnedness was inherited as a two-factor difference in each cross, with apparent complete dominance in a factor pair for length of awns and partial domiance in a factor pair for normal versus reduced lateral awns and length of awns. The factor for normal versus reduced lateral awns was designated Lr_1. This factor was carried in the recessive condition in Arlington Awnless and in the dominant condition in the two Atrada varieties. The factors for length of awns were designated Lk_4 and Lk_5. Arlington Awnless carried both of these factors in the dominant condition; Atrada, C. I. 5641, carried Lk_4 in the dominant condition and Lk_5 in the recessive; and Atrada, C. I. 5638, carried Lk_4 in the recessive condition and Lk_5 in the dominant. True-breeding long-awned types were obtained in each cross. These carried all three factors in the dominant condition. True-breeding awnless segregates carrying Lr_1 and Lk_5 in the recessive and Lk_4 in the dominant condition were obtained in Arlington Awnless x Atrada, C. I. 5641. No awnless segregates were obtained in Arlington Awnless x Atrada, C. I. 5638; the segregates carrying Lr_1 and Lk_4 in the recessive and Lk_5 in the dominant condition had awns similar to those of the Arlington Awnless parent.

Blue versus white aleurone, spring versus winter habit, and lax versus dense spikes were each inherited on a single-factor basis. In each case, the dominant character is listed first. Xenia was observed in the inheritance of aleurone color.

The linkage relationships of spring versus winter habit in Arlington Awnless x Atrada, C. I. 5638, were not determined because the ratio obtained for this character in the F_2 generation did not fit a monohybrid ratio closely, although the F_3 segregation indicated a single-factor difference.

Long versus short awns was linked with lax versus dense spikes with 24.18 ± 6.30 percent crossing over. All other combinations of characters studied showed independent assortment.

The genotypes of the parent varieties as determined for the characters used in this study are:

Variety	Lateral awns	Awn length	Aleurone color	Spike density	Growth habit
Atrada, C. I. 5641	Lr_1Lr_1	Lk_4 Lk_4 lk_5 lk_5	Bl_2Bl_2	L_6L_6	E E
Arlington Awnless	lr_1lr_1	Lk_4 Lk_4 Lk_5 Lk_5	Bl_2Bl_2	L_6L_6	e e
Atrada, C. I. 5638	Lr_1Lr_1	lk_4 lk_4 Lk_5 Lk_5	bl_2bl_2	l_6l_6	E E

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DESCRIPTION OF PLATES

Plate I. Representative heads of each of the parent varieties and the F_1 type of Arlington Awnless x Atrada, C. I. 5638, and of Arlington Awnless x Atrada, C. I. 5641.

Plate II. Heads of barley representative of each of the six phenotypic awn classes established for this study. The number of each figure in the plate corresponds to the number of the awn class represented. Figure 1, awnless type; figure 2, Arlington Awnless type; figure 3, reduced Atrada type; figure 4, Atrada type; figure 5, F_1 type; and figure 6, fully awned type.

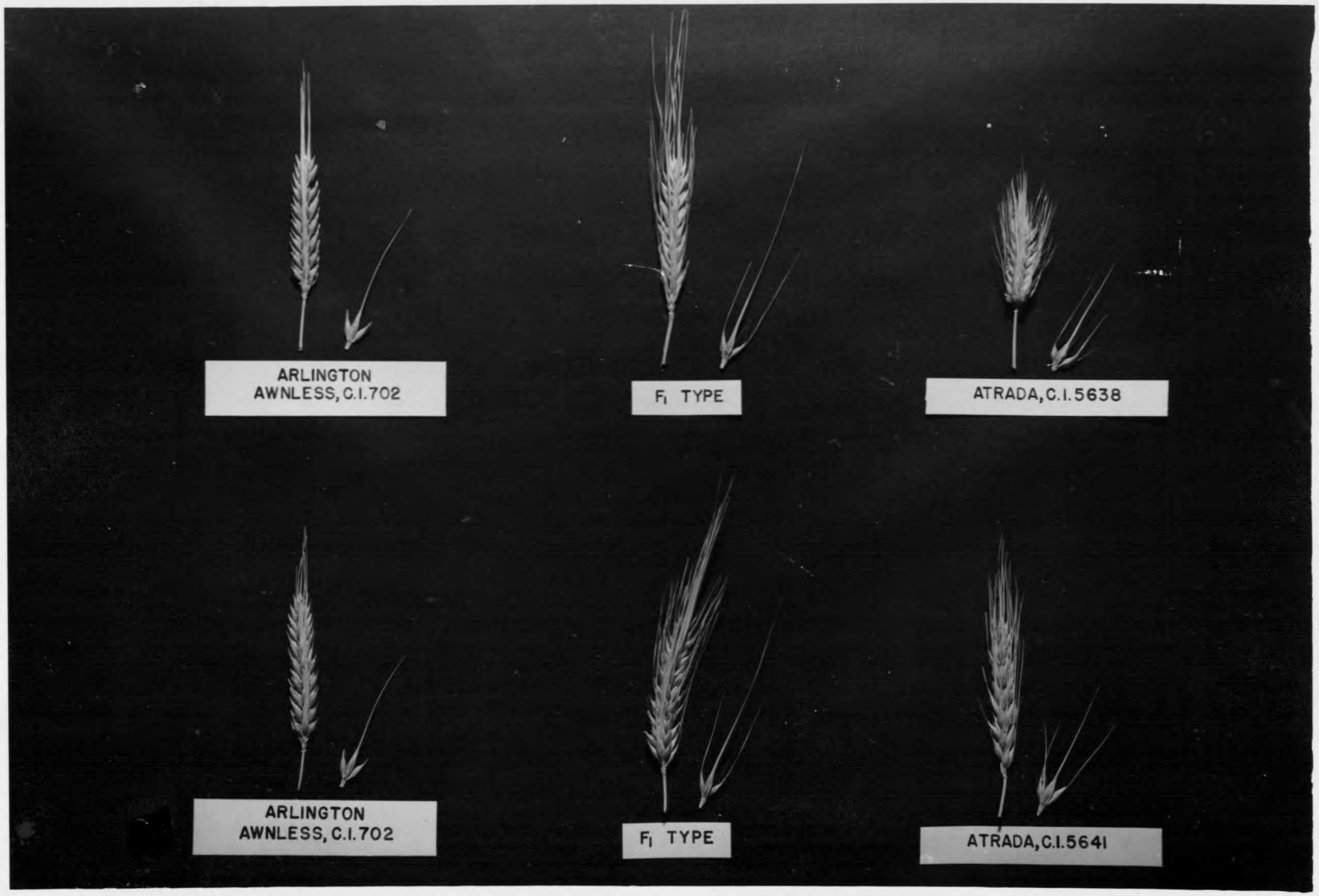
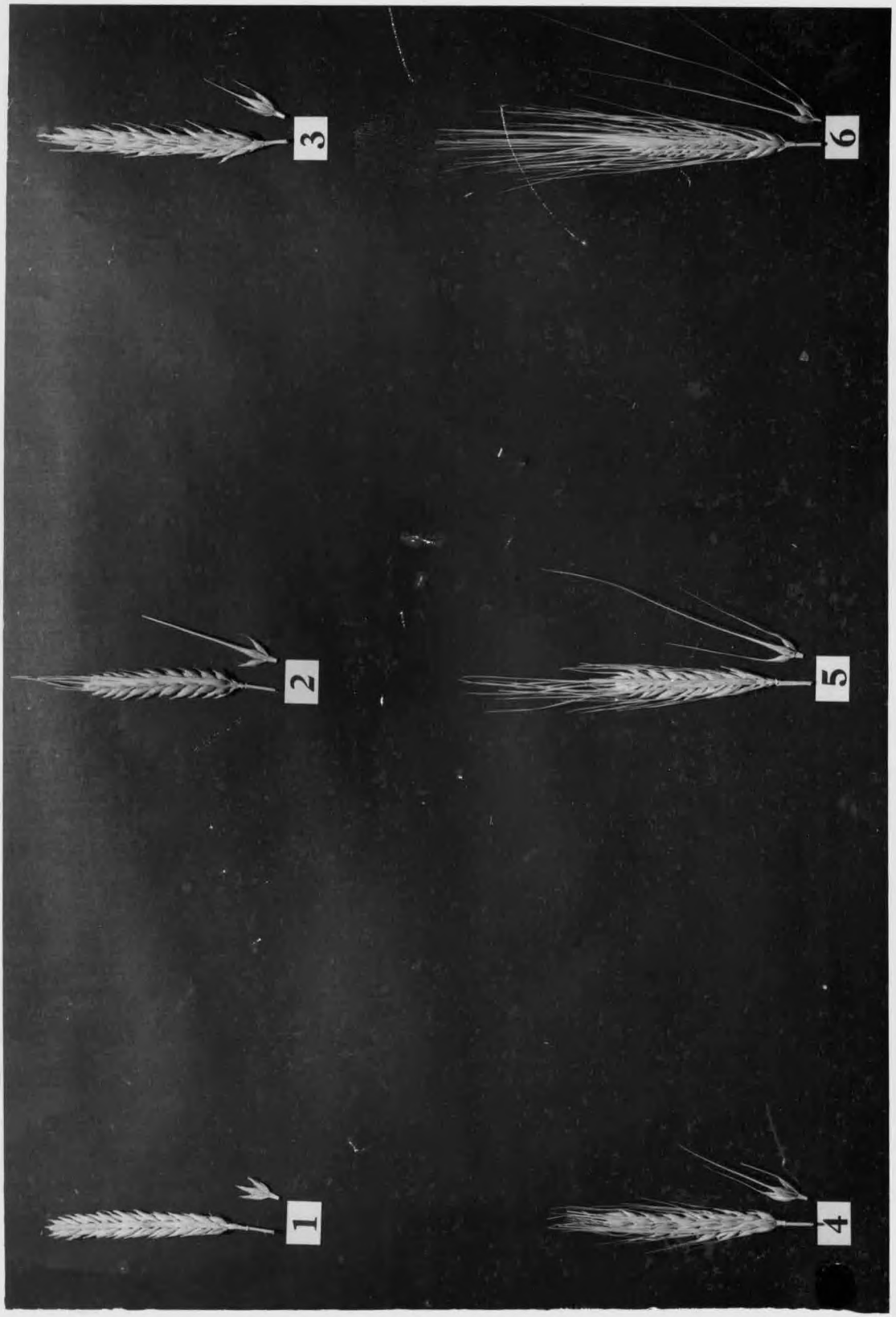

ARLINGTON
AWNLESS, C.I. 702
F1 TYPE
ATRADA, C.I. 5638
ARLINGTON
AWNLESS, C.I. 702
F1 TYPE
ATRADA, C.I. 5641

PLATE I

PLATE II



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