



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 was studied in crosses of Arlington Awnless, 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. 5638, long versus short awns were linked with lax versus dense spikes with  $24.18 \pm 6.30$  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 F3 generation indicated a single factor difference. All other characters segregated independently of each other.

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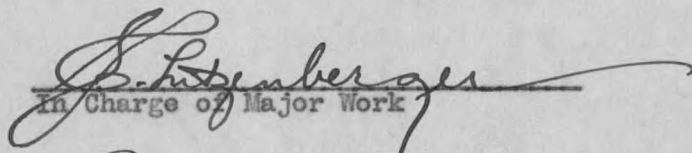
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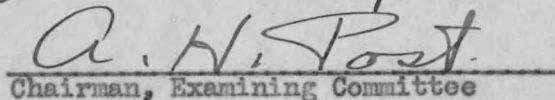
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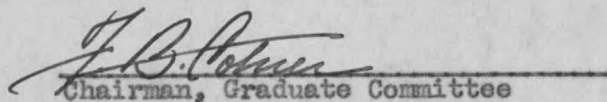
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TABLE OF CONTENTS

	Page
LIST OF TABLES . . . . .	5
ABSTRACT . . . . .	7
INTRODUCTION . . . . .	8
REVIEW OF LITERATURE . . . . .	8
Awn Length . . . . .	8
Normal versus Reduced Lateral Awns . . . . .	10
Blue versus White Aleurone Color . . . . .	11
Spring versus Winter Habit of Growth . . . . .	13
Lax versus Dense Spikes . . . . .	14
Linkage Groups in Barley . . . . .	15
MATERIALS AND METHODS . . . . .	16
Description of Parents and Characters Studied . . . . .	16
Method of Growing the Filial Generations . . . . .	17
Methods of Classification . . . . .	18
Symbols for Genetic Characters . . . . .	21
Analysis of Data . . . . .	21
EXPERIMENTAL RESULTS . . . . .	23
Variation in Awn Length . . . . .	23
Inheritance of Awnedness . . . . .	23
Arlington Awnless x Atrada, C. I. 5641 . . . . .	23
Arlington Awnless x Atrada, C. I. 5638 . . . . .	26
Inheritance of Aleurone Color in Arlington Awnless x Atrada, C. I. 5638 . . . . .	32

Inheritance of Growth Habit in Arlington Awnless x Atrada, C. I. 5641 . . . . .	33
Inheritance of Growth Habit in Arlington Awnless x Atrada, C. I. 5638 . . . . .	34
Inheritance of Density of Spike in Arlington Awnless x Atrada, C. I. 5638 . . . . .	35
Linkage Relationships in Arlington Awnless x Atrada, C. I. 5641 . . . . .	37
Characters inherited independently . . . . .	37
Linkage Relationships in Arlington Awnless x Atrada, C. I. 5638 . . . . .	37
Characters inherited independently . . . . .	37
Characters linked in inheritance . . . . .	39
DISCUSSION . . . . .	42
SUMMARY . . . . .	46
LITERATURE CITED AND CONSULTED . . . . .	48
DESCRIPTION OF PLATES . . . . .	51
PLATE I . . . . .	52
PLATE II . . . . .	53

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LIST OF TABLES

		Page
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	24
Table II	Observed and calculated $F_2$ phenotypic ratios for awn types in Arlington Awnless x Atrada, C. I. 5641	25
Table III	Observed and calculated $F_2$ genotypic ratios for awn-ness as determined by the $F_3$ segregation in Arlington Awnless x Atrada, C. I. 5641	26
Table IV	Observed and calculated $F_2$ phenotypic ratios for awedness in Arlington Awnless x Atrada, C. I. 5638	27
Table V	Observed and calculated $F_2$ genotypic ratios for awn-ness as determined by the $F_3$ segregation in Arlington Awnless x Atrada, C. I. 5638	28
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	29
Table VII	Hypothetical genotypes and observed breeding behavior of the $F_2$ generation segregates in Arlington Awnless x Atrada, C. I. 5641, and Arlington Awnless x Atrada, C. I. 5638	31
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	33
Table IX	Observed $F_2$ phenotypic ratios for spring versus winter growth habit in Arlington Awnless x Atrada, C. I. 5638, and Arlington Awnless x Atrada, C. I. 5641	34
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 Arlington Awnless x Atrada, C. I. 5641	35

	Page
Table XI Observed and calculated $F_2$ phenotypic ratios for lax versus dense spike in Arlington Awmless x Atrada, C. I. 5638	36
Table XII Observed and calculated $F_2$ genotypic ratios for lax versus dense spike as determined by the $F_3$ segregation in Arlington Awmless x Atrada, C. I. 5638	36
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 Awmless x Atrada, C. I. 5641	38
Table XIV Observed and calculated $F_2$ genotypic ratios as determined by the $F_3$ segregation for characters inherited independently in Arlington Awmless x Atrada, C. I. 5638	38
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 Awmless x Atrada, C. I. 5638	40
Table XVI Observed and calculated $F_2$ phenotypic ratios for long versus short awns and lax versus dense spikes in Arlington Awmless x Atrada, C. I. 5638	41

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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)<sup>1/</sup>. 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 aaauvv, short awns. Density of

<sup>1/</sup> 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,<sup>2/</sup> an awnless variety. All were six-rowed barleys. The two awn factors for which segregation was observed were designated Lk and Lk<sub>1</sub> 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<sub>1</sub> in the dominant condition were "awnletted"; and those recessive for both factor pairs were awnless. The "awnletted" type had awns on the central spikelets

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<sup>2/</sup> 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 ( $Mn$ ) 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, Colseess IV, Colseess 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  $33.58 \pm 1.20$  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 ( $X_c x_c$ ), and green versus chlorina seedlings ( $F_c f_c$ ). 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 Colseess 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  $22.58 \pm 0.82$  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  $Bl_1Bl_1Bl_1Bl_1$  and that the white parent has either  $Bl_1Bl_1bl_1bl_1$  or  $bl_1bl_1Bl_1Bl_1$ . The factor pair  $Bl_1bl_1$  was found to be linked with hooded versus awned with  $24.72 \pm 1.73$  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  $Bl_1bl_1$  was found to be linked with hulled versus naked ( $Nn$ ) with  $9.88 \pm 0.44$  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:

<u>Linkage Group:</u>	<u>Character Pair</u>	<u>Symbol</u>
I	Long versus short awns	Lklk
	Normal versus reduced lateral spikelet appendages	Lrlr
	Dense versus lax spikes	Ll
	Dense versus lax spikes	L <sub>4</sub> <sup>1</sup> <sub>4</sub>
III	Dense versus lax spikes	Ll
	Dense versus lax spikes	L <sub>1</sub> <sup>1</sup> <sub>1</sub>
	Dense versus lax spikes	L <sub>a</sub> <sup>1</sup> <sub>a</sub>
	Dense versus lax spikes	L <sub>2</sub> <sup>1</sup> <sub>2</sub>
	Long versus short awns	Lklk
IV	Dense versus lax spikes	Ll
	Blue versus white aleurone	Blbl

## MATERIALS AND METHODS

### Description of Parents and Characters Studied

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

Arlington Awless is characterized by a decumbent type of growth in the seedling stage, blue aleurone, lax spikes, occasional awn points on usually awless 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 Awless 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 Awmless 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 Awmless x Atrada, C. I. 5641

Long versus short awns

Normal versus reduced lateral awns

Spring versus winter habit

Arlington Awmless 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<sub>3</sub> 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<sub>2</sub> plant. The seed planted in 1942 was from the F<sub>2</sub> heads not used for seeding in 1941. The seed from each F<sub>2</sub> plant was space planted in an eighteen-foot row which gave an F<sub>3</sub> family. The F<sub>3</sub> families were pulled just before ripening and were stored for classification.

The F<sub>2</sub> and F<sub>3</sub> generations were seeded in the spring. Both spring and winter segregates headed and matured when seeded in the spring.

#### Methods of Classification

The F<sub>1</sub> plants of each cross were classified for the characters being studied. A description of the F<sub>1</sub> type in each cross follows:

Arlington Awless 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 Awless 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<sub>2</sub> generation plants was made on the basis of their phenotypes; this classification was corrected and the F<sub>2</sub> genotypes were determined by checking the breeding behavior of each F<sub>2</sub> plant in the F<sub>3</sub> 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<sub>1</sub> 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<sub>2</sub> and F<sub>3</sub> segregation, the segregates were divided into six phenotypic awn classes as described below:

<u>Class No.</u>	<u>Description</u>	<u>Lateral Awns</u>	<u>Central Awns</u>
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 <sub>1</sub> 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:

Long versus short awns  
Normal versus reduced lateral awns  
Blue versus white aleurone color  
Spring versus winter habit  
Lax versus dense spikes

#### Symbols Used:

Lk<sub>4</sub>lk<sub>4</sub>, Lk<sub>5</sub>lk<sub>5</sub>  
Lr<sub>1</sub>lr<sub>1</sub>  
Bl<sub>2</sub>bl<sub>2</sub>  
Ee  
L<sub>6</sub>l<sub>6</sub>

#### Analysis of Data

All phenotypic ratios observed in the F<sub>2</sub> generation and all genotypic ratios as determined by the F<sub>3</sub> 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.

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## 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										Mean S.E.
	1	2	3	4	5	6	7	8	9	10	
<u>Length of lateral awn points in millimeters</u>											
1	0	0	0	15	0	0	0	0	0	0	0
2	0	0	0	5	0	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	
<u>Length of central awns in millimeters</u>											
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<sub>2</sub> phenotypic ratios for awn types in Arlington Awnless x Atrada, C. I. 5641

Item	Number of indicated phenotype						Totals	X <sup>2</sup>	P
	Fully awned (6)	F <sub>1</sub> type (5)	Atrada type (4)	Reduced Atrada type (3)	Arlington Awnless type (2)	Awnless (1)			
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<sub>2</sub> genotypic ratio as determined by the F<sub>3</sub> 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<sub>2</sub> genotypic ratios for awnedness as determined by the F<sub>3</sub> 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	$\chi^2$	P value
Lr <sub>1</sub> Lr <sub>1</sub> Lk <sub>5</sub> Lk <sub>5</sub>	6	6	6.0625		
Lr <sub>1</sub> Lr <sub>1</sub> Lk <sub>5</sub> lk <sub>5</sub>	6	13	12.1250		
Lr <sub>1</sub> lr <sub>1</sub> Lk <sub>5</sub> Lk <sub>5</sub>	5	11	12.1250		
Lr <sub>1</sub> lr <sub>1</sub> Lk <sub>5</sub> lk <sub>5</sub>	5	31	24.2500		
Lr <sub>1</sub> Lr <sub>1</sub> lk <sub>5</sub> lk <sub>5</sub>	4	5	6.0625		
Lr <sub>1</sub> lr <sub>1</sub> lk <sub>5</sub> lk <sub>5</sub>	3	13	12.1250		
lr <sub>1</sub> lr <sub>1</sub> Lk <sub>5</sub> Lk <sub>5</sub>	2	7	6.0625		
lr <sub>1</sub> lr <sub>1</sub> Lk <sub>5</sub> lk <sub>5</sub>	2	8	12.1250		
lr <sub>1</sub> lr <sub>1</sub> lk <sub>5</sub> lk <sub>5</sub>	1	3	6.0625		
Totals		97	97.0000	5.392	0.71

Arlington Awnless x Atrada, C. I. 5638.— The F<sub>1</sub> 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<sub>2</sub> 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

Item	Number of indicated phenotype					Totals	$\chi^2$	P
	Fully awned (6)	$F_1$ type (5)	Atrada type (4)	Reduced Atrada type (3)	Arlington Awnless type (2)			
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<sub>2</sub> genotypic ratios for awnness as determined by the F<sub>3</sub> segregation in Arlington Awnless x Atrada, C. I. 5638

Genotype	Awn class	Observed counts	Calculated 1:2:2:4:1:2:4 ratio	X <sup>2</sup>	P value
Lr <sub>1</sub> Lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub>	6	3	5.0625		
Lr <sub>1</sub> Lr <sub>1</sub> Lk <sub>4</sub> lk <sub>4</sub>	6	12	10.1250		
Lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub>	5	7	10.1250		
Lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> lk <sub>4</sub>	5	27	20.2500		
Lr <sub>1</sub> Lr <sub>1</sub> lk <sub>4</sub> lk <sub>4</sub>	4	6	5.0625		
Lr <sub>1</sub> lr <sub>1</sub> lk <sub>4</sub> lk <sub>4</sub>	3	9	10.1250		
lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub>	2				
lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> lk <sub>4</sub>	2	17	20.2500		
lr <sub>1</sub> lr <sub>1</sub> lk <sub>4</sub> lk <sub>4</sub>	2				
Totals		81	81.0000	5.193	0.52

An attempt was made to separate the three genotypes, lr<sub>1</sub>lr<sub>1</sub>Lk<sub>4</sub>Lk<sub>4</sub>, lr<sub>1</sub>lr<sub>1</sub>Lk<sub>4</sub>lk<sub>4</sub>, and lr<sub>1</sub>lr<sub>1</sub>lk<sub>4</sub>lk<sub>4</sub>, that were grouped into the phenotypic awn class 2. The central awns of fifteen F<sub>3</sub> families grown from F<sub>2</sub> 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<sub>3</sub> 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<sub>3</sub> families grown from fifteen F<sub>2</sub> 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 awnness 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<sup>3/</sup>. 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,  $Lr_1Lr_1Lk_4Lk_4lk_5lk_5$ , 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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<sup>3/</sup> 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<sub>2</sub> generation segregates in Arlington Awnless x Atrada, C. I. 5641, and Arlington Awnless x Atrada, C. I. 5638

Genotypic ratio	F <sub>2</sub> genotype	Numerical awn class	Phenotypic ratio	Segregation observed in the F <sub>3</sub> generation
Arlington Awnless x Atrada, C. I. 5641				
1	Lr <sub>1</sub> Lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	6	3	True breeding.
2	Lr <sub>1</sub> Lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> Lk <sub>5</sub> lk <sub>5</sub>	6		Segregating for classes 4 and 6.
2	Lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	5	6	Segregating for classes 2,5 and 6.
4	Lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> Lk <sub>5</sub> lk <sub>5</sub>	5		Segregating for all classes, 1 to 6.
1	Lr <sub>1</sub> Lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> lk <sub>5</sub> lk <sub>5</sub>	4	1	True breeding (Atrada type)
2	Lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> lk <sub>5</sub> lk <sub>5</sub>	3	2	Segregating for classes 1,3, and 4.
1	lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	2	3	True breeding (Arlington Awnless type).
2	lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> Lk <sub>5</sub> lk <sub>5</sub>	2		Segregating for classes 1 and 2.
1	lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> lk <sub>5</sub> lk <sub>5</sub>	1	1	True breeding.
Arlington Awnless x Atrada, C. I. 5638				
1	Lr <sub>1</sub> Lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	6	3	True breeding.
2	Lr <sub>1</sub> Lr <sub>1</sub> Lk <sub>4</sub> lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	6		Segregating for classes 4 and 6.
2	Lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	5	6	Segregating for classes 2,5, and 6.
4	Lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	5		Segregating for classes 2 to 6.
1	Lr <sub>1</sub> Lr <sub>1</sub> lk <sub>4</sub> lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	4	1	True breeding (Atrada type).
2	Lr <sub>1</sub> lr <sub>1</sub> lk <sub>4</sub> lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	3	2	Segregating for classes 2,3, and 4.
	lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> Lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	2	4	True breeding (Arlington Awnless type).
4	lr <sub>1</sub> lr <sub>1</sub> Lk <sub>4</sub> lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	2		Apparently true breeding.
	lr <sub>1</sub> lr <sub>1</sub> lk <sub>4</sub> lk <sub>4</sub> Lk <sub>5</sub> Lk <sub>5</sub>	2		True breeding.

the progeny of Arlington Awmless 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 awms was partially dominant over reduced since the segregates carrying  $Lr_1lr_1$  in the heterozygous condition were less awmed 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 awms with long awms partially dominant over short. The central awms in class 2 were short, in class 5, intermediate, and in class 6, long.

In each of the factor pairs affecting awm 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 Awmless 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<sub>2</sub> plants was observed in the F<sub>3</sub> generation. The observed and calculated F<sub>2</sub> genotypic ratios as determined by the F<sub>3</sub> 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<sub>2</sub> genotypic ratios for blue versus white aleurone as determined by the F<sub>3</sub> segregation of Arlington Awless x Atrada, C.I. 5638

	Number of indicated genotype			Totals	X <sup>2</sup>	P
	Bl <sub>2</sub> Bl <sub>2</sub>	Bl <sub>2</sub> bl <sub>2</sub>	bl <sub>2</sub> bl <sub>2</sub>			
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 Awless x Atrada, C. I. 5641

The plants of the F<sub>1</sub> generation made an erect type of growth, indicating that spring habit of growth was dominant over winter.

The F<sub>2</sub> phenotypic and genotypic ratios as determined by the F<sub>3</sub> 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/		Totals	$\chi^2$	P
	Spring	Winter			
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<sub>2</sub> 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<sub>2</sub> genotypic ratios for spring versus winter growth habit as determined by the F<sub>3</sub> 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 <sup>2</sup>	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<sub>1</sub> plants were lax, indicating that lax was dominant over dense.

The observed and calculated F<sub>2</sub> phenotypic ratios are presented in table XI. Of the 81 F<sub>2</sub> plants grown, 65 were classified as lax and 16 as dense. When this observed ratio was compared with a calculated 3:1





































