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APPARENT INSTABILITY IN
TITAN BARLEY


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N. F. Putnam

INTRODUCTION

There has long been a need for a variety of feed barley which is more suited to the conditions of western Canada, and particularly of Alberta, and which might partially or wholly replace those varieties now being grown. The breeding of smooth-awned barley has received considerable attention in the past few years. The advantages of a variety of this type are obvious and have been pointed out by Harlan (5) and Hayes and Wilcox (10). It is important that other desirable characteristics be associated with that of smooth awn. Resistance to disease, particularly loose and covered smut which are prevalent under Alberta conditions, is an important factor. Because of the favorable moisture and soil conditions of the barley-producing areas of Alberta, strength of straw is also important. Other factors such as high yield, early maturity, and hardiness, must be given equal consideration in selecting a new variety of barley.

During the past fifteen years, work on barley breeding

at the University of Alberta has been directed toward the production of a more suitable smooth-awned feed barley. In 1943 Titan, a new variety developed here, was registered for distribution. It has many of the desired characteristics mentioned. It has, however, shown considerable variability, particularly with respect to barbing of the awn. The present investigation was undertaken to study the apparent instability and to ascertain as closely as possible its nature.

Variability of seed color was also noted. Seeds with blue aleurone and some with black lemma and palea were found in the foundation stock Titan produced at the University farm in 1944. These off-type characteristics also came under investigation.

This investigation is not primarily concerned with a genetic study of the inheritance of factors in barley, but rather it tries to explain the origin and nature of the off-type segregates in Titan in the light of genetic investigations already carried out by many workers.

Four possible sources of contamination were considered in attempting to explain the origin of the segregates in the foundation stock of Titan grown in 1944:

1. The foundation stock was heterozygous for the characters concerned;
2. Natural crossing took place;
3. Mutations occurred;
4. Mixtures were present.

Any one or all of these possibilities could be responsible for the apparent instability in Titan.

PARENT MATERIAL

In approaching the problem and planning the investigation, consideration was first given to the parentage, selection, and handling of Titan.

Titan is a smooth-awned feed barley developed at the University of Alberta. It has a strong straw and does not "neck-over" when ripe. It is highly resistant to loose smut. Also, considering that it is fairly early-maturing and gives good yields, this variety shows promise as a crop for Alberta.

Titan is a selection from a cross between Trebi and Glabron, made at the University of Alberta in 1929 by Johnston (11). His original investigation was a study of the inheritance of smooth awn and disease reaction in barley. Trebi and Glabron have been described by Johnston (11). Trebi is a selection from a variety imported from the Black Sea region. Glabron is a selection from a double cross (Lion x Manchuria)Manchuria. Glabron is not pure as to color, containing both white and blue strains (6). Harlan and Martini (6) have given brief descriptions of all the varieties involved in the parentage of Titan. These descriptions are included here as a background for the discussion of inheritance of characters in Titan.

Trebi is a barley of exceptional vigor. It is one of the highest-yielding varieties now grown in Alberta. It is six-rowed and rough-awned and has large blue kernels. It is entirely unsatisfactory as a malting barley in Canada.

A barley from the south side of the Black Sea was secured by the United States Department of Agriculture in 1905. It was grown in cooperation with the Minnesota Agricultural Experiment Station. A number of distinct types were isolated and tested, and from these Trebi was selected. It was released in 1918.

Glabron is one of the more important smooth-awned barleys. It has a very strong straw, yields well, and is resistant to smut, spot blotch, and root-rot.

Glabron was distributed from the Minnesota Agricultural Experiment Station in 1929. In the early development of smooth-awned barleys Lion was crossed with Manchuria. A smooth-awned segregate from this cross was used to cross again with Manchuria. From the second cross, Glabron was isolated.

Lion has been widely used as a parent in hybrids. It is smooth-awned, black, six-rowed, and of fair yielding ability. Its main contribution is a smooth awn which is highly stable for smoothness.

In 1911 the United States Department of Agriculture received a black, six-rowed barley from Taganrog, Russia. Both smooth- and rough-awn types were present in the material. H. V. Harlan made a number of selections, one of which (Lion)

was used in crosses. Lion is of little commercial value.

Manchuria is a vigorous, six-rowed, rough-awned, early barley. The first importations of Manchuria were made in 1861 from Germany. This barley contained a large number of strains, some with blue aleurone layer and some with white.

Johnston (11) made numerous reciprocal crosses between Glabron and Trebi and, in the subsequent generations, selections of smooth-awned segregates were made for disease resistance, strength of straw, and maturity. H-29-8, one of these selections, proved superior and was introduced into the standard comparative test at the University of Alberta in 1935. It was subsequently tested at several stations in western Canada and was accepted for registration in 1943 under the name "Titan".

From an examination of Johnston's original data, it is seen that H-29-8 was intermediate-smooth-awned in the F_2 , but in the F_3 and F_4 intermediate-smooth and smooth awns appeared. The F_4 seed was bulked and grown in an increase plot in 1934. The first record of H-29-8 in the rod-row trials at the University did not give the source of seed but it apparently came from the F_4 bulked seed grown in the increase plot in 1934. The original results are summarized in Table I.

The seed of H-29-8 was increased from year to year in the rod-row tests and in 1941 several strains were given to Mr. J. W. Hopkins, Field Superintendent, Department of Plant Science. It was from this seed, grown as foundation stock in

TABLE I

A summary of the early history of Titan
from "Barley Genetic Studies",
University of Alberta,
1931 - 1934

Selection	Generation	Year	Row number	Awn character	Remarks
H-29-8	F ₁	1930	49-1	Rough	
"	F ₂	1931	45-137	Intermediate-rough	
"	F ₃	1932	1530-5	33 int.-rough 11 smooth	Promising
"	F ₄	1933	328		Harvest row Bulked selections for increase plot
"	F ₅	1934	14		Harvest row

1944, that the off-type material was rogued.

Counts on plots of Titan showed about ten plants per ten thousand with rough awns. This agrees with the field inspection reports made on registered Titan in 1944 by Mr. L. B. Goodall of the Plant Products Division, Dominion Department of Agriculture.

MATERIAL AND METHODS

The off-type heads of Titan used in this investigation were obtained from the foundation stock seed grown at the University of Alberta in 1944. The material was carefully rogued for all off-type agronomic characteristics such as rough and intermediate-rough awns, height of plant, and "nodding" habit. These off-types were grouped into three classes: (a) rough awn; (b) intermediate-rough awn; and (c) smooth awn. Each head was classified by passing the awns between the fingers to determine the degree of barbing.

The awn index system of classification was used on a small population grown in the greenhouse. Figure 1 shows the degree of barbing in each of the awn classes. The awn index used in classifying the segregates was that established by Robertson, Deming and Koonce (16).

The seeds with blue aleurone and those with black lemma and palea used in this study were obtained from the foundation stock seed during the cleaning process. These off-types were grown in the greenhouse during the winter of 1944-45 and a second generation was grown in head rows in the field the following summer.

Titan seed from four different sources was also grown in comparative plots:

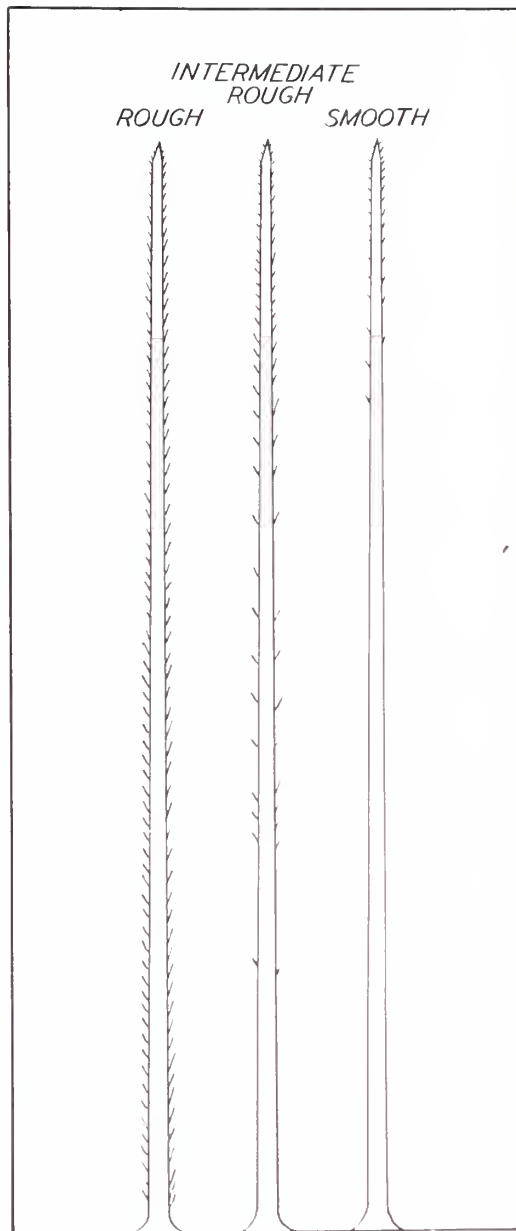


Figure 1

Diagrammatic representation of an average awn of each of the three classes, rough, intermediate-rough, and smooth, used in the classification of the off-types of Titan

1. Foundation stock seed produced in 1942#.
2. Foundation stock seed produced in 1943#.
3. 1944 foundation stock seed which had been rogued#.
4. Foundation stock seed produced in 1944, un-rogued (obtained from border rows).

The border rows around the barley plots in 1944 were grown from foundation stock Titan seed. Since these rows had not been rogued they were harvested and used as a source of seed to obtain some information on the percentage of off-type segregates in the foundation stock.

The author inspected a field of registered Titan grown by Mr. J. L. Squance, Sunnybrook, Alberta, in the summer of 1945. The crop was grown from seed produced in 1944. The original sample had been secured from the University. The crop had not been rogued and several rough and intermediate-rough awn segregates were collected for investigation.

During the winter of 1944-45 some material was sown in the greenhouse. Owing to a failure in the heating system a severe frost occurred just as the barley heads were in the boot. Only a few plants set seed. The mature heads were harvested and the seed sown in head rows in the field the following summer.

Supplied by J. W. Hopkins, Field Superintendent.

All the crossing was done during the summer of 1945 and the F_1 was grown in the greenhouse during the present winter.

The seed of Lion was obtained from the 1940 Barley Cereal Garden. Newal was obtained from the barley seed plots, and is the equivalent of foundation stock seed.

The designations F_1 and F_2 are generally limited to the first and second generations following a cross of two parental types. In this paper, however, the terms have been used in a different sense. The off-type plants selected from Titan for the investigation were considered as parents. F_1 and F_2 are the first and second generations of these parent plants.

INHERITANCE OF CHARACTERS

Barbing of Awns

Literature Review

Extensive studies have been conducted on the inheritance of the rough- and smooth-awn character in barley. In one of the earliest studies recorded, Harlan (5) found rough awn to be dominant and a single factor involved.

Hayes et al, as reported by Johnston (11), found the F_1 generation of a cross between Lion and Manchuria to be rough-

awned, while the F_2 segregated giving three rough-awned plants to one smooth. By using an awn index, found by dividing the total length of the awn by the barbed portion, they were able to segregate varying degrees of smoothness. From their results they conclude that, in addition to a single-factor difference for rough and smooth awn, modifying factors influence the degree of smoothness.

Griffiee (4), investigating a cross, Svanhals x Lion, found all the F_1 plants to be as rough as Svanhals. The F_2 plants were classified into two groups: (a) awn fully barbed, and (b) awns partially or wholly smooth. Using the awn index of Hayes et al, Griffiee was able to group the segregates into three classes; the distribution suggested a two-factor difference. He suggests that a factor, R, when present, gives rough awns; and a second factor, S, which is hypostatic to R produces intermediate-smooth awns in the absence of R. Smooth-awned plants would carry the double recessive $rrss$.

In two crosses, Bearer x Lion and Chinese x Lion, Sigfusson (17) obtained results similar to those of Griffiee (4). He, however, classified the segregating lines into four distinct groups: rough, intermediate-rough, intermediate-smooth, and smooth awned, and suggested that R and S are cumulative in effect but that R is the main factor and produces a greater effect than does S. He obtained a close approximation to the 9:3:3:1 ratio.

Robertson, Deming, and Koonce (16), studying the F_2

segregation of a cross between Coast and Lion, were able to divide the population into three groups: rough, intermediate-rough, and smooth awned, in approximately a 12:3:1 ratio. This agrees with the results of Griffee (4). The awn index used by Robertson, Deming, and Koonce (16), for each group, was as follows:

Rough	1.0
Intermediate-rough	1.1 to 2.7
Smooth	2.7 and higher.

Wexelson (20) also reported a single-factor difference between rough and smooth awn but found variability in the degree of smoothness, and suggests that there may be a second factor giving intermediate types. Daane (3) reports a single-factor pair for inheritance of rough and smooth awns.

Other workers, however, have not been in complete agreement with the two-factor hypothesis. Vavilov, as reported by Hayes and Garber (8) and Johnston (11), made numerous crosses and obtained more complicated ratios in the segregating generations. He obtained smooth-awned types in the F_2 and F_3 in crosses between two rough-awned parents. He suggests a multiple-factor difference. Hayes and Garber (8) suggest that his results showed a varietal difference in awn inheritance in barley. Johnston (11) was not able to distribute the F_2 of reciprocal crosses Trebi x Glabron into three phenotypes in a 12:3:1 ratio, although he obtained a very good fit to the 12:3:1 ratio in the F_2 of reciprocal crosses Trebi x Velvet. In reviewing Johnston's original data a few instances were noted

where smooth-awned F_2 plants of the Trebi x Glabron cross did not breed true in the F_3 but segregated into intermediate-smooth and smooth awn types. These results would suggest that there is a varietal difference in the inheritance of characters and that more than two factors are involved in the inheritance of barbing of the awn in the Trebi x Glabron cross; or at least that the results cannot be explained by the two-factor hypothesis of Griffée (4).

Johnston (11) also reports that David, working with a similar cross, Trebi x Glabron, arrived at different conclusions from most of the other workers. The distribution of the F_3 of the cross could not be explained by the two-factor difference of Griffée (4). David suggested that there was a factor, A, for smooth awns and a second factor, I, inhibiting smooth awns. The smooth-awned variety had the constitution AAii and the rough-awned, aaII.

Methods and Experimental Results

The off-type segregates rogued from the foundation stock Titan in 1944 were grouped according to awn type. Three groups were established: rough, intermediate-rough, and smooth. The degree of barbing of the awn was determined simply by passing the awn between the fingers. The rough-awned group had barbs the total length of the awn. The smooth-awned heads had awns as smooth as Titan. Some of the seeds of each group were

sown in the greenhouse in 1944-45. As already mentioned, however, a mechanical failure in the heating system resulted in a severe frost just when the plants were in the shot blade. Only a few heads matured, with the result that no counts were made. Some heads were salvaged and the seed planted in head rows in the field in the summer of 1945. Table II gives a summary of the number of heads and the awn character of the F_1 from the greenhouse test. —

TABLE II

Total number of heads and awn character
of F_1 generation from greenhouse
studies, 1944 - 1945

Awn type of parent	Awn type of F_1 generation			Total number of heads
	Rough	Intermediate- rough	Smooth	
Rough	8	4	1	13
Intermediate-rough	8	7	1	16
Smooth	1	3	4	8

The most important feature noted from the study of the results in Table II is the segregation of the smooth-awned parent. If we consider smooth awn to be homozygous for the double recessive $rrss$, as suggested by Griffée (4) and Sigfusson (17), then the F_1 progeny should all be smooth-awned. This is not the case, however, and the segregation into smooth

and non-smooth fits a 1:1 ratio. Since the number of plants is not large, we cannot draw any conclusions as to what the genotype of the parent is, but since there is an occurrence of intermediate-rough and rough awn segregates, we can say that it is not homozygous for the smooth awn character. The intermediate-rough and rough awned parents exhibit a heterozygous condition for barbing of the awns. As before, the population is not large enough to draw any conclusions.

Continuing the investigation further, the F_1 phenotypes within each parental group were sown in head rows during the summer of 1945 and the awn character studied in the F_2 . The results are given in Table III.

From this table it will be seen that all smooth-awned-selections breed true. Again counts are too small to establish any accurate phenotypic ratios and, in fact, from the results shown, no consistent ratios of any kind can be established. All of the rough-awned and intermediate-rough-awned phenotypes in the F_1 were heterozygous and segregated in the F_2 .

Because of the apparent heterozygous nature of the inheritance of barbing of the awn it was assumed that other agronomic characters of the segregates might show variability. During the summer of 1945 a plot of rough awn selections from Titan was grown in a comparative trial with a pure strain of Titan. These plots were about 10 feet long and included about 20 rows in each of two plots. The rough-awned selection

TABLE III

Behavior of F_1 phenotypes, of smooth, intermediate-rough, and rough awn parents, when grown in head rows in the F_2

Parent awn type	Number of F_1 plants	Awn type F_1	F_2 generation		
			Rough	Intermediate-rough	Smooth
Rough	1	Smooth	0	0	5
	4	Interme- diate	19	0	9
	8	Rough	78	0	3
Intermediate- rough	1	Smooth	0	0	3
	7	Interme- diate	0	9	24
	8	Rough	14	9	5
Smooth	4	Smooth	0	0	26
	3	Interme- diate	0	2	17
	1	Rough	0	3	5

showed variability with respect to barbing of awn, height of plant, days to maturity, and strength of straw. On the average, the rough-awned selections were about six inches taller than Titan and five days later in maturing. Many of the rough-awned plant selections tended to "neck-over". This was particularly true of the taller segregates. Figure 2 shows a few of the selections made from the rough-awned plot compared with Titan.

The rough-awned selections segregated into several groups in the F_1 . The segregates could be readily classified



Figure 2

Off-type selections of Titan barley compared
with pure Titan

- A. Tall rough-awned selection
- B. Short rough-awned selection
- C. Titan
- D. Tall intermediate-rough-awned selection
- E. Tall smooth-awned selection

into tall rough, tall intermediate-rough, and tall smooth awn; short rough, short intermediate-rough, and short smooth. The tall plants averaged thirty-six to thirty-eight inches in height and the short ones were about thirty inches high. The average height of Titan was thirty inches.

The results demonstrate the extreme heterozygous nature of the rough-awned plant selections, not only for barbing of the awn but for other agronomic characteristics as well.

A series of crosses was made during 1945 to test the heterozygous nature of the awn inheritance of the segregates of Titan. Each of the segregates, rough awn, intermediate-rough awn, and smooth awn, was crossed with a pure strain of Titan and with Newal, another smooth-awned feed barley. These crosses were grown in the greenhouse during 1945-46 and the F_1 progeny was studied. Tables IV and V give the results obtained.

TABLE IV

Number of rough, intermediate-rough, and smooth awned F_1 progeny from crosses between Titan and each of the three groups of segregates

Cross	Number of crosses	F_1 generation		
		Rough	Intermediate-rough	Smooth
Titan x smooth-awned selection	10	0	1	27
Titan x intermediate-rough-awned selection	2	0	5	5
Titan x rough-awned selection	4	11	1	0

No ratios can be established in the F_1 population, but we can immediately see from the table that the parent smooth-awned selection must be heterozygous since an intermediate-rough-awned plant was obtained in the first generation. By similar deductions we can say that the rough-awned parent was not homozygous for rough awn, since there appears an intermediate type in the F_1 of the cross. These interpretations are made with the assumption that the pure strain of Titan used as the parent is homozygous for smooth awn. Since no evidence to the contrary could be found in any of the Titan, it is fairly safe to say that the Titan used in the cross is homozygous.

Table V gives the results of crosses made between off-type selections of Titan and Newal.

TABLE V

Number of rough-, intermediate-rough-, and smooth-awned F_1 progeny from crosses between Newal and each of the three groups of segregates

Cross	Number of crosses	F_1 generation		
		Rough	Intermediate-rough	Smooth
Newal x smooth-awned selection	4	0	0	16
Newal x intermediate-rough-awned selection	5	3	3	2
Newal x rough-awned selection	6	24	0	0

The crosses Newal x smooth-awned selection and Newal x rough-awned selection give an expected F_1 progeny, considering the parents to be homozygous for the awn characters with rough awn dominant.

Because there were rough-awned segregates in the F_1 progeny of the cross Newal x intermediate-rough-awned selection, the results cannot be explained by the two-factor theory proposed by Griffée (4), Sigfusson (17), and others (11, 15, 16).

A number of heads were taken from the rough, intermediate-rough, and smooth awn selections and the awn indices calculated. The seeds were grown in the greenhouse during the winter of 1945-46, and the progeny were grouped into rough, intermediate-rough, and smooth awn types by the awn index. The results are given in Table VI.

TABLE VI

Segregation in F_1 of rough-, intermediate-rough- and smooth-awned parental lines using the awn index as a basis of classification

Parent type	Awn index	No. of plants	F_1 generation		
			Rough	Intermediate-rough	Smooth
Rough	1.0	26	26	0	0
Intermediate-rough	1.1 - 2.6	14	4	7	3
Smooth	2.7 & up	40	1	1	38

All rough-awned parent selections appear to be homozygous for the rough-awned character. The intermediate-rough- and smooth-awned parents, however, segregate in the F_1 into phenotypes which again cannot be explained by the two-factor theory. The smooth-awned parental selections exhibit a heterozygous condition when the F_1 progeny is examined.

Inheritance of Color of Lemma and Palea

Literature Review

In crosses between varieties with black lemma and palea and varieties with white lemma and palea, most workers have found a single-factor difference for inheritance of color, black being dominant. Biffin (1) was one of the first workers to report a single-factor difference.

Robertson (15) used two white-hulled varieties, Colsess and Trebi, and two black-hulled varieties, Hordeum distichon nigrinudum and Minnesota 90-5 as parents in the following crosses: Colsess x Hordeum distichon nigrinudum; Colsess x Minnesota 90-5; and Trebi x Minnesota 90-5. He found a single-factor pair for inheritance of color of lemma and palea. The F_1 in all the crosses was black, indicating dominance. The F_2 segregated in the ratio three black to one white.

Powers (13) used a black-hulled variety, Brachytic,

to cross with white-hulled B_1 . He found a single-factor pair, Bb, responsible for inheritance of color.

Sigfusson (17) crossed Bearer with Lion and Chinese with Lion. All the F_1 were as black as the Lion parent. The F_2 segregated into three black and one white. All the white F_2 plants bred true. The black segregated in the F_3 , giving one homozygous black and two heterozygous black. Thus the phenotypes of the F_2 were 1 BB: 2 Bb: 1 bb. This ratio satisfies the single-factor hypothesis for inheritance of color.

Buckley (2), Daane (3), Hayes and Garber (8), and Robertson (14) also report a single-factor pair for inheritance of color of the lemma and palea.

Methods and Results

A number of seeds having black lemma and palea were found in the Titan foundation stock. These seeds were culled from the 1944 foundation stock during the cleaning operation.

These black-hulled seeds were grown in the greenhouse the following winter. The F_1 plants all had black lemma and palea. The heads of the F_1 plants were harvested and seeded in head rows in the field during 1945. Here again only plants having black-hulled seeds appeared. This would indicate that the black-hulled off-types were homozygous for the character and would be of the genotype BB, according to Robertson (14, 16), Sigfusson (17), and others (1, 2, 3).

Crosses were made between the F_2 black-hulled plants and a pure strain of Titan, using Titan as the female parent. The lemma and palea of all the F_1 plants of the cross were as black as the male parent. This would also indicate that the black-hulled parent was homozygous for the character, while Titan carried the homozygous recessive bb . Within the limitations of the investigation the results agree with those of other workers already mentioned. A study of the F_2 phenotypes of the cross between Titan and the black selection is necessary however, to prove these conclusions.

The black-hulled strain might have come from a mixture. Lion was grown in a test plot with the black selections in order to compare the two varieties and to see if they had any other similar agronomic features besides the black lemma and palea. The black selections differed from Lion in several respects including the length of rachilla hairs, a character which is used in classifying barley varieties (9). This precludes the possibility that the black-hulled seeds were from Lion. No other black-hulled varieties could have caused a mixture.

Inheritance of Aleurone Color

Literature Review

There has been little work published on the inheri-

tance of aleurone color.

Kuckuck, as reported by Buckley (2) found a single-factor pair for the inheritance of blue aleurone color. He suggests that the intensity of the blue aleurone color is affected by environmental conditions.

Buckley (2) crossed a variety with blue aleurone and one with white aleurone. He found all the F_1 plants to have blue aleurone. The F_2 segregated giving three blue and one white aleurone. He found difficulty in segregating the phenotypes in the F_3 , and makes this comment, "However, environmental conditions make it difficult to separate the homozygous blues from the heads which are segregating". By grouping the plants having homozygous and segregating blue aleurone seeds, he obtained a close fit to the expected 5:3 ratio in the F_3 , indicating a two-factor difference, blue aleurone color being dominant.

Robertson, Deming, and Koonce (16) studied aleurone color inheritance. They used Colsess (blue aleurone) and Minnesota 72-8 (white aleurone) as parents. All the F_1 seeds had blue aleurone. The F_2 gave a close fit to the expected three blue to one white ratio, indicating a single-factor difference.

Hayes and Immer (9) and Robertson (14) also list a single-factor difference for inheritance of blue aleurone color.

Myler and Stanford (12) crossed three varieties, Algerian, Kwan, and Awnless, each having blue aleurone with

Nepal, a white variety. Their results agree with those of Buckley (2) that aleurone color inheritance is controlled by a single-factor difference. In a cross between two white aleurone varieties, Nepal and Goldfoil, however, the F_2 segregated, giving nine plants with blue aleurone seeds and seven non-blue. They suggest two complementary factors for the inheritance of blue aleurone color, $B1\ b1$ and $B1_1\ b1_1$.

According to Myler and Stanford, Algerian, Kwan, and Awnless would have the genotypic constitution $B1B1B1_1B1_1$; Goldfoil would have $blblB1_1B1_1$; and Nepal, $B1B1bl_1bl_1$. They found these factors to be in different linkage groups.

Methods and Results

The aleurone layer of Titan is not white, but is rather a dull bluish-grey color. This color seems to be stable in the pure strains. Several seeds found in the 1944 foundation stock Titan had an intense blue aleurone color which showed up very prominently.

These off-types were grown in the field in 1945 to try to learn something of the inheritance of the aleurone color. The blue aleurone color did not appear to be stable. None of the F_1 seeds showed the deep blue color, and appeared to be more like Titan than the parent with respect to aleurone color. Environmental conditions may have influenced the intensity of the aleurone color in the foundation stock, giving rise to the

off-types. It could similarly be argued that the aleurone color of the F_1 plants grown from the parent selections may have been influenced by the abnormal environmental conditions in 1945 when moisture was very limited.

Environmental conditions may not have been altogether responsible. Manchuria showed variability of aleurone color. Glabron also showed variability with both blue aleurone and white aleurone strains appearing. Some genetic factor or factors, of which nothing is understood yet, may have been responsible for this variability both in Manchuria and Glabron, and may have been transmitted to Titan from the Glabron parent. Further study on inheritance of blue aleurone is necessary before any definite conclusions can be reached.

DISCUSSION

Titan barley has many agronomic characteristics which will ensure its popularity in many of the barley-producing areas of western Canada. Already the demand for this new barley has far exceeded the supply and the University, in cooperation with Alberta seed growers, has pursued a program to increase the present supply of seed as rapidly as possible for distribution to the farmers. Before any new variety of crop can be registered and distributed for seed purposes, it must meet the rigid requirements of the Canadian Seed Growers'

Association and pass careful inspection. The high frequency of off-type segregates in the Titan grown in 1944 caused some alarm and steps were taken to ensure a purer strain. The 1944 crop of Titan was carefully rogued for all off-type segregates to ensure as nearly as possible homozygous seed. This was done not only to meet the standards of purity of the Canadian Seed Growers' Association, but also to maintain the good reputation of the University.

The source of the segregates was questioned. If they were the result of mixtures, then, by careful roguing, they could be eliminated. If the Titan seed was heterozygous for the characters in question, however, then these off-types might reoccur in subsequent generations and reselection for purity would be necessary. If the off-type characters were controlled by a single-factor pair, then selection for the desired type is quite simple; but if the inheritance concerns several factors, then selection for purity becomes complicated.

In following the history of Titan (H-29-8), some information is gained regarding inheritance of the smooth awn character. As already demonstrated in Table I, the F_2 generation of H-29-8 was heterozygous for the intermediate-rough awn character, and segregation occurred in the F_3 . Selections were again made in the F_3 and the F_4 grown in an increase plot. Presumably this was the source of seed for H-29-8 grown in the rod-row trials in 1935. From the records, the only other seed produced in that season was in the Barley Genetic Study

rows. There is evidence that the original seed used in the rod-row trials was not completely homozygous for smooth awn. Any off-type segregates would be carried over from year to year as no attempt is made to select for purity in the rod-row trials.

The genetic study indicates that the inheritance of smooth awn in a cross between Trebi and Glabron cannot be explained on the two-factor theory of Griffee (4), Sigfusson (17), and others, with the smooth awn plants having the double recessive $rrss$. The smooth-awned segregates, when selfed and also when crossed with other stable smooth-awned varieties, have produced rough- and intermediate-rough-awned progeny. Selections of Titan in this investigation did not breed true even in the second generation, after the F_1 had been reselected.

Considering the other possible sources of the off-types in Titan, as outlined in the introduction, no evidence can be derived from the investigations to support these theories.

A change or mutation may have occurred in one of the genes responsible for barbing of the awn--a change from recessive to a dominant effect, i.e. $rrss \rightarrow Rrss$, or $rrss \rightarrow rrSs$. If such a change took place, the awn would be totally rough or intermediate-rough, and could be readily detected and eliminated and no further segregation would take place.

Natural crossing cannot explain the origin of these off-types. According to Stevenson (18) there is very little

natural crossing in barley--less than 1%. Furthermore, the Titan grown as source of seed was well isolated from any other barley variety, so the only crossing that could take place would be inter-plant crosses. If Titan were homozygous for smooth awn, then the F_1 of such a cross would also be smooth-awned and no off-types would occur in following generations.

No attempt has been made to establish the genetic constitution of these off-type segregates, because of the small population and the limited time in which to grow enough generations to study the segregations. Since the population under investigation was heterozygous and there was nothing known of the number of variable characters, many crosses would have to be made with plants which were homozygous for the characters concerned and of known genetic constitution before attempting to explain the nature of the inheritance of the off-type characteristics. The nature of the inheritance of degree of barbing of the awn in the material studied would seem to be a quantitative character with more than two-factor pairs involved.

The evidence compiled from this investigation suggests that the seed of Titan used in the production of the foundation stock grown in 1944 was not a pure strain and the rough-awned impurities arose as a result of segregation of the heterozygous factors concerned. With rigid selection and care in handling Titan seed, the off-types can be eliminated. This is shown in

a report submitted by Weir (19). In 1944, forty-nine rough-bearded plants were reported in forty-two 10,000 counts on farmers' fields of Titan grown from seed supplied by the University of Alberta. In similar counts made in 1945 on fields of Titan grown from seed which had been carefully rogued for off-types, only one rough-bearded plant was found in twelve counts. This shows that by careful selection the off-type segregates can be eliminated. Because of the apparent complicated method of inheritance of the smooth awn factor, it would be advisable to reselect for purity in at least two or even three generations. It would also be advisable to keep a close check on all seed that has already been distributed to growers and replace this seed as soon as possible with a pure strain.

The black-hulled seed selections were completely stable for the character both in the F_1 and F_2 generations. Therefore, they would carry the homozygous dominant BB for color of lemma and palea, according to the work of Biffen (1) and Buckley (2) and others already mentioned.

Evidence for the homozygous dominant was further demonstrated in crosses between a pure strain of Titan and the black selections. All the F_1 had lemma and palea as black as the black-hulled parent. A further study of the F_2 phenotypes of the cross is necessary to determine definitely the genotype of the black selection parent.

The origin of these black selections is questionable.

At first it was thought that they were mixtures of Lion. However, when grown in the field beside Lion in comparative rows, they show distinct agronomic characteristics. The length of rachilla hairs is a character used in identifying varieties. The black selections have short rachilla hairs and Lion has long ones. The selection is certainly not Lion.

Mutations have been responsible for alteration of gene characters. The possibility of a mutation was not overlooked. The black selection apparently carried the two dominant allelomorphs, BB; and Titan would have the double recessive bb. A mutation may occur in Titan to give a new black selection Bb. It would, however, be highly improbable that mutations would occur simultaneously in the two allelomorphs, bb, of Titan to give BB of the black selection. Thus, if a mutation occurred, a heterozygous genotype would arise which would segregate in the subsequent generations. These heterozygous genotypes would be black and would be easily rogued. The mutation theory is inadequate, then, because all the black-hulled selections bred true for two generations and were homozygous for the black character.

There seems to be no logical explanation of the source of the black-hulled seeds found in Titan. They should not give rise to much concern, however, because such plants can be easily rogued from the crop and the black color, being dominant, shows up in the homozygous or heterozygous genotypes. It might be well to note that the blackening of the lemma and palea, in plants carrying the character, does not occur until

the plant begins to ripen; therefore roguing should be done at that time in order to recognize the black-hulled plants.

The kernels with blue aleurone color, obtained from the seed of Titan barley, were grown only for one generation under abnormal climatic conditions and therefore no definite conclusions can be made regarding the inheritance of this character. The number of seeds with blue aleurone found in the Titan was not large enough to cause particular concern.

Studies by other investigators on the inheritance of aleurone color have been limited, and conflicting results have been reported (2, 12). Because of the limitations of the investigation it is not possible to explain in this paper the inheritance of the blue aleurone color in the segregates.

It is worth repeating that pure strains of Titan have a rather bluish-grey aleurone color which might be described as intermediate between blue and white. This might suggest that inheritance of aleurone color is not a single-factor difference as reported by Buckley (2), but rather is controlled by complementary factors.

The degree of expression of the genetic factor or factors is modified, in the phenotype, by environmental conditions, as is shown by Buckley (2) and Robertson, Deming, and Koonce (16).

Variability of aleurone color is reported in Glabron and Manchuria (6), both varieties giving white and blue strains.

This variability may have been transmitted to Titan through the Glabron parent. If this is true, then blue aleurone strains may reoccur in Titan.

All the seeds with blue aleurone that were grown in this study did not breed true for the color, nor was there any segregation. All the F_1 seeds showed an aleurone color more like that of Titan than like that of the off-type parent. It would be logical to suppose, therefore, that the blue aleurone color of the off-types was a modification due to environmental conditions, and when conditions were changed the color intensity became normal again.

It might also be argued that the color intensity of the F_1 had been influenced by environment and, under more favorable conditions, would have shown the deep blue of the parent segregates. More generations would have to be grown to study the inheritance of aleurone color before any definite conclusion could be reached.

Since this variation in aleurone color has not appeared again in the pure strain of Titan, it may therefore be assumed that variation in aleurone color was due to environmental conditions.

It seems, then, that the original strain of Titan used in the production of foundation stock seed was heterozygous for several characters. The highest incidence of off-type segregates was in the rough awn types. These appeared in

excess of the maximum number allowed for registration by the Canadian Seed Growers' Association. Seeds with black lemma and palea and some with blue aleurone occurred less frequently. By further careful selection of pure strains of Titan, these off-types can be eliminated.

SUMMARY

1. Titan is the name of a new variety of smooth-awned, feed barley developed at the University of Alberta. It is a selection from a cross between Trebi and Glabron.
2. Foundation stock seed of Titan, grown at the University of Alberta in 1944, was unstable for several characters. Degree of barbing of the awn, color of lemma and palea, and color of aleurone, have been studied in this investigation.
3. The rough-awned segregates gave the highest incidence of off-types. In counts made on experimental plots, ten rough-awned plants per ten thousand were found.
4. Inheritance of rough awn in the segregates could not be explained by a two-factor difference. Although the nature of inheritance was not determined, it appeared to be controlled by several quantitative factors.

5. A review of the parentage, selection, and handling of Titan was made. Titan (H-29-8) was selected in the fourth generation of a cross between Trebi and Glabron. At the time the selection was made, Titan apparently was not homozygous for the smooth awn character. The rough- and intermediate-rough-awned off-types found in the 1944 foundation stock Titan are segregates and are not mixtures.

6. The black-hulled type found in the foundation seed of Titan is homozygous for black lemma and palea. Black is dominant and a single-factor pair is responsible for the inheritance of color. The black-hulled type is not Lion.

7. Seeds with blue aleurone were grown for one generation so only limited information can be obtained from the investigation. The blue aleurone color was not stable. None of the seeds of the F_1 plants were blue but appeared to be more like Titan. Environmental conditions may have been responsible for modifying the intensity of aleurone color of the off-types.

8. By reselection in one or more generations, and by careful roguing, it should be possible to get a pure strain of Titan. There is no certainty, however, that the rough-awned off-types will not reoccur.

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REFERENCES

1. BIFFIN, R.H. Hybridization of barleys. Jour. Ag. Sci. 2:183-206. 1907.
2. BUCKLEY, G.F.H. Inheritance in barley with special reference to the color of caryopsis and lemma. Sci. Ag. 10 460-492. 1930.
3. DAANE, A. Linkage relations in barley. Minn. Tech. Bul. 78. 1931.
4. GRIFFEE, F. Correlated inheritance of botanical characters in barley and manner of reaction to Helminthosporium sativum. Ag. Res. Jour. 30:915-935. 1925.
5. HARLAN, H.V. Smooth awn barleys. Jour. Am. Soc. Agron. 12:205-208. 1920.
6. _____ and MARTINI, M.L. Problems and results in barley breeding. U.S.D.A. Yearbook, pp. 303-346. 1936.
7. HAYES, H.K. Breeding improved varieties of smooth-awned barleys. Jour. Hered. 17:370-381. 1926.
8. _____ and GARBER, R.J. Breeding Crop Plants. McGraw-Hill Book Co. Ed. 2. 1927.

9. HAYES, H.K. and IMMER, F.R. Methods of Plant Breeding. McGraw-Hill Book Co. N.Y., 1st Ed., pp. 152-164. 1942.
10. _____ and WILCOX, A.N. The physiological value of smooth-awned barleys. Am. Soc. of Agron. J. 14:113-118. 1922.
11. JOHNSTON, W.H. Inheritance of smooth-awn and disease reaction in barley crosses. M.Sc. Thesis. U. of Alta. 1933.
12. MYLER, J.L. and STANFORD, E.H. Color inheritance in barley. Am. Soc. Agron. J. 34:427-436. 1942.
13. POWERS, LEROY. The nature of the interaction of genes affecting four quantitative characters in a cross between Hordeum deficiens and vulgare. Genetics 21: 398-420. 1936.
14. ROBERTSON, D.W. Summary of linkage studies in barley. Am. Soc. Agron. J. 33:47-64. 1941.
15. _____ Linkage studies in barley. Genetics 14: 1-36. 1929.
16. _____, DEMING, G.W. and KOONCE, D. Inheritance in barley. Jour. Ag. Res. 44:445-466. 1932.
17. SIGFUSSON, S.J. Correlated inheritance of glume color, barbing of awns and length of rachilla hairs in barley. Sci. Ag. 9:662-674. 1929.
18. STEVENSON, F.J. Natural crossing in barley. Jour. Am. Soc. Agron. 20:1193-1196. 1928.
19. WEIR, C.A. Private communication. March, 1946.
20. WEXELSEN, H. Quantitative inheritance and linkage in barley. Hereditas. 18:307-348. 1934.

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