THE INHERITANCE OF AWN-LENGTH IN WHEAT

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THESIS

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Introduction

The object of this work is to make a thorough study of the manner of inheritance of awn-length. This is taken as a typical problem of inheritance to illustrate the principles of genetics and also to furnish a practical problem for the plant breeder.

The material used in this investigation was the first, second, third, and fourth generation hybrids derived from a cross between an awned variety of wheat, Red Turkey, and an awnless variety, Sonora; also, successive generations of each of the parents. Data relating to the inheritance of awn-length in the first, second, and third generations of the above-mentioned cross were taken from the permanent records of the Department of Plant Breeding of the University of Arizona, while data for the fourth generation studies were obtained from the fourth generation plants grown in the plant breeding plots this year.

The problem will be discussed under the following topics:

1. The method used in the studies.
2. Analyses of the data of each generation.
3. A study and review of the literature relating to similar problems of inheritance.
4. A general summary setting forth the results obtained by the investigation, and the application of these results in practical plant breeding.

THE METHOD USED IN THESE STUDIES

In 1916, cross pollination was made between the awnless Sonora wheat as male parent and the awned Red Turkey as a female parent. Thirty-three crosses were obtained in this manner and were planted in the next season (1917). The progenies of these plants compose the first filial generation (F_1). In 1918, the seeds from each of the plants in the(F_1) generation were planted in a separate row, and the whole population formed the second filial generation (F_2) . The third (F_3) and fourth (F_4) generations were planted in the same manner; that is, each plant in a separate row.

The awns were measured as soon as the heads were in full maturity and before they were brittle enough to be broken by the wind, or any other factor. The ordinary scale measure was used and measurements were taken to the nearest millimeter. Measurements were taken from the top of the head to the tip of the awn. All the plants that were as awnless as the Sonora were given the zero mark (O) in the records, and those whose awn-lengths were less than 5 mm. were recorded as having traces of awns (T) and the actual measurements of all the rest were recorded.

The plants in the (F_2) generation had a wide distribution of awn-lengths, ranging from plants as awnless as the Sonora up to plants with awns as long as those of the Red Turkey. For the purpose of simplification, these plants were graded in different classes, each class higher than the preceding one by 10 mm., and each the average mean of all the plants lying within the class. Thus, the (O) and (T) plants formed one class, which was considered xx awnless; the 6-15 mm. formed the next class, whose average value was 10 mm.; and the 16-25 formed another, with average value of 20 mm. and so on.

In the case of the (F_3) generation, all the awnless and traces were studied, and from the other classes a population of 10 rows each.

As some of the rows in a class of the F_3 generation showed a tendency to fluctuate around the mean of that class, a selection of 10 plants showing that tendency was made from each class and planted in the F_4 generation for the purpose of determining whether or not it is possible to breed different varieties of wheat with different awn-lengths.

With each of the four generations some rows of the original awned Turkey and awnless Sonora were planted in order to provide a thorough comparison between them and their progenies in the different generations. Thus, by comparing the progenies of each generation with the original stock raised in the same soil and in the same season, the differences which may occur from seasonal and environmental factors will be eliminated. The statistical constants used in these studies were those commonly used by biometricians. The constants used were the mode, arithmetical mean, standard deviation, and coefficient of variability. The probable error for each constant used was also calculated. Curves constructed from the frequency distribution of certain families were used to illustrate the similarity of these families, the nature of their genotypical constitution, together with other genetical facts to be discussed in the analyses of the different generations.

The adding machine and calculating machines were used in adding, subtracting, multiplying, dividing, and extracting the square root.

THE ANALYSES OF THE DATA IN EACH GENERATION

The First Generation (F_1)

Table I shows the different statistical constants of the F_1 generation and also those of the two parents.

Table I-The Constants of F_1 and its Parents

Samples	No.of Pop. (N)	Mode	Arithmetical Mean (A.M.)	Standard Devn. (σ)	Coef.of Variability (C)
			mm.	mm.	%
F_1 Gen.	30	40	27.6667±1.2568	10.2064±.8887	36.8905±3.6231
Red.Tur	80	90	87.2223 ± .6800	9.5507±.4808	10.9498±2.1875
Sonora	00	00	-----	-----	-----

The mode of F_1 is just half that of the Red Turkey, and the arithmetical mean of the former is about one-third that of the latter. This shows that the inheritance of awn-length is of a blending type. The variability in F_1 is more than three times that in the Turkey parent, and this is easily seen by comparing the two coefficients of variability. The higher degree of variation in F_1 can probably be explained by the small number of the plants in the population.

The Second Generation (F_2)

The F_2 plants had all grades of awn-length, from pure awnless to 100 mm. awned plants. The method used in measuring considered plants having less than 5 mm. awns as having traces of awns and represented them by (T). The first question then which presents itself to the student of such a case is how he is going to treat these (T) plants. Is he going to consider them as awnless, or as the lowest grades of the intermediate type of his F_2 generation ? The safest method is to treat them in both ways in the F_2 calculation, and compare the results with their behavior in the F_3 generation.

Table II shows the distribution of F_2 plants with the assumption that all the (T) plants were pure awnless.

Table II showing the distribution of F_2 plants

Plt. No.	Population	Awnless	Awned	Ratio	Remarks
	plt.	plt.	plt.		
1	367	83	284	1:3	
7	168	40	128	1:3	Average
9	165	42	123	1:3	371:1243 or
13	128	28	100	1:3	1:3
21	240	51	189	1:3	
22	152	41	111	1:3	8 families contain-
25	177	39	138	1:3	ing 1614 plants
31	217	47	170	1:3	
4	113	21	92	1:4	Average
11	134	27	107	1:4	158:681 or
14	191	34	157	1:4	1:4
19	182	34	148	1:4	6 families con-
28	138	25	113	1:4	taining 839 plants
32	81	17	64	1:4	
2	276	44	232	1:5	Average
5	141	23	118	1:5	202: 1055 or
8	86	13	73	1:5	1:5
26	219	34	185	1:5	6 families con-
27	180	28	152	1:5	taining 1257 plants
33	355	60	295	1:5	
3	180	24	156	1:6	Av. 44:278 or 1:6
17	142	20	122	1:6	2 fams. with 322 plts
6	106	13	93	1:7	Average 66:452 or
15	83	11	72	1:7	1:7
16	209	27	182	1:7	4 fams, containing
18	120	15	105	1:7	516 plants
30	86	9	77	1:8	One family
29	171	16	155	1:10	One family
Whole averge	4807	866	3941	1:4.55	50% lower than 1:3

This table shows that a good number of the families behaved in a simple Mendelian manner, with the awnless character as recessive to the awned character, and both forming a simple allelomorph, giving a distribution in F_2 as one awnless to 3 awned. But a larger number of the plants gave different ratios; 1:4, 1:5, 1:6, 1:7, 1:8, and 1:10 . Also the whole population gave the ratio of 1:4.55 which is more than 50 percent different from the expected ratio 1:3. Therefore, there must be some factor or factors interfering with the occurrence of the ratio 1:3, or it may be that the (T) plants which were considered as awnless were not awnless but the lowest grades of intermediate awned plants, which case will change the inheritance of awn-length from the simple assumption of one factor-difference to a more complex inheritance.

Table III shows the behavior of F_2 plants with the assumption that the traces were short intermediates and not pure awnless .

Table III-F_2 distribution on the assumption that (T) plants were intermediate and not awnless.

Plant No.	Population	Awnless	Awned	Ratio	Remarks
	pl.	pl.	pl.		
1	367	10	366	1:36	On the assumption of one factor difference these families have the following ratio:-
7	168	4	164	1:41	
9	165	0	165	0:165	
13	128	4	124	1:32	
21	240	6	234	1:39	
22	152	4	148	1:37	1:3
25	177	7	170	1:25	
31	217	4	213	1:53	
4	113	3	110	1:37	
11	134	2	132	1:66	
14	191	8	183	1:24	
19	182	3	179	1:60	1:4
28	138	1	137	1:137	
32	81	2	79	1.40	
2	276	0	276	0:276	
5	141	0	141	0:141	
8	86	1	85	1: 85	1:5
26	219	3	216	1:216	
27	180	5	175	1: 35	
33	355	5	350	1: 70	
3	180	1	179	1:179	1:6
17	142	3	139	1: 46	
6	106	0	106	0:106	
15	83	0	83	0: 83	1:7
16	209	4	205	1: 51	
18	120	1	119	1:119	
30	86	0	86	0:86	1:8
29	171	0	171	0:171	1:10
Whole avge.	4807	81	4726	1:58.34	1:4.55

This table shows different ratios, but the average of the whole population gives a ratio of 1:58.34, which is very much nearer to the ratio 1:63, expected in F_2 if there are three cumulative factors concerned in such inheritance; that is, the pure Turkey has three similar determinants for awn-length which will be inherited independently, while the Sonora has none. Therefore, if the (T) plants prove in F_3 to be intermediates, there will be a possibility that there are three cumulative factors concerned in the inheritance of awn-length in the present case. The probability will be greater if a right explanation can be given for the great variability in the ratio of the different families within the whole population.

A careful study of the ratios indicates that they are merely modifications of the ratio 1:63 caused by the addition or omission of one or more awnless plants in a family. For instance, if there is a family with a population of 128 plants and an extra awnless plant is wrongly added to them, the ratio instead of being 2:126, or 1:63 will become 3:126 or 1:42. There are in the modified ratios 1:41,1:40 and 1:41. Also, if one extra awnless plant be added to a population of 64 the ratio will change from 1:63 to 2:64 or 1:32 and there is in the modified ratios 1:32. Again, if one extra awnless be added to a population of 192 it changes the ratio from 3:189 to 4:189 or 1:47 and there is in the modified ratios 1:46. On the other hand, if one awnless is omitted from a population of 256 it changes the ratio from 4:252 to 3:252 or 1:84, and there is 1:85. Again, if one awnless is omitted from a population of 126, it changes the ratio from 2:126 to 1:126 and there are 1:119 and 1:137. Also, there are ratios which are very much nearer to 1:63, such as 1:60 and 1:66, which when added together will give 1:63, the exact expected ratio. The other ratios actually obtained can probably be explained in a similar manner.

From all that has been said, it is plain that all the different ratios obtained in Table III are modified ratios of 1:63, caused by the addition or omission of one or more awnless plants to a family of 63 or more individuals. One more fact in favor of this explanation is that the law of chance makes equal chances for adding as well as for omitting awnless plants. But the law of chance works only in the case of large numbers; so that, if the average of a large population is calculated, the law of chance will cause the addition to nullify the omission, and a ratio very much nearer to the exact expected ratio will be obtained. This was exactly the case when the ratio of the whole population was calculated, as it was 1:58.34 which is very much nearer to 1:63.

But what caused such extra addition or omission ? This can be easily understood if the wide environmental fluctuations, even of the pure strains such as the Red Turkey will be taken into account. Red Turkey in F_2 has a mode of 90 mm. but there was a wide fluctuation on both sides up to 120 mm. and down to 60 mm. If this is taken into account then the (T) plants which are supposed to be of heterozygous nature since they are assumed to be intermediates, fluctuate more widely, and their lower fluctuations may appear with minute beaks such as are found on the awnless Sonora. Hence, they may be erroneously counted as awnless. If the (T) plants prove to be intermediate in F_3, this explanation will account for most of the modifications of the ratios given in Table III. All the ratios above 1:63 such as 1:32 or 1:46 or

1:25, etc., will be thus explained . On the other hand, the omission of one or more awnless plants may result from the same cause of fluctuation ; that is, the minute beaks found on the Sonora may fluctuate as widely as the other pure strains of Red Turkey have done, and its higher fluctuations may look like plants with minute traces and may be erroneously counted as (T) plants. Also, the factor of sterility caused by hybridization may play a part here, as it is well known now that , though hybridization may increase the fertility of the crosses in the first generation, yet a tendency towards lessened fertility or towards sterility in some cases , as in cotton, has been shown in the next generations.

The study of the behavior of F_2 plants in F_3 will throw much light upon the nature of inheritance of awn-length and will show which of the two hypotheses , one-factor or three-factor difference is more probable.

The Third Generation (F_3)

The plants for each class value were taken at random from (F_2) and their progenies in 10 rows of F_3 were studied, and their constants were calculated (Table IV).

Table IV - The Constants for Class Groups in F_3

Class Value in F2	Frequency	Average mean in mm.	Standard deviation in mm.	Coef. of variability	Remarks
0	3	behaved as (0) #fluctuating to (T)			
T	15	8 behaved as intermediate and 7 behaved as (0)			
10	203	42.9557 ± 1.1161	23.5753 ± .7891	54.8828 ± 2.3255 %	all intermediate
20	195	42 .5641 ± 1.1075	22.9288 ± .7843	53.8688 ± 2.3163	" "
30	181	45.8563 ± 1.1701	23.4099 ± .8299	51.0505 ± 2.2322	2 plts awned, rest inter.
40	172	54.3023 ± 1.0897	21.1880 ± .7705	39.0186 ± 1.6205	3 " awned, 1 awnless, rest inter.
50	216	64.7685 ± .7774	16.9406 ± .5497	26.1556 ± .9050	9 " " , 1 inter.
60	223	67.8924 ± .4715	10.4408 ± .3335	15.3784 ± .5023	all awned
70	225	74.6667 ± .4871	10.8320 ± .3444	14.5071 ± .4708	" "
80	271	72.3247 ± .5902	14.4052 ± .3834	19.9174 ± .5531	" "
90	46	70.6521 ± 1.0652	10.7141 .7534	15.1645 ± 1.0906	" "
			Intermediates		
10	203	42.9557 ± 1.1161	23.5753 ± .7891	54.8828 ± 2.3255	
20	195	42.5641 ± 1.1075	22.9289 ± .7843	53.8688 ± 2.3163	
30	179	45.8563 ± 1.1701	23 .4099 ± .8299	51.0505 ± 2.2322	
40	109	48.1651 ± 1.4490	22.4288 ± 1.0240	46.5664 ± 2.5471	
50	21	not enough distribution to obtain fair representation for the class.			
			Awned Plants		
30	42	26.9524 ± 1.5341	14.7405 ± 1.0918	54. 6908 ± 5.0878	not enough populn.
40	65	64.4615 ± 1.1370	13.5908 ± .8040	21. 0835 ± 1.3013	
50	197	67.8173 ± .6197	12.8958 ± .4388	19. 0155 ± .6621	
60	223	67.8924 ± .4716	10.4408 ± .3335	15. 3784 ± .5032	
70	225	74.6667 ± .4871	10.8320 ± .3444	14. 5071 ± .4708	
80	271	72.3247 ± .50902	14.4052 ± .3834	19. 9174 ± .5531	
90	46	70.6521 ± 1.0652	10.7141 ± .7534	15.1645 ± 1.0906	not enough populn.
			Red Turkey		*
50-100	79	79.9874 ± .6342	8.3582 ± .4485	10.4493 ± .5846	

Table IV shows that there were awned rows in F_3 deriving from 30, 40, 50, up to 90 awned plants in F_2. It also shows that the (T) plants were not all pure awnless, and that the awned plants fluctuated around different means, an evidence of their different genotypical nature. This result suggested to the writer to study every plant in each group separately, and the results of such studies were as follows-

The behavior of F_2 awnless and (T) plants in F_3 - Only three awnless plants in all of the families that gave the ratio 3:1 as awned to awnless in F_2, on the assumption that the traces were pure awnless, were planted in F_3, and every one of them bred true to awnless. All the (T) plants were also studied separately and the result was that eight plants behaved as intermediates and seven behaved as pure awnless. The conclusion is that the (T) plants differ in their genotypical constitution. Some of them behaved as plus fluctuations from pure awnless to (T) plants and thus bred true to awnless. Others behaved as minus fluctuations from higher intermediate classes and thus behaved in F_3 as intermediates. These results support the previous assumption for the explanation of the modified ratios of the hypothesis of three-factor difference in F_3, which assumption explains the modified ratios caused by the adding or omitting of an awnless plant to the population through the fluctuation of (T) plants to awnless plants and the fluctuation of awnless plants to (T) plants. The results also show that more than 50 per cent of the (T) plants that were considered awnless in the families giving in F_2 the ratio (3:1) on the assumption of one-factor difference were intermediates, and this of course changes that ratio (3:1) and makes it much lower (7:1) as awned to awnless. Then, there were no plants in F_2 that gave the ratio (3:1) . Few members of the plants that bred true to awnless fluctuated to plants with minute traces (T) of awns, a further evidence of the correctness of the assumption made for the explanation of the modified ratios of three-factor difference in F_2.

The behavior of F_2 10 mm. awned plants in F_3.

All plants behaved as intermediates forming bimodal curve, with a very high mode at 20 mm. and much lower one at 70 mm. This is evidence of its heterozygous constitution and mixed population.

The behavior of F_2 20 mm. plants in F_3.

All plants behaved just the same as the 10 mm. awned plants.

The behavior of F_2 30 mm. plants in F_3 .

Plants No. 1815 and 1990 gave only awned plants in F_3 with a mean of 26.47 and 30.21 mm. respectively . The rest of the plants behaved as intermediates giving awnless and awned plants in F_3, with a bimodal curve having a high mode at 30 mm. and another much lower one at 80 mm, an evidence of its heterozygous mixed nature.

The behavior of F_2 40 mm awned plants in F_3.

Plant No.1912 bred true to awns forming one modal curve and a mean of 50 mm. Plants No. 1870-1934 also bred true to awns giving one modal curve each and a mean of 69 mm. The rest of the plants behaved as intermediates giving awnless and awned plants and forming a bimodal curve with a high mode at 40 mm and a much lower one at 80 mm.

The behavior of F_2 50 mm. awned plants in F_3

Plants No. 1833, 1972,and 2017 bred true to awns with a mean of 78 mm. and a mode at 80 mm. each. Plant No. 1984 also bred true to awns but with a mean of 52 mm. and a mode of 50 mm. ,while plants No. 1877, 1882, 1907, 1933, and 1944 had a mode between 60 and 70 each and a mean of 64.6 mm. Plant No.1901 behaved as intermediate with a bimodal curve.

The behavior of F_2 60 mm. awned plants in F_3

Plants No. 1811, 1830, 1890, 1909, 1975, 1992, 2013, and 2030 behaved as awned with a mode between 60 and 70 mm. each and a mean of 65 mm. Plants No. 1825 and 1851 were also awned with a mode of 80 mm. each and a mean of 77.55 mm.

The behavior of F_2 70 mm. awned plants in F_3

Plants No. 1843, 1900, 1910, 1936, 1970, 2025, and 2039 had a mode of 80 mm. each and a mean of 76.2 mm. Plant No. 2000 had a mode between 60 and 70 and a mean of 68 mm.

The behavior of F_2 80 mm. awned plants in F_3

Plants No. 1951- 52, 1999, 2007, 2015-16, 2090, and 2139 had a mode at about 80 mm. and their average mean was 78.18 mm. . Plants No.1987, 2004, and 2036 had a mode between 60 and 70 mm. and a mean of 68.87. Plant 2080 had a mean of 53.6 mm.

The behavior of F_2 90 mm. awned plants in F_3

One plant only, 2008-09, had a mode of 70 and a rather wide distribution with a mean of 70.65 mm.

The behavior of all the different F_2 groups of awn length in F_3 -

(1) The awnless plants in F_2 behaved as pure awnless in F_3 but they were only three in number,and therefore not enough to give accurate results.

(2) More than 50 per cent of the (T) plants behaved as intermediates and the rest as pure awnless. The awnless showed a fluctuation towards (T) plants as the latter had also fluctuated to the former.

(3) The 10 mm. and 20 mm. awned plants behaved as intermediates with identical bimodal curves.

(4) The 30 mm. 40 mm. and 50 mm. awned plants gave intermediate and awned plants, while the 60 mm., 70 mm., 80 mm., and 90 mm. gave only awned plants in F_3. The awned plants in F_3 from F_2 30 awned plants were of one type only with a mean of about 26 mm, while the awned plants in F_3 from 40 and the other higher classes of F_2 were of three different types; (a) those with a mode of 50 mm. and a mean around 52 mm., (b) those with a mode between 60 and 70 mm., and a mean around 65 mm., and (c) those with a mode at 80 mm. and a mean around 78 mm.

Discussion of F_3 Studies

Before trying to discuss the data obtained from these studies, it is important to go back to the two different hypotheses assumed for the inheritance of awn-length in F_2, one-factor and three-factor differences, and to show the genotypical and phenotypical distribution of F_2 plants in either of these two hypotheses, as well as the expected behavior of each of F_2 groups in F_3 .

The expected distribution of F_2 plants and their behavior in F_3 on the assumption of one-factor difference between awned Red Turkey wheat and awnless Sonora wheat are shown in Table V.

Table V - The distribution of F_2 plants and their behavior in F_3 on the assumption of one-factor difference

Genotype	Phenotype	Distribution	Behavior in F_3	Mean in F_3
A A	Pure awned 80 mm	1	Breeds true to awns	80 mm.
A a	Intermediate 40 mm.	2	Gives 1(80): 2(40): 1(0)	40 mm.
a a	Pure awnless (0)	1	Breeds true to awnless	0

The phenotypical nature shown in this table was obtained by determining the value for each dose of the determinant,(A). The Red Turkey with a constitution of (AA) had a mean of about 80 mm. awn-length; therefore each dose (A) will be $\frac{80}{2} = 40$ mm. On the other hand, the Red Turkey had a genotypical constitution of (AAAAAA) on the assumption of three-factor difference, and therefore each dose (A) in such assumption will be $\frac{80}{6} \doteq$ 13 mm. Then the expected genotypical and phenotypical distribution in F_2 on the assumption of three-factor difference, and the behavior of the plants in F_3 will be shown in Table VI.

Table VI- The expected distribution of F_2 plants and their behavior in F_3 on the assumption of 3-factor difference

Genotype	Phenotype	Frequency	Behavior in F_3	Mean in F_3
A A A A A A	Awned 78 mm.	1	Breeds true to 78 mm.	78 mm.
A A A A A a	Awned 65 mm.	6	Gives 1(78):2(65):1(52)	65 mm.
A A a A A a	Awned 52 mm.	15	Breeds true to 52 mm.	52 mm.
A A a A a a	Intermediates 39 mm.(av.)	20	Gives 1(78):6(65):15(52): 20(39):15(26): 6 (13):1(0)	39 mm
A a a A a a	Awned 26 mm.	15	Breeds true to 26	26 mm.
A a a a a a	Intermediates 13 mm.(av.)	6	Gives 1(o):2(13):1(26)	13 mm.
a a a a a a	Awnless (o) mm.	1	Breeds true to awnless	(0) mm.

To begin the discussion, it will be important to construct the distribution curves of the different intermediates and different awned plants observed in the F_3 studies; also, to show the constants of each type of plants ; and then to compare the results with those shown in Tables V and VI.

Figure I shows the curves of the different intermediates obtained in F_3 from F_2 10, 20, 30, and 40 mm. plants.

This figure shows a bimodal curve for each group of plants, an evidence of a heterozygous nature. In each curve, the first mode is much higher than the second. The first mode, therefore, is the mode of the majority of individuals in the population.

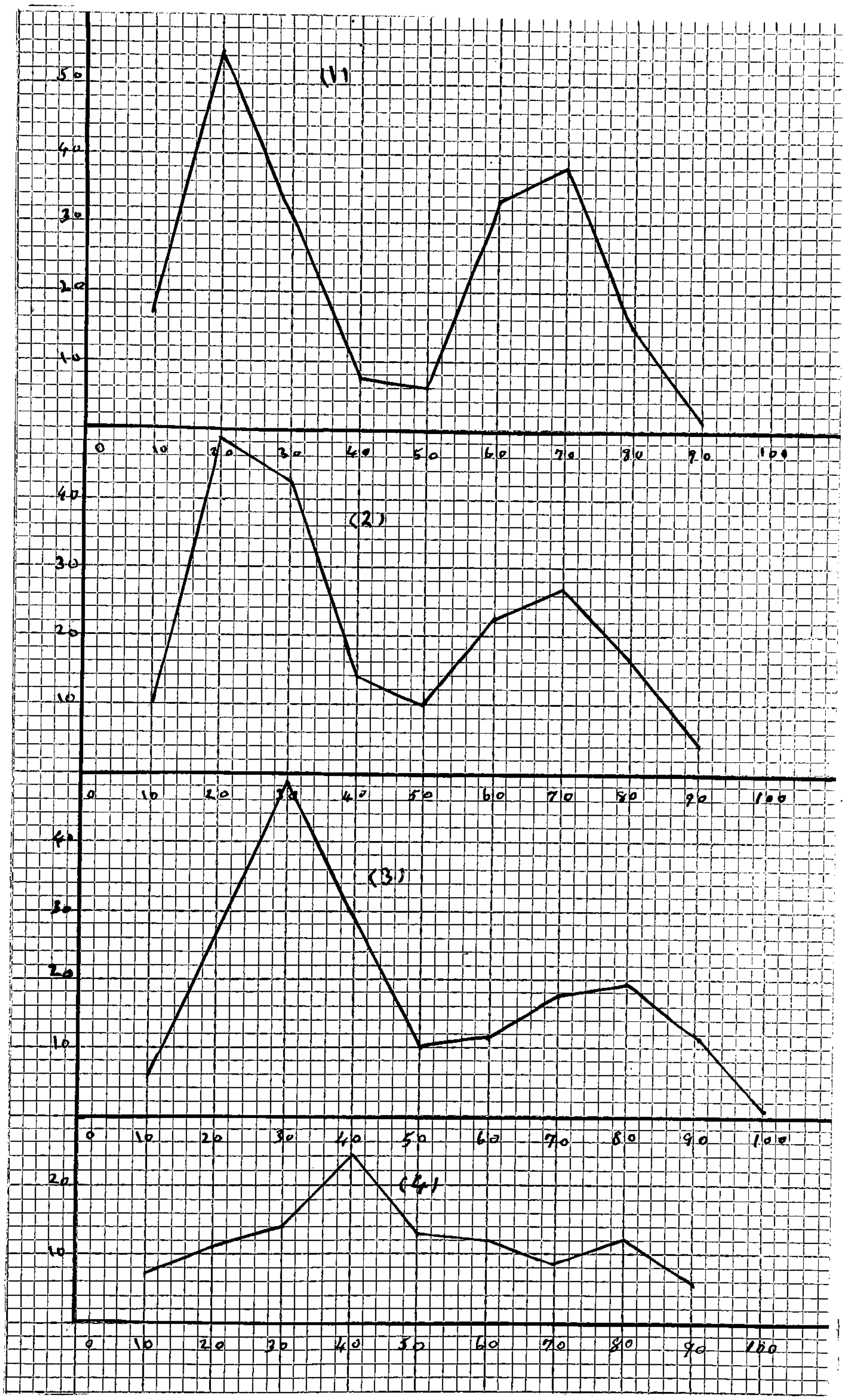

Fig. I Intermediate plants in F_3
Bred from F_2 plants having :(1) 10 mm. awns (2) 20 mm. awns (3) 30 mm. awns, and (4) 40 mm. awns.

A comparison of the four curves shows that the first and second are practically identical; therefore, the two populations forming them are of the same nature. The fourth curve is greatly different from the first two in at least two respects. First, it has a higher value for the first mode, being at 40 mm. instead of 20 mm. as in the first two. Second, there is a much lower frequency for the second mode in the fourth curve than in the first two curves. This condition makes the former look more uniform and much nearer to a single mode curve. The third curve is practically an intermediate between the first two curves and the fourth . To conclude, it can be said that the intermediate plants are not all of the same nature, but they have at least two different constitutions, one forming the majority of the plants of the first and second curves and the other forming the majority of the plants in the fourth curve. The third curve may be a mixture of the two types of intermediates.

Figure II shows four different curves formed from different types of awned plants observed in F_3. Three of the curves are strictly with single modes and the fourth is slightly bimodal, which condition, together with its wide distribution, arouses some suspicion concerning its homozygous nature. The majority of plants in the slightly bimodal curve have a mode between 20 and 30, while the single mode curves have modes at 50, 60-70, and 80 mm. respectively . Therefore, the awned plants in F_3 are of more than one genotypical nature and probably of four different natures. The biometrical constants for the plants in each of the four curves in

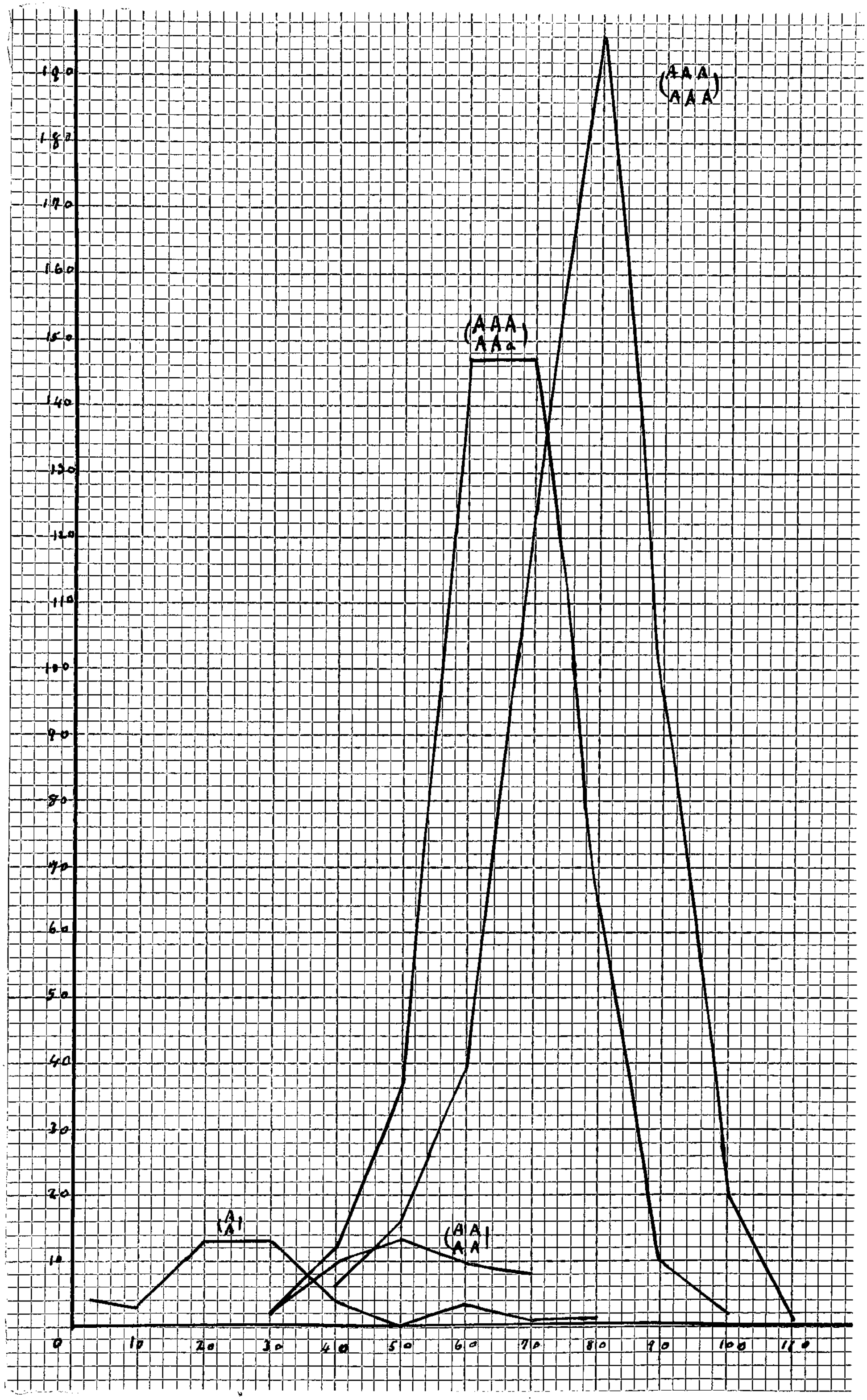

Fig. II - Awned plants in F_3

figure II were calculated as shown in table VII.

Table VII- The Constants of Awned Plants in F_3 -

Frequency	Mode	Mean	Standard Dev.	Coef. of Variability
	mm.	mm.	mm.	%
42	20 & 30	26.9524±1.5341	14.7405±1.0918	54.6908±5.0878
43	50	52.7904±1.1806	11.4781± .8348	21.7426±1.6545
422	60 & 70	65.8767± .3524	10.7344± .2492	16.2947± .3881
686	80	77.0834± .3524	11.5171± .2491	14.9411± .3303
			Red Turkey	
79	80	79.9874± .6342	8.3582± .4485	10.4493± .5846

From this table it is seen that there is only one group of the awned plants in F_3 that resembles the awned parent in every respect; in the mean, the mode, and the other constants. There are three other different groups of awned plants which greatly differ from the pure awned parent.

It is interesting now to compare the results obtained from the present studies with each of the expected results of the two previous hypotheses assumed as bases for the inheritance of awn-length ; i.e., the assumption of one-factor and three-factor differences between the awned Red Turkey wheat and the awnless Sonora wheat.

On the assumption of one-factor difference , the following results are obtainable:

(1) The F_2 plants must be distributed on the ratio of three awned to one awnless (3:1).

(2) The awned F_2 plants which breed true to awns in F_3 must fluctuate around one mean which must be very much nearer to if not the same as the mean of the pure awned parent.

(3) All the intermediates in F_3 must be of the same nature as those in F_2 and must fluctuate around one mean and have one type of curve (see table V)

On the other hand , the hypothesis of three-factor difference will give in F_2 :

(1) Awned to awnless plants as 63:1 .

(2) The F_2 awned plants which breed true to awns in F_3 will be of four types (a) one with a mean and a mode like those of the pure Turkey and having its genotypical constitution (AAAAAA) , (b) the second will have the constitution of (AAAAAa) and a mean around 65 mm. , (c) the third will have the constitution of (A A A A) and a mean around 52 mm. and (d) the last will have a constitution of (A A) and a mean around 26 mm. (See table VI)

The actual results of the studies made in F_2 and F_3 generations in the present instance were : -

(1) The distribution of awned to awnless plants in F_2 generation was as 58.34 :1 which is very much nearer to the ratio 63:1 than to any other expected ratio.

(2) The awned plants of F_2 which bred true to awns in F_3 had been of the following types: (a) plants with a mean of 77.0834 and a mode of 80 mm. which are nearly identical with those of Red Turkey, whose constitution on the assumption of three-factor difference is (AAAAAA) and whose expected mean is around 78 mm. (b) Plants with a mean of 65.8767 mm. and a mode of 60-70 which are identical with those of the group of plants whose constitution , on the assumption of three-factor difference, is (AAAAAa) and whose expected mean is

around 65 mm. (c) Another group of plants with a mean of 52.7907 and a mode af 50 mm. which are identical with those of the plants of the constitution (AAAA) and whose expected mean is around 52 mm. (d) a fourth group with a mean of 26.9524 and a mode of 20-30, which are the same as those of the expected group of the constitution (AA) and whose expected mean is around 26 mm. But the last group has another very low mode at 60 mm. and a rather wide distribution, which two conditions, though they may have occurred through an insufficient number of population in this group, yet arouse some suspicion concerning the expected homozygous nature of that group, (see table VI).

Conclusion for F_2 and F_3 Studies

To conclude the foregoing studies, it is easy to deduce the following statements for the present instance of inheritance:

(1) The awned character is dominant.

(2) The awnless character is recessive.

(3) The dominance here is incomplete and the nature of inheritance is of the blending type.

(4) The awn-length in the present case is a quantitative character.

(5) The universal belief that the awn-length in wheat is inherited on a simple Mendelian basis with the assumption of one-factor differ-ence between the awnless and awned plants, is not true for this pres-ent case.

(6) There is a greater probability that there are three cumulative factors between the Red Turkey awned wheat and the awnless Sonora wheat; that is, factors of the same type which are inherited inde-pendently.

(7) The inheritance of awn-length seems to be different in different strains of wheat, because while the F_1 generation obtained by crossing the Red Turkey and Sonora is of the intermediate type, the same generation obtained this year by crossing the awned Early Baart(as female parent)and the awnless Federation Hard (as male parent) in the wheat garden of the Plant Breeding Department of the University of Arizona , has been noticed to be practically awnless. This result proves that the awned character in Early Baart is recessive to the awnless character in Federation Hard.

THE FOURTH GENERATION (F_4)

Ten plants for each class were selected at random from (F_3) and planted in (F_4) each in a separate row. To study the awned plants, all the plants in the different classes which had in (F_3) the same assumed constitution were studied as one class and the results were :

The behavior of (F_3) 10, 20, 30, and 40 mm intermediate awned plants in (F_4). Each class gave similar results to those given by the same class in (F_3).

The behavior of (F_3) 26 mm (AA) awned plants in (F_4) - All behaved as intermediates proving that the suspicion which arose in (F_3) about their homozygous nature was true.

The behavior of (F_3) 52 mm (AAAA) awned plants in (F_4) - All behaved as pure awned with one modal curve and a mean of 45.44 mm awn-length.

The behavior of (F_3) 65 mm (AAAAAa) awned plants in (F_4) - All behaved as pure awned with one modal curve and a mean of 57.70 mm. awn-length.

The behavior of (F_3) 78 mm (AAAAAA) awned plants in (F_4) - All behaved as pure awned plants with one modal curve and a mean of 56.14 mm awn-length.

The behavior of (F_3) awnless plants in (F_4) - One plant behaved as intermediate and the rest bred true to awnless with trace of awns like those on the pure Sonora.

The behavior of the pure Sonora in (F_4) - Bred true to awnless with traces of awns.

The behavior of the Red Turkey in (F_4)- Bred true to awns with a mean of 95.06 mm. awn-length.

DISCUSSION OF (F_4) STUDIES

(1) The awnless plants as well as the lowest grades of intermediates have traces of awns. This makes it difficult to isolate the awnless plants except through continuous selection for several generations.

(2) The awned plants, though bred true to awns yet every class of them had in (F_4) shorter awns than was expected.

(3) The (F_3) awned plants of the assumed nature (AAAAAa) and those of the assumed nature (AAAAAA) gave in (F_4) similar results with nearly the same means; while the plants with the assumed nature (AAAA) bred around a much lower mean.

(4) Though the (F_4) generation did not sustain the assumption that the Red Turkey wheat contains three cumulative factors for awn-length, yet it did not disprove that the awned character is a quantitative one.

A STUDY AND REVIEW OF THE LITERATURE RELATING TO SIMILAR PROBLEMS OF INHERITANCE

1- Nilsson-Ehle, H: Multiple allelomorphism and complex mutation in wheat - Hereditas 1:277-31, 1920 - Spike characters : beardless, half-bearded, and bearded. The last two types originated from the first one through complex mutation and linkage. Beardlessness is dominant over the other two types, and the half bearded is dominant over the bearded. In F_2 the segregation was in the ratio (3:1).

2- Kezer,Alvin,Breeze,and Boyak:Mendelian inheritance in wheat and barley crosses, with probable error studies on class frequencies, Colorado Agric.Exp.Sta.Bull. 249, Oct.1918 - Beardlessness and beardedness were studied in wheat and were found to appear in the F_2 generation as (3:1). Hooded and bearded barley appeared in F_2 as (3:1).

3- Kajanus, B. : Bot.Notiser, No.5, 1918, pp. 245-247 - The author described a cross between an awned type of wheat, designated as Mazoulo and employed as the male parent, and an awnless variety from Svalof known as Pearl. Awning behaved as a recessive character, and the ratio of awned to awnless plants in F_2 was as (1:3).

4- Hayes and Garber : Breeding of Crop Plants, 1921 , p.85- Three to one ratio has been generally obtained in the F_2 generation of crosses between what is commonly known as awnless (tip-awned) and awned wheats. The Howards (1915) explained results by assuming two homozygous factors in the awned plants and one homozygous factor in the tip-awned ones which are usually considered as awnless. In crossing a tip-awned wheat like the Marquis with an awned variety, the F_1 crosses will have intermediate awns; while in crossing a real awnless with an awned wheat the F_1 plants will be as awnless as the pure awnless parent.

5 - Martin: Botany for Agric.Students, 1919 , p.552
A photograph of an awned wheat (Turkey), an awnless (Blue Stem), and their F_1 cross with intermediate awns, is given as an illustration of the inheritance of quantitative characters. A quantitative character is represented by more than one similar factor, each being responsible for a part of the character and each inherited independently of the others.

6. Bailey and Gilbert : Plant Breeding, 1916, p.194-
Mr.Spillman , Agriculturist of the United States Depsrtmment of Agriculturem worked on the inheritance of awn-length in wheat. The wheat parents were an awned variety (Little Club) and an awnless strain (Valley). The F_1 plants were practically awnless (with minute traces of awns). In the F_2 the distribution of the awnless to the awned plants was as (3:1).

7- Percival : Agricultural Botany , 1913, p.295 - Awnless and awned characters in wheat form a pair of allelomorphs with the awnless character as dominant and the awned as recessive giving in F_2 the ratio (3:1).

8- Punnet : Mendelism, 1919, p.69- The awned character is an additional character and, according to the Presence and Absence Theory, cannot be recessive to awnlessness which is the absence of awns. The author suggested that the awned plants are always dominant over the awnless ones, and explained the cases in which awnlessness was shown to be dominant by assuming that such awnless wheats contain an inhibitor which suppresses the growth of the awns. He said also that his assumption was confirmed by Howard who was able to find two sorts of awnless wheats, one of them recessive and the other dominant over the awned plants.

GENERAL SUMMARY

The following three different hypotheses have been developed by different authorities at different times to explain the nature of the inheritance of awn-length.

(1) The first assumption is the oldest and the most prevailing one. It states that the awnless character is dominant over the awned. The F_1 crosses will be awnless (plate II), while the F_2 generation will be distributed in the ratio of (3:1) as awnless to awned plants.

(2) The second hypothesis worked out by the Howards (1915) considered the awned character as a quantitative one represented in the constitution of an awned plant by two homozygous cumulative factors. The awnless plants were divided into two types, one with traces of awns like the Sonora, and the other completely awnless like the Federation Hard (plate IV). The last type (completely awnless) was the only one considered as really awnless, while the tip-awned type was considered as awned with one homozygous factor for awns. If a true awnless plant (Federation) be crossed with an awned plant (Early Baart), the F_1 generation will be awnless (plate II) while crossing a tip-awned variety (commonly known as awnless: Sonora) with

the same awned plant the F_1 plants will have intermediate awns (plate I).

(3) The third theory was suggested by Punnet, who considered the awned character as dominant and divided the awnless plants into two groups, one with an inhibiting factor for awns, and the other without it. If an awnless plant with the inhibitor be crossed with an awned one, the awns will be inhibited in all of the F_1 crosses (plate II); while crossing an awnless without the inhibitor with an awned plant, the F_1 generation will have intermediate awns (plates I and III).

The first assumption does not explain cases like that of the crosses of the Sonora and Turkey, or the Sonora and Early Baart, when the F_1 plants have intermediate awns (plates I and III); also the awned character is an additional one and, according to the Presence and Absence Theory, cannot be considered recessive.

The Howards' hypothesis does not explain cases like that of the Sonora and Red Turkey crosses, because if the Sonora is not awnless but short awned wheat with one homozygous factor for awns, as the Howards had assumed, and if the Red Turkey has two homozygous factors for awns, as they also assumed, the Sonora should have awns with a length half that of the Red Turkey, which is not the actual case. Also the distribution of the F_2 plants in the Sonora and Red Turkey crosses does not agree with the Howards' assumption.

The writer, as a result of his present studies of awn-length, prefers the theory of Punnet and adds to it that the awned character may be represented by one or more cumulative factors. This explains every case yet known for the inheritance of awn-length in wheat.

As a result of the present studies, the writer draws the following conclusions:

(1) An awnless plant with the inhibitor of awns will appear completely awnless without the slightest traces of awns, as the Federation Hard (plate IV)

(2) An awnless plant without the inhibitor of awns will have traces of awns, especially at the top of the spike, as the Sonora (plate IV).

(3) If an awned plant like the Early Baart be crossed with an awnless plant with the inhibitor (Federation Hard), the F_1 plants will be awnless; (plate II) while if the same awned plant be crossed with an

awnless one without the inhibitor of awns (Sonora) the F_1 crosses will have intermediate awns (plate IX)

(4) If an awnless plant without the inhibiting factor be crossed with an awnless with the inhibiting factor, the F_1 crosses will be as awnless as the one with the inhibitor (plate IV).

(5) The case of the Red Turkey and Sonora crosses can probably be explained by assuming that the Red Turkey contains three homozygous cumulative factors for awns, while the Sonora contains none. The Sonora having no inhibiting factor must give with Red Turkey F_1 plants with intermediate awns (plate III)

(6) In crosses between an awnless with the inhibiting factor and awned plants, all the F_2 awned plants breed true to awns, but the pure awnless , although these may be distinguished from the heterozygous awnless plants in the F_2 generation, yet they can be surely isolated only in the F_3 generation.

(7) In crosses between awnless plants without the inhibitor and awned plants, neither the awnless nor the pure awned plants can be isolated except in the F_3 generation.

(8) As the awned character is a quantitative one, several pure strains of wheat with different awn-lengths,

can be isolated in the F_3 generation; and it will be useful to study the correlations between awn-lengths and different important economic characters, such as tillering of plants, disease resistance, yield, etc.

PLATE I

From left to right: a head of an awned variety of wheat (Early Baart), a head of the F_1 cross between the awned variety and an awnless variety of wheat (Sonora), a head of the awnless Sonora. Notice that the F_1 cross has intermediate awns, and that the awnless Sonora has traces of awns. The Sonora does not contain an inhibiting factor for awns.

Plate I

PLATE II

From left to right: a head of an awned variety of wheat (Early Baart) a head of the F_1 cross between the awned variety and an awnless variety of wheat (Federation Hard), a head of the awnless Federation Hard. Notice that the F_1 cross is awnless and that the awnless Federation Hard has no traces of awns. The Federation Hard contains an inhibiting factor for awns.

PLATE II