U. M.

THE UNIVERSITY OF MINNESOTA

GRADUATE SCHOOL

Report

of

Committee on Examination

This is to certify that we the undersigned, as a committee of the Graduate School, have given Carl Kurtzweil final oral examination for the degree of Master of Science. We recommend that the degree of Master of Science be conferred upon the candidate.

Minneapolis, Minnesota

May 27 1919

H. K. Hayes
Chairman

C. O. Rosendahl

M. J. Dorsey

THE UNIVERSITY OF MINNESOTA

GRADUATE SCHOOL

Report

of

Committee on Thesis

The undersigned, acting as a Committee of the Graduate School, have read the accompanying thesis submitted by Carl Kurtzweil for the degree of Master of Science. They approve it as a thesis meeting the requirements of the Graduate School of the University of Minnesota, and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science

H K Hayes
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M. J. Dorsey

May 27 1918

First Copy

DIFFERENTIATING CHARACTERS AND THEIR
INHERITANCE IN MARQUIS, PRESTON,
AND BLUESTEM SPRING WHEATS.

A THESIS

Presented to the Faculty of the Graduate
School of the University of Minnesota
in partial fulfilment of the re-
quirements for the Degree of
Master of Science

By

Carl Kurtzweil

June, 1919

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CONTENTS

INTRODUCTION

The study of the wheat characters and their inheritance reported in the following pages was made in the Plant Breeding Laboratory of the College of Agriculture of the University of Minnesota during the year 1917-1918.

The primary purpose of the study was to determine what characters of the wheat head were correlated with the growth factors which go to make high production. It was hoped that some correlations would be found which would afford a much easier method of determining the higher yielding strains than by the usual field tests which must necessarily extend over a period of years. At the same time other characters of only general interest were included in the data taken.

HISTORICAL REVIEW OF WHEAT BREEDING

Before 1890. Previous to the year 1890 when Vilmorin (Nilsson-Ehle 49) advanced his "pedigree isolation principle", all wheat breeding had been done by the mass selection method. The process of improving the varieties of wheat was slow and more or less uncertain. It was necessary, in the first place, to have a variety consisting of a mixed population. If the good qualities of two wheats were to be combined it was necessary to cross them.

Rimpau (56) crossed a large number of wheats. He was more successful than most workers which was probably owing to his observation of the intermediate condition appearing in the first generation to be followed by the appearance of all forms in later generations. He must also have practiced very rigid selection since he was able to produce constant forms in eleven years.

Vilmorin (73 , 74) also did a great amount of wheat breeding. A large part of his work was between different species. He also noticed the uniformity of the first generation which was intermediate and the segregation in the second generation.

Before 1900 After the advancement of Vilmorin's isolation principle, wheat breeding became a more definite science. However the principle was limited in its application with mixed populations, and economic conditions did not demand the high-yielding varieties which they did a few years later. The work done during this period was largely of an experimental nature with the practical side of the problem more or less obscured.

Stoll (66 , 67) is an instance of this type of work. He crossed wheat with spelt and studied the following generations. He reports a uniform intermediate F_1 with segregation in the F_2. He also found types which he called "monstrosities". These were probably transgressive segregations.

Since 1900. After the rediscovery of Mendel's law, by Correns, Tschermak, and De Vries, breeding work of all kinds was carried on in many places. Wheat breeding along with the other crops felt the stimulus of the new conditions. Owing to the practical advantage of better wheat many investigations were also made with regard to the inheritance of its characters.

Johannsen's pure line theory and Nilsson's application of the principle to cereals gave added impetus to the work. Pure lines had been produced before. Patrick Sheriff, Vilmorin, and W.M.Hays had produced wheat varieties which have later been found to be pure lines. However, these were produced by men who certainly did not know the genetic principles of which they were making use.

Investigations started before 1900 were continued. Many crosses were made between the various species to determine which ones would cross and also with the idea of determining the original wild wheat. The origin was thought to be from various sources until Aaronsohn (2) in June, 1906 found a wild emmer growing in Palestine. He declared this to be the prototype of the cultivated wheat. Later it was found that Kotschy had found the same plant on Mt. Hermon about 1885 and had sent it to Körnicke who named it Triticum dicoccum dicoccoides. Cook (21) suggests that the name should be Triticum hermonis.

The fact that wheat species are very closely related has been demonstrated by a number of workers, such as Vilmorin (73 & 74) and Tschermak (69) though much work was done by Buffum (16), Kondo (42), Vaviloff (72), Stoll (66), Gmelin (30) and Blaringhem (11). Vilmorin and Tschermak obtained all five forms when any two were crossed. However Tschermak did not find a pure monococcum or polonicum though he did obtain similar forms. He also limits the cross to solid stemmed x hollow stemmed varieties.

The breeding of wheat along the present lines depends upon its habit of maturing the pollen and ovules before the glumes are opened, so that the plant is called self fertilizing and on that account comes under the pure line conception. A number of references were found of cases of naturally crossed plants. Kajanus (40) and Saunders (61) give individual instances. Smith (63) lists the following men as having found natural crosses; Saunders, Rimpau, Hildebrand, Kornicke, Nowacki, Delpino, and Howard. Howard noted two hundred and twenty-six cases, which is the largest number noted until Hayes (32) reported a larger number from Minnesota in 1916 and 1917. Whether natural crosses occur more often in some localities or whether observation has been more careful in the above instances is very important. Inheritance studies will need to be carried on under conditions of control which have hitherto been thought unnecessary.

The wheat plant is subject to a large number of fungous diseases which materially injure the plant and reduce the yield. The rusts are the chief ones and Orton (51) estimates the annual loss to be "hundreds of millions".

It has long been noticed that there was a wide difference in resistance and susceptibility to the disease. Where resistance was found in a good variety no work was necessary. However, in many cases the high-yielding varieties are the ones most susceptible to the disease. Hence breeding is necessary to produce high-yielding wheats. Jackson (38) gives the following methods of producing disease resistant varieties: (a) selection of resistant individuals; (b) selection of varieties; (c) hybridization followed by selection of individuals.

The cause of resistance has been a much debated question. Ward (75) found that it was not due to the morphological characters of the plant. Jackson (38) thinks it due to chemical substances in the plant. Comes (19, 20) finds resistance due to the acidity of the cell-sap. Plants with an acid sap are resistant. However, if the plant is grown on soil highly fertilized with nitrogen a greater growth of chlorophyl tissue is found with consequent decreasein acidity and in disease resistance. Lewton-Brain thinks that a fungus is able to adapt itself to a plant. Stakman (64, 65) finds that this is not true of the stem rust of wheat. Stakman also found that the stem rust of wheat (Puccinia graminis tritici Erikss. and Henn.) has more than one form with different infection powers on different varieties of wheat. This will explain the conflicting results secured in different countries in regard to the resistance or susceptibility of varieties of wheat.

Biffen (7, 8, 9) crossed a susceptible variety, Michigan Bronze, with a resistant variety, Club. The first generation was susceptible and the second segregated in the ratio of 3:1. Eriksson (Reed 60) found a mildew on one of Rimpau's wheat-rye hybrids. It produced full infection on wheat but no infection on rye, showing that susceptibility was dominant in this case also.

The following outline gives the characters on which work has been done and the manner of their inheritance.

CHARACTERS

	F_1	F_2	Authority
Glume, long x short	Intermediate	1:2:1	Backhouse (4)
" " "	"	"	Biffen (6)
" " "	"	15:1 and 3:1	Tschermak (69)
" hairy x smooth	Hairy, int. or smooth		Rimpau (59)
" " "	Hairy	3:1 inhibited by long glumes	Backhouse (4)
" " "	"	3:1	Biffen (6)
" " "	Not always dominant		Henkemeyer (33)
" " "	Intermediate	3:1 or 15:1 Two kinds of hairs	Howard and Howard (36)
" " "	Hairy	3:1	Gmelin (30)
" " "	"	3:1	Tschermak (68)
" hairy grey x smooth black		3:1:1:3	Engledow (22) Biffen (10)
" red x white	Red	3:1 Two shades of red	Biffen (6)
" white x brown	Intermediate	Segregation	Stoll (66)
" red x white	Red	3:1	Gmelin (30)
" brown x white	Not always dominant	Segregation	Henkemeyer (33)
" red x white	White or intermediate	"	Tschermak (68)
" red x bluish	Red or bluish	"	"
" bluish x white	Bluish	"	"
" red gray x white	White	"	"
" white x red brown	White or brown	"	"
Caryopses, red x white	Red	63:1	Gmelin (30)
Presence or absence of awns			
Bearded or beardless	Beardless		Rimpau (59)
" "	"	3:1	Biffen (6)
" "	Intermediate	3:1	Kezer and Boyack (41)
" "	"	15:1	Howard and Howard (36)
" "	Beardless		Tschermak (68)

CHARACTERS	F_1	F_2	Authority
Density of head			
Dense x lax	Intermediate	Segregation and transgressive segregation	Parker (53)
" "	Dense		Rimpau (59)
" "	Lax	3:1 or 1:2:1	Biffen (6)
" "	Intermediate	Segregation. Transgressive for very dense	Gmelin (30)
" "	Lax		Tschermak (68)
Thrashing of grain			
Hulled x naked	Thrashing	Segregation	Tschermak (68)
Disease resistance			
Ergot susceptibility		15:1	Biffen (9)
Rust resistance	Susceptibility	3:1	
Awn color, black x white	Intermediate	3:1	Howard and Howard(35)
Kernel characters			
Red x white	Red	3:1	Biffen (6)
" "	Intermediate	1,2, or 3 factors	Howard and Howard(35)
Soft x hard	"	1:2:1	" "
" "	Hard	3:1	Biffen (6)
Other characters			
Shattering of ear	Intermediate	15:1	Howard and Howard(35)
Hollow straw x solid	Hollow	3:1	Biffen (6)
Rough leaf x smooth	Rough		"
Broad leaf x narrow	Broad	1:2:1	"
Late maturity x early	Late	1:2:1	"
Long x short grains		Segregation	

THE EXPERIMENTAL STUDY

THE INHERITANCE OF SIZE

The greater part of this study is on those characters known as size characters. Most of the work which has had to do with size inheritance has been on those plants which are more easily controlled or with a long growing season. The reason for this is that environment plays an important part in the expression of the character in question. This is so well known that it requires no proof.

Wheat has then been cast aside in favor of such crops as corn and tobacco which have a much longer growing season and which are more easily controlled under unfavorable weather. Another tremendous advantage is the larger size of the plant parts to be measured.

The literature on the inheritance of size in wheat characters has been little more than general observation.

Backhouse (4) has found the length of glume in crosses of Polish wheat with durum and club wheats to be intermediate in the F_1 and to segregate 1:2:1 in the F_2. Tschermak was unable to determine the ratio in the second generation.

Parker (53,54) found density of the spikelet to be correlated with the number of spikelets per head, in a single variety of wheat. He also found the F_1 of a Polish-durum and club wheat cross to be intermediate in the F_1 and segregation to take place in the F_2, both ordinary and transgressive.

Biffen (6) found seed length not to segregate until the F_3 (endosperm). The F_2 was larger than either parent. He also found length to be correlated with length of the glume.

DESCRIPTION OF THE MATERIAL

All the material used was grown during the summer of 1917 in the spring wheat nursery on the farm of the Minnesota Agricultural Experiment Station at St. Paul, Minnesota. It consisted of nearly one thousand single plants of wheat. The heads from each plant were harvested separately and placed in paper envelopes. The parent wheats, Marquis, Preston, and Bluestem, had originally been selected from single plants. The crosses were made in the summer of 1915, the F_1 was grown in 1916, and the F_2 on which the study was made in 1917. The F_2 plants were from the crosses (a) Preston x Marquis, (b) Marquis x Preston, and (c) Bluestem x Marquis. The grain for the determination of the number of seeds necessary to make a reliable sample, was obtained from strains of Marquis and Preston wheats grown in rod rows. Each strain represents the progeny of an individual plant selected a number of years previously.

METHODS OF WORK

In taking the data the degree of accuracy of measurement was as far as possible commensurate with the variability of the character. For the single plants, three heads were usually measured. However, if the plant was a large one, four or even more were used. Care was practiced in selecting the heads not to include immature and undeveloped ones and at the same time not to select the best heads only. If a plant did not have three good heads it was discarded entirely.

The instruments used in measuring the size and weight were:

1. Six centimeter celluloid rule, graduated to millimeters.
2. Vernier calipers, graduated to tenth millimeters.
3. Chemical balance, graduated to tenth milligrams.

In measuring the length of the head, the centimeter rule was used. For measuring the length of the beak, and for the length and width of the seed, the vernier calipers were used. In weighing the 100 seeds per plant and for the weighing of the twenty-five seed samples, the chemical balance was employed.

The following data were taken on each head. The average of three heads being taken as the measurement for the plant in question.

1. The length of head in millimeters.
2. The number of spikelets per head.

3. The index of density of the head. This was obtained by dividing the length of the head by the number of spikelets per head, less one.

4. The length of the beak in tenth millimeters. The beak on the fifth spikelet from the base was measured.

5. Presence or absence of awns.

6. Presence or absence of hairy chaff.

7. The length of the seed in tenth millimeters.

8. The width of the seed in tenth millimeters.

9. The index of size of the seed. This was obtained by dividing the length by the width.

10. The date on which the central culm of the plant came into full head.

11. The weight of one hundred seeds in milligrams. This was taken on the plant as a whole since no single head contained one hundred seeds.

In the study of the inheritance of the seed weight the question arose regarding the number of seeds it was necessary to weigh in order to have a representative sample. To state the question another way would be to ask: how accurate can the weight of 100 seeds of a variety of wheat be considered in judging the true average weight of the variety?

To determine this point four hundred and eighty samples of twenty-five seeds each were taken from the two varieties, Marquis and Preston. The counting of the samples was done as carefully as possible, taking the seeds as they came, in order to reduce the human equation in the counting. The seeds were well developed. The two varieties were selected because they were the ones with which the study was to be concerned. However it would be almost impossible to find better ones for the purpose. As can be seen from Tables 7A and 7B they are entirely different in shape. Marquis is wide and short. Preston is long and narrow.

The samples were weighed to the third place on a chemical balance. To increase the accuracy the practice was made of splitting the fourth place.

The four hundred and eighty samples were then re-combined so as to make two hundred and forty samples of fifty seeds each. This recombination was continued until there were samples of from twenty-five up to one thousand seeds each. The recombination was so done that no twenty-five seed samples were used twice in making the samples of any one population. A study of the columns giving the number of seeds per sample and the number of samples in the population will show this.

All the population were then arranged according to their frequency distributions. See Tables A and B.

The first parts of the tables showing the frequency distribution of the populations needs no explanation. It is interesting to note that the extent of distribution is exactly two hundred milligrams in both varieties.

In the second part of each table is given the Means, Standard Deviations, and the Coefficients of Variability together with their Probable Errors.

These Means, as would be expected, have only a slight variation. Marquis is about eighty milligrams heavier.

Table A

The Number of Seeds Necessary to Make an Average Sample

Frequency Distribution of Classes of the Population by Weight.

Marquis

Class centers for the average weight of twenty-five seeds in milligrams

No. of seeds in sample	675	680	685	690	695	700	705	710	715	720	725	730	735	740	745	750	755
25	1	1			2	1	1	4	4	2	7	14	6	19	17	17	18
50									1	1		1	2	7	5	11	7
75													1	7		6	6
100											1			1		4	4
125																3	2
150																1	1
200																1	
250																	
300																	
500																	
800																	
1000																	

No. of seeds in sample	760	765	770	775	780	785	790	795	800	805	810	815	820	825	830	835	840	845	850	855	860	865	870	875	Total no. of samples
25	30	28	26	31	30	30	20	29	27	32	14	10	13	11	11	7	2	4	3	3		2	1	2	480
50	12	18	23	22	26	19	19	18	13	10	7	9	5		2	1			1						240
75	5	11	19	14	18	26	13	8	10	6	5	1	1	1	1	1									160
100	3	8	15	13	19	13	13	9	8	5	4														120
125	5	12	6	15	9	15	14	6	5	2	2														96
150	2	7	7	17	14	10	8	6	3	1	3														80
200	1	4	7	9	16	7	9	3	2				1												60
250	2	3	6	9	10	7	6	5																	48
300		2	8	5	6	9	7	2		1															40
500		1		7	8	5	2	1																	24
800				4	8	1	2																		15
1000				3	3	6																			12

Table A (Continued)

Total no. of seeds weighed	No. of seeds per sample	No. of samples	Mean	S.D.	C.V.
12000	25	480	779.6 ± 1.00	32.62 ± .71	4.18 ± .09
"	50	240	779.8 ± .95	21.78 ± .67	2.79 ± .09
"	75	160	779.5 ± .99	18.61 ± .70	2.38 ± .09
"	100	120	780.2 ± .96	15.57 ± .68	2.00 ± .09
"	125	96	779.6 ± .94	13.61 ± .66	1.75 ± .09
"	150	80	780.5 ± .92	12.21 ± .65	1.56 ± .08
"	200	60	780.4 ± .96	11.00 ± .68	1.41 ± .09
"	250	48	779.6 ± .91	9.35 ± .64	1.20 ± .08
"	300	40	780.9 ± .98	9.14 ± .69	1.17 ± .09
"	500	24	780.4 ± .86	6.28 ± .61	.80 ± .08
"	800	15	780.3 ± .81	4.64 ± .57	.59 ± .07
"	1000	12	781.3 ± .84	4.33 ± .60	.55 ± .07

Table B.
The Number of Seeds Necessary to Make an Average Sample

Frequency Distribution of Classes of the Population by Weight.
Preston

Class centers for the average weight of twenty-five seeds in milligrams

No. of seeds in sample	600	605	610	615	620	625	630	635	640	645	650	655	660	665	670	675	680	685	690	695	700	705	710	715	720	725	730	735	740	745	750	755	760	765	770	775	780	785	790	795	800	Total no. of samples
25	3		1	1	5	5	8	5	8	6	10	10	6	10	25	18	26	23	25	36	18	16	39	17	20	27	21	14	24	12	10	5	5	8	6	4		1	1		1	480
50									3	5	4	2	5	6	8	11	20	10	12	21	17	12	19	24	19	13	9	6	4	7	1	2										240
75									1		1		3	4	4	8	11	9	14	16	17	15	16	9	10	8	4	6	2	1			1									160
100										1		2	2	2	3	2	8	4	11	15	16	15	10	4	12	6	6	1														120
125											1		1		2	3	4	5	15	8	8	16	12	10	7	4																96
150															2	3	2	4	10	16	11	13	2	7	3	6		1														80
200															1	2	1	6	9	9	5	8	8	2	5	3	1															60
250																	1	7	5	3	7	13	7	3	2																	48
300																		2	4	9	9	8	4	2	2																	40
500																		1	2	7	4	5	3	2																		24
800																				3	7	4	1																			15
1000																			1	2	3	5	1																			12

Table B (Continued)

Total no. of seeds weighed	No. of seeds per sample	No. of samples	Mean	S.D.	C.V.
12000	25	480	700.06 ± 1.12	36.32 ± .79	5.19 ± .11
"	50	240	699.94 ± 1.08	24.86 ± .76	3.55 ± .11
"	75	160	700.13 ± 1.08	20.20 ± .76	2.88 ± .11
"	100	120	700.00 ± 1.12	18.17 ± .79	2.59 ± .11
"	125	96	700.21 ± 1.02	14.87 ± .72	2.12 ± .10
"	150	80	700.25 ± 1.04	13.71 ± .73	1.95 ± .10
"	200	60	700.50 ± 1.19	13.67 ± .84	1.95 ± .11
"	250	48	700.65 ± 1.00	10.24 ± .70	1.46 ± .10
"	300	40	700.88 ± .91	8.51 ± .64	1.21 ± .09
"	500	24	700.63 ± 1.08	7.81 ± .76	1.11 ± .11
"	800	15	700.33 ± .85	4.90 ± .60	.70 ± .09
"	1000	12	701.25 ± .92	4.71 ± .65	.67 ± .09

The Standard Deviation shows a steady decline as the size of the sample increases. This is true of both varieties, though for some reason Preston is more variable than Marquis. This increased variability is probably a varietal characteristic and in this case may be due to the smaller mean weight.

The Coefficient of Variability also shows a steady decline in value as the size of the sample increases. Looking at this column in the Marquis wheat it is seen that the difference between twenty-five and fifty seed samples is greater than ten times the probable error. Between fifty seeds and seventy-five and between seventy-five and one hundred the difference is about five times the probable error. The difference between one hundred seeds and one hundred and twenty-five is less than three times the probable error. To conclude, it seems reasonable that one hundred seeds is the smallest number that should be weighed, though two hundred and fifty is more accurate and five hundred still more so. It is probably never necessary to weigh more than five hundred.

The same is true of Preston though not to the same extent as is true of Marquis. It will be necessary to weigh more seed in the case of the Preston variety to equal the Marquis variety.

Practicability then will decide whether one hundred or more seeds must be weighed. In the case of the grain from single plants it will be found that one hundred will be the best, since, in most varieties of wheat, conditions must be exceptional in order to have an average of many more than one hundred seeds per plant.

DIFFERENTIATING CHARACTERS

The three wheats on which this study was made are the most widely grown varieties of spring wheat in Minnesota.

The following table gives their differentiating characters in comparison with each other

Character	Marquis	Preston	Bluestem
Awns	absent	present	absent
Chaff	smooth	smooth	hairy
Average beak length	.62 mm.	1.72 mm.	.67 mm.
Average head length	80.89 mm.	95.23 mm.	92.28 mm.
Average head density	4.77 mm.	4.97 mm.	4.66 mm.
Average weight of 100 seeds	3.31 gm.	2.99 gm.	
Average seed length	5.22 mm.	5.73 mm.	
Average seed width	3.14 mm.	2.83 mm.	
Average index	1.66 mm.	2.03 mm.	
Date of heading	6-29+	6-29+	7-5+

Marquis and Bluestem are both classed as awnless. However, according to Howard and Howard (36) they should both be classed as having long tips, (i.e. awns, usually not very long, growing at the tip of the head). Since none of the commercial wheats grown in the United States are really awnless, the above varieties are called awnless and are so considered throughout this study.

INHERITANCE OF THE DIFFERENTIATING CHARACTERS

The mode of inheritance of each differentiating character is first discussed separately and this is followed by a study of correlation between several of the characters.

Awns versus beardless. Data obtained from a study of the second generation of reciprocal crosses between Preston, a bearded wheat, and Marquis, which is classified as awnless (it has slight tip awns), are given in Table I. The F_1 generation has considerably longer awns than Marquis and the F_2 was classified as awnless, intermediate, and awned; ratios being obtained of 1:1.1:1.3 and 1:1.1:1.4 respectively. However, when the awned are considered as one class and the intermediate and awnless as another, the ratio is fairly close to expectation for a single factor difference or 1:3.15. This shows the difficulty in all cases of classifying the heterozygous types, especially when preserved material is used. The populations are too small to give conclusive evidence. Howard and Howard (35,36) found ratios very close to theoretical expectation for a single factor difference from similar crosses.

According to Tschermak (68) inheritance of beards follows Mendel's law strictly, the beardless condition being dominant. Vilmorin (73) in a cross of a common wheat with a durum, found tip awns in the F_1 and four forms in the F_2. Two were like the parents and the others were similar to those found on poulard and spelt. Biffen reports that beardless is strictly dominant with no intermediate and the F_2 segregating 3:1. Rimpau (59) also found the beardless condition dominant. Howard and Howard (35,36) have demonstrated at least two factors for awns. They describe four types of wheat heads -- bearded, short tips, long tips, and totally beardless. The factors are described as a factor for long beards, B; a factor for short beards, T; B is an intensifier; T serves to distribute the tips over the entire length of the head.

Hairy versus smooth chaff. The Bluestem parent has hairy chaff, while the Marquis parent has smooth chaff. The F_2 generation gave 210 hairy to 72 smooth, or a ratio of 3:.93. These wheats apparently differ by a single factor for presence and absence of hairy chaff. While the F_1 is somewhat less densely hairy than the Bluestem parent it is impossible to separate with accuracy homozygous and heterozygous hairy sorts in the F_2 generation of this cross.

According to Howard and Howard (35,36) there are two types of hairs found on the glumes of the head. One is short and dense, the other long and silky. Each is due to a single factor and is inherited separately. Biffen (6) found in some crosses that the velvet chaff was dominant in the first generation and segregated in the second. In other cases the ratio was 2:1 in the F_2 and the degree of felting was not the same in all cases. Tschermak (68) says that hairy chaff follows Mendel's law strictly in its inheritance. Rimpau (56 , 59) found hairy chaff to be dominant, recessive or intermediate in the F_1. Henkemeyer (33) also says that it is not always dominant in the first generation.

Head length. Table III is a presentation of head length of the three parent sorts, Marquis, Preston, and Bluestem and F_2 generations of crosses between Preston and Marquis and its reciprocal, and Bluestem x Marquis. From a study of the frequency distribution, the F_2 seems somewhat more variable than the parent. Comparing the more variable Marquis with the least variable F_2 cross between Marquis and Preston, a difference in coefficients of variability of $1.33 \pm .46$ is obtained which is about three times its probable error. The difference between the coefficient of variability of Bluestem and the F_2 Bluestem x Marquis is only $.67 \pm .52$.

Further discussion of the inheritance will be found in the discussion of head density. This is done because all previous work on head length has considered the problem from the viewpoint of the density of the head. This has been unfortunate, as our knowledge of the character would be greater if each character had been worked upon separately as well as in combination. The number of spikelets per head is probably correlated with the head length in some cases. Tables III and IV show that this is the case with the wheats studied. Parker (53) found a correlation coefficient of 0.9909 between the average

Table No.I
The Inheritance of Awns

Variety	No. Awned	No. Awnless	No. Intermediate	Total No.	Ratio
Marquis		110		110	
Preston	39			39	
Preston x Marquis F_2	76	97	87	260	1:1.3:1.1
Marquis x Preston F_2	27	39	31	97	1:1.4:1.1

Table No. II
The Inheritance of Hairy Chaff

Variety	No. Hairy	No. Smooth	Total No.	Ratio
Marquis		110	110	
Bluestem	67		67	
Bluestem x Marquis F_2	210	72	282	3:0.93

Table III
Inheritance of Head Length

Variety	Head length classes in millimeters																	Total population	Mean	S.D.	C.V.
	63	66	69	72	75	78	81	84	87	90	93	96	99	102	105	108	111				
Marquis	1	1	1	8	5	20	33	26	8	6		1						110	80.89 $\pm$.032	4.98 $\pm$.023	6.16 $\pm$.28
Preston				1				1		4	5	14	13	1				39	95.23 $\pm$.060	5.57 $\pm$.043	5.85 $\pm$.45
Bluestem					1	2	5	3	4	14	12	11	11	1	1	1	1	67	92.28 $\pm$.060	7.30 $\pm$.043	7.91 $\pm$.46
Preston x Marquis F_2			1	5	7	11	29	34	44	45	45	15	14	5	5			260	88.23 $\pm$.033	7.98 $\pm$.024	9.04 $\pm$.27
Marquis x Preston F_2			1	1	3	3	5	12	22	22	9	9	7	3				97	88.73 $\pm$.046	6.65 $\pm$.032	7.49 $\pm$.36
Bluestem x Marquis F_2	1	1	2	8	9	22	27	51	43	53	35	15	11	2	3	1		284	86.71 $\pm$.030	7.44 $\pm$.021	8.58 $\pm$.24

Table IV
Inheritance of Number of Spikelets per Head

Variety	Number of spikelets per head 14	15	16	17	18	19	20	21	22	23	Total population	Mean	S.D.	C.V.
Marquis		2	2	23	45	33	5				110	18.10 ±.062	.96 ±.044	5.29 ±.24
Preston						6	16	15	2		39	20.33 ±.086	.80 ±.061	3.92 ±.30
Bluestem					1	3	12	37	12	1	67	20.58 ±.061	.75 ±.043	3.62 ±.21
Preston x Marquis F_2		1	4	19	69	91	60	16			260	18.88 ±.046	1.10 ±.033	5.85 ±.17
Marquis x Preston F_2	1		1	4	21	35	28	7			97	19.05 ±.078	1.14 ±.055	5.98 ±.29
Bluestem x Marquis F_2			5	15	48	109	82	20	5		284	19.15 ±.045	1.12 ±.032	5.83 ±.17

length of the internode and the total length of the ear in Squarehead's Master wheat. Bringing the number of spikelets per head into consideration with the head length has been the cause of added difficulties, always found where more than one character is being studied. The fact that both characters are variable ones, Parker (54) does not add to the ease of solution of the problem.

Number of spikelets. The number of spikelets of the parents and F_2 generation crosses is given in Table IV, Preston and Bluestem average somewhat higher than Marquis in number of spikelets. Segregation occurs in F_2 although the coefficient of variability of Marquis is nearly as large as in the F_2 generations. The difference, for example, in the coefficient of variability of the F_2 of Preston x Marquis and Marquis is only $.56 \pm .29$. Preston and Bluestem have, however, significantly lower variabilities than any F_2 generations.

The number of factors concerned can not be accurately determined from the data presented. However, it is very plain that the character is inherited and that segregation does take place.

Head density. The parents do not differ very widely in this regard. Preston has a somewhat more lax head than Marquis or Bluestem. The F_2 generations are approximately as lax as the more lax parent and are somewhat more variable than the parents. For example the difference in coefficients between Bluestem and the F_2 cross between Bluestem and Marquis is $.88 \pm .35$.

Table No. V
Inheritance of Head Density

Variety	Head length divided by number of spikelets								Total population	Mean	S.D.	C.V.
	3.9	4.2	4.5	4.8	5.1	5.4	5.7	6.0				
Marquis		4	29	54	21	1		1	110	4.77 ± .017	.26 ± .012	5.49 ± .25
Preston	1		2	14	17	5			39	4.97 ± .031	.29 ± .022	5.77 ± .44
Bluestem		7	24	31	4	1			67	4.66 ± .02	.25 ± .014	5.30 ± .31
Preston x Marquis F_2		6	37	90	85	33	9		260	4.95 ± .013	.32 ± .095	6.46 ± .19
Marquis x Preston F_2		5	11	30	32	18	1		97	4.95 ± .023	.33 ± .016	6.65 ± .32
Bluestem x Marquis F_2	3	12	72	115	68	13	1		284	4.79 ± .012	.30 ± .084	6.18 ± .17

Rimpau (56, 59) states that density of the ear is dominant. Tschermak (68) found density recessive but adds that the question needs further investigation. Biffen(6) says that deneness may be recessive or intermediate in the F_1. In the F_2 he obtained different results. In some crosses the ratio was 1:2:1, though in most of the trials the ratio was irregularly 3:1. Parker (54) states that Nilsson-Ehle also obtained different results with different crosses. He says further that Spillman, Strampelli, and Rumker all obtained an intermediate F_1 and a ratio of 1:2:1 in the F_2. Parker found in crosses made between a dense and a lax wheat that the F_1 was intermediate, tending toward dense. The F_2 gave transgressive segregation for both laxness and denseness beside all the intermediate forms. In the F_3 nearly all the lax bred true and a portion of the dense also. Gmelin (30) also found density intermediate in the F_1 and transgressive segregation for very dense ears in the F_2.

Length of beak. The beak is the extension of the outer glume. Results for the measurements of this character are found in Table VI.

In the inheritance of this character an entirely new condition presents itself. Transgressive segregation has taken place to a remarkable extent. Furthermore this condition is found only in the crosses between Marquis and Preston wheats, i.e. between a beardless and a bearded wheat. The cross between the two awnless wheatsshows no such tendency. Why a cross between two wheats whose average beak length is less than two millimeters should produce a beak with a length

Table No. VI
Inheritance of Beak Length

Variety	Beak length classes in millimeters .5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0
Marquis	84	26																				
Preston		1	21	16	1																	
Bluestem	66	1																				
Preston x Marquis F_2	62	106	13		3	3	7	11	7	8	9	3	5	7	3	3	3	2	1	1	1	2
Marquis x Preston F_2	23	47			1	2	2	4	3	4	2	2	3	2	2							
Bluestem x Marquis F_2	178	106																				

Table No. VI (Continued)

Variety	Beak length classes in millimeters 11.5	12.0	12.5	13.0	Total population	Mean
Marquis					110	.62 ±.040
Preston					39	1.72 ±.016
Bluestem					67	.51 ±.050
Preston x Marquis F_2				1	260	2.33 ±.105
Marquis x Preston F_2					97	2.01 ±.140
Bluestem x Marquis F_2					284	.81 ±.098

of thirteen millimeters is hard to determine. Furthermore almost exactly twenty-five per cent of the F_2 of the Marquis-Preston crosses have beaks longer than twice the average of the parents. This suggests the explanation of an intensifier in the Marquis parent but not in the Preston parent. The intensifier would satisfy the condition found in the Marquis x Bluestem cross also, as no awns are present. Further study is of course necessary but the ratio found is very suggestive.

Width, length, and index of kernels. The study of seed size character was made in the Preston x Marquis cross only, and even then the number of measurements is too small to be very conclusive. Ten seeds for each plant were used, only average seeds of normal plumpness being selected. Data for width, length, and index are given in Table VII, A, B, and C. The difference in seed width is so small that measurements are not very reliable, However, forms like the parents for both width and length were obtained in F_2 as well as narrow short seeded plants and those with long, broad kernels (see Fig. 1).

These results show that it is possible to obtain recombination and thus new varieties which have short seeds like Marquis and narrow seeds like Preston as well as long broad seeded sorts.

In part C of the table, the parent and F_2 generations are compared for seed index, i.e. length divided by breadth. The F_2 generation is somewhat more variable than the parent sorts. Comparing Marquis with a population of 51 and a

Table No. VII, A.B.C.
Inheritance of Size of Seed
A. Width of seed.

Variety	Average width of ten seeds in millimeters									Total population	Mean	S.D.	C.V.
	2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3	3.4				
Marquis			2	1	7	16	15	8	2	51	3.14 ±.012	.130 ±.009	4.14 ±.277
Preston	3	4	10	13	2	1				35	2.83 ±.013	.113 ±.009	3.99 ±.322
Preston x Marquis F_2		1	5	17	17	13	6	1		60	3.00 ±.011	.124 ±.008	4.13 ±.254
Marquis x Preston F_2		3	4	18	33	26	6			90	3.00 ±.008	.111 ±.006	3.70 ±.186

B. Length of seed.

Variety	Average width of ten seeds in millimeters														Total population	Mean	S.D.	C.V.
	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9	6.0				
Marquis		1	2	3	7	17	14	6			1				51	5.22 ±.014	.149 ±.010	2.85 ±.190
Preston						1		1	1	6	10	6	5	3	35	5.73 ±.019	.166 ±.013	2.89 ±.239
Preston x Marquis F_2						8	10	15	10	8	5	3			60	5.43 ±.017	.192 ±.012	3.54 ±.218
Marquis x Preston F_2		1	1	2	2	8	18	20	12	16	4	4	1	1	90	5.43 ±.015	.208 ±.010	3.83 ±.193

C. Index

Variety	Length of seed divided by width of seed													
	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.05	2.10	2.15	2.20
Marquis	7	8	20	18	1	1								
Preston								1	6	12	9	5	1	2
Preston x Marquis F_2			1	3	15	13	17	6	4	1				
Marquis x Preston F_2			5	10	13	27	20	9	2	2	1		1	

C. (Continued)

Variety	Total population	Mean	S.D.	C.V.
Marquis	51	1.66 ±.005	.049 ±.003	2.95 ±.197
Preston	35	2.03 ±.007	.064 ±.005	3.15 ±.254
Preston x Marquis F_2	60	1.82 ±.006	.071 ±.004	3.88 ±.240
Marquis x Preston F_2	90	1.81 ±.006	.083 ±.004	4.59 ±.336

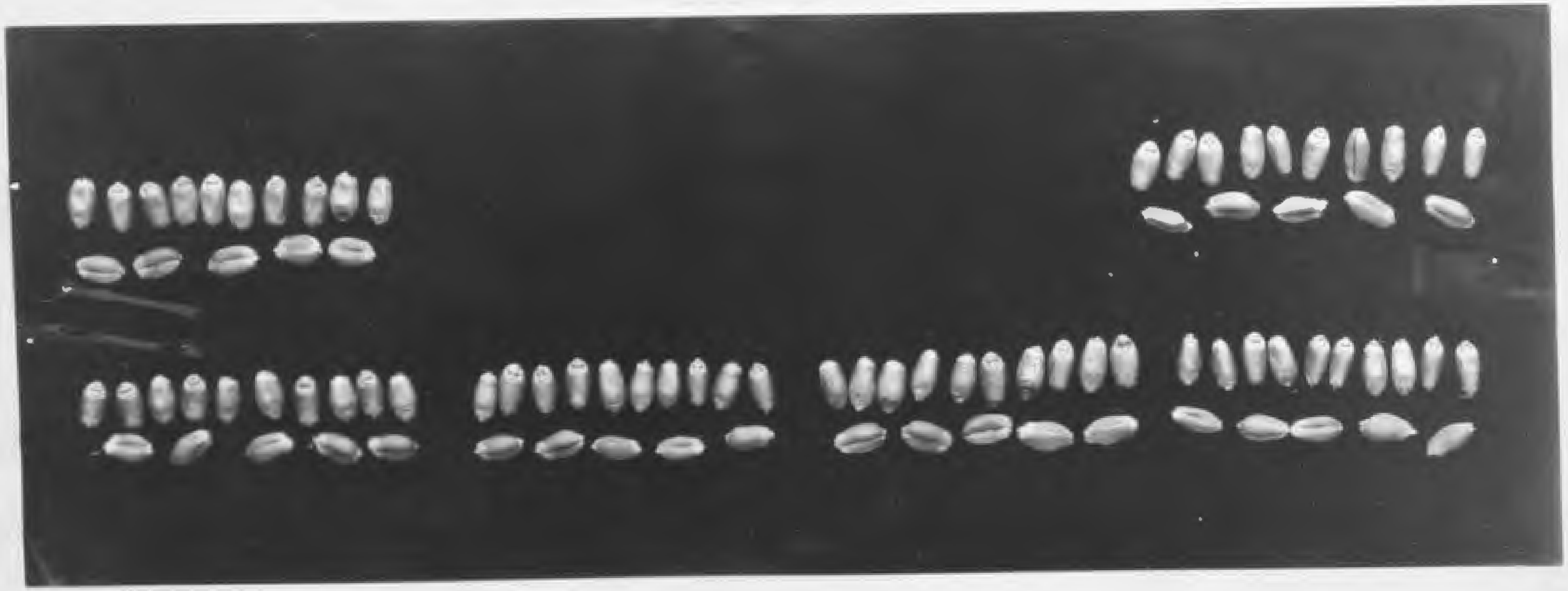

Fig. 1. Upper left, Marquis parent; Upper right, Preston parent; below, kernels of four individual F_2 plants, left to right respectively, resembling the Marquis parent; a plant with the seed length of Marquis and seed width of Preston; a plant with the seed width of Marquis and seed length of Preston and an F_2 plant resembling Preston.

coefficient of variability of 2.95 ± .197 with Marquis x Preston F_2 with a population of 90 and a coefficient of variability of 4.69 ± .236 gives a difference of 1.74 ± .31 which is approximately 5.6 times the probable error.

Seed weight. Determinations of seed weight are given in Table VIII, the average weight of 100 seeds being somewhat greater for Marquis than for Preston. The F_2 generation approaches Marquis in this particular although the differences between the parents and crosses are not very large. There is some indication that transgressive segregation has occurred for this character and it seems resonable to suppose that a plant with the seed width of Marquis and the seed length of Preston might have heavier seeds than either parent variety.

The practical value of this conclusion is very great. Grabner (31) has found a positive correlation of yield with the weight of one thousand grains. This then would show that it is possible to produce higher yielding wheats by crosses such as the ones under consideration.

Date of maturity. Data obtained at the Minnesota Station and by other investigators have shown that date of heading is an accurate means of determining the genotypic maturity of small grains. Marquis and the strain of Preston used in these experiments mature at about the same time, while Bluestem is about a week later. The cross between Bluestem and Marquis has a mean intermediate between Marquis and Bluestem and is somewhat more variable than the parental varieties. Comparing Marquis with a coefficient of varia-

Table No. VIII.
Inheritance of Seed Weight

Variety	Weight of 100 seeds in grams												
	2.35	2.50	2.65	2.80	2.95	3.10	3.25	3.40	3.55	3.70	3.85	4.00	4.15
Marquis			1	2	2	8	10	16	11	2			
Preston	1	1	2	3	12	9	6	1					
Preston x Marquis F_2				1	5	10	9	8	5	3			
Marquis x Preston F_2			4	3	5	13	27	19	10	5			1

Table No. VIII(Continued)

Variety	Total population	Mean	S.D.	C.V.
Marquis	52	3.31 ± .021	.23 ± .015	6.89 ± .46
Preston	35	2.99 ± .025	.22 ± .018	7.29 ± .59
Preston x Marquis F_2	41	3.26 ± .024	.23 ± .017	6.96 ± .52
Marquis x Preston F_2	90	3.29 ± .020	.28 ± .014	8.45 ± .42

Table No. IX
Inheritance of Maturity

Variety	Date heading														
						7/1	7/2	7/3	7/4	7/5	7/6	7/7	7/8	7/9	7/10
	6/26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Marquis		2	9	29	50	4	4	5	1						
Preston				17	14	4	2								
Bluestem						1	2	3	7	29	18	7			
Preston x Marquis F_2	2	9	36	37	81	18	37	30	6				1		
Marquis x Preston F_2		2	17	11	48	2	11	3							
Bluestem x Marquis F_2				2	11	8	61	68	14	66	16	4		1	1

Table No. IX (Continued)

Variety	Total population	Mean	S.D.	C.V.
Marquis	104	29.79 ± .082	1.24 ± .085	4.16 ± .19
Preston	37	29.76 ± .095	.85 ± .067	2.86 ± .22
Bluestem	67	35.13 ± .100	1.21 ± .071	3.44 ± .20
Preston x Marquis F_2	256	30.39 ± .077	1.82 ± .054	6.00 ± .18
Marquis x Preston F_2	94	29.81 ± .093	1.33 ± .066	4.47 ± .22
Bluestem x Marquis F_2	252	33.42 ± .073	1.72 ± .052	5.16 ± .16

Note: In the above table the July dates of heading are given as June dates 31-40. This is done in order to maintain numerical sequence.

bility of 4.16 $\pm$ .19 and the F_2 of Marquis x Bluestem with a coefficient of 5.16 $\pm$ .16 gives a difference of 1.00 $\pm$ .25.

There is some indication that transgressive segregation has occurred in the cross between Preston and Marquis. Thus crossing two varieties with similar maturity may produce by recombination new sorts which are earlier and later than the parents. In this case we may suppose that the genotypic factors for maturity are different in the parental varieties.

Biffen (6) found, studying the inheritance of the time of maturity, that an approach to the late condition was obtained in the first generation and that the second generation segregated with the ratio of 1:2:1.

Correlation between index of seed size and presence of awns. Frequency populations for length of seed divided by width for the F_2 Marquis x Preston segregating classes, awnless, bearded, and intermediate, are given in Table X. In both crosses the mean index is higher for the bearded than for the awnless plants. This is of considerable interest and merits further investigation. There are two possibilities, either that the factor for beards has also an effect on seed size or that the factor for seed length of the Preston is genetically linked in inheritance with the factor for beards. If this is so, crossing-over evidently occurs, for low index bearded plants are occasionally obtained as well as high index awnless ones.

Beards in wheat have often been considered to be of considerable physiological importance. Perlitius (55) has shown that the awns of the wheat head exert an important

Table X A and B.
Correlation of Index of Seed Size and Presence of Awns or Beards

A. Marquis x Preston F_2

	Length of seed divided by width; in millimeters.											Total population	Mean	S.D.
	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.05	2.10	2.15			
Awnless	1	6	8	13	5	4						37	1.80 ±.006	.057 ±.004
Bearded			2	4	10	2	2	2	1		1	24	1.90 ±.010	.071 ±.007
Intermediate	2	4	5	10	5	3						29	1.80 ±.005	.035 ±.003

B. Preston x Marquis F_2

	Length of seed divided by width; in millimeters								Total population	Mean	S.D.
	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00			
Awnless	1	3	6	7	5	2	1		25	1.78 ±.010	.075 ±.007
Bearded			7	3	7	3	2	1	23	1.83 ±.014	.096 ±.010
Intermediate			2	3	5	1	1		12	1.82 ±.021	.108 ±.015

influence on the quality and weight of the grain. He found that the transpiration of the head was increased as much as one hundred per cent by the presence of awns. He also found that the intensity of transpiration was in close relation with the development of the grain and was greatest at the time of greatest development of the grain. Fleischmann (26) found that bearded wheat had the following advantages: It was more resistant to yellow rust, more frequently high yielding, had stronger straw, and greater weight per thousand grains. As has been stated, Grabner (31) found that the weight per thousand grains is positively correlated with the yield of the variety. The data given, together with the references quoted, show then that the bearded wheat has a distinct advantage over the beardless. That this advantage is so great as to make the selection of bearded wheats alone advisable is doubtful, especially when it is remembered that two beardless wheats, Marquis and Bluestem, are grown more widely in Minnesota than any bearded variety. However, the advantage is sufficient to show that the possibility of finding the high-yielding wheats is greater among bearded wheats than among beardless ones; and this fact should be remembered in breeding for increased yield.

<u>The correlation of the beak length and the presence of awns.</u> The correlation found in this table, while much greater than that of the preceding ones, is probably not so important. If it were not for the few exceptions found in Part B of the table, the long beaks would afford a decisive

Table XI A and B.
Correlation of Beak Length and Presence of Awns or Beards

A. Marquis x Preston F_2

	Length of beak in millimeters															Total population	Mean	S.D.
	.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5			
Awnless	21	18														39	.73 $\pm$.027	.25 $\pm$.019
Bearded					1	2	2	4	3	4	2	2	3	2	2	27	5.06 $\pm$.182	1.40 $\pm$.128
Intermediate	2	29														31	.97 $\pm$.016	.13 $\pm$.011

B. Preston x Marquis F_2

	Length of beak in millimeters																									
	.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0
Awnless	53	42	2																							
Bearded			1		3	3	7	11	7	8	9	3	4	7	3	3	3	1		1	1					1
Intermediate	9	64	10										1					1	1		1					

B. (Continued)

Awnles	Total population	Mean	S.D.
Awnless	97	.74 $\pm$.018	.27 $\pm$.013
Bearded	76	5.45 $\pm$.155	2.01 $\pm$.120
Intermediate	87	1.37 $\pm$.121	1.68 $\pm$.086

means of determining the plants with intermediate awns, which are found on the heterozygous plants in the crosses of bearded with beardless. The criterion would be useful, not only in the first generation where it would be an evidence of hybridity, but also in the later generations when the plants heterozygous for beards could be determined very easily. It is very possible that the exceptions noted will prove to be, on further study, nothing more than mistakes made when the data were taken.

SUMMARY

1. The progress made in breeding wheat was very slow in the years preceding 1890. Owing to the pedigree principle of Vilmorin, the rate of advance was increased. It was not until 1900, when Mendel's law was rediscovered, that wheat breeding became a promising field of study. The progress made since then has been very rapid, both from an economic as well as a scientific standpoint.

2. The study of size inheritance is a complex one requiring a large amount of data and very careful study to determine its nature, so that conclusions drawn from small populations can be only general in nature, though very valuable in indicating the direction for continued study.

3. In weighing a sample of wheat to determine the average of the variety, at least 100 seeds are necessary and 250 are still better. Samples of more than 500 are not enough more accurate to advise their use.

4. The inheritance of awns is not so simple as is generally thought to be the case. Sometimes two factors are concerned.

5. Hairy chaff, when of the simple dense type found in Bluestem wheat, is due to a single factor which

segregates in the ratio of 3:1 in the second generation.

6. The length, width, and density of the head, together with the weight of the seed and the time of maturity, are all due to a complex of factors and while each is inherited with segregation in the second generation the data presented in this paper are not sufficient to determine more in regard to their inheritance.

7. Beak length as well as seed size segregate in F_2 and in some cases transgressive segregation occurs.

8. There is a correlation between seed index and beak length with presence of awns.

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