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A Study of Size Inheritance in Wheat

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A STUDY OF SIZE INHERITANCE IN WHEAT

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INTRODUCTION

The results presented in this paper are from data accumulated by a study of the F3 generation of a cross between the two varieties, Sevier and New Zealand wheat. This cross was made during the summer of 1920 by Professor George Stewart with the object of combining the high-yielding power of Sevier with the strong straw of New Zealand. In the fall of 1922 the problem was assigned to me, at which time I selected about 150 superior plants, possessing the desired characteristics, at least so far as appearance was concerned. Since then these plants and the F3 generation have been studied mainly with the object of finding out whether size characters behave in Mendelian fashion or not. Other characters received attention incidentally, and will also be reported briefly.

To study a variable problem with any degree of accuracy there must of necessity be a definite means by which variations may be measured. Size differences in straw are extremely difficult of measurement, and measurements at best can only be approximations. It was decided, therefore, to make a careful study of size variations in wheat heads, and only estimate straw strength.

The study of this problem is valuable for two main reasons:

1. If high-yielding power and straw strength can be combined from two different varieties it is worth knowing because of the economic value of such a combination.

From this point of view the original object of the cross under discussion itself justifies the investigation.

2. Since it is not a definitely settled question as to whether heritable size fluctuations behave according to the principles of Mendelism the problem has both interest and value from the point of view of genetics.

REVIEW OF LITERATURE

Since (15) the re-discovery of Mendel's original papers, the point of interest among geneticists and plant and animal breeders, has been centered around the question: "Are the principles involved in the discoveries of Mendel of limited or of universal application"? This question is not yet answered, but the results of many experiments show affirmative evidence.

For some time (25) following the publication of Mendel's principles (1900) the followers of Mendelism placed exaggerated emphasis upon the phenomena of dominance and recessiveness. Many (13) investigators, however, were distrustful. The application of Mendelism broadened gradually, though, as dominance moved toward the background and other theories such as presence and absence, plus and minus came into use. It was found in later years that "perfect dominance was the exception rather than the rule, and that cases where dominance was entirely lacking were frequently found".

One of the main stumbling blocks to Mendelism (13) was the comparative frequency of quantitative variations. Most variations which behaved in a simple Mendelian fashion were qualitative in character. But a possible explanation of quantitative inheritance was given by Nilsson - Ehle in 1908, although he presented no experimental data to support his hypothesis. He arrived at this explanation through investigations with oats and wheat in which he found that certain colors were determined not by single gametic factors but by several.

East developed and presented a similar theory in the same year that Nilsson - Ehle published his. East arrived at his conclusions as a result of investigations with color inheritance in maize.

Following this, data supporting the idea of Mendelian inheritance of size characters accumulated rapidly.

At this point just a brief statement should be made regarding one type of size characters which segregate in simple definite ratios.

Mendel (1) dealt with one case of size inheritance in his original experiments. He found that when a tall pea is crossed with a dwarf pea the FI generation consists entirely of tall peas, and that the F2 generation breaks up into approximately the proportion of 3 tall to 1 dwarf. He noticed also that in the F3 generation the dwarfs bred true to dwarfness, and that one third of the tall peas bred true to tallness, but the other two thirds again segregated into the same ratio as was obtained in the F2 generation.

Similar results (1) are quite common in size studies involving differences between tall and dwarf plants. In a study of beans, (14) Emerson points out that "differentiating factors are factors for indeterminate as opposed to a determinate habit of growth". In this case it is possible to state definitely what size differences depend upon.

There are cases, however, (15) which can be explained by hypotheses other than those based upon Mendelian principles. Many characters which are expressed quantitatively may be cited as examples. In many such cases the F1 generation appears to be intermediate between the parents, and the F2 and subsequent generations show continuous segregation. Castle has reported a case which seems (7) to contradict a Mendelian explanation. The following quotation describes this case:

"A cross between rabbits differing in ear length produces offspring with ears of intermediate length, (12) varying about the mean of the parental ear lengths. - - - - - A study of the offspring of the primary cross-breds shows the blend of the parental characters to be permanent. No reappearance of the grand-parental ear lengths occurs in generation F2, nor are the individuals of the second generation as a rule more variable than those of the first generation of cross-breds. - - - - It seems probable that skeletal dimensions, and so proportions of skeletal parts, behave in general as blending characters. The linear dimensions of the skeletal parts of an individual approximate closely the mid-parental dimensions." ----

He then goes on to say: "It is probable that in plants, as well as in animals, linear dimensions are in general blending in their inheritance".

On the other hand (10) East aggressively defends the Mendelian interpretation of quantitative characters. The following quotation illustrates his attitude towards those who oppose the Mendelian explanation of size inheritance: "The true reason for objecting to the theory, therefore, seems to be - as is often the case - that those who disapprove of it have not given it sufficient study to be convinced that any real evidence in its favor can be cited".

He then lays down eight conditions which he says should be met by the pedigree-culture data when all populations succeeding the original cross are obtained by self-fertilization.

"1. Crosses between individuals belonging to races which from long continued self-fertilization or other close inbreeding approach a homozygous condition, should give F1 populations comparable to the parental races in uniformity.

"2. In all cases where the parent individuals may reasonably be presumed to approach complete homozygosis, F2 frequency distributions arising from extreme variants of F1 population, should be practically identical, since in this case all F1 variation should be due to external conditions.

"3. The variability of the F2 population from such crosses should be much greater than that of the F1 population.

"4. When a sufficient number of F2 individuals are available, the grant-parental types should be recovered.

"5. In certain cases individuals should be produced in F2 that show a more extreme deviation than is found in the frequency distribution of either grand-parent.

"6. Individuals from various points on the frequency curve of an F2 population, should give F3 populations differing markedly in their modes and means.

"7. Individuals either from the same or from different points on the frequency curve of an F2 population should give F3 of diverse variabilities extending from that of the original parents to that of the F2 generation.

"8. In generations succeeding the F2, the variability of any family may be less but never greater than the variability of the population from which it came."

Emerson in his extensive studies (12) is led to the conclusion that size characters behave in Mendelian fashion. He has reported inheritance of size in several plant crosses. In maize, from a cross of Queen's Golden pop-corn having small grains, with Black Mexican sweet corn having medium-sized grains, he found that the F1 generation was intermediate while F2, though uniform for any one plant, shows marked variation between different plants. Grains were found that were fully as large as those of the Black Mexican, and others that were quite as small as those of Queen's Golden.

In a cross between Tom Thumb pop-corn, a dwarf variety averaging 90 centimeters in height, and Missouri dent with an average height of 225 centimeters, the F1 generation was as uniform as either parent and had an average height of about 182 centimeters. The F2 generation ranged in size from that of the Tom Thumb parent to above that of the F1 plants, but no plant was as tall as the tall parent.

He crossed a Yellow Crookneck Squash with a White Scallop. The Crookneck has a long neck with a bowl of only medium diameter. Scallop has very flat fruits. The F1 generation was intermediate in both dimensions and in shape, while F2 showed a complete series of dimensions and shapes ranging from one parent to the other.

He also studied a cross of a Striped Spoon gourd with Philipino Horned gourd. The Spoon gourd is relatively small and long, the Horned is relatively short and thick. The F1 generation was above the mid-parent in most dimensions and varied no more than either parent. The variation of the F2 plants was wide enough to include the variation of both parents.

In his three crosses of beans Longfellow crossed with Snowflake, Fillbasket with Longfellow, and Fillbasket with Snowflake, varieties varying in size and shape of seed, he noticed that the F1 hybrids were practically intermediate and exhibited no greater variation than either parent, while the F2 hybrids, on the contrary, showed a variation more than twice as great as that of the F1.

In 1913 Emerson and East (13) presented conjointly an extensive study of the inheritance of quantitative characters in maize. They describe in their report ten different kinds of quantitative data carefully tabulated, showing distributions with the calculated constants given in detail.

Inheritance of number of rows per ear was studied in eight different crosses. The parent varieties were of 8, 12, 16, and 20 rowed types. In nearly every case F1 was intermediate between the parents, though in the case of one cross of an 8 rowed with an apparently 12 rowed variety, the latter condition seemed to be dominant. In most cases the F2 generations had a wider range of variation than the F1, a range that included both parent types.

Inheritance of ear-length was studied in three crosses of distinct varieties. In each case the ear length of one parent was approximately two and one half times that of the other parent. In the cross of Tom Thumb with Black Mexican, the F1 ear length was distinctly intermediate between the parental ear lengths. In the cross of Missouri dent with California pop, on the other hand, the F1 generation had ears practically as long as those of the long eared parent, but the authors attribute the extreme length of the F1 ears in part to heterozygosis, as the means of the F2 families were distinctly intermediate between the parental means. In every case the F2 fraternities were more variable than the F1 lots, and in most cases the F2's completely bridged the gap between the parents. In one case the F2 range of variation was from practically the shortest ears of the short parent to beyond the longest ears of the long parent.

Two crosses were investigated for inheritance of diameter of ears. F1 ears were intermediate in diameter between those of the parents, but somewhat nearer the large eared than the small eared parent. The F2 ranges of variation little more than filled the gap between the parent races.

In crosses of Missouri with California pop and Tom Thumb, also Tom Thumb with Black Mexican, inheritance of weight of seed showed F1's as distinctly intermediate and F2 as markedly greater in variability than F1 or the parents.

Four different crosses were studied for inheritance of height of plants. A peculiarity of these crosses is that in three of them the F1 plants were almost as tall as the tall parent and in the fourth were considerably taller than the mean of the two parents. The authors do not ascribe this to dominance of tallness but rather to increased vigor accompanying heterozygosis, which they say, is indicated by the fact that in every case the mean height of the F2 plants is about half way between the heights of the parents. The F2's also overlap the inner extremes of the parents.

They report inheritance of number of nodes in two crosses, with the result that F1 families were strictly intermediate. The mean number of nodes in F2 was practically the same as in F1, which the authors explain indicates that number of nodes is not affected appreciably by heterozygosis. The F2 generation exhibited a wide range of variation.

Internode length showed a great increase which, it is explained, is due to heterozygosis. Frequently F1 plants were found to be as tall as the tall parent. The F2 plants extended above the plus and below the minus extremes of the parents, and above the plus extremes of the F1 generation.

Results in the two crosses studied showed an intermediate condition in the F1 generation for number of tillers and a wide variation in F2. The F3 generation showed a few one-stalked types.

In studying total length of stalks per plant, it was found that the short parent had many tillers, while the tall parent had relatively few. The total stalk length per plant was about equal for both parents. The F1 plants had an intermediate number of stalks, but a total stalk length exceeding that of the parents, and almost equal to the combined lengths of the parents. The range of variation in the F2 was considerably greater than in the parents, but due to an unfavorable season the F2 plants showed no unusual height.

The F1 plants were intermediate according to observations on inheritance of duration of growth. The F2 plants more than filled the gap between the parents in all cases.

In general the authors interpret the results as being what might be expected if quantitative differences were due to numerous factors inherited in a strictly Mendelian manner. They present evidence in favor of the view that length of ear is directly correlated with height of plant and inversely correlated with number of rows per ear. They also state that the multiple factor hypothesis furnishes a satisfactory and simple interpretation not only of all the results secured from maize experiments, but also of the results from experiments previously reported for other plants and for animals. They express themselves as being unfamiliar with any hypothesis not based upon Mendelian principles of segregation and recombination of factors which furnishes a plausible explanation of many of the facts regarding the inheritance of quantitative characters.

In the cases cited thus far size inheritance may be quite satisfactorily explained on a Mendelian basis in plants by the multiple factor hypothesis. The explanation is less simple in the case of animals, and yet an examination of a few investigations reveals the fact that the behavior of size inheritance in plants and animals is similar. But as (7) Castle points out, animals make less favorable material for study than plants because of being less pure.

Philips (7) crossed two breeds of ducks, Roun and Mallard which differ greatly in size. The F1 was intermediate and not more variable than either parent. The F2 was also intermediate but more variable than F1 or the parents. MacDowell (24) has reported similar results for rabbits.

In a cross (30) of Southdown with Rambouillet sheep Ritzman found the F2 generation more variable than F1, but neither generation showed sizes that exceeded those of either the large or the small foundation parent. He noticed also that different size characters did not inherit equally.

Quantitative studies of heads that have been reported (2,18,27) have been studied on the basis of rachis internode length. Boshnakian studied squareheadedness and density in wheat and found that squareheadedness was a quantitative character which did not segregate into "clear-cut Mendelian classes and ratios". Density, on the other hand was dominant over laxness and ratios obtained approached 3:1.

Nilsson - Ehle (26) crossed a compact variety of wheat with other varieties varying in density from average to low. Extremes which appeared to be quite new forms arose. In one cross described a compact variety crossed with one of average density he obtained the following results:

F1: all compact.

F2: segregated into 61 compact (of which 5 were decidedly more compact than either of the parent parts); 5 somewhat more out-drawn-compact; 28 of the foregoing group were sharply defined as average to more open-headed than either parent.

The F2 when planted gave the following results:

5 compact: very dense F3: 5 constant compact.

56 compact: F3 { 18 constant compact. 38 segregating into compact and 'not-compact'.

5 somewhat more out-drawn compact. F3: 5 segregating into compact and 'not-compact'.

28 'not-compact' F3 -- all progeny remained 'not-compact'.

Similar results (19) to those just described for wheat have been obtained for barley. From a study of several crosses of barley the following conclusions were reached by Hayes and Harlan:

"That internode length in the barley rachis is a stable character; that segregation occurs in the F2 generation and forms homozygous for density occur in this generation, their purity being demonstrated in F3; that in some crosses new lines with densities differing much from those of their parents cannot be secured, while in others lines with very different densities may be isolated; that inheritance of internode lengths may be interpreted on the factor hypothesis.

MATERIAL AND METHODS

Sevier wheat (34) was discovered and named by Professor George Stewart in Sevier County, Utah, during a small-grain variety survey in the summer of 1918. He tentatively classified it as a durum wheat. Samples of the wheat were sent to the office of cereal investigations of the United States Department of Agriculture, where J. A. Clark also pronounced it a variety of durum. However, later studies led the cereal office to classify it as common wheat.

Sevier is a spring (8) wheat, also adapted for use as a winter wheat. The head is short, awned and compact but not clubbed. The chaff has a brownish bronze color and is quite long and stiff. The kernels are white, long, semi-hard to hard when grown with abundant moisture, and extremely hard and flinty when grown under dry-farm conditions. The straw is tough, slender, and especially under irrigation lodges to an undesirable extent.

The history (8) of New Zealand wheat is not known to any degree of completeness. Its origin is also somewhat undetermined. The office of cereal investigations of the United States Department of Agriculture explain that it is possibly the Ble'de Le'lande wheat described by Henze', of France. Stewart, believes it to be the same thing as is called Ninety-Day in Salt Lake County, Utah, and Ruby in Sanpete County, Utah. If the last statement is correct, New Zealand is likely to be one of a large number of Blount's hybrids produced at the Colorado Agricultural College.

It is a spring wheat, resembling Pacific Bluestem, except that it has a longer and more lax spike. The straw is coarse, strong, and white and grows to be tall. The spike is awnless, long, and medium loose; the glumes long, narrow, and white; the kernels long, white, and soft.

In yield (35) tests conducted at Nephi and Logan by the Utah Experiment Station, Sevier wheat has proved to be the highest yielder. But under ordinary field conditions, great losses are often sustained with Sevier wheat because of its lodging habit. It was for the purpose, as stated in the beginning of this paper, of producing a variety having the high-yielding power of Sevier and the ability to stand erect that Professor Stewart crossed this variety with New Zealand.

Unfortunately no measurements were made of the F1 generation of this cross. Little can be said, therefore, regarding the F1 plants except that they were apparently intermediate between the two parents. The heads resembled the Sevier parent in color, but were slightly less compact and somewhat longer.

Through the courtesy of Professor Stewart I was permitted to study the data collected by Mr. Leo Mortensen of the F2 generation. This data is fairly complete except that no measurements of heads were taken. However, the estimations of straw strength are taken more accurately for F2 than for F3 plants because the F2's were planted far enough apart to permit of inspection of single individuals.

Tables 1, 2, 3, 4, 5, and 6 show the distribution of plants for various characters studied in the F2 generation. An examination of these tables shows that two of the characters studied, kernel structure and compactness segregates in a simple 3:1 ratio. The others are apparently di-hybrids segregating into ratios which approach 9:7 for color, 9:3:4 for awns, 9:7 for straw strength, and 9:3:3:1 for head shape respectively.

Table No. 1 - Showing Plant Distribution for Kernel Structure in F2. (After Mortensen)

	Tot. No. Plants	Soft	Hard	Ratio
Experimental	4452	3013	1439	2.707:1.292
Theoretical	"	3339	1113	3:1

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Table No. 2 - Showing Plant Distribution for Color in F2. (After Mortensen)

	Tot. No. Plants	White	Bronze	Ratio
Experimental	4452	2460	1992	8.84:7.159
Theoretical	"	2504.25	1947.75	9:7

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Table No. 3 - Showing Plant Distribution for Awns in F2. (After Mortensen)

	Tot. No. Plants	Awnless	Awntipped	Awned	Ratio
Experimental	4453	2830	644	979	10.168:2.31:3.51
Theoretical	"	2504.79	834.93	1113.24	9:3:4

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Table No. 4 - Showing Plant Distribution for Straw Size in F2. (After Mortensen)

	Tot. No. Plants	Coarse	Slender	Ratio
Experimental	4452	2847	1605	10.23:5.768
Theoretical	"	2504.25	1947.75	9:7

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Table No. 5 - Showing Plant Distribution for Head Shape in F2. (After Mortensen)

	Tot. No. Plants	Club Compact	Long Club	Long Compact	Long Loose	Ratio
Experimental	4452	2012	1096	295	1049	7.2:3.9:1.06:3.76
Theoretical	"	2504.25	834.75	278.25	834.75	9:3:1:3

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Table No. 6 - Showing Plant Distribution for Compactness in F2. (After Mortensen)

	Tot. No. Plants	Compact	Loose	Ratio
Experimental	4452	3403	1049	3.057: .942
Theoretical	"	3339	1113	3:1

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Before the F2 generation was harvested this Sevier and New Zealand cross, known as cross "A", was assigned to me for further investigation. My task was to select a group of superior plants, take them to the laboratory, study them and record the data, thresh the plants, prepare them for the F3 planting, and then study the F3 generation. The plants selected were from the centers of the rows, or at least not near the ends or near other openings where plants would have any apparent environmental advantage. The selected plants, with about three exceptions, had 12 or more culms per plant.

All club-compact heads were above 4 centimeters in length: long-club heads were 5 centimeters long or more;

long-compact heads had a length above 5½ centimeters; no long-loose heads were less than 8½ centimeters in length. All plants selected had coarse straw so far as field observations were concerned. But, in the laboratory it was observed that there were two grades of coarseness which wererecorded as coarse and medium coarse.

Table 7 shows the number of plants of each head type selected, and gives the average number of culms, average head lengths, and degree of coarseness of straw:

Table No. 7 - Showing F2 Plants selected for F3 Planting.

Head Type	No. of Plants	Av. No. Culms	Av. Head Length	Straw Size Coarse	Straw Size Medium Coarse
Club-Compact	31	16	4.42 Cm.	28	3
Long-Club	37	17	5.0 "	32	5
Long-Compact	39	16.3	6.7 "	26	13
Long-Loose	27	14.81	9.8 "	17	10

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For lack of space in the plant nursery the F3 seed was rather compactly planted in rod rows, the rows being about two feet apart. This made the inspection of individual plants in the field an impossibility. As a consequence straw strength was estimated by judging an entire row, and giving it a percentage number, according to the degree of erectness observed. The data given in Table 8 are observations of the author. Those in Table 9 are comparisons made by Professor Stewart.

Table No. 8 - Showing Straw Strength in F3.

Percentage Str. Stren.	Club Compact	Long Club	Long Comp.	Long Loose	Total
90	3	-	-	1	4
85	4	2	-	2	8
80	-	-	1	3	4
75	1	1	-	1	3
70	1	2	-	1	4
65	-	1	-	2	3
60	-	-	-	1	1

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Table No. 9 - Showing Straw Strength in F3.

Percentage Str. Stren.	Club Compact	Long Club	Long Comp.	Long Loose	Total
95	5	2	-	-	7
90	10	3	-	-	13
85	9	2	1	-	12
80	5	3	2	2	12
75	2	2	-	1	5
70	2	1	-	1	4
60	-	-	-	1	1
50	1	1	1	-	3
30	-	1	-	-	1

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The rows in the nursery were all handled as uniformly as was possible. But in spite of all care in the field management some rows were necessarily discarded because of varying soil conditions. The nursery was located on the College Hill Farm where anything like an approach to homogeniety of soil is out of the question.

At harvest time all rows having the appearance of pure lines were turned over to the Agronomy Department to be tested for yield, and other values. The various pure lines are listed in Table 10, a table which gives an encouraging bit of information regarding straw size.

Table 7 shows that 31 plant selections were listed as medium coarse under straw size. Ten of these plants bred true for medium coarse straw. An examination of Table 10 shows that only two rows planted as medium coarse were as high as 85 percent in strength. The other medium coarse parents produced plants which varied in strength from 60 to 80 percent. No parent planted as a coarse straw type, and showing evidence of being a pure line, had a percentage straw strength below 70. It is also noticeable that only three coarse-strawed individuals produced progeny that came so low, and these, because of environmental encouragement, were abnormally tall.

Table No. 10 - Various Pure Lines from F3 Selections.

Row No.	Head Shape	Awns	Chaff Color	Pub-escence	Str. Stren.	Kern. Struct.	Plant Height	Straw Size
1	CC	Awd	B	Sm	85	H	76 Cm.	Coarse
2	CC	Awd	B	Sm	85	H	76 "	Coarse
5	CC	Awd	B	Sm	90	H	76 "	Coarse
6	CC	Awd	W	Sm	90	H	76 "	Coarse
7	CC	Awd	LB	Sm	85	S YB	76 "	Coarse
14	CC	Awt	W	Sm	90	H	74 "	Coarse
20	LC	Awd	B	Sm	85	H	70 "	Coarse
33	LL	Awd	B	Sm	80	H	65 "	Coarse
35	LL	Awd	B	Sm	85	H	66 "	Medium
37	LL	Awd	B	Sm	85	H	74 "	Medium
38	LCC	Awd	B	Sm	80	H	74 "	Medium
42	LL	Awt	B	Sm	90	H	75 "	Coarse
52	LL	Awl	W	Sm	80	H YB	75 "	Coarse
53	LC	Awd	B	Hry	75	RS	70 "	Medium
69	LC	Awd	B	Sm	70	H	103"	Coarse
71	CC	Awl	W	Sm	70	S	104"	Coarse
72	CC	Awt	W	Sm	75	H	100"	Coarse
81	LC	Awd	B	Sm	65	S YB	98 "	Medium
87	LC	Awl	W	Sm	70	H YB	98 "	Coarse
98	LC	Awd	B	Sm	85	S?	80 "	Coarse
17	LC	Awt	B	Sm	85	S	78 "	Coarse
21	LL	Awd	W	Sm	70	H	64 "	Medium
22	LL	Awd	Pink	Sm	75	S	64 "	Medium
24	LL	Awt	W	Sm	60	H	65 "	Medium
29	LL	Awd	W	Sm	80	H	65 "	Coarse
33	LL	Awd	B	Sm	65	S	65 "	Medium
35	LL	Awd	B	Sm	65	S	70 "	Medium

Key to Table

CC - Club-compact	Awt - Awntipped	H - Hard
LC - Long-club	Awl - Awnless	S - Soft
LCC - Long-compact	B - Bronze	Sm - Smooth
LL - Long-loose	LB - Light bronze	Hry- Hairy
Awd - Awned	W - White	YB - Yellowberry

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Thirty-five rows (populations) numbering 7135 plants, having grown under practically uniform environmental conditions were selected for further study in the laboratory. These were all pulled by the roots, and each separate row bound into a bundle, labeled, and taken to the laboratory.

Since the characters of awned habit, chaff color, and structure of kernel are valuable both from the point of view of genetics and practical field operations, they were studied incidentally along with study of size inheritance of heads. Tables 11, 12, 13, 14, 15, and 16 show tabulations of the results obtained from the study of these three characters.

Table No. 11 - Showing Segregation for Kernel Structure in F3.

	Planted as	Hard	Soft	Ratio
Experimental	(Soft)	192	234	7.21:8.79
Theoretical		186.34	239.58	7:9

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Table No. 12 - Showing Segregation for Kernel Structure in F3.

	Planted as	Hard	Soft	Ratio
Experimental	(Hard)	410	325	8.92:7.07
Theoretical		413.37	321.51	9:7

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Table No. 13 - Showing Segregation for Awns in F3.

	Planted as	Awl	Awt	Awd	Ratio
Experimental	Awnless	245	279	192	5.47:6.23:4.3
Theoretical		179	402.75	134.25	4:9:3

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Table No. 14 - Showing Segregation for Awns in F3.

	Planted as	Awl	Awt	Awd	Ratio
Experimental	(Awn-tipped)	326	1191	502	2.58:9.438:3.97
Theoretical		378.54	1135.62	504.72	3:9:4

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Table No. 15 - Showing Segregation for Color in F3

	Planted as	Bronze	White	Ratio
Experimental	(Bronze)	909	355	2.87:1.12
Theoretical		948	316	3:1

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Table No. 16 - Showing Segregation for Color in F3

	Planted as	Bronze	Light Bronze	White	Ratio
Experimental	(Bronze)	157	752	355	1.98:9.52:4.49
Theoretical		237	711	316	3:9:4

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A study of Table 11 would indicate that softness is dominant over hardness; Table 12 indicates the opposite. The parental plants in the first case were soft; while in the second case they were hard. It seems, therefore, that kernel structure, at least in this instance, shows a case of reversed dominance.

Tables 13 and 14 support the fact that has frequently been demonstrated in wheat studies, that awnlessness is dominant. This dominance is incomplete, however, since the heterozygous plants are awntipped.

Table 15 reveals the fact that bronze color in this cross, is dominant over white. In this case also (Table 16) dominance is incomplete as the heterozygous plants show an intermediate or light bronze color.

Two characters are considered here in the study of segregation in head types, namely, compactness and length. The first segregates as a unit character, while the second is more complex.

A glance at Tables 17, 18, and 19, and curves 2 to 6 inclusive, justifies the conclusion that compactness is a purely dominant character having looseness as its recessive. In every instance, in the cross under consideration, segregation for compactness has been in a simple 3:1 ratio. Table 17 shows ten populations (each one the progeny of a single long-compact parent) which segregate very uniformly, with the exception of P-62, into a ratio of 3 compact to 1 loose. Each of these populations also segregate into the four head types with a marked predominance of long-compact.

Four populations are listed in Table 18 of long-compact parentage which segregated into only three head types, but a 3:1 ratio for compactness still persisted. Similarly in P-99, while segregating only into two head types the 3:1 ratio for compactness still obtains.

Table No. 17 - Showing Segregation of Long-Compact Parents - F3 Generation.

Row No.	CC	LC	LCC	LL	Tot. Comp.	Tot. Loose	Ratio
101	54	41	125	65	220	65	3.08:.912
63	52	43	192	76	287	76	3.16:.837
105	34	37	87	63	158	63	2.86:1.14
62	33	35	60	80	128	80	2.46:1.54
64	14	29	80	40	123	40	3.02: .98
116	33	26	77	48	136	48	2.96:1.04
100	25	40	170	77	235	77	3.01: .987
108	36	24	117	58	177	58	3.01: .987
112	22	10	67	29	99	29	3.09: .906
26	23	57	143	78	223	78	2.96:1.036
Tot.	326	342	1118	614	1786	614	2.97:1.03
Theoretical	- - -	- - -	- - -	- - -	1800	600	3 :1

\- - - - - - - -

Table No. 18 - Showing Segregation into Three Head Types of Long-compact Parents - F3.

Row No.	LC	LCC	LL	Tot. Comp.	Tot. Loose	Ratio
118	43	92	60	135	60	2.769:1.23
61	22	85	57	107	57	2.61:1.39
31	39	93	56	132	56	2.8 :1.19
113	42	81	54	123	54	2.78:1.22
Tot.	146	351	227	497	227	2.75:1.25
Theoretical	- - -	- - -	- - -	543	181	3 :1

\- - - - - -

Table No. 18a - Showing Segregation into Two Head Types of Long-compact Parent - F3.

Row No.	LCC	LL	Tot. Comp.	Tot. Loose	Ratio
99	164	60	164	60	2.9:1.07
Theoretical	- -	- -	168	56	3 :1

\- - - - - - -

Eight populations (Table 19) having a long club parentage segregated into four head types and a ratio of 3 compact to 1 loose. P-17 and P-18, planted as long-club, segregated for head type but only within the compact group. P-23, for some unknown reason, did not follow the same line of action as the other long-club parents.

Only three populations (Table 20) segregating for head type were studied which had club compact parents. These segregated into club compact and long club only without following definite ratios.

No individuals planted as long-loose segregated for head shape, which clearly indicates that looseness is a recessive character.

Table No. 19 - Showing Segregation of Long-club Parents - F3 Generation.

Row No.	CC	LC	LCC	LL	Tot. Comp.	Tot. Loose	Ratio
19	37	58	46	55	141	55	2.88:1.12
83	20	26	84	43	130	43	3.005:.994
90	16	58	110	57	184	57	3.053:.946
86	34	45	50	30	129	30	3.245:.754
77	53	59	22	46	134	46	2.98:1.02
89	34	23	89	52	146	52	2.95:1.05
128	22	45	63	48	130	48	2.92:1.08
93	34	47	76	47	157	47	3.08:.92
Tot.	250	361	540	378	1151	378	3.01:.99
Theoretical - - - - - - -					1146.75	382.25	3. :1.

\- - - - - -

Table No. 19a - Showing Segregation of Long-club Parents into Three Head Types - F1.

Row No.	CC	LC	LCC	Tot. Comp.	Ratio
17	41	82	52	175	Indefinite
18	19	132	42	193	"

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Table No. 20 - Showing Segregation of Club-compact Parents into Two Head Types - F3

Row No.	CC	LC	Tot. Comp.	Ratio
10	122	83	205	Indefinite
13	92	103	195	"
12	48	173	221	"

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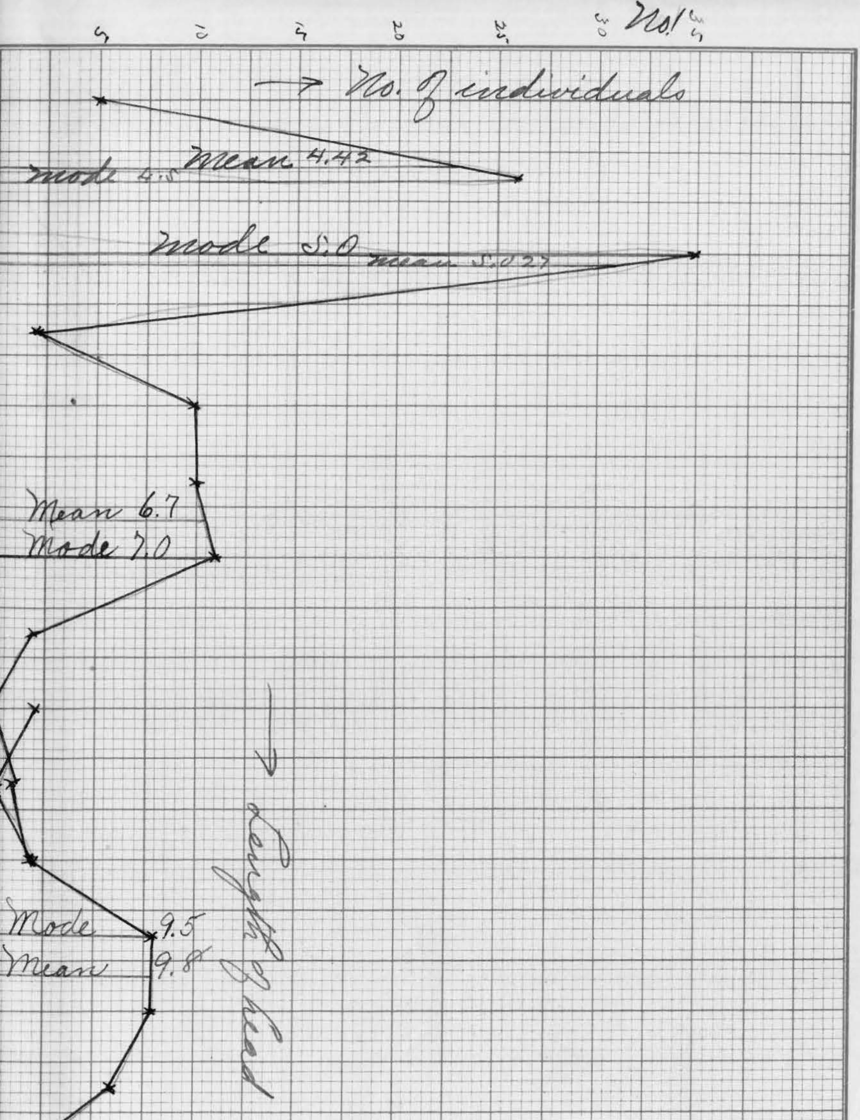
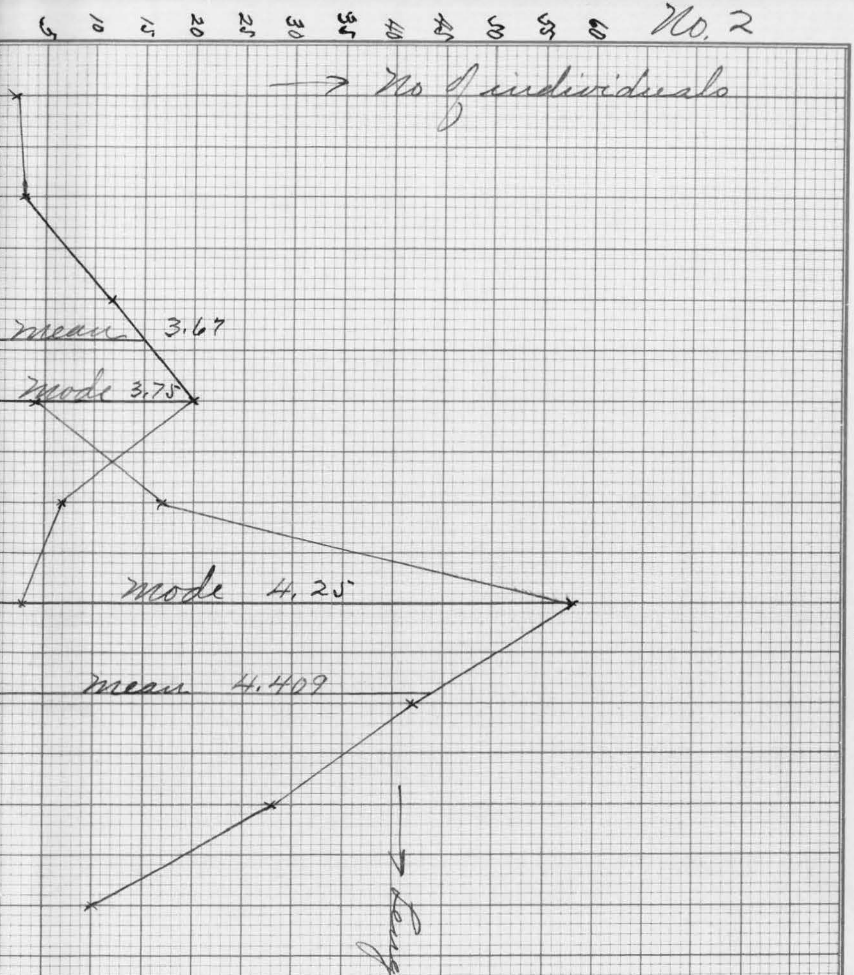
Due to the apparent complexity of length inheritance no definite ratio has been assigned to this character. But that there is a distinct segregation into various mean head lengths is demonstrated by curves 2 to 6 inclusive.

The data represented in these curves were obtained as follows: The head lengths of five typical populations, a total of 946 individuals were measured with a rule to as near as .25 centimeters. Only what appeared to be the longest head on each plant was measured. All measurements of a particular population were arranged into a table, so modes could be marked, and means calculated. The data were then plotted on a curve.

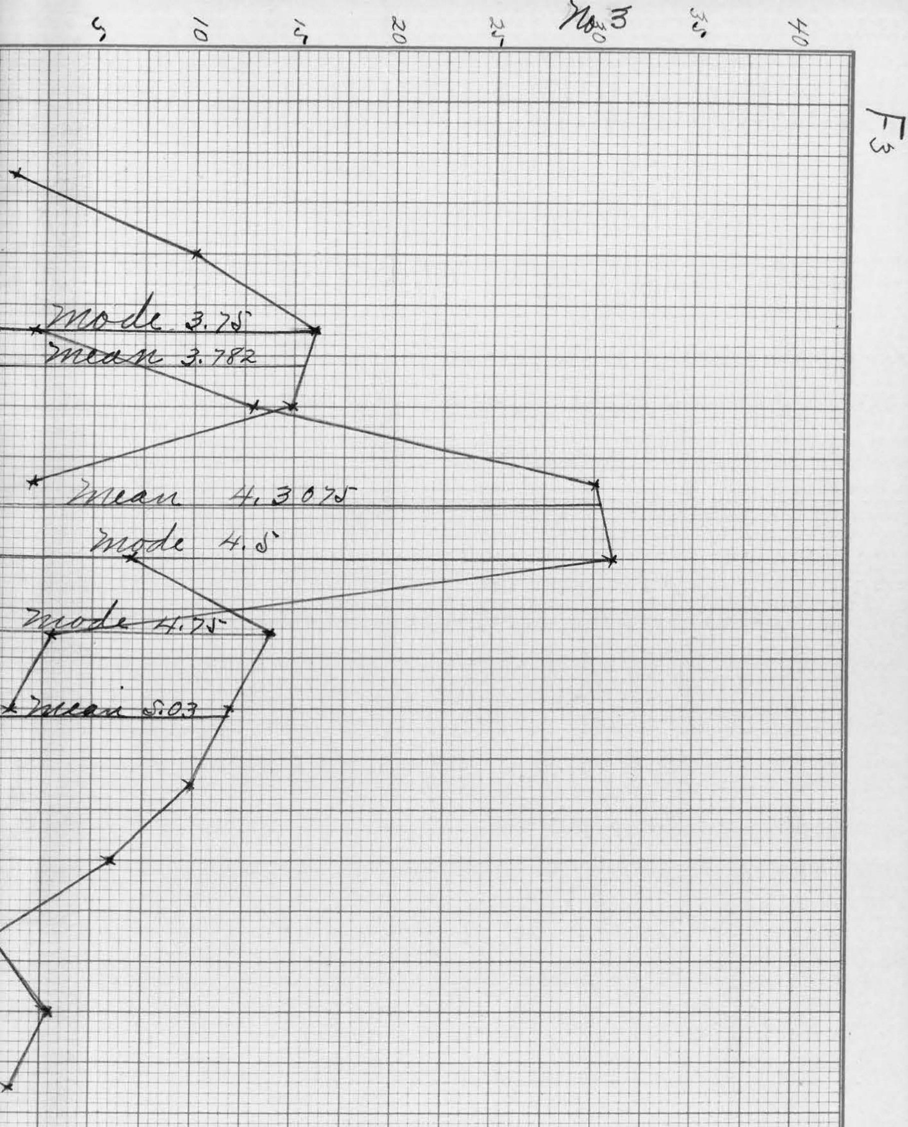


5
10
15
20
25
30
35
No.
→ No. of individuals
mode 4.5
Mean 4.42
mode 5.0
mean 5.027
Mean 6.7
Mode 7.0
Mode 9.5
Mean 9.8
→ Length of head
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17



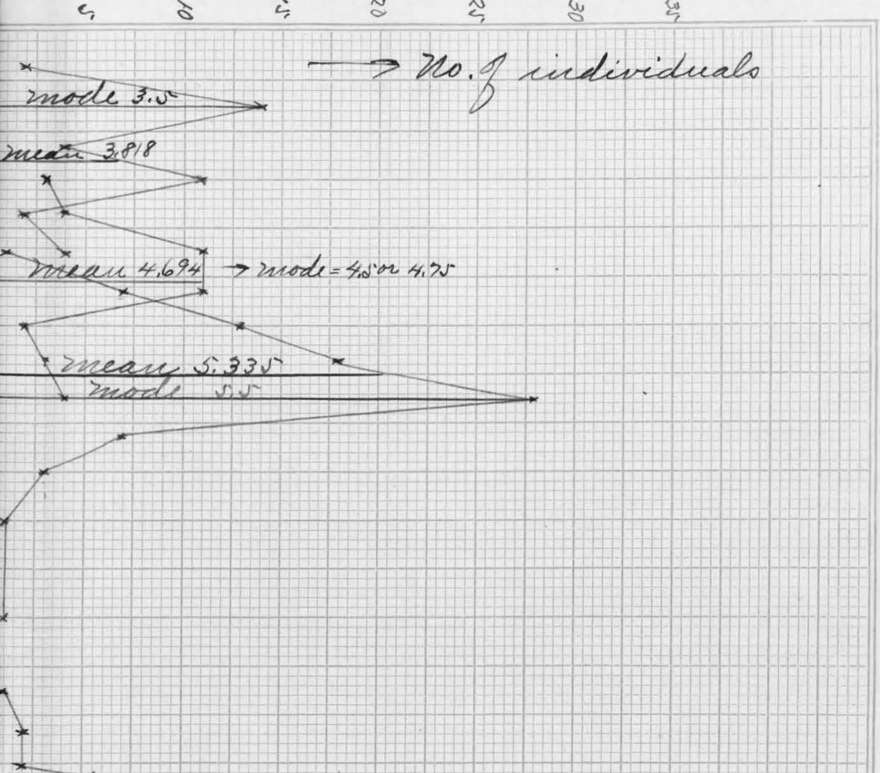
No. 2
5 10 15 20 25 30 35 40 45 50 55 60
→ No of individuals
mean 3.67
mode 3.75
mode 4.25
mean 4.409
→ Length of head
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17

F3



No 3
F3
5 10 15 20 25 30 35 40
mode 3.75
mean 3.782
mean 4.3075
mode 4.5
mode 4.75
mean 5.03
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17

No. 4



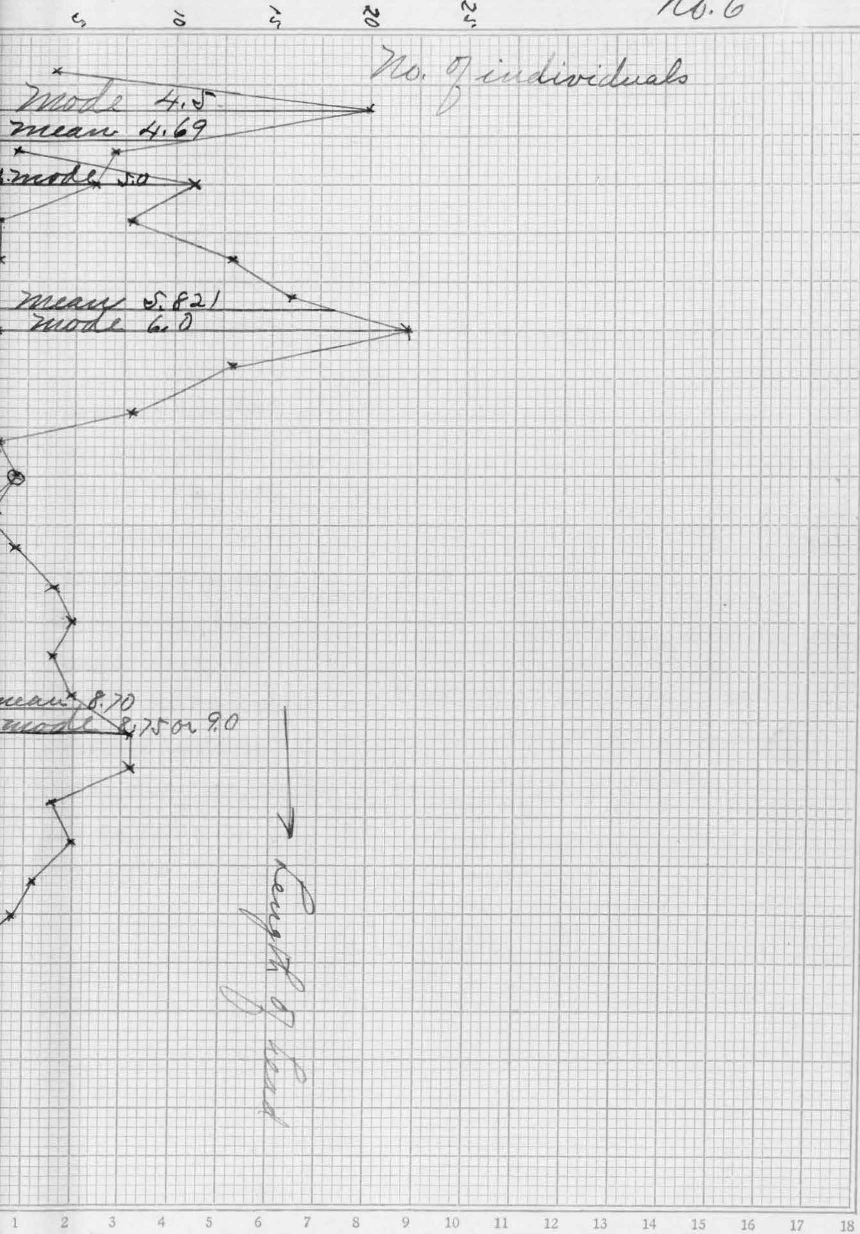
5
10
15
20
25
30
35
→ No. of individuals
mode 3.5
mean 3.818
mean 4.694
→ mode = 4.5 or 4.75
mean 5.335
mode 5.5
mode 8.25
mean 8.853
mode 9.5
→ Length of head
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

F3


No. 5
5
10
15
20
25
No. of individuals
mode 3.75
mean 3.909
mode 4.5
mode 5.5
mean 5.85
mean 9.35
mode 9.5
Length of head.
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

F3

No. 6


5
10
15
20
25
No. of individuals
mode 4.5
mean 4.69
mode 5.0
mean 5.821
mode 6.0
mean 8.70
mode 8.75 or 9.0
Length of head
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18

F3

A study of Tables 17 and 19, shows that where segregation is complete, or where the four head types show up there is a strong predominance of long compact. This would be expected in cases where long compact was the parent. But the number of long-compacts is also greatest among the segregates from long-club parentage.

Just why this is so is difficult of explanation. A possible explanation might be that since the F1 generation was intermediate in size a predominance of intermediates would follow in succeeding generations. This statement is not supported, however, by the F2 data. Yet the regularity with which intermediates excell in numbers; the regularity of the appearance of the other three head lengths, in apparently definite proportions; the regularity with which the variation completely fills the gap between and includes the variations of both parents indicate that in this case head length is a typical size character, segregating according to Mendelian principles as explained by the multiple factor hypothesis.

Summary

The data presented in this study support the follow- conclusions:

(1) That color, awnlessness, and kernel structure do not segregate as characters showing complete dominance when crossed because intermediate forms appear in F2 and F3, which breed true.

(2) That kernel structure shows reversed dominance.

(3) That compactness behaves as a distinctly dominant character with looseness as its recessive.

(4) That straw size, though difficult to measure, does show regular systematic segregation in cases where crosses of two different straw sizes are made.

(5) That there are several factors involved in straw size segregation because pure lines representing several different straw sizes appear in the F2 and F3 generations.

(6) That head length is a stable size character, which upon being crossed, shows a predominance of intermediate sizes.

(7) That F2 and F3 variations in head length fill the gap between the parents, and that pure lines of at least four different mean lengths appear in these two generations.

(8) That size inheritance is a complex character which behaves in a Mendelian fashion, and explainable by the multiple factor hypothesis.

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