THE HEREDITY OF QUANTITATIVE CHARACTERS IN WHEAT

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INTRODUCTION

This paper forms a report on certain phases of a series of investigations in wheat breeding under the supervision of the writer, in the Department of Plant Breeding of the ARIZONA AGRICULTURAL EXPERIMENT STATION. The work was initiated by the making of a number of reciprocal crosses between an Algerian white macaroni wheat, an Algerian red bread wheat and two local white bread wheats, Early Baart and Sonora. The original hybridizations were made at Yuma, Arizona, in the spring of 1913, the F_1 was grown at Tucson in 1913-'14 and the F_2 and F_3 on the experimental farm at Yuma in 1915, 1916, respectively. The data concerning time relations, width of leaf, height, rust resistance, etc., were, of course, taken in the field. At the time of ripening, the heads of each plant were harvested and placed together in a paper bag, care being taken to label each bag so that it could be completely identified. All other data were taken in the laboratory of the Department of Plant Breeding at the UNIVERSITY OF ARIZONA at Tucson. The summation and analysis of this data begun some months earlier, has been continued throughout the present year by the writer while on sabbatical leave from the UNIVERSITY OF ARIZONA. The writer here wishes expressly to thank the officers and management of the BUSSEY INSTITUTION for laboratory and library facilities throughout the year and especially Dr. E. M. EAST for many valuable criticisms and suggestions. He also wishes to recall with appreciation the assistance rendered by Mr. DONALD F. JONES who made the original crosses, by Mr. LEONHARDT SWINGLE to whose careful and accurate work may be credited a large proportion of the field and laboratory notes of the second generation, and finally, by Mr. W. E. BRYAN in his efficient assistance with the field and laboratory notes for the third generation.

Since the re-discovery and publication of MENDEL's original papers, the question of paramount interest among geneticists and plant and animal breeders has been that as to whether or not the principles involved in the discoveries of MENDEL are of limited or universal application. Practically all real progress in the study of heredity has arisen through experiments and observations designed to test the validity and universality of MENDEL's laws.

At the present time, the inheritance of a large number of characters, including those both of a qualitative and quantitative nature, in a wide series of both plants and animals, are almost universally considered to be best explained by the Mendelian hypothesis. These include all characters which in the F_2 and subsequent generations, show definite, discontinuous segregation. Most of the cases of peculiar and unusual ratios have been satisfactorily explained as due to multiple factors, lethal factors, gametic coupling, gametic selection, partial sterility, etc.

There are cases, however, which admit of explanation by hypotheses other than those based upon Mendelian principles. Examples may be cited among characters which may be expressed quantitatively. In many such cases the F_1 is more or less intermediate between the parents, and the F_2 and subsequent generations show segregation, but such segregation as does occur is perfectly continuous. Where a sufficiently large number of variants are grown, there is found every degree of size from the lowest to the highest extreme of the hybrid distribution. The extremes of this distribution may or may not reach or extend beyond the extremes of the parental races.

There are some geneticists who believe that such a type of inheritance is not Mendelian. They advocate the application of the Mendelian principles in many cases, but maintain that we have no proof that Mendelism is universal and that cases such as those described above may be just as easily explained by assumptions other than those of gametic purity and unchanged segregation.

The literature on the subject of the inheritance of quantitative characters has been collected by SHULL (1914) and MACDOWELL (1914), and has been summarized with excellent clearness by these writers. It is therefore not necessary to re-summarize these earlier papers. The results of original research bearing upon the inheritance of quantitative characters which have appeared since SHULL'S and MACDOWELL'S summaries may now be reviewed briefly.

NILSSON-EHLE (1914) shows a genetic linkage between a factor for yellow glume color and an inhibitor which shortens beard length in oats.

PHILLIPS (1914) crossed Rouen and Mallard ducks which differ greatly in size. The F_1 was intermediate in size between the parents and not more variable than the most variable parent. The F_2, while still intermediate in average size, was markedly more variable than either the F_1 or the parents.

PUNNETT and BAILEY (1914) in crosses of bantam with larger breeds of fowl found the F_1 intermediate and the F_2 highly variable, transgressing the extremes of both parents. Small F_2 fowl bred together gave an F_3 all of small size; large F_2 individuals bred *inter se* produced altogether large offspring. The F_3 obtained by mating intermediate F_2 individuals was highly variable. They interpret the results as being due to the segregation of Mendelian unit factors and give a factorial scheme to account for the phenomena observed.

HAYES and EAST (1915) crossed flour corn with a flint variety and found that the endosperm character was determined by the mother only, although it was proved that endosperm character, first visible in the next generation could be inherited through the pollen. The authors conclude that this behavior is due to the fact that the endosperm is produced from a union between two female polar nuclei and one male cell and that the presence of two factors dominates one in either the direction of starchy or flinty endosperm. In other flint-starchy crosses, the ratios were not so definite, due possibly to the difficulty of classifying the seed. It was thought, however, that the same principles were involved as in the previous crosses. Crosses involving grains of different shape were made between rice pop corn, pearl pop corn and a dent corn. The results of these experiments indicated that several factors were involved which segregated in a Mendelian fashion in the F_2 and F_3. Parental types when once recovered bred true.

EAST (1916 a) records the crossing of *Nicotiana Langsdorffii* and *N. alata* which differ markedly in corolla length. The F_1 was intermediate and no more variable than the more variable parent. The F_2 also had an intermediate average but the variability was much higher than in the F_1. There was a wide range in the variability of the different F_3 races but they were all lower than in F_2. He showed by F_3 pedigrees that segregation had occurred in F_2 but did not attempt to determine the number of factors.

EAST (1916 b) in a second paper reports the results of crossing a variety of *Nicotiana longiflora* having the corolla about 93 mm long with another variety of the same species having a corolla length of about 40 mm. He carried the study through the first, second, third, and in a few races as far as the fourth generation, with sufficient numbers to calculate the coefficients of variation in the separate races. The author lays down eight conditions which he assumes the data must fulfill in order to be interpreted as complying with the conditions of Mendelian inheritance. Tables and distributions with the calculated constants are given in detail and the conclusions are that no single phenomenon has occurred which cannot be interpreted as Mendelian.

PHILLIPS (1915) after a study of the results of color inheritance in various duck crosses and pheasant crosses says that "it is almost certain that the ordinary subspecies of the ornithologist is very far from being a unit variation."

Since the work of JOHANNSEN on the effect of selection in beans, there has been no similar work with plants which can compare in volume and significance with that of FRUWIRTH (1915). FRUWIRTH followed the system of pure line selection as practiced by JOHANNSEN. Choosing a variety of *Lens esculenta* with flecked seed, he endeavored through selection to bring about greater flecking on the one hand and the diminution of the flécks on the other. After 13 generations he had made no progress in either direction. Chevrier beans (*Phaseolus vulgaris*) produce seeds which, for the most part, have seed coats of a slightly greenish color rather than creamy white but a few seeds are white on one or both sides. It was attempted, through selection within a pure line, to secure complete inheritance of the green type. Though carried out for 14 generations no change was produced. In a race of vetch which produced both green and cream-colored seeds on the same plant, he tried for 10 generations to fix the green coloration by selection but made no progress. Likewise two years selection of yellow seed made no progress in the direction of fixing the type. In a Victoria pea variety with yellowish green and yellow seed three years of selection was without effect. In a variety of Soja bean having lighter and darker brown seed, three years of selection could make no progress in either direction of darker or lighter seed coats. In a certain variety of *Pisum arvense* the seeds are variable in color. They may be pure yellowish green, or yellowish green with violet flecks or bands, or the violet color may be so extended as to leave the yellowish green appearing only as flecks, or finally the violet color may prevail altogether. FRUWIRTH endeavored by selection to increase the amount of violet color in the seeds on the one hand and to reduce it on the other. In the selection for more violet color in the seed coats, 10 generations produced no results. The results of the selection in the opposite direction can best be given in FRUWIRTH's own words as follows (FRUWIRTH 1915, p. 200):

"In beiden JOHANNSEN'SCHEN Linien 1 und A ist die Anlage zur Ausbildung violette Farbe der Samenschale vorhanden, die Anlage ist aber stark modifikabel und ausserdem sind beide Linien geneigt spontan Zweige abzuspalten, in welchen diese Anlage ihre Wirksamkeit ganz (in 1 die Zweige II von Ernte 1909, und IV von 1910 Ernte) oder fast ganz (in 1 der Zweig III der von Ernte 1908 abgeht und die Auslese A) eingebüsst hat. Eine Neigung rein violettsamige Zweige abzuspalten, besteht nicht."

"In beiden JOHANNSEN'SCHEN Linien ist die Anlage zur Ausbildung violette Farbe in der Hülsenschale vorhanden, und zwar ist die Anlage—sowie jene violetter Farbe der Samenschale—stark modifikabel. In beiden Linien ist die Neigung vorhanden, spontan Zweige abzuspalten, in welchen die Wirkung der Anlage durchschlagend, ohne Modification auftritt, so dass dann nur violette Hülsen gebildet werden. Violette Färbung der Samenschale ist ganz unabhängig von violetter Färbung der Hülsenschale."

"Auslese nach grüner Farbe der unreifen Hülse ist wirkungslos, Auslese nach violetter Farbe derselben nur dann—und dann sofort—von einer

Wirkung begleitet, wenn spontan ein violetthülsiger Zweig abgespaltet worden ist."

In a selection carried out upon a variety of lupine (*Lens esculenta*) having mottled seed, FRUWIRTH sought by selection to produce both dark- and light-seeded strains. Six years selection in one direction and eight years in the other produced some divergence in the selected lines but was not effective in producing either self-colored dark- or light-seeded races.

In a variety of vetch which normally produced either greenish or cream-colored seed (see selection experiment described above) after five generations of self-fertilization, there appeared in the harvest of 1910, 2 plants having mottled seeds. In 1912 after 7 generations of self-fertilization and selection the same line produced 4 plants having mottled seeds. Finally, "trat diese Variation auch als Variation einer ganzen Pflanze bei 5 Individuen der Ernte 1910 auf, nach 9 Generationen aus Selbstbefruchtung, fünf in der Linie, vier während der vorangegangenen Massenauslese." All mottled seed bred true.

In selection work with Soja beans one or two spontaneous variations were observed. All effects of selection (from a mass lot), however, were produced in the first year. The spontaneous origin of a white-flowered vetch is also noted.

White mustard (*Sinapis alba*) with which FRUWIRTH worked, produces both yellow and brown seed. After eight years of selection of close-fertilized seed, he was unable to fix the type or even materially to diverge the tendency in one direction or the other.

In extensive selection experiments with oats which for some characters were carried through ten generations he decides that selection within pure lines is without effect.

FRUWIRTH (1915, p. 450) finally sums up by saying:

"Bei einer Reihe von äusseren Eigenschaften zeigte sich durchweg, dass in einer JOHANNSEN'SCHEN Linie bestimmt gerichtete Auslese auch bei Fortsetzung durch eine grössere Zahl von Generationen keine Änderung des Liniencharakters mit sich bringt."

MACDOWELL (1915) has reported the results of selection experiments upon a race of Drosophila which possessed more than the normal 4 bristles on the thorax. The average number of bristles increased for 6 generations of selection. The same selection was carried on for 5 more generations without additional effect. The author concluded that there were several accessory factors limiting extra bristles which were gradually eliminated by selection. MACDOWELL has also shown a very strong correlation of extra bristles with body size. The present writer strongly suspects that the real factors here concerned were size factors and that MACDOWELL'S extra bristle selection was merely an indirect means of selecting for larger size.

The paper by YUZO HOSHINO (1915) on the flowering time of peas and rice has been the subject of much interesting recent comment. HOSHINO crossed early- and late-blooming varieties of peas. He found that the variation behaviors of the F_1, F_2, F_3 and F_4 races (detailed distributions of which are given) could for the most part be interpreted by assuming the Mendelian segregation of two allelomorphic pairs, A and a, which determined early- and late-blooming respectively and two modifiers B and b. Those variation behaviors which could not be explained by these factors, he supposed to have been caused by a "contamination" of genes. What he means by contamination of genes is not clear for he distinctly states that he does not refer to such a contamination as is assumed by CASTLE in rodent crosses. He suggests "secondary factors." This is the same as assuming additional factors of secondary importance such as are assumed by NILSSON-EHLE in the report of his *compactum*-squarehead-Landweizen wheat crosses.

HOSHINO has also shown a gametic coupling of early-blooming with white flowers and late-blooming with red flowers. This coupling is broken (by physiological interference or crossing over) approximately 1 time in 7.

In crossing early- with late-shooting rice varieties he finds the F_1 intermediate, the F_2 showing strong segregation. The behavior of the F_3 and F_4 races were such as would be normally expected of segregating Mendelian factors.

CASTLE (1917) has re-stated certain data and conclusions previously published (CASTLE 1912, pp. 163-168). In crossing + variants of hooded rats with wild rats he found that "wild" was dominant in F_2 and that the hooded extractives of the F_2 were often higher in hood grade than were their hooded grandparents. In crossing "mutant" hooded rats (a race which suddenly appeared with a very high + hooded condition) with wild rats, the F_1 was of the wild type but the hooded extractives of the F_2 did not drop lower than the range of the original "mutant" race. CASTLE concludes that these facts cannot be interpreted as Mendelian and must be explained as the results of changes in a single unit factor.

The present paper is offered as the first in a series of further contributions to the knowledge of the inheritance of quantitative characters. Wheat has proved an especially favorable subject for such an experiment inasmuch as its small size renders feasible the production of large numbers without prohibitive expense and the fact that it is close-pollinated greatly simplifies the genetic analysis of the F_2 and subsequent generations.

The characters here studied are the date of the appearance of the first head on each plant, the total height of the plants measured in centimeters from the ground to the top of the tallest head (not including beards) and the width of the broadest leaf.

MATERIAL AND METHODS

A brief description of the four varieties of wheat used may be given as follows:

Algerian macaroni (No. 1)

Late, tall; stems large, stiff; leaves broad, dark green, medium width; heads large, cylindrical, flattened, long; glumes bearded, pubescent, light straw yellow; grain large, mostly translucent light amber, and very hard, but with some grains having spots of opaque starch in the endosperm. Originally obtained from R. MARIE, Algiers, Algeria.

Algerian red bread (No. 3)

Late, tall; stem medium in size; leaves medium in width and color; heads medium size, square; glumes bearded, smooth, light straw yellow; grain red, medium soft, opaque. Originally obtained from R. MARIE, Algiers, Algeria.

Early Baart (No. 34)

Early, low; stem medium in size; leaves medium width, medium green; heads medium size, square; glumes bearded, smooth, light straw yellow; grain white, medium soft, medium size, opaque. Originally obtained locally.

Sonora (No. 35)

Early, low; stem medium in size; leaves broad, light green; heads cylindrical, square, medium size; glumes beardless, pubescent, reddish brown; grain white, opaque. Soft. Originally obtained locally.

All planting was done with a nursery row machine by which each grain was covered 2 inches deep and spaced 3 inches in rows 10 inches apart. There were fifty hills in each row. Strips of barley were planted on either side of the plot in order that the end plants should not have more space than those within the plots. All plants of the pure varieties grown in 1914 were from mother plants which were selected from the 1913 general mass cultures as true to the types of their respective varieties. Of these selected 1913 plants there were 14 of macaroni (No. 1), 3 Algerian red bread wheat (No. 3), and 5 early Baart. The head records for Sonora (No. 35) in 1914 came from 12 typical heads of this variety selected from a mass culture. In 1915, of the 9 nursery rows of pure macaroni (No. 1), 6 were plant rows from the previous year's culture and 3 were from a mixture of seeds resulting from threshing together a number of typical heads of this variety selected from a field culture. The 3 nursery rows of No. 35, 1 of No. 3 and 1 of No. 34 were plant rows from the previous year's harvest. In 1916, 5 of the nursery rows of No. 1 came from a single mother plant in 1915 (No. 52-4-1-4) and the remaining 2 from a single other 1915 mother plant (No. 3-12-1-5). The 5 nursery rows of each of the other varieties originated from single plants in 1915 as follows: No. 35 from No. 35-11-1-4; No. 3 from No. 32-2-38; No. 34 from No. 1-13-3-1-24. In all of the discussions, the word culture is used in the sense of a group of plants, grown in a single nursery row and originating from a single mother plant of the previous season. This applies alike to the pure varieties and hybrids. The exception in the case of the 3 nursery rows of mass-selected macaroni, grown in 1915, has been noted. The expression "pure race" is often used to distinguish plants belonging to one of the parental varieties from those of hybrid origin.

The statistical methods used in these investigations were those commonly employed by biometricians. The constants used were the arithmetical mean, standard deviation and coefficient of variation. The means were calculated to the nearest unit employed in the taking of the original data. The standard deviations were calculated from the mean class as a mean, i.e., with the middle of the mean class as the assumed mean, no correction being made for the true mean. This was considered sufficiently accurate in view of the fact that different plant rows of the same pure race (pure line originating from a single mother plant) often showed more difference in standard deviation in the same season than could possibly arise from failure to correct for the true mean. An example will suffice. All of the plantings of pure No. 3 (Algerian red bread) arose from the seeds of a single plant in 1914. In 1916 there were 5 plant rows of this culture grown in different parts of the experimental plots for comparison with the various hybrids into which this culture entered. The data for height and the statistical constants calculated therefrom by various methods are given below. The original measurements were made to the nearest centimeter and in the summation of the data the classes were made to include 5 cm with the middle points at 2.5 and 7.5, thus 62.5, 67.5, etc.

TABLE I A

Height of pure No. 3, 1916, in centimeters.

Row No.	45 to 49	50 to 54	55 to 59	60 to 64	65 to 69	70 to 74	75 to 79	80 to 84	85 to 89	90 to 94	95 to 99	100 to 104	105 to 109	110 to 114	115 to 119	120 to 124	125 to 129	130 to 134	135 to 139	140 to 144	145 to 149	150 to 154
105A ...	1*												1	3	3	19	8	8	2			
105B ...															2	2	4	10	13	15	3	
105C ...															1		2	12	21	10	3	1
105D ...															1	8	18	14	6	1		
105E ...																	7	13	9	10	6	5

* Not used in calculation of constants given in table I B.

TABLE IB

Statistical constants.

Row No.	Number of variants	True mean (A)	Mean used in the calculation of σ used in the discussions (B)	Approximate mean given in the tables and discussions	Standard deviation calculated on (A)	Standard deviation calculated on (B)
105A	44	122.85	122.5	123	6.4	6.4
105B	49	135.00	137.5	138	7.0	7.3
105C	50	137.40	137.5	138	5.8	5.8
105D	48	129.50	127.5	128	5.2	5.5
105E	50	138.50	137.5	138	7.7	7.7
Averages and totals	243	132.65	132.5	133	8.5	8.6

Now the greatest difference in standard deviation arising from different methods of calculating was .3 or about 3.5 percent of the average standard deviation, whereas the greatest difference between the different lines was 2.5 (that between 105D and 105E) or 29.4 percent, a little over eight times the error introduced by the different methods of calculation. In view of such facts it was not considered worth while to waste time in accuracy of calculation which could not possibly add any significant value to the constants so obtained.

Although the probable errors of a large proportion of the constants here given have been calculated they are not given in the text on account of lack of space and the difficulty of placing them in complicated tables of distribution, etc. In nearly every case, however, in which the reader is interested, the probable errors can readily be calculated from the data given. In the F_2 hybrids most of the cultures had from 85 to 95 individuals and in the F_3, from 40 to 48.

It has been necessary to devise some means of comparing the variability of a series of hybrid races with their pure line parents, each of which may perhaps be grown in several different plant rows in different parts of the experimental plots. Moreover, if we accept high variability as a measure or indication of heterozygosity, it will be of interest to compare the variability of second generation hybrids with the third generation (F_3). In close-pollinated plants like wheat, as the average of heterozygosity certainly decreases from generation to generation, the average variability of plant populations (populations arising from single mother plants) should also decrease. This average increase in homozygosity with respect to any one character is, however, not uniform in all lines. The recombinations may be such that an F_2 plant is just as heterozygous with respect to the factors governing height, for instance, as was its F_1 parent and the same may be said of certain individuals in the comparison of the F_3 plants with their F_2 parents. We will therefore have some F_2 plants just as heterozygous as their F_1 parents that will give rise to cultures of F_3 which are just as variable as were the F_2 cultures, but the majority of the F_2 plants will be less heterozygous than their F_1 parents and will therefore give rise to F_3 cultures less variable than were the F_2 cultures. Now since the quantitative characters concerned, as well as the variability of the same, are subject to environic modification (see behavior of pure lines in table 1) there must be some means of comparing statistically the variability of the F_3 cultures with the F_2 cultures in order to demonstrate this general decrease of variability in the succeeding hybrid generations.

Three methods are available as follows:

(a) Throw all the cultures of a given generation into a single population and calculate the standard deviation of the same.

(b) Superimpose the means of the several hybrid cultures, sum the equal deviations on each side of this mean and calculate therefrom a standard deviation for the whole series.

(c) Calculate the standard deviation and coefficient of variation of each hybrid culture separately and show the average and distribution of these constants.

These methods and the value of the constants so obtained will now be discussed in order:

(a) The standard deviation calculated by this method from a population consisting of several plant rows of a single pure line is always greater than the average of their standard deviations taken separately. This is caused not necessarily by differences in the standard deviations of the plant rows entering into the total population (these may be all identical) but by differences (environic) in the means of the several rows whereby the distribution of the population as a whole is much broadened. The distribution of this total population and the standard deviation derived from it are therefore measures of the total effects of the given different environments in modifying the character concerned. If now we are dealing with an F_2 generation all of which originated from genetically equivalent F_1 plants, part of the differences in the F_2 plants would be due to environic effects and part to the effects of genetic recombination. The distribution and standard deviation of a hybrid population calculated by method (a) would therefore give the total combined effect of environment and recombination in producing variability. When now we come to consider an F_3 population arising from genetically unequal F_2 plants we simply re-measure (if we plant all the seeds of all of the F_2 plants or a sufficiently large random sample) the influence of the same factors as were measured in the F_2, i.e., the sum of the effects of environment and all of the factors entering the cross from the original parents. We cover up the possibility of discovering any decrease in the heterozygosity of the F_2 plants since differences in the means of the F_3 cultures, due to the genetically different parents, will have the same effect in broadening the distribution of the total population, as differences in the individuals of a single highly variable culture.

(b) The method of superimposing the means introduces a small but unavoidable mathematical error where the standard deviation is used as a measure of the average variability of a number of separate cultures. It is well known, however, that where the means differ, the standard deviation is not a good measure of comparative variability. In order to overcome this difficulty and obtain abstract numbers which may be compared, the coefficient of variation has been devised. This is the percentage which the standard deviation is of the mean. It is therefore apparent that a given deviation from the mean has more weight in the determination of the coefficient of variation when it is a deviation from a small mean than when it is a deviation from a large mean. When now we superimpose small means and large means we give equal values to deviations which are of unequal value in determining the coefficient of variation. Hence if our data have to do with cultures differing widely in their means, where the coefficients of variability rather than the standard deviation must be used in the comparison of variabilities, we are not justified mathematically either in averaging standard deviations or superimposing means. As a matter of fact, however, it may be said that the error introduced by this means is not large. Taken alone, however, the method of superimposing the means has one serious fault. It covers up wide differences in the variability of different individual F_3 cultures. For the purposes of genetic analysis it is necessary to know whether all of the F_3 cultures have decreased in variability or whether this decrease is confined to the offspring of certain only of the F_2 plants. It is therefore necessary to calculate the standard deviations and coefficients of variation of each of the cultures separately.

(c) Since, as just stated, a knowledge of the distribution of the coefficients of variation of a series of hybrid cultures is probably even more important than a single general expression of the average variability as a whole, method (c) which gives all of these details is usually to be preferred.

In general the coefficient of variation was used as a measure of variability. In time relations, however, this is difficult on account of the necessity of selecting arbitrarily some point from which to estimate the means. In the case of the date of first heading, if some date in March, say the first or fifteenth were chosen, it was feared that the differences in means would be so great as to unduly distort the coefficients of variation. One may readily see that the later such a basal date be chosen the greater will be the distortion on this account. On the other hand, if the chosen date be moved backward, the various means, in comparison with each other, approach unity, and the coefficient of variation becomes then more and more dependent upon the size of the standard deviation. Although all of the plots were planted within a period of seven days in the fall and all came up at approximately the same time, it would be questionable whether the total vegetative period would be the best basis of a determination of the variability of date of first heading on account of the fact that some strains were more active in winter than others and were therefore given unequal starts in the rapid vegetative period of spring. In view of these difficulties it was decided to use the standard deviation (expressed in days) alone as the measure of variability in all time relations.

In the studies on size relations, the coefficients of variation only are given.

Where averages of a series of standard deviations are given, or standard deviations are calculated from artificial populations produced by superimposing the means of different races, such fact has been expressly stated, but it must not be understood that the writer would infer that these are strictly comparable mathematically to an average of a series of coefficients of variability, for reasons already given. Rather than true arithmetical averages, such means should be considered as foci around which the distribution of the given series of constants (here standard deviations) cluster, and therefore form, as it were, a locus for thinking specifically.

DATE OF FIRST HEAD

The dates of the first head of the parents and the F_1 plants in 1914 were not taken.

Macaroni × bread wheat crosses. Algerian macaroni (No. 1) × Sonora (No. 35)

In 1915, 3 pure races of No. 35, 9 pure races of No. 1, and 37 cultures of (1 × 35) F_2, were grown at Yuma. The following results were obtained:

TABLE 2 A

Date of first head in F_2 of cross 1 × 35 and in the parent strains, 1915.

	Number of cultures	Number of individuals	Average dates of first head	σ of population	Average σ of cultures
Pure No. 35...	3	168	March 17	2.14	1.66
(1 × 35) F_2...	37	2546	" 27	4.00	3.56
Pure No. 1...	9	650	" 31	3.30	1.87

TABLE 2 B

Distribution of standard deviation of cultures.

	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75
Pure No. 35............		1	1	1							
(1 × 35) F_2...........				2	7	12	5	8	2	1	
Pure No. 1............		1	5	2		1					

The 37 hybrid cultures were from the seed of the 37 F_1 plants secured in 1914 which were sown in plant rows in 1915. It should here be noted that the standard deviation of the whole population is markedly higher than the average standard deviation of the plant rows taken separately. This was also true of the pure races and can be attributed in part to the place variation of the different plant rows. Part of this difference may also be due to slight differences in the genetic composition of the individuals of the parental varieties used in the original cross. However, these individuals, although not all belonging to one pure line, in their respective varieties, were carefully selected as belonging to the type of the variety which they were to represent. The differences between the average standard deviation of the pure lines taken separately and of their respective populations is therefore an approximation of the error introduced by place varation (modification) and whatever genetic differences there might have been in the several individuals of the parental cultures.

The greater variability of the hybrid cultures as compared with the parental varieties is in accordance with what would be expected from the recombination of genetic factors in the F_2 generation. The mean of the hybrid cultures was 3 days later than the mean of the parents and 4 days earlier than the late parent. The heading dates of both parents and of the F_2 cultures may be summarized as follows:

TABLE 3

Date of first head in (1 × 35) F_2, 1915.

Cultures	March									April									
	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21
Pure No. 35	25	85	47	7	4														
(1 × 35) F_2	4	18	74	21	403	796	306	403	266	98	86	42	17	8	1	2			1
Pure No. 1						11	78	153	132	134	81	54	5	2					

Means of cultures.

Pure No. 35			2	1															
(1 × 35) F_2					1	7	17	12											
Pure No. 1							1	4	1	2	1								

From the 2546 F_2 plants, 230 were selected and planted in plant rows at Yuma in the fall of 1915. These selections were, for the most part, based upon economic characters. However, the dates of first heading of the plants in the spring of 1915 varied from March 15 to April 9 and thus furnished material for the study of the segregation of the factors relating to time of heading.

For comparison of the parental varieties with these F_3 hybrids, 7 pure cultures of No. 1 and 5 pure cultures of No. 35 from plants selected as types from these same varieties of the previous year, were grown. The results may first be summarized as follows:

TABLE 4

Date of first head in (1 × 35) F_3, 1916.

Culture	Number of cultures or plant rows	Number of individuals	Average date of first head	σ of total population	Average σ of culture
Pure No. 35...	5	247	March 25	1.34	1.27
(1.× 35) F_3...	230	9772	April 11	6.24	3.14
Pure No. 1....	7	343	April 15	1.99	.91

Distribution of standard deviation.

Culture	.25	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75	7.25
Pure No. 35.......	1	3	3												
(1 × 35) F_3)......		2	9	20	38	35	45	41	17	8	9	4	1		1
Pure No. 1........		2	1	1	1										

The increase in the variability of the F_3 population of hybrids over the F_2 population is striking and surprising. Knowing that only selected individuals of the F_2 were planted, one, at first thought, might be inclined to attribute this to the selection of extremes from both ends of F_2 as parents, but observation of the column showing number of cultures in table 4 will show that the distribution of F_2 parents forms practically a normal curve. One can therefore only attribute this increase to climatic differences in the two seasons which emphasized the effects of extreme combinations more in 1916 than in 1915, or else to the following, which probably accounts for the greater part of the increase. It will be noted that the standard deviations of both the populations and cultures, averaged separately, of the parental varieties, was less in 1916 than in 1915, and also that the same was true of the average standard deviation of the separate cultures of F_3 as compared with that of the separate cultures of F_2. These facts indicate that the season of 1916 did not emphasize the extremes either in the pure cultures of that year or in the F_3 cultures taken separately, or at least that in the latter case the increasing homozygosity of the F_3 over the F_2 was a little more than able to offset this effect and thereby reduce the variability of the F_3 cultures as compared with the F_2 cultures taken separately. Now in this increase in homozygosity of the F_3 cultures probably lies the increase in variability of the population as a whole. We have already seen that the heterozygotes here tend to take an intermediate position. Hence as the percentage of heterozygous forms decreases with the approach toward homozygosity, the percentage of intermediate types will grow less, i.e., the curve will be flattened, and the standard deviation of the population, thereby slightly increased.

TABLE 5

Date of first head in (1 ×35) F_3, 1916.

	Number of cultures	March									April															May			Number of individuals
		15	17	19	21	23	25	27	29	31	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	2	4	6	
		16	18	20	22	24	26	28	30	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29	1	3	5	7	
Pure No. 35	5				1	3	8	161	69			4																	246
(1 × 35) F_3	230		3	26	46	43		267	136	356	432	767	693	863	2	2893	2156	578	103	355	103	69	48	20	1	3		1	9772
Pure No. 1	7															88	164	84	6	2									344

Average dates of heading of separate plant rows.

Pure No. 35	5							4	1																				
(1 × 35) F_3	230						3	2	4	6	8	13	17	21	33	58	38	8	13	3	3								
Pure No. 1	7															2	3	2											

A summary of the distribution of the dates of first head in the plants of the parental cultures and the F_3 hybrids is shown in table 5.

It should now be noted that, considering individual plants, there were among the hybrids, 29 plants earlier than the earliest of No. 35 and 293 plants later than the latest of pure No. 1. Moreover, considered as cultures, there were three cultures whose average date of first head was earlier than the earliest average of any of the cultures of pure No. 35 and that there were 19 cultures averaging later than the latest pure culture average of No. 1. There were in fact three cultures whose average date of first head was later than the latest individual of pure No. 1. Does this indicate that by recombination we may be able to isolate races which are earlier than the early parent and later than the late parent?

Table 6 shows the distribution of the F_3 individuals and cultures arranged according to the date of first heading of the parent F_2 plants. **+** = the date of the first head on the selected F_2 parent. **O** = the average date of the population arising from such parents (reading horizontally). In the same grouping of cultures there are also shown the distribution of the means of the F_3 cultures taken separately and the distribution of the standard deviations of these cultures. The first vertical column at the left shows the number of F_2 plants (hence F_3 cultures) in each category. In a vertical column are also shown the average of the standard deviations of the cultures taken separately in that category.

Table 7 shows the distribution of the F_3 individuals and cultures arranged according to the means of the F_3 cultures. **O** = the average date of first head of the cultures going to make up the population in that group (horizontal). This table also shows the distribution of the selected F_2 plants which were the parents of the several cultures making up the corresponding culture groups. The distribution of the standard deviations of the several races taken separately which make up its corresponding category is given. The vertical columns are the same as in table 6.

Table 6 shows us that the differences observed in the date of first heading of the individual plants of F_2 were largely genetic, since their offspring (F_3) exhibits but little regression toward the general mean. Again the same thing is perhaps better shown in table 7 where the F_3 cultures are grouped and arranged in accordance with their own means. We then have the distribution of the parents of these groups of F_3 cultures. It will be observed that in no case does the distribution of the parents, for any group of F_3 means extend beyond the normal limits of

TABLE 6

Date of first head in (1 × 35) F_3, 1916. Distribution based upon date of first head of the selected F_2 parents.

	F₃ individuals																							
	March								April															May
ber of	15	17	19	21	23	25	27	29	31	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	2
tures	16	18	20	22	24	26	28	30	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29	1	3
1	+		11	9	8	O	13	1		1	6														
5		+ 3	12	25	25		O 81	25	28	8	10	2							1						
7			+ 3	10	9		88	O 51	54	32	14	11	6		10	1									
1				2	+ 1		81	46	163	225	O 348	210	226		363	93	18	1	4		1	1			
0					1	+	4	9	102	144	235	268	336	O 1	867	504	88	11	29	9	5	6			
7							+	3	3	12	92	116	78		O 362	233	55	3	39	9	12	6	3		1
0								+ 1	6	10	54	61	85	1	630	O 580	153	21	95	30	17	8	6	1	2
8									+	1	8	22	27		333	O 214	128	40	113	31	34	16	6		1
6										+		3	1		5	105	O 71	7	38	7	17	2	4	1	
2											+					49	O 8		22	1	1	2			
2												+				3	18	13	17	O	31	6	3		5/6 = 1
1													+			1	17	O 3		15	1				

= Selected F_2 parents.
= Mean of F_3 group.

		Means of F₃ cultures														
		March				April										
Number of cultures	Average σ of F₂	25 26	27 28	29 30	'31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23
1	5.21	1														
5	3.88	3		1	1											
7	3.83		1	2	3	1										
41	3.39			1	2	5	10	7	7	5	3	1				
60	3.00					3	3	7	10	14	15	7	1			
37	3.21							3	3	8	16	6			1	
40	3.00							1	1	6	14	10	5	3		
28	2.81										8	12	1	4	1	2
6	3.34											2	1	3		
2	2.78											1		1		
2	3.51														1	1
1	2.58													1		

TABLE 6 (continued)

Date of first head in (1 × 35) F_3, 1916. Distribution based upon date of first head of the selected F_2 parents.

Number of cultures	Standard deviation of F_3 cultures													
	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75	7.25
1										1				
5					2		1		1		1			
7			1			2		3				1		
41			5	3	6	10	10	3		1	2			1
60	1	5	6	8	6	15	10	4	2	3				
37	1	2		7	6	5	10	4	1	1				
40		2	3	10	7	7	5	1	2	2	1			
28			5	9	3	3	5	1	2					
6				1	1	3				1				
2					2									
2					1			1						
1					1									

variation of the most variable parental culture. If the differences in the means of the F_3 cultures in tables 6 and 7 are due to genetic causes, one would expect the intermediate cultures to be more variable than the extremes, thus assuming that the extreme cultures are more nearly homozygous than those which are intermediate.

Now noting the distribution of standard deviations in the F_3 cultures as given in tables 6 and 7 and the average of the standard deviations for separate cultures as shown in the vertical columns, we are unable to discover such a decrease in variability toward the extremes. In the present material, however, this is not surprising for the following reason: No. 1 and No. 35 differ in so many genetic factors that there is an extremely wide range in the products of their recombination. As a matter of fact many of these recombinations are so radical and unbalanced that they are no longer automatic (i.e., are unable to give rise to a living organism). Hence there is a large percentage of sterility in the F_2 and later generations. Now the recombination of factors which govern (by their interaction) the time of heading in this particular cross are likely so many and so widely different that all of the possible recombinations would give a range of heading time far beyond (both toward the early and late extremes) the limit of physiological possibilities of a normal wheat plant. Hence in the range of variation observed in the F_2 or F_3 of this cross we have only a small section taken from some part of the larger theoretical curve. It would therefore appear much flatter than the corresponding curve of a pure race and there would be but little difference in the heterozygosity, hence, variability, i.e., standard

TABLE 7

Date of first head in (1×35) F_3, 1916. Distribution based upon the means of the F_3 culture.

	F₃ individuals																								
	March								April															May	
Number of cultures	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23	24 25	26 27	28 29	30 1	2 3
4		3	23	34	31	O	59	6	9	2	9	1							1						
1			1	4	6		O 18	13	6	1															
4				2	1		88	O 32	32	10	1				1	1									
6			2	4	3		62	40	O 65	45	20	11	9		7										
9				3			28	22	101	O 95	66	17	7		8	3									
13					1		15	12	75	117	O 187	73	43		50	13	1								
18								6	28	79	229	O 150	128		135	29	2	1	2						
21								5	10	38	161	159	O 209		288	64	5		1						
33								1	1	23	64	167	269	O 1	618	200	21	1	6	3	1				
56									1	8	32	110	166	1	O 1175	788	137	12	43	8	10	3	3		
39										1		10	17		545	O 768	230	27	78	30	9	6			1
8											1	7	1		28	153	O 46	33	43	5	9	6	1		
13											1	2	1		27	128	112	O 10	122	44	31	12	6	2	1
3															6	11	29	17	O 26	5	30	4	6		1
3																4	10	3	43	O 7	28	15	4		

O = Mean of group.

		Distribution of F₂ parents												
		March								April				
Number of cultures	Average σ of F_3	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9
4	4.84	1	3											
1	3.07			1										
4	2.70		1	2		1								
6	3.77		1	3		2								
9	2.80			1		5	3							
13	3.34					10	3							
18	3.43					7	7	3	1					
21	3.63					7	10	3	1					
33	3.31					5	14	8	6					
56	2.85					3	15	16	14	8				
39	2.59					1	7	6	10	12	2	1		
8	3.47						1		5	1	1			
13	3.56								3	4	3	1		1
3	4.14							1		1			1	
3	3.24									2			1	

TABLE 7 (continued)

Date of first head in (1 × 35) F_3, 1916. Distribution based upon the means of the F_3 culture.

Standard deviation of F_3 cultures.

Number of cultures	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75	7.25
4							1		1	1	1			
1						1								
4			1	1	1			1						
6					2	2		1				1		
9	1	1	1	2		1	1	1			1			
13			3	1		3	3	1	1	1				
18			1	1	4	4	5	1	1	1				
21					3	8	5	3		1	1			
33			2	7	5	5	9	3	1					1
56	1	6	6	9	8	12	9	3	1	1				
39		2	5	12	10	5	3	1	1					
8				3		2	1			2				
13				1	3	3	1		2	1	1			
3					1			1		1				
3			1				1	1						

deviation, of the cultures arising from individuals selected from either the middle or extremes.

Bread wheat crosses. Red Algerian bread (No. 3) × early Baart (No. 34)

In 1915, 1 culture of pure No. 3, 1 culture of pure No. 34 and 6 plant rows of the F_2 of 3 × 34 were grown. These hybrid rows were from the 6 F_1 plants of this cross obtained in 1914. As noted above, dates of first heading were not taken in the F_1 plants. A summary of the results in 1915 is given in table 8:

TABLE 8

Date of first head in (3 × 34) F_2, 1915.

	Number of cultures	Number of individuals	Average date of first head	σ of population	Average σ of cultures
Pure No. 3....	1	42	March 28	1.60	1.60
(3 × 34) F_2...	6	538	March 23	3.98	2.95
Pure No. 34...	1	93	March 16	1.75	1.75

Distribution of σ of separate cultures.

	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75
Pure No. 3..........................			1						
(3 × 34) F_2..........................		1		1	1		2	1	
Pure No. 34			1						

As previously, it may be noted again that the standard deviation of the hybrids both as a population and as separate cultures was higher than that of the parental varieties. The mean of the F_2 hybrid population was only 1 day later than the mean of the parents. The heading dates of the populations of parental cultures and F_2 hybrids may be given in table 9.

TABLE 9

Date of first head in (3 × 34) F_2, 1915.

	March												April
	9	11	13	15	17	19	21	23	25	27	29	31	2
	10	12	14	16	18	20	22	24	26	28	30	1	3
Pure No. 3									2	24	10	6	
(3 × 34) F_2	1			18	33	61	136	47	62	130	40	8	2
Pure No. 34				53	33	6		1					

Means of cultures.

Pure No. 3										1			
(3 × 34) F_2							2	3		1			
Pure No. 34				1									

From these 538 F_2 plants 112 were selected, for economic reasons, for planting in the fall of 1915. For comparison 5 cultures of each of the parental varieties were also grown. These were selected from typical plants of the parental varieties of the previous season. The range of dates of first heading of the selected F_2 plants extended from March 10th to the 29th, thus covering 19 of the 23 days of total variation of the F_2. The first summary of results are given in table 10.

TABLE 10

Date of first head (3 × 34) F_3, 1916.

	Number of cultures or plant rows	Number of individuals	Average date of first head	σ of total population	Average σ of cultures
Pure No. 3	5	242	April 13	1.52	.82
(3 × 34) F_3	112	5321	April 5	6.43	2.95
Pure No. 34	5	244	March 25	3.10	2.17

Distribution of standard deviations.

	.25	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25
Pure No. 3	2	2		1									
(3 × 34) F_3	2	2	7	14	15	15	7	10	14	8	9	4	3
Pure No. 34		1			2	1	1						

The general features of this table are the same as those for the other crosses, namely, that the average standard deviations for the cultures are less than those of their respective populations and that the hybrid cultures are much more variable than the pure lines. Moreover, as in the comparison of tables 1 and 4 we here note also an increase in the variability of the F_3 population of hybrids over that of the F_2. (Compare tables 8 and 10.) The failure of the average standard deviation of the hybrid cultures to decline from 1915 to 1916 should be noted. Does this indicate a lack of progress toward homozygosity?

Such an inference would be natural were it not for the peculiar behavior of the parental pure race No. 34.

It will be observed that the variability of this race was strongly increased in 1916 over 1915, although all of the 5 cultures belong to one and the same pure line, i.e., the single pure line grown the previous year, which had originated from a single plant in 1914. Perhaps the same factors which caused this increase in the variability of the pure line No. 34 were also able to increase the variability of the hybrid cultures which arose from No. 34 as one parent and that this influence upon the variability was sufficient to offset that of increasing homozygosity and thus maintain the variability for the two seasons at approximately the same figure.

The distribution of the dates of first head in the parental races and in the F_3 hybrids for 1916 is shown in the following table:

TABLE 11

Date of first head in (3 × 34) F_3, 1916.

	March								April										
	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23
Pure No. 3.......										1	1		14	87	138	1			
(3 × 34) F_3......		12	17	43	139	415	761	675	597	842	391	195	157	30	1103	21	17	1	1
Pure No. 34......	1	30	41	56	23	74	17	1											

Means of cultures.

Pure No. 3.......														3	2				
(3 × 34) F_3......					1	12	9	14	15	21	9	6	10	7	8				
Pure No. 34......			1	1	2	1													

It is interesting to note here that no hybrid plant was earlier than the earliest individual of the early culture and that there were only 19 later than the latest of the late parent. Again considered as cultures, the means of the hybrid cultures all fall within the limits set by the extreme means of the parental variety cultures. Here recombination does not seem to have extended the variability definitely beyond the limits of the parents.

Tables 12 and 13 show the segregation of the F_3 to be just as marked in this cross as in the cross already discussed. The greater variability of the intermediate classes is also quite evident. This fact taken in connection with the fact that there was no indication of partial sterility among the hybrids seems significant. It is exactly what should be expected if the segregation of the F_2 plants and F_3 cultures were due to recombination. This should be contrasted with the absence of greater variability of intermediates in the semi-sterile hybrids of the bread wheat—macaroni wheat crosses.

TABLE 12

Date of first head in (3 × 34) F_3, 1916. Distribution based upon dates of first head of the selected F_2 parents.

Number of cultures	F₃ individuals																						
	March											April											
	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23
1	+						1	2	1		13	O 11	14	5					3				
2				+						56	O 16			22									
7					+	2	6	37	16	O 172	47	30	3	21									
13						+		1	16	72	153	103	O 30	158	10	22	4	3	56	2	1		
38						10	+ 10	3	104	91	481	O 396	248	214	59	45	26		101	6			
13								+	2	3	49	85	121	O 170	37	26	15	12	84		5		
14									+	11	1	37	57	195	O 151	36	31	14	124	4	8	1	
21										+	1	13	24	57	134	O 56	80	1	619	2			
3											+					14	1		O 125	1			1

+ = Selected F_2 parents.
O = Mean of group.

Number of cultures	Average σ of F₃ cultures	Means of F₃ cultures														
		March			April											
		25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23
1	6.30				1											
2	1.47		1		1											
7	2.01	1	4	1	1											
13	3.79		1	3	1	3	5									
38	3.46		6	5	9	9	7	1		1						
13	4.02				1	3	4	3	1	1						
14	3.82					1	3	4	3	3						
21	2.46						1	1	2	5	6	6				
3	2.03										1	2				

TABLE 12 (continued)

Date of first head in (3 × 34) F_3, 1916. Distribution based upon dates of first head of the selected F_2 parents.

Standard deviations of F_3 cultures.

Number of cultures	.25	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75
1													1	
2	1					1								
7			1	3	1	2								
13			1	1	2	1			5		1		2	
38			1	5	7	4	3	4	2	5	4	2		
13				2	1			2	2	1	3	1		
14				1		3	1	2	4	1	1	1		
21	1	2	3	1	4	3	3	2	1	1				
3			1	1			1							

TABLE 13

Date of first head in (3 × 34) F_3, 1916. Distribution based upon means of F_3 cultures.

	F_3 individuals																						
Number	March													April									
of cultures	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23
1						2	4	24	O	15	1												
12						8	9	16	79	O 200	214	38	1	1	1								
9							3		30	72	O 195	108	13	6	1				1				
14						1	1	2	20	40	157	O 222	101	92	7		3		17				
16									9	55	116	136	O 108	221	37	18	6	2	59	2			
20						1		1	1	20	78	136	192	O 291	58	24	31	2	101	8	1		
9										13	1	27	69	150	O 71	7	19	5	79		1		
6											1	1	9	52	84	O 45	26	7	52	3	5		
10													4	27	112	58	O 46	13	213		6	1	
7														2	19	40	24	O 1	248				
8															3	8	2		O 352	2	1		1

O = mean of group.

TABLE 13 (continued)
Date of first head in (3 × 34) F_3, 1916. Distribution based upon means of F_3 cultures.

		Selected F_2 parents												
		March											April	
Number of cultures	Average σ of F_3 cultures	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3
1	2.55					1								
12	2.05				1	4	1	6						
9	2.05					1	3	5						
14	3.35	1			1	1	1	9	1					
16	4.18						3	9	3		1			
20	4.32						5	7	4		1			
9	4.18							1	3	4	1			
6	3.74								1	3	2			
10	3.63							1	1	3	5			
7	2.53										6	1		
8	1.21										6	2		

Standard deviations of F_3 cultures.

Number of cultures	.25	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75
1						1								
12	1		1	3	3	3	1							
9			2	2	4			1						
14				4	1	3	1		1	1	1	1	1	
16				1	1	1	1	1	5	2	2	1	1	
20		1		2	1			1	4	3	4	2	2	
9						2		2	1	2	2			
6						1	1	1	2	1				
10							4	4	2					
7				1	2	4								
8	1	1	4	1	1									

Summary; date of first head

In both crosses the parents had wide differences in heading dates and the averages of the F_2 and F_3 were in every case intermediate and nearer to the late parent. The range of the individual hybrid plants in no case extended significantly beyond the range of the early parent toward extreme precocity of heading. Toward the late extreme, however, in the macaroni—bread wheat crosses, there was a long extension of the range, much beyond that of the late parent. As a matter of fact many plants never headed, but remained as dark green, grass-like tufts until they were killed by the heat and dryness of the summer. Among the bread wheat crosses the extension of the range of date of first head beyond the extreme of the late parent was never marked and could, in fact, be accounted for by the normal extension of the curve due to greater numbers.

The same observations made above with regard to the relation of the means of the hybrid populations to their parental means, apply also to the distribution of the means of the hybrid cultures, as compared with their parents, in the F_2. In the F_3, however, the matter was somewhat different. In the macaroni—bread wheat cross there were 3 cultures whose average dates of first head were earlier than the earliest parental average and there were altogether 19 cultures averaging later than the latest parental average. Since there were 230 cultures concerned, 8.2 percent are thus seen to lie outside of the parental range. In the bread wheat cross, on the other hand, there was no case where the average of a hybrid culture was outside the range of averages for the parental varieties. As regards individuals in the F_2 the parental types were abundantly recovered in every case. As regards means of F_3 cultures (a better criterion of the genetic constitution of the F_2 plants) the parental types were also recovered in all cases.

In all cases where more than one culture was involved the standard deviations of the population were greater than the average of the standard deviations of the cultures taken separately and in all cases the standard deviations of the hybrids[1] were greater than those of either parent both as regards that of the populations and the averages of the cultures taken separately.

In comparing the standard deviations of the hybrid F_3 populations with their respective F_2 parental populations we may note the following observations: (1) the standard deviation of F_3 populations are so dependent upon the range of F_2 parents chosen, that conclusions drawn from the calculation of this constant should be carefully guarded. The standard deviation of the F_3 population of both crosses was greater than that of the F_2 population. Since heading time appears to be imperfectly dominant in these hybrids, the number of intermediate types will tend to be reduced as the population approaches homozygosity. If therefore we assume a Mendelian inheritance, whenever the selected F_2 parents practically cover the range of distribution of the F_2 population and form a random sample thereof, we would expect the F_3 population to have a higher standard deviation than the F_2 population.

When we come to compare the average variability (here measured by standard deviation) of the F_3 cultures taken separately with the average

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[1] It should be remembered that the F_1 is not here included.

variability of the F_2 cultures we are not hampered in our conclusions, to so large an extent as mentioned above in comparing the variability of the F_2 and F_3 populations. With a Mendelian interpretation there is no genetic reason why any F_3 culture should be significantly more variable than the most variable F_2 culture. Moreover, the average variability of the F_3 should be equal to or less than that of the F_2, whatever the mode of selection. We may now observe as follows: (1) In the macaroni—bread wheat cross, 1 × 35, the average variability of the F_3 cultures was significantly below that of the F_2 cultures. (2) In the bread wheat cross some complications arose. The average standard deviations of the F_2 and F_3 cultures of the 3 × 34 were the same (2.95). This, however, cannot be assumed as evidence of a lack of progress toward homozygosity, for the following reasons: It will be observed that the variability of pure race No. 34 was strongly increased in 1916 over 1915 (2.17 and 1.75, respectively) although all 5 of the cultures grown in 1916 came from the 1 culture grown in 1915, which in turn came from a single plant in 1914. Perhaps the same factors which caused this increase in the variability of the pure line No. 34 were also able to increase the variability of the hybrid cultures which were grown from No. 34 as one parent and that this influence upon the variability was sufficient to offset that of increasing homozygosity and thus maintain the variability for the two seasons at the same figure.

The strongly fluctuating nature of the variability of date of first head is shown by a study of the distribution of the standard deviations of the F_2. In every case the range of distribution of the standard deviations of the F_2 overlapped the range for one or both parents. This could be explained by assuming a partial-blending inheritance and assuming that in some F_1 plants the blend was more complete than in others. If this were true the F_3 cultures grown from these low-variable F_2 cultures should also show a low variability. The results are given in table 14.

TABLE 14

Number of F_2 cultures as little variable as one parent	Number of F_3 cultures arising from these	Average σ of these F_3 cultures	Number of F_2 cultures more variable than either parent	Number of F_3 cultures arising from these	Average σ of these cultures
22	148	3.12	21	194	3.05

It is thus seen that the low-variable F_2 cultures gave rise to the higher-variable F_3 cultures. This is what would be expected upon a Mendelian interpretation if we assumed that the low variability of the F_2 cultures in question were so because but few of the extreme combinations chanced to occur. It must be admitted however that the difference shown is not large enough to be significant. We may therefore safely conclude that the differences in standard deviations of the F_2 cultures were wholly fortuitous and without genetic significance.

In the F_3 generation, in all cases, cultures occurred with as low variability as that of the parents, i.e., there were cultures which, insofar as variability is concerned, appeared as nearly homozygous as the pure lines.

With a Mendelian interpretation we are accustomed to expect those F_2 plants which take a position relative to the parents similar to that occupied by the mode of the F_1, to give rise to F_3 cultures which are more variable than the F_2 plants otherwise located. In the macaroni—bread wheat crosses we are not able to observe any relation of this kind. This fact, however, does not argue the absence of Mendelian segregation for the following reasons: The macaroni and bread wheats here crossed, differ in so many genetic factors that there is an extremely wide range in the products of their recombination. Many of these recombinations are so radical and unbalanced that they are no longer automatic. Hence there is a high percentage of sterility in the F_2 and later generations. Such sterility may have the effect of flattening the distribution curve of the F_2 or perhaps even limiting it to one end or the middle or even the extremes of a curve which would be formed by all of the recombination possibilities. As already pointed out many of the F_2 plants never got beyond the rosette stage and many plants which made a robust vegetative growth were completely sterile. The study of sterility in these crosses will be reserved for a future paper. In circumstances such as these it is apparent that there may occur very little difference in the heterozygosity, hence variability, of the cultures from individuals selected from either the middle or extremes of the fertile F_2 of such a population. In the 3 × 34 cross there is a very apparent greater variability of the cultures arising from the modal F_2 plants (see tables 12 and 13). It should be noted that here there was complete fertility and the F_2 selections covered nearly the whole of the range of the F_2 population. A glance at tables 6 and 12, where the F_3 individuals are grouped with reference to the heading date of the F_2 parents, yields abundant evidence that some sort of segregation has occurred. The F_2 plants were not alike genetically. All of the phenomena observed can be explained by assuming that heading date is governed by three or more Mendelizing unit factors. No attempt has been made to determine the number of factors in any case but the fact that many of the intermediate groups (see tables 6 and 13) show cultures with low variability would indicate that the number of factors concerned was rather large, thus providing the possibility of securing several genetically different but still homozygous types.

HEIGHT

Macaroni—bread wheat crosses. Algerian macaroni (No. 1) × Sonora (No. 35)

In this study all height measurements were made from the ground to the top of the highest head (not including the awns). Lengths were taken to the nearest centimeter and expressed in the summaries to the nearest five centimeters. No pure No. 35 was grown in 1914 which was comparable with the pure No. 1 and the (1 × 35)F_1. The No. 1 grown in 1914 was not a single pure line but was from seed of several different mother plants of this variety. A summary of the results for 1914 is shown in table 15.

TABLE 15
Heights in centimeters in (1 × 35) F_1, 1914.

	Number of plants	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	Average	C.V.
Pure No. 1..........	151	1		1	3	9	26	43	49	18	1	134	10.0
(1 × 35) F_1.........	39				1		1	4	8	21	4	147	8.0

The F_1 was taller but no more variable than the parent given. Thirty-eight of these hybrid plants gave rise to hybrid cultures in 1915. The results are summarized in table 16.

TABLE 16
Heights in (1 × 35) F_2, 1915.

	Number of cultures	Number of individuals	Average height	Coefficient of variation of population	Coefficient of variation of separate cultures
Pure No. 1..........	9	648	147	8.5	6.7
(1 × 35) F_2.........	38	2535	122	19.6	19.0
Pure No. 35.........	3	166	128	11.1	6.4

Distribution of the coefficients of variation of cultures.

	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Pure No. 1............		3	2	2	1					1											
(1 × 35) F_2...........													2	8	3	9	8	4	2	1	1
Pure No. 35...........	1		1			1															

It should be noted here that, whereas the F_1 was taller than No. 1, the tall parent, the average of F_2 (where all of the F_1 was planted) was lower than either parent. The high sterility of the F_2 plants has already been noted. As usual the hybrids were more variable than either parent. It should also be noted that the F_2 hybrids were much more variable than the F_1.

Table 17 gives the distribution of the populations and means of both parents and the F_2 hybrids as regards height.

TABLE 17

Heights in centimeters in (1 × 35) F_2, 1915.

	Distribution of individual heights																Distribution of means of cultures				
	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	110 119	120 129	130 139	140 149	150 159
Pure No. 1						1	4	4	4	25	89	155	217	139	10				2	3	4
(1 × 35)F_2	5	2	18	29	51	104	178	226	311	409	447	399	248	94	11	3	4	30	4		
Pure No. 35								8	25	29	52	38	13	1				1	1	1	

Only three of the hybrid plants were taller than the tallest individuals of the tall parent, but there were 95 lower than the lowest individual of either parent. No hybrid culture averaged as tall as the highest average for the low parent, but 4 cultures averaged lower than the lowest average of either parent. All recombinations so far obtained appear therefore to be less vigorous than the parental races. Since the F_1 plants showed considerable range in height, it would be interesting to know whether this was inherited to any degree in F_2, i.e., was the range in F_1 due solely to modification or were these differences partly genetic? Table 18 shows the F_2 cultures grouped according to the parental height. The class in which the parental height fell is marked **+**, and the mean of the population arising from such parents is marked **O**.

While the last class is 8 cm higher than the first class, considering the small number of races in each, this difference is not above the probable error. We may therefore safely conclude that for all practical purposes the F_1 plants were uniform genetically.

Two hundred and thirty of the F_2 plants were selected for planting in the fall of 1915 and gave rise to hybrid cultures which were measured just before ripening in 1916. For comparison 7 pure cultures of No. 1 and 5 pure cultures of No. 35 were grown. The first summary of results follow.

TABLE 18

Heights in centimeters in (1 × 35) F_2, 1915.

Number of cultures	Height of parent	Average height of offspring	Number of individuals	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199
1	120 129	118	37				3		2	6		O 4	+ 6	10	3	3				
4	130 139	123	228	1		3		8	6	18	20	25	O 34	+ 48	38	21	6			
8	140 149	122	485	2		2	7	3	20	39	40	57	O 68	87	+ 78	51	27	2	2	
21	150 159	123	1488	1	2	11	16	37	65	98	143	199	O 249 O	253	223	+ 139	46 +	5	1	
4	160 169	126	297	1		2	3	3	11	17	23	26	52	49	57	34	15	4		

TABLE 19

Height in centimeters in (1 × 35) F_3, 1916.

	Number of cultures	Number of individuals	Average height	Coefficient of variation of the population	Average C.V. of separate cultures
Pure No. 1....	7	344	137	8.4	6.6
(1 × 35) F_3..	230	10084	118	20.3	15.4
Pure No. 35...	5	246	123	7.1	6.3

Distribution of coefficients of variation in (1 × 35) F_3, 1916.

	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52
Pure No. 1...		4	2	1																					
(1 × 35) F_3..		6	15	24	35	38	28	21	20	19	11	3	4	3	1			1							1
Pure No. 35..	1	2	1	1																					

As usual it may be observed that the pure races are less variable than the hybrids and that the average coefficient of variation of the cultures is smaller than those of the populations. It should be further noted that the average coefficient of variation of the F_3 hybrid cultures is smaller than that of the F_2. This is to be expected in the case of increasing homozygosity.

Table 20 shows the distribution of the populations in 1916.

TABLE 20

Heights in centimeters in (1 × 35) F_3, 1916.

	10 19	20 29	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199
Pure No. 1....								2	2	1	9	83	114	95	33	6			
(1 × 35) F_3..	1	12	15	62	127	217	404	496	862	1335	1723	1757	1435	1077	471	75	8	5	2
Pure No. 35...							1	3	1	10	72	141	17	1					

Distribution of means.

	10 19	20 29	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199
Pure No. 1....												2	2	3					
(1 × 35) F_3..						1	2	13	21	49	53	42	36	12	1				
Pure No. 35...											2	3							

Only 15 hybrid plants were taller than the tallest individuals of the tall culture. Considering the large number of hybrids in comparison with the number of No. 1, these few taller plants are without significance. At the other end of the scale, however, we find 474 plants lower than the lowest of the lower parent. Considering means we also note with interest that there were 86 hybrid cultures averaging lower than the lowest average for the low parent and one hybrid culture averaging lower than the lowest individual of the low parent.

TABLE 21

Heights in centimeters in (1 × 35) F_3, 1916.

Number of cultures	Arrangement of F_3 individuals grouped according to F_2 parents																		
	10 19	20 29	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199
3				9	12	13	11	+ 9	O 17	27	29	5							
8		1	2	3	5	11	32	30	+O 67	83	52	21	5	4	1				
12			1	2	11	13	21	35	65	O+ 96	123	62	31	22	3	1			
24		7	1	10	21	32	54	72	160	O 226	+ 240	128	71	21	6	1			
35		1		12	24	33	79	106	144	250	O 326	+ 304	168	56	16	2			
55	1	2	7	20	31	61	99	107	174	310	O 473	507	+ 328	223	89	6	2		
48			4	5	12	36	62	76	124	186	271	O 428	423	+ 351	138	15		2	2
40		1		5	5	21	38	47	92	141	178	O 282	385	354	+ 174	41	5	2	
4				1	4	2	8	11	11	11	15	O 19	21	39	31	+ 3	1		
1													1	27	O 17	5	+		

Number of cultures	Distribution of means of F_3 cultures										Average coefficient of variation
	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	
3	1				2						16
8			1	2	4	1					18
12			3		5	3		1			16
24		1	2	6	7	8					17
35			3	4	11	10	5	2			15
55		1	3	4	11	17	11	6	2		16
48			1	4	5	7	14	14	3		14
40				1	3	8	10	13	5		14
4					1	1			2		18
1									1		5

Number of cultures	Distribution of coefficients of variation																									
	1 2	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52
3						2						1														
8						1	1	2	1	1	1	1														
12			1	2	1		2	2	1		2								1							
24			1	1	2	3	4	2	4	3	1			2												1
35				2	4	4	5	8	2	2	6		2													
55				2	9	10	9	3	5	4	4	3	1	2	2	1										
48			2	3	7	8	6	6	4	7	3	1			1											
40			1	5	1	6	11	3	5	3	1	4														
4						1		1			1	1														
1			1																							

TABLE 22

Heights in centimeters in (1 × 35) F_3, 1916.

Number of cultures	Distribution of F_3 individuais																		
	10 19	20 29	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199
1				9	12	○ 12	7			1	1								
2		4	1	12	10	7	○ 6	5	4	4	4	3	1	1	1				
13		4	3	10	23	46	73	○ 74	93	55	32	13	5	3					
21		1	5	15	31	51	90	125	○ 207	176	134	55	20	7	1		1		
49		2	2	12	13	56	118	175	292	○ 534	526	292	91	27	5				
53	1			7	10	27	70	66	144	375	○ 627	625	280	95	23	5			1
42			4	2	7	15	30	30	71	131	269	○ 481	484	264	75	12	1	2	
36					1	6	9	13	35	47	96	234	○ 470	493	183	17	1	2	1
12					1		2	5	6	8	17	43	81	○ 180	172	35	6		
1													1	27	○ 17	5			

Number of cultures	Distribution of F_2 parents										Average coefficient of variation
	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	
1	1										24
2				1		1					41
13		1	3	2	3	3	1				23
21		2		6	4	4	4	1			21
49	2	4	5	7	11	11	5	3	1		17
53		1	3	6	10	17	7	8	1		14
42				2	5	11	14	10			14
36			1		2	6	14	13			11
12						2	3	5	2		11
1										1	5

Number of cultures	Distribution of coefficients of variation																									
	1 2	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52
1												1														
2															1											1
13									1	1	7	1		1		1			1							
21							1	5	1	5	1	3	1	2	2											
49			1		3	6	7	9	5	6	6	3	2	1												
53				6	7	10	8	6	6	4	4	2														
42				2	3	9	11	4	8	4	1															
36			3	5	9	7	8	2	1			1														
12			1	2	2	3	3	1																		
1			1																							

Table 21 shows the height of the F_3 plants grouped according to their F_2 parents, the means of the F_3 cultures and the coefficients of variation of these cultures, respectively, making up each population group. Table 22 shows the height of the F_3 plants grouped according to the means of the F_3 cultures, the heights of the parents giving rise to these groups and the standard deviations and coefficients of variation of the F_3 cultures, respectively. It should be noted in table 21 that, while there was considerable regression toward the mean, there was a nearly uniform correlation between the height of the F_2 parent and the F_3 offspring. By comparing table 21 with table 20 it will be observed that the distribution of the means in any group of hybrids is no wider than the range of variation of the individuals in either of the parental varieties. Observing the averages and distribution of the coefficients of variation we note an irregular but yet fairly definite lessening of variability in the taller groups.

Again comparing table 22 with table 20 we note that for any F_3 group (in table 22) the distribution of the parents was not wider than the distribution of the individuals of the parental varieties. The differences in the heights of the individuals of these parental groups (which gave rise to cultures having the same mean) could therefore be assumed to be environmental modifications of plants of the same or equivalent heredity so far as height is concerned.

The column showing the average coefficient of variation and the distribution of these constants in table 22 shows a very decided decrease in variability of those cultures which have high means.

One conclusion stands out prominently from these tables. The factors for height were not uniform in the F_2 plants. Recombination had occurred so that on the average (i.e., excluding environmental modifications), tall parents gave rise to tall offspring and the grading of the parents into a series of ascending heights resulted in a slightly less marked but still regularly ascending series of offspring groups. The completeness of this series indicates that the number of factors was large.

Algerian macaroni (No. 1) × Algerian red bread (No. 3)

In 1914, 151 plants of pure No. 1 and six plants of pure No. 3 together with 5 plants of (1 × 3) F_1 were measured for height.

The following table shows the distribution of the heights of these plants and their means. Except for the pure No. 1, the numbers were too small for the calculation of the standard deviations with any degree of accuracy.

TABLE 23

Heights in centimeters in the (1 × 3) F_1, 1914.

	Number of plants	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	Mean
Pure No. 1	151	1		1	3	9	26	43	49	18	1	134
(1 × 3) F_1	5				2			1	2			124
Pure No. 3	6				2	1	2	1				118

The numbers are too small to give results of any particular significance, but it may be noted that the range of the F_1 hybrids lies within the range of the most variable parent and that the mean of the hybrids lies between the means of the two parent cultures.

The 5 F_1 hybrid plants gave rise to 5 hybrid F_2 cultures in 1915. For comparison in the same year 9 cultures of No. 1 and 1 culture of No. 3 were available. Table 24 gives a summary of the results.

TABLE 24

Heights in the (1 × 3) F_2, 1915.

Culture	Number of cultures	Number of individuals	Average height	Coefficient of variation of the population	Average C.V. of the separate cultures
Pure No. 1	9	648	147	8.5	6.7
(1 × 3) F_2	5	406	118	21.1	20.4
Pure No. 3	1	42	146	4.2	4.2

Distribution of coefficients of variation.

	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32
Pure No. 1		5	3			1									
(1 × 3) F_2				1			1		1			1			1
Pure No. 3	1														

Whereas the F_1 hybrids were intermediate between the parent races, the F_2 averaged lower than either, the two parent races being of practically equal height. The variability of the hybrids was strikingly higher than that of the parental cultures.

Table 25 gives the distribution of the populations and the means of both parents and the F_2 hybrids as regards height.

None of the hybrid plants was taller than the tallest individual of the parental cultures but there were 29 lower than the lowest individual of the parents. It is striking that all of the means of the hybrid cultures save one were lower than the lowest parental mean. All recombinations, therefore, appear to be less vigorous than the parental cultures.

TABLE 25

Heights in centimeters in the (1×3) F_2, *1915.*

	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 1....					1	4	4	4	25	89	155	217	139	10
(1×3) F_2....	7	5	8	9	17	27	39	57	61	87	34	27	8	
Pure No. 3....										3	18	21		

Distribution of means of cultures.

	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 1....										2	3	4		
(1×3) F_2....							2	1	1	1				
Pure No. 3....											1			

Table 26 shows the F_2 cultures grouped according to the height of their respective F_1 parents. The class in which the parental height fell is marked + and the means of the population arising from such parents are marked O..

TABLE 26

Heights in centimeters in the (1×35) F_2, *1915.*

Number of cultures	Height of parent	Average height of offspring	Number of individuals	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169
2	100 109	105	82		2	4	5	4	9	10	O + 9	10	12	9	6	2	
1	130 139	110	54		3	1		2	4	3	5	O 9	9	+ 13	3	2	
2	140 149	126	270		2		3	3	4	14	25	38	O 40	65	+ 45	23	8

Although the range of each of these groups is practically the same, the distinct correlation between the height of parent and height of offspring cannot be disregarded. This would indicate that one or the other of the parental stocks was not pure as regards the factors influencing height and that the F_1 plants were, therefore, not all equivalent genetically in this respect. In order, therefore, to avoid complications, the subsequent discussion of this cross will be based upon the product of a single F_1 plant (145 cm high) in 1914 from which a culture (No. 32-1) was grown in 1915, of which the following data may be given:

TABLE 27

Heights in centimeters in the (1×35) F_2, *1915.*

Culture	Height of parent	Average height of offspring	Number of individuals	Average C.V.	Distribution of heights of individuals 70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169
32-1	145	130	71	15	1	1	4	10	7	11	9	13	10	5

From this culture 40 plants were selected as parents in 1915-'16. A first summary of the results may be given as follows:

TABLE 28

Heights in centimeters in (1 × 3)F_3, 1916.

Cultures	Number of cultures	Number of individuals	Average height	Coefficient of variation of the population	Average C.V. of separate cultures
Pure No. 1....	7	342	137	8.5	6.6
(1 × 3) F_3....	40	1758	123	20.6	14.2
Pure No. 3....	5	243	133	8.0	6.6

Distribution of coefficients of variation

Cultures	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44
Pure No. 1...............		4	2	1																	
(1 × 3) F_3...............	1	6	3	5	5	3	3	2	5	2	2	1				1					1
Pure No. 3...............	2	1	1		1																

Again we perceive that the averages of the coefficients of variation of the cultures are less than the coefficients of variation of their respective populations, and that the pure lines are less variable than the hybrids. The average variability of the F_3 is markedly less than that of the cultures in F_2.

Table 29 gives the distribution of the populations and means of both the hybrid and parental cultures.

TABLE 29

Heights in centimeters in (1 × 3)F_3, 1916.

	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 1..............					1	1	1	1	11	91	123	84	26	3	
(1 × 3) F_3..............	8	6	21	21	67	73	100	157	244	274	252	320	170	36	8
Pure No. 3..............		1			1			1	10	68	108	48	6		

Distribution of means.

Pure No. 1..............										2	2	3			
(1 × 3) F_3..............						2	4	5	9	6	3	9	2		
Pure No. 3..............										3	2				

Observing tables 28 and 29 it is evident that on the average, height-vigor in the F_3 hybrids was again less than for the two parental cultures but that there were two hybrid cultures taller than the tallest average for the taller parent. On the other hand 20 hybrid cultures were lower than the lowest average of the low parent.

Table 30 shows a fairly uniform correlation between the height of the selected F_2 parent and the average height of its F_3 offspring. Table 31 exhibits rather strikingly the fact that the taller F_3 cultures are much less variable than those which averaged lower. Now if one will compare the distribution of the selected F_2 parents (table 30) with the total F_2 population as shown in table 25, it will be observed that the selections just cover the upper half of the range. As regards the variability of the F_3, therefore, table 31 and the accompanying column of average coefficients of variation might be assumed to represent only a half curve. The low selections were therefore really intermediate F_2 individuals. The higher variability of these lower F_3 cultures, and the very evident decline in variability as we approach the taller, real, extreme, can be interpreted as being in accord with the idea of hybrid recombination of height factors with the intermediate forms most heterozygous and hence more variable.

TABLE 30

Heights in centimeters in $(1 \times 3)F_3$, *1916.*

Number of cultures	10	20	30	40	50	60	70	80	90	100	110	120	130	140	150	160	170
	19	29	39	49	59	69	79	89	99	109	119	129	139	149	159	169	179
2					1		4	7	13	+ 11	O 13	31	8	1			
3			2	1	6	4	12	17	O 16	19	+ 20	10	3	4			
7			1	3	4	5	19	16	22	42	O 87	+ 67	36	19	2		
9			3	2	6	7	20	17	21	47	O 66	81	+ 57	45	10	3	1
11			2		2	5	8	9	18	27	32	49	O 80	+ 147	89	27	7
6					1		4	7	9	10	22	30	O 54	72	+ 48	1	
2									1	1	4	7	14	O 32	21	+ 5	

+, Selected F_2 parents.
O, Means of F_3 groups.

Number of cultures	Distribution of means of F_3 cultures									Average coefficient of variation
	70	80	90	100	110	120	130	140	150	
	79	89	99	109	119	129	139	149	159	
2				1	1					15
3		1	1	1						25
7		1		1	3	2				16
9			2	1	2	3		1		17
11			1	1	1		3	3	2	11
6					2	1		3		12
2								2		10

TABLE 30 (continued)

Heights in centimeters in (1 × 3) F_3, 1916.

Number of cultures	Distribution of coefficients of variation in F_3 cultures																				
	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44
2					1			1													
3						1			1												1
7			1	1		1	1		1	1	1										
9			1	2		1	1		1	1	1					1					
11	1	3	1		4			1				1									
6		3					1		2												
2				2																	

TABLE 31

Heights in centimeters in (1 × 3)F_3, 1916.

Number of cultures	Distribution of F_3 Individuals																
	10 19	20 29	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
2			1	2	4	5	20	**O** 20	21	9	5	4					
4			4	3	11	10	17	11	**O** 20	18	17	24	6	7	1		1
5			2		1	2	10	18	25	**O** 49	55	32	10	2			
9					4	2	10	15	23	55	**O** 114	109	46	13	5		
6			1	1	1	2	8	6	8	20	38	**O** 73	66	38	5		
3							2	3	2	3	8	17	**O** 43	49	13	1	
9									1	2	7	15	77	**O** 194	108	10	
2										1			4	17	**O** 38	25	7

O, Means of F_3 groups.

Number of cultures	Distribution of F_2 parents							Average coefficient of variation
	100 109	110 119	120 129	130 139	140 149	150 159	160 169	
2		1	1					22
4		1		2	1			31
5	1	1	1	1	1			16
9	1		3	2	1	2		15
6			2	3		1		15
3					3			12
9				1	3	3	2	6
2					2			7

TABLE 31 (continued)
Heights in centimeters in (1 × 3) F_3, 1916.

Number of cultures	Distribution of coefficients of variation in F_3 cultures																				
	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44
2									1		1										
4									1			1				1					1
5						1	2	2													
9			1	1	2	1			2	2											
6				2		1	1		1		1										
3					3																
9	1	5	1	2																	
2		1	1																		

Height in bread wheat crosses, 3 × 35

No pure No. 35 was grown in 1914 for comparison with the pure No. 3 and the F_1 hybrids of 3 × 35. The following table summarizes the data for the pure No. 3 (6 plants, not a pedigree line) and the (3 × 35) F_1 hybrids.

TABLE 32
Heights in centimeters in (3 × 35) F_1, 1914.

Culture	Number of plants	Average height	Distribution of heights of individuals							
			100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 3	6	118	2	1	2	1				
(3 × 35) F_1	18	142			1	5	8	3	1	

The hybrids are thus seen to be taller than the pure No. 3 and the range is slightly greater, but not more than would be expected with the larger number of individuals grown, i.e., one could not infer that the hybrids were more variable than the pure race.

Each of the 18 F_1 plants gave rise to an F_2 culture in 1915. For comparison 3 cultures of No. 35 and one of No. 3 are available. Table 33 summarizes the results for 1915.

TABLE 33
Heights in centimeters in (3 × 35) F_2, 1915.

Culture	Number of cultures	Number plants	Average height	Coefficient of variation of the population	Average C.V. of separate cultures	Distribution of C.V.			
						3 4	5 6	7 8	9 10
Pure No. 3	1	42	146	4.2	4.2	1			
(3 × 35) F_2	18	1611	148	7.4	6.0		15	1	2
Pure No. 35	3	166	128	11.1	6.4	1	1		1

It is here interesting to note that the hybrids are somewhat taller than the tall parent.

Table 34 gives the distribution within the populations of F_2 hybrids and parental races. In the hybrids, the cultures are arranged in groups with regard to the height of their F_1 parents.

TABLE 34

Heights in centimeters in (3 × 35) F_2, 1916.

	Number of cultures	Parental height	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 3	1									3	18	21		
(3 × 35) F_2	1	120 129				1		1	+ 4	8	O 40	30	2	
"	5	130 139	1				1		14	+ 46	144	O 169	65	9
"	8	140 149				1	2	3	18	80	+O 236	286	93	3
"	3	150 159				2	1	1	5	12	57	+O 105	55	4
"	1	160 169							2	5	13	O 52	+ 20	
(3 × 35) F_2 Totals	18		1			4	4	5	43	154	O 508	663	235	16
Pure No. 35	1						8	25	29	52	38	13	1	

Distribution of means of cultures.

Pure No. 3											1			
(3 × 35) F_2										1	6	11		
Pure No. 35									1	1	1			

+, Selected F_1 parent.
O, Mean of group.

No appreciable correlation between the height of the F_1 parent and the average of the F_2 offspring is apparent. We may therefore consider that so far as the height factors are concerned, the F_1 plants were all equivalent. The range of distribution of the hybrid population slightly exceeded that of the most variable parent in both directions but no more than would be expected considering the larger number of plants grown.

From the above F_2 hybrids 80 selections were made for growing in 1915-16. These ranged from 118 to 173 cm high, thus covering all of the upper but not quite all of the lower end of the range of the F_2. For comparison with these, 5 cultures of each of Nos. 3 and 35 were grown. A first summary of the results are shown in table 35.

TABLE 35

Heights in centimeters in (3 × 35) F_3, 1916.

Culture	Number of cultures	Number of individuals	Average height	Coefficient of variation of the population	Average C.V. of separate cultures
Pure No. 3....	5	243	133	8.0	6.6
(3 × 35) F_3...	80	3849	143	8.4	6.3
Pure No. 35...	5	246	123	7.2	6.3

Distribution of coefficients of variation.

	3 4	5 6	7 8	9 10	11 12	13 14
Pure No. 3.......	2	1	1		1	
(3 × 35) F_3......	8	43	21	4	3	1
Pure No. 35......	1	2	1	1		

It should here be noted that the average height of the hybrids is again greater than that of the taller parent and that there is no diminution in the variability of the F_3 from the F_2. Moreover, the hybrids are no more variable than the pure races.

Table 36 gives the distribution of the populations of the hybrids and their parental races as well as the distributions of the means of the cultures of each.

TABLE 36

Heights in centimeters in (3 × 35) F_3, 1916.

	Distribution of individuals														Distribution of means of cultures				
	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	110 119	120 129	130 139	140 149	150 159
Pure No. 3..	1			1			1	10	68	108	48	6				3	2		
(3 × 35) F_3.				1	3	1	37	164	519	1045	1350	611	104	14		12	26	34	8
Pure No. 35.				1	3	1	10	72	141	17	1				2	3			

That we should here have 42 hybrid cultures (slightly more than half) whose average heights were higher than the highest average for the tall parent is somewhat surprising. Especially is this so when we reflect that the variability of the hybrids is no greater than that of the pure lines.

From table 37 we observe that the regression of the offspring of extreme selections is quite strong, but it is not complete. The difference between the means of the offspring of selected extremes is greater than between the means of the parental races (compare table 35). Comparing the distribution of selected F_2 parents forming the groups in table 38 with the distribution of the individuals of their parental varieties in table 34, we will note that they are not more widely distributed. They can therefore be assumed to be environic modifications of individuals representing equivalent genetic combinations so far as height is concerned. There was a fairly well marked decrease in the variability of the taller cultures.

TABLE 37

Heights in centimeters in (3 × 35) F_3, 1916.

Number of cultures	Arrangement of F_3 individuals grouped according to F_2 parents										
	69 78	79 88	89 98	99 108	109 118	119 128	129 138	139 148	149 158	159 168	169 178
1				5	+ 11	O 10	5	15	3		
2				2	13	+ 12	O 21	24	23	2	
9	1	2		7	43	110	O+ 79	96	73	19	1
20			1	15	33	188	O 265	+ 314	132	17	2
35			1	7	53	148	484	O 669	+ 273	43	10
12		1		1	12	48	176	O 212	98	+ 23	1
1						2	15	O 24	9		+

Number of cultures	Distribution of means of F_3 cultures				Average C.V. of F_3 cultures	Distribution of coefficients of variation of F_3 cultures					
	119 128	129 138	139 148	149 158		3 4	5 6	7 8	9 10	11 12	13 14
1	1				12.0					1	
2	1		1		8.0		1			1	
9	3	2	4	1	8.2		4	1	3		1
20	4	6	9	1	6.1	2	10	7	1		
35	3	13	15	4	5.9	4	23	7		1	
12		5	5	2	5.9	2	4	6			
			1		5.0		1				

Red Algerian bread (No. 3) × early Baart (No. 34)

In 1914 there were grown 6 plants of pure No. 3, 12 plants of pure No. 34 and 6 plants of (3 × 34) F_1. These numbers are too small to warrant the calculation of coefficients of variation but the distribution and averages may well be given.

TABLE 38

Heights in centimeters in (3 × 35) F_3, 1916.

Number of cultures	F_3 individuals arranged in accordance with the means of the F_3 cultures										
	69 78	79 88	89 98	99 108	109 118	119 128	129 138	139 148	149 158	159 168	169 178
12	1	1	1	25	108	O 242	150	46	6		
26		2	1	10	43	213	O 542	402	45	1	1
34				2	13	61	231	O 797	390	32	2
8						3	22	105	O 170	71	11

Number of cultures	Distribution of F_2 parents							Distribution of coefficients of variation of F_3 cultures						
	109 118	119 128	129 138	139 148	149 158	159 168	169 178	Average C.V. of F_3 cultures	3 4	5 6	7 8	9 10	11 12	13 14
12	1	1	3	4	3			8.1		4	4	1	3	
26			2	6	13	5		6.3	1	14	9	1		1
34		1	3	9	15	5	1	5.8	7	17	8	2		
8			1	1	4	2		5.8		8				

TABLE 39

Heights in centimeters in (3 × 34) F_1, 1914.

Cultures	Number of plants	Average height	100 109	110 119	120 129	130 139	140 149	150 159	160 169
Pure No. 3....	6	118	2	1	2	1			
(3 × 34) F_1...	6	123		1	1	4			
Pure No. 34...	12	150				1	2	7	2

The F_1 is here seen to be intermediate in height between the parents and with a smaller range of variation than either.

Each of the 6 F_1 plants gave rise to an F_2 culture in 1915. For comparison, one culture of No. 3 and one of No. 34 were available. Table 40 gives first summary of the results.

TABLE 40

Heights in (3 × 34) F_2, 1915.

Culture	Number of cultures	Number of plants	Average height in centimeters	Coefficient of variation of the population	Average C.V. of the cultures	Distribution of C. V.	
						3 4	5 6
Pure No. 3..	1	42	146	4.2	4.2	1	
(3 × 34) F_2.	6	537	150	7.1	5.0	1	5
Pure No. 34.	1	92	137	4.1	4.8		1

As in the last bread wheat cross (No. 3 × 35) and unlike either of the bread wheat × macaroni wheat crosses (1 × 35 and 1 × 3) the average height of the F_2 is greater than the mean of the parents, in fact greater than either of the parents. As usual the coefficient of variation of the F_2 taken as a population was greater than the average of this constant for the separate cultures and the average coefficient of variation of the hybrid cultures was greater than that of the pure parent cultures.

Table 41 gives the distribution of height in the parental races and the F_2 hybrids of this cross.

TABLE 41
Heights in centimeters in (3 × 34) F_2, 1915.

Culture	Distribution of individuals										Distribution of means of cultures		
	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	130 139	140 149	150 159
Pure No. 3.......						3	18	21				1	
(3 × 34) F_2......	1			1	6	26	151	232	111	9		2	4
Pure No. 34......					2	29	55	6			1		

That we should have 4 hybrid cultures averaging taller than the tall parent is interesting, but may be ascribed to hybrid vigor.

The following table (table 42) gives the distribution of the F_2 population grouped according to the height of the F_1 parents, + being the height of F_1 parent, and O the mean of F_2 individuals arising from such parents:

TABLE 42
Heights in centimeters in (3 × 34) F_2, 1915.

Number of cultures	Parental height	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	Average height
1	110 119				+ 1	6	6	O 41	27	9		147
1	120 129					+	4	29	O 42	12		152
4	130 139	1					+ 16	81	O 190	99	9	155

There is thus seen to be a slight correlation between the height of the F_1 parents and the height of the F_2, indicating a possibility of some genetic differences in the F_1 in respect to height. In all further discussion of this cross, as regards height, it will be necessary to segregate the data into groups so as to consider at one time only plants originating from a single F_1 parent. Since nearly all of the F_3 population arose from one or the other of the original F$_1$ plants, Nos. 25-1 and 44-2, all F$_3$ cultures except such as originated from these two will be excluded from this study, and these will be kept separate. The distribution of the F$_2$ of these two cultures were as follows:

TABLE 43

Heights in centimeters in (3 × 34) F$_2$, 1915.

Culture	Parental height	Number individuals	Average height	Distribution of individuals						Average C.V.
				120 129	130 139	140 149	150 159	160 169	170 179	
(44-2) F$_2$, 1915	120	87	152	1	3	29	42	12		4.5
(25-1) F$_2$, 1915	135	90	155			12	42	33	3	4.9

The selections for the F$_3$ covered the full range of both of these parents. Table 44 gives a summary of the results in F$_3$.

TABLE 44

Heights in centimeters in (3 × 34) F$_3$, 1916.

Culture	Number of cultures	Number of individuals	Average height
Pure No. 3..........................	5	243	133
(3 × 34,F$_3$ (44-2)..................	50	2408	133
(3 × 34) F$_3$ (25-1)................	50	2396	131
Pure No. 34	5	243	121

Coefficient of variation

Culture	Population	Average of separate cultures	Distribution of C.V.						
			3 4	5 6	7 8	9 10	11 12	13 14	15 16
Pure No. 3.............	8.0	6.6	2	1	1		1		
(3 × 34) F$_3$ (44-2)......	9.8	6.5	9	23	10	4	2		2
(3 × 34) F$_3$ (25-1).....	7.7	5.9	10	26	10	3	1		
Pure No. 34............	7.4	6.2		3	2				

In 1916, it will be observed that the average height of the F$_3$ is practically the same as the taller parents. The coefficient of variation of the hybrid population is greater than that of the populations of either parent but the average coefficient of variation of the hybrid cultures taken separately was not significantly below that of the pure cultures.

The distribution of the heights of the individuals of the F$_3$ population and the parental cultures and also of the means of the separate cultures are given in table 45.

Whereas the ranges of the hybrid populations extend beyond the limits of the parents, this is here not surprising considering the much larger

TABLE 45

Heights in centimeters in (3×34) F_3, *1916.*

Culture	Distribution of individuals														Distribution of means of cultures					
	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	100 109	110 119	120 129	130 139	140 149	150 159
Pure No. 3......	1			1			1	10	68	108	48	6					3	2		
(3×34)F_3 Total			5	12	13	29	87	453	1570	1819	1068	292	13	1	1	3	41	50	14	3
(3×34)F_3 (44-2)			3	8	8	18	50	215	652	769	493	179	13		1	2	15	23	8	1
(3×34)F_3 (25-1)			2	4	5	9	31	184	770	934	428	29				1	21	24	4	
Pure No. 34.....			1			2	22	85	119	14						1	4			

numbers used. It is interesting, however, to note that 17 hybrid cultures had average heights higher than the highest average for the parental cultures.

Table 46 shows the distribution of the F_3 grouped according to the selected F_2 parents. In table 47 the F_3 is grouped according to the means of the F_3 cultures. Table 46 shows a definite correlation between the height of the selected F_2 parent and the mean of the F_3 classes, but there is a strong regression, especially in the higher groups. The F_2 selections, it may be noted, covered practically the entire range of the F_2 population. The distribution of the parents in the F_3 groups of cultures having equal means, was not greater than the normal distribution of individuals in a pure culture. They could therefore be assumed to be modifications (environic) of genetically equivalent individuals.

TABLE 46

Heights in centimeters in (3×34) F_3, *1916.*

Number of cultures	Arrangement of F_3 individuals grouped according to F_2 parents												Distribution of means of F_3 cultures, 1916					
	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	100 109	110 119	120 129	130 139	140 149	150 159
(44-2)																		
1	2	2	1	9	O 15	5	+ 10	1	1				1					
8		1	1	2	10	93	O 171	+ 91	14					1	5	2		
16		3	3	4	11	71	218	O 233	+ 180	53	4			1	7	4	4	
23	1	2	3	3	11	42	218	‘O 410	281	+ 124	9				3	15	4	1
2					3	5	35	O 34	17	2	+					2		
(25-1)																		
4		1			5	23	O 86	54	+ 19						3	1		
22	1	2	2	5	13	97	382	O 410	129	+ 6				1	9	12		
22	1	1	3	4	13	64	279	O 423	254	20	+				9	10	3	
2							23	O 47	26	3		+				1	1	

+, Selected F_2 parent.
O, Mean of F_3 group.

TABLE 46 (continued)

Heights in centimeters in (3 × 34) F_3, 1916.

Number of cultures	Mean of F_3	Average C. V. per cent	Distribution of coefficients of variation of F_3 cultures						
			3 4	5 6	7 8	9 10	11 12	13 14	15 16
(44-2)									
1	107	16.0							1
8	125	5.8	3	2	2	1			
16	130	6.3	3	8	2	1	2		
23	137	6.4	3	12	5	2			1
2	132	7.0		1	1				
(25-1)									
4	122	6.3	1	1	2				
22	130	6.3	1	15	3	3			
22	133	5.6	7	9	5		1		
2	136	4.0	1	1					

TABLE 47

Heights in centimeters in (3 × 34) F_3, 1916.

Cultures	Arrangement of F_3 individuals grouped according to means of F_3 culture											Distribution of selected F_2 parents					
	69 60	79 70	89 80	99 90	109 100	119 110	129 120	139 130	149 140	159 150	169 160	129 120	139 130	149 140	159 150	169 160	179 170
(44-2)																	
1	2	2	1	9	O 15	5	10	1	1			1					
2			1	1	7	‘O 47	39	2					1	1			
16		5	6	8	18	129	O 340	207	34	2			5	7	4		
22	1	1			9	35	257	O 504	235	25			2	4	14	2	
8					1		6	52	‘O 206	130	6			4	4		
1								3	17	O 22	7				1		
(25-1)																	
1					1	O 22	23	1							1		
21		1	3	4	23	129	O 517	296	28					3	9	9	
24	2	3	1	1	7	32	225	‘O 629	287	12				1	12	10	1
4						1	5	58	O 113	17						3	1

TABLE 47 (continued)

Heights in centimeters in (3 × 34) F_3, 1916.

Cultures	Mean of F_3	Average C. V.	Distribution of coefficients of of variation of F_3 cultures						
			3 4	5 6	7 8	9 10	11 12	13 14	15 16
(44-2)									
1	107	16.0							1
2	118	6.0		2					
16	123	7.6	2	3	6	2	2		1
22	134	6.0	1	16	3	2			
8	147	4.5	6	1	1				
1	153	5.0		1					
(25-1)									
1	120	4.0	1						
21	126	6.2	2	12	6	1			
24	135	5.8	6	12	3	3			
4	142	5.3	2	1	1				

Summary; height

The number of F_1 plants grown were too small to give significant results except in the case of the 1 × 35 and 3 × 35 crosses. In both of these cases the F_1 averaged taller than the tall parent. In the other two cases the F_1 was intermediate. In the two macaroni—bread wheat crosses (1 × 35 and 1 × 3) the F_2 and F_3 averaged below both parental races. In the two bread wheat crosses (3 × 34 and 3 × 35) the F_2 averaged taller than either parent and the F_3 of the 3 × 35 cross was taller than either parent, but in the 3 × 34 cross the average of the F_3 was 1 cm shorter than the taller parent. The distribution of heights in F_1 did not go significantly beyond the limits of the parental cultures in any case except that of 3 × 35 in which the whole distribution was pushed upward about 24 cm. The range of distribution of the individual heights of the F_2 and F_3 in neither case of the macaroni—bread wheat crosses extended significantly above that of the parents, but in both cases extended markedly below the parental range. On the other hand in the bread wheat crosses the range in both cases extended distinctly above, but not significantly below, the parental ranges in F_2 of both crosses and the F_3 of the 3 × 35 cross, but in the F_3 of the 3 × 34 cross it did not extend significantly either above or below the parental range. The same observations made with reference to the distribution of the individual heights of the F_2 and F_3 of both kinds of crosses also apply with perhaps greater emphasis to the distribution of the means of the F_2 and F_3 cultures taken separately.

Now, referring to the appropriate tables, note that the average height of F_1 in one of the species crosses (macaroni—bread wheat). was above the tall parent and in the other intermediate between the parents. We must therefore assume that the maximum heterozygosity of these crosses will give plants at least taller than the low parent. In both the F_2 and F_3 of these crosses, however, the average F_2 and F_3 height was below the parent. We are therefore compelled to conclude that recombination and not antagonistic heterozygosis is the cause of the low averages of the F_2 and F_3. A complete double set of macaroni factors, a complete double set of bread wheat factors, or the combination of one complete set of factors from each species, was able to produce a plant of standard vigor, but a large majority of the recombinations of these factors where a complete set from one of the species was lacking, resulted, through failure of coördination, in the production of plants of reduced vigor.

Now it should be noted that no F_2 plant, tall because it was completely heterozygous, could give rise to an F_3 culture which had a high average height, for the reasons above given. Hence the majority of tall F_3 cultures must have arisen from F_2 plants, tall because they were genetically completely, or nearly completely, like one of the parents. Now this is in harmony with the fact (see tables 22 and 31) that the taller F_3 cultures were markedly less variable than were those with a less average height. Now let us remember that the completely heterozygous F_1 plants of the 1 × 35 cross were tall plants with wrinkled seeds. If we examine the F_2 plants selected and pick out all of those which were taller than the average of the low parent and which also had wrinkled seed, thus again resembling the F_1 plants we find that the average height of the F_3 cultures arising from these were 110 cm with an average coefficient of variation of 19.5 percent, whereas the average height of the offspring of all of the remaining selected F_2 plants taller than the average of the low parent was 123 cm with an average coefficient of variation of 14.1 percent. Again, if we pick out all of the selected F_2 plants which were taller than the average of the low parent and which also had smooth seeds, thus resembling one or the other of the parents, we find that the average height of the F_3 cultures arising from these was 126 cm with an average coefficient of variation of 12.6 percent.

A similar study in the 1 × 3 cross gave for the F_1-like F_2 plants F_3 cultures with an average height of 131 cm and an average coefficient of variation of 12.9 percent, whereas the parent-like F_2 plants gave F_3 cultures with an average height of 143 cm and an average coefficient of variation of 6.6 percent.

While these facts coincide completely with the assumptions above made, the story does not end here. Returning to the 1 × 35 cross we found that there were 30 tall F_1-like F_2 plants and 73 tall parent-like F_2 plants. If now we cast the F_3 cultures arising from these two groups respectively into subgroups arranged according to the average heights of the F_3 cultures and find the average coefficients of variation of each subgroup we may tabulate the results as in table 48.

TABLE 48

Average heights of F_3 cultures in centimeters.

		70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	15 15
30 F_3 cultures from tall F_2 plants hav-the wrinkled seed (F_1-like F plants)	Distribution of heights	1	2	3	6	8	5	5		
	Average coefficients of variation	30.0	26.0	23.7	20.5	18.5	16.2	16.0		
73 F_3 cultures from tall F_2 plants having smooth seed (parent-like F_2 plants)	Distribution of heights		1	2	5	12	27	20	5	1
	Average coefficients of variation		23.0	16.0	15.6	13.7	13.8	10.0	9.4	5.

With these results we must conclude that we have not yet succeeded in separating out genetically equivalent groups and that those F_3 plants which gave rise to tall F_3 cultures are genetically more nearly homozygous or else we must postulate some other cause for the suppression of variability in the taller F_3 cultures. This last analysis in no way interferes with the conclusions already drawn, for it clearly shows that in F_3 subgroups of equal height, those cultures arising from F_1-like plants were always more variable than those which came from parent-like plants.

Now turning to the bread wheat crosses we note that the average coefficients of variation of the F_2 and F_3 generations were in no case significantly higher than that of the most variable parental culture (see tables 33, 35, 40, 44). If, however, we consult tables 38 and 47 we shall observe a distinct lowering of the variability of the taller cultures. Let us also remember that the F_1, F_2 and F_3 of the 3 × 35 cross all averaged taller than the tall parent and note (table 38) that the reduction of the variability of the taller F_3 cultures was uniform, whereas the F_1 of the 3 × 34 cross was intermediate, the F_2 taller and the F_3 again intermediate, and while the reduction in variability of the F_3 cultures (table 47) was still apparent (with the exception of 1 erratic extreme) there was some indication that the intermediate F_3 classes (F_1-like) had a tendency to be a little more variable. There appears, therefore, to be two conflicting forces at work, one (heterozygosis) tending to make the cultures arising from the F_1-like F_2 plants more variable, and another which tends to suppress variability in the taller cultures.

A means of testing for the presence of a factor suppressing variability, which is independent of heterozygosity, is found in the F_2 cultures which came from supposedly genetically equivalent F_1 plants. In the F_2, the means and variabilities of the several cultures from any given cross should be the same. Where slight differences occur, they are in all probability environic. Nevertheless if the cultures be grouped according to these slight differences in the F_2 means, and the average coefficients of variation of these groups calculated, if there be a factor suppressing variability in the taller groups it should become apparent, provided there is a sufficient number of F_2 cultures to give valid averages. Such an analysis of the F_2 hybrid cultures for 1915 is given in table 49.

TABLE 49

Correlation between average height and coefficient of variation in F_2 hybrids.

		Total number	Average heights, 1915					
			100 109	110 119	120 129	130 139	140 149	150 159
(1 × 35) F_2	Number of cultures	38		4	30	4		
	Average C. V.			19.2	19.0	18.9		
(1 × 3) F_2	Number of cultures	5	2	1	1	1		
	Average C. V.		28.5	20.2	10.4	14.5		
(3 × 34) F_2	Number of cultures	6					2	4
	Average C. V.						5.5	4.8
(3 × 35) F_2	Number of cultures	18				1	9	8
	Average C. V.					7.0	5.9	6.0

The differences, while not large, are as uniform as could be expected from such small numbers and indicate the presence of a suppression factor of some sort which slightly reduces the variability of the taller cultures.

The presence of this suppression factor for variability in the taller cultures is even more strikingly shown in the pure races. Grouping the cultures according to their means (without regard to year in which they are grown) and calculating the average coefficient of variability for each group we have the result shown in table 50.

Having now shown that there is a factor which, independent of heterozygosity, may suppress the variability of the taller cultures, we may conclude as follows:

(1) Some factor for suppressing variability has been able to com-

TABLE 50

Correlation between average height and coefficient of variation in pure races.

		Total number	Average height				
			110 119	120 129	130 139	140 149	150 159
Pure No. 1	Number of cultures	16		2	4	6	4
	Average C. V.			7.5	7.5	6.5	5.5
Pure No. 35	Number of cultures	8	3	3	1	1	
	Average C. V.		6.7	6.7	6.4	3.9	
Pure No. 3	Number of cultures	6		2	3	1	
	Average C. V.			7.5	5.6	4.2	
Pure No. 34	Number of cultures	6	1	4	1		
	Average C. V.		6.9	6.1	4.8		

pletely mask the effect of heterozygosity in a cross where the F_2 and F_3 cultures averaged taller than the tall parent (3 × 34).

(2) This same factor has largely suppressed, but not entirely masked, the variability due to heterozygosity in a cross where the F_2 and F_3 cultures were approximately as tall as the taller parent (3 × 35).

(3) The factor for the suppression of variability in tall cultures is apparent in crosses where the averages of the F_2 and F_3 cultures are below those of the low parent, but was in no case able to obliterate the effect of heterozygosity (see 1 × 35 and 1 × 3).

The question as to the nature of this suppression factor will be reserved for future discussion. The fact that the average variability of the F_2 and F_3 cultures was not significantly higher than that of the pure-line parents in the bread wheat crosses might be cited as showing that a blending inheritance has occurred with the production of a single new race no more variable than the most variable of the parental races, were it not for the fact that tables 37 and 46 show a definite positive correlation between the height of the F_2 parents and the means of the F_3 cultures derived therefrom. A distinct segregation occurred in the formation of the gametes of the F_1 plants whereby the F_2 plants were different genetically and exhibited these differences in the means of their offspring, thus giving rise, not to one race, but to a number of distinct races. The theoretically expected greater variability of the F_2 and F_3 cultures are simply here suppressed, but in the macaroni—bread wheat crosses where this suppression factor was ineffective in masking the variability due to heterozygosis the variability of the F_2 and F_3 cultures in all cases averaged markedly above that of the pure-line parents.

In the F_3 of all crosses, cultures were secured having the parental types both as regards average height and variability. In the bread wheat crosses the average variability of the F_3 cultures was slightly larger than that of the F_2 cultures in both cases. This is in accordance with the circumstance that in both, the average height of the F_2 cultures was markedly greater than that of the F_3 cultures and thus called into more active effect the variability-suppressing factor already shown to influence the taller cultures. In the macaroni—bread wheat crosses, on the other hand, the average height of the F_2 was greater than that of the F_3 in one case and less in the other, but still the average variability of the F_2 cultures was markedly above that of the F_3 cultures in both cases. This is in harmony with the fact pointed out above that the variability-suppressing factor visible in all of the crosses was not sufficient to mask the influence of heterozygosity in macaroni—bread wheat hybrids.

Finally we may conclude that all of the facts observed in the study of the inheritance of height in the wheat crosses here considered are in harmony with the hypothesis of the segregation of a number of simple Mendelian unit characters and that there is present some factor (as yet unknown) which suppresses variability in the taller cultures of both pure lines and hybrids and that this factor is sometimes able to completely mask the variability which would normally be produced by heterozygosity.

WIDTH OF LEAF

In the following study of the inheritance of width of leaf in wheat hybrids, all measurements are given in millimeters. Averages are therefore given to the nearest millimeter.

Macaroni (No. 1) × Sonora (No. 35)

No pure No. 35 was available for comparison in 1914. The data with reference to the pure No. 1 and the F_1 hybrid plants are given in table 51.

TABLE 51

Width of leaf in millimeters (1 × 35) F_1, 1914.

	Number of plants	Distribution of individuals															Average	Coefficient of variation
		13	14	15	16	17	18	19	20	21	22	23	24	25	26	27		
Pure No. 1	151	2	1	1	3	11	11	19	25	24	32	5	10	3	3	1	20	13
(1 × 35) F_1	39					2	1		4	4	8	9	9	1	1		22	9

We will here pause only to notice that both the range and variability of the pure No. 1 were greater than for the hybrid. The average leaf width for the hybrid was greater than for the pure No. 1, but since the No. 1 is here the more narrow-leafed parent we have as yet no indication as to whether or not we are dealing with imperfect dominance or hybrid vigor.

In 1915 there were available for comparison 4 cultures of No. 35, 9 cultures of pure No. 1 and 37 cultures of the (1 × 35) F_2. A summary of these data is presented in table 52.

TABLE 52

Width of leaf in (1 × 35) F_2, 1915.

	Number of head rows	Total number of plants	Average width of leaf	Coefficient of variation of the population	Average C. V. of cultures
Pure No. 1....	9	651	17	13.0	10.3
(1 × 35) F_2...	37	2537	15	30.2	29.3
Pure No. 35...	4	169	20	13.5	13.0

Distribution of coefficients of variation

	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 20	31 32	33 34	35 36
Pure No. 1..............	1	5	1	1	1										
(1 × 35) F_2.............									2	6	6	9	8	5	1
Pure No. 35	1			1	2										

The average of the hybrids is below that of either parent. The standard deviations of the populations are greater than the averages of the standard deviations of the separate cultures making them up, and the variability of the hybrids is much greater than that of the pure cultures. All hybrid cultures were more variable than the most variable pure culture.

Table 53 gives the distribution of the several populations and the distribution of the means of the cultures.

Studying these distributions we note that there were 16 hybrid plants having leaves wider than the widest individual of the widest-leaved parent, but there was no hybrid culture averaging as wide as the most narrow average for Sonora, the wider-leaved parent. On the other hand more than half of the hybrid cultures averaged lower than the lowest average of any macaroni head-row and there were 121 hybrid plants having more-narrow leaves than the narrowest-leaved individual of the macaroni parent.

TABLE 53

Width of leaf in millimeters in (1 × 35) F_2, 1915.

	Distribution of widths in individuals																												Distribution of means of cultures							
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	14	15	16	17	18	19	20	21
Pure No. 1						2	1	2	1	2	6	28	62	75	117	130	107	78	26	11	3										4	1	2	2		
(1 × 35) F_2	3	11	25	46	36	63	93	119	85	198	190	193	260	229	174	190	146	171	103	69	40	39	29	8	9	4	2	1	3	22	11	1				
Pure No. 35							1			1	1	4	2	6	16	13	19	32	25	24	13	6	4	2										1	2	1

TABLE 54

Width of leaf in millimeters (1 × 35) F_2, 1915.

Width of parent in 1914	Number of cultures	Average width in 1915	Distribution of leaf widths in individuals																										
			3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
17	1	17		1	1					1	2			3	2	4	+O 3	3	3	6	2	4		1	1				
18	1	16			2		2		1	1	3	6	6	8	3	O 11	2	+ 4	5	2	2	3	2	1	1				
20	4	15		3	1	3	3	8	7	7	8	19	19	19	O 27	24	20	23	16	+ 12	8	3	4	5	2				
21	4	15		1	1	8	5	8	8	13	8	16	21	15	O 31	17	21	15	10	24	+ 11	6	4	3	2	5	3	1	1
22	8	15		4	6	9	6	15	27	32	22	55	43	49	O 68	54	36	41	29	41	16	+ 21	9	9	2	1	1	1	
23	8	15		4	8	12	13	12	18	27	19	44	46	49	O 58	54	33	48	31	37	30	13	+ 10	9	9	2	2		
24	9	16	1	2	4	11	6	17	28	23	18	48	45	42	55	O 53	46	47	44	40	29	16	9	+ 10	12		3		1
25	1	15				1		1	3	7	3	4	5	3	O 8	7	4	5	3	6	3	2			+			1	
26	1	15			2	1	1	2		5	4	6	4	6	O 9	5	9	4	5	3	2	1	2	1		+			

Referring to table 51 it will be observed that there was considerable variation in the width of leaf of the F_1 plants. Table 54 groups the 1915 F_2 plants in accordance with the leaf width of their F_1 parents in 1914.

A glance at this table is sufficient to show that there is no correlation whatever between the parental leaf width in 1914 and the average leaf width of the offspring in 1915. We may therefore conclude that all of the variation observed in the F_1 plants was nutritional and that they were all equivalent genetically so far as the factors governing width of leaf were concerned.

From these F_2 hybrids 230 selections were made which gave rise to a like number of F_3 hybrid cultures in 1916. For comparison with these there were available seven head-rows of No. 1 and five head-rows of No. 35. The selected F_2 plants used as parents ranged in width of leaf from 10 to 35 mm. The very wide-leaved individual was very striking in appearance and was nearly sterile. Table 55 gives a first summary of the results in 1916.

TABLE 55

Width of leaf in millimeters in (1 × 35) F_3, 1916.

Class	Number of cultures	Number of individuals	Average width of leaf	Coefficient of variation in the population	Average coefficient of variation of separate cultures
Pure No. 1....	7	344	16	12.0	10.1
(1 × 35) F_3...	230	10123	15	24.9	20.9
Pure No. 35...	5	246	17	15.2	14.0

Distribution of coefficients of variation

Class	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52	53 54
Pure No. 1.......	5	1	1																				
(1 × 35) F_3.....	1	3	24	35	31	42	29	11	17	5	11	5	7	1	3	3	1						1
Pure No. 35......			3	2																			

The average for the hybrids is less than either of the parents; in every case the coefficient of variation of the population is greater than the average for the pure cultures of the same class and the coefficient of variation for the hybrids is greater than for either parent. The coefficient of variation both for population and average of cultures among the hybrids was lower in 1916 than in 1915. This was also true of the pure

TABLE 56

Width of leaf in millimeters in (1 × 35) F_3, 1916.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Pure No. 1..											14	24	47	53	78	57	40	21	9		1									
(1 × 35) F_3..	4	27	41	64	53	151	161	255	467	642	1076	904	1208	1074	1151	755	751	383	370	217	196	75	64	15	12	4	2		1	1
Pure No. 35..									1		4	10	24	35	48	27	30	18	21	10	16	1	1							

Distribution of means of cultures

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Pure No. 1..													1	1	4	1														
(1 × 35) F_3..							2		2	15	22	30	45	48	27	18	13	5	1	2										
Pure No. 35..															2	1	2													

cultures, and therefore may be in part environic. One thing, however, remains to indicate progressive increase in homozygosity among the hybrids. This is the much greater difference in the coefficient of variation of population and average of cultures, which was apparent in 1916.

Table 56 shows the distribution of the populations of pure cultures and hybrids of this cross in 1916.

The hybrid population shows a distribution far beyond both extremes of the parents. This is also true of the means of cultures. Part of this greater distribution is of course due to the normal extension of the curve from the much larger number of hybrids grown. That the curve of variation is more flat, however, is shown by differences in the shapes of the curves of variation which are rendered comparable by reducing each group class to a percentage of the total number in the population and disregarding all percentages less than one-half of one percent and expressing all percentages to the nearest integer (see table 57).

TABLE 57

Width of leaf in millimeters in (1 × 3) F_3, 1916.

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Pure No. 1...........								4	7	14	15	23	17	12	6	3					
(1 × 35) F_3..........	1	1	1	2	2	4	6	11	9	12	11	11	8	7	4	4	2	2	1	1	
Pure No. 35...........								2	4	10	14	20	11	12	7	9	4	7			

When reduced to equal areas the polygon of the F_3 hybrid distribution is thus seen to be limited by a curve much more flat and with more extended limits than either of the parent races. This indicates that the extension of the range of variations of the F_3 hybrids over the parental races is genetic. This is further shown in table 58 where F_3 cultures are thrown into groups or populations in accordance with the leaf width of the selected F_2 parental plants.

Though somewhat erratic at the extremes, these results show a very definite genetic segregation of leaf width in the F_2 as exhibited by the means of their offspring. The distribution of the means of the cultures in each of these groups is shown in table 59.

TABLE 58

Width of leaf in millimeters in (1 × 35) F_3, 1916. Distribution of F_3 individuals grouped according to the leaf width of the F_2 parents.

Number of cultures	Leaf width of parent	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	35
3	10		3	2	3	2	8	8	10	+ 18	O 20	16	6	11	2	3	2	2	1	1												
2	11						1		3	10	+ 4	12	O 7	6	5	6	1	3						1								
4	12		4	3	3		7	3	16	14	23	O+ 26	31	26	22	9	3				1											
14	13	1	9	10	14	10	15	13	32	44	79	O 96	+ 62	84	62	47	21	13	3	5	3											
10	14		1	1	2	2	3	6	11	30	51	84	O 60	+ 68	38	46	28	11	3	2												
23	15		1	5	3	4	16	24	34	79	87	113	118	O 125	+ 104	114	75	49	24	17	16	19	7	9	1	1	1					
19	16	1	1	3	6	4	14	14	33	36	51	105	98	O 107	88	+ 101	66	48	34	20	23	6	3	1	1							
24	17	1		7	11	10	24	19	31	53	92	127	91	O 130	118	114	+ 73	66	27	23	8	17	2	2								
28	18		8	2	6	7	17	24	16	57	81	157	119	O 172	144	135	79	+ 85	33	43	20	15	3	3			1	1				
12	19			1	4	5	8	5	12	20	23	69	55	O 54	73	78	40	41	+ 17	20	8	3	1	1								
32	20		2	1	2	3	10	12	24	36	54	119	101	176	O 167	181	132	153	82	+ 67	30	34	15	8		3	1				1	
22	21			2	1	2	15	10	11	28	33	54	65	107	112	O 123	94	96	57	58	+ 30	23	8	6	1	2						
13	22	1	3	3	3	1	4	4	9	14	15	27	39	66	53	O 67	38	54	30	39	23	+ 23	15	10	7	3		1				
4	23							2	1	5	2	17	10	8	14	22	O 24	34	15	9	8	3	+ 5	2	2							
8	24		2	1	4	2	5	15	3	13	10	23	14	31	O 36	61	34	35	15	13	25	9	3	+ 4								
7	25		3		2	1	4	2	5	6	6	17	15	19	23	32	O 37	45	25	32	12	21	5	5	+	1				1		
1	26									1			1	1	1	1	2	2	6	O 9	3	12	4	6	1	+						
1	27								2	2	7	8	9	O 4	4	1	1	2	4		2						+					
2	28								2	1	1	5	2	12	5	7	2	O 6	5	8	2	9	4	3		2		+				
1	35										2	1		1	3	3	3	6	O 2	4	3	2		3	2		1					+

+, leaf width of parent; O, mean of F_3 groups.

TABLE 59

Width of leaf in millimeters in (1 × 35) F_3, *1916. Distribution of means of* F_3 *cultures grouped according to the leaf width of the* F_2 *parents.*

Number of cultures	Parental leaf width in 1915	Mean of group in 1916	8	9	10	11	12	13	14	15	16	17	18	19	20	21
3	10	11	1		1			1								
2	11	13						2								
4	12	12				2	1	1								
14	13	12	1		1	1	6	2	2	1						
10	14	13				1	2	4	3							
23	15	14				3	3	3	6	4	2	1		1		
19	16	14				2	2	3	2	5	4	1				
24	17	14				4	1	5	4	7	2	1				
28	18	14					3	3	14	3	1	3	1			
12	19	14					2		4	3	3					
32	20	15				1	2	3	2	9	7	4	3			1
22	21	16						1	5	5	3	5	3			
13	22	16				1		1		4	2	1	3			1
4	23	17							1		1		2			
8	24	15						1	1	4		1	1			
7	25	17								2	2	1		2		
1	26	20													1	
1	27	14							1							
2	28	18								1				1		
1	35	19												1		

This table exhibits even more plainly than the preceding the correlation between the parental leaf width and the mean leaf width of the offspring.

In order to determine whether the offspring of narrow-, medium-, and wide-leaved F_2 mother plants exhibited any definite difference in their variability table 60 was constructed.

There is shown here an irregular but still evident diminution of variability among the offspring of the wider-leaved parents.

It may be suggested, moreover, that since width of leaf is highly influenced by the environment and there is therefore a strong regression of the mean of the offspring of extreme variants toward the general mean of the population, we may get a better idea of the segregation of leaf-width factors, by grouping the F_3 cultures according to their own means and then calculating the variability of these groups and observing the distribution of the parents which gave rise to them. We thus measure backward, determining the range of environic modification of individuals which are able to give rise to genetically equivalent progenies.

TABLE 60

Width of leaf in millimeters in (1 × 35) F_3, 1916. Distribution of coefficients of variation of F_3 cultures grouped according to the leaf width of the F_2 parents.

Number of cultures	Parental leaf width	Average C. V. for group	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52	53 54	55 56
3	10	26.0							1	1					1											
2	11	23.0						1			1															
4	12	24.0		1						1			1	1												
14	13	25.6			1	1	2		4			1	2		1		1								1	
10	14	18.5				3	4	1	1		1															
23	15	20.3		1	1	2	3	7.	5	1	1	1			1											
19	16	20.6			1	4	2	5	2	2	1		1					1								
24	17	22.0			4	4		1	3	3	4		1	2	2											
28	18	21.5			4	2	2	8	4	2	1		3					1	1							
12	19	20.1			2	1	3	2	1		2			1												
32	20	18.3		1	2	9	10	3	1	1	4	1														
22	21	19.9	1		4	4	1	7			1	1			1	1		1								
13	22	21.5			3	1	2	2	1			1	1		1		1									
4	23	17.8			1	1		1	1																	
8	24	22.9					1	2	2		1		2													
7	25	22.1			1	1	1	1	1					1			1									
1	26	15.0				1																				
1	27	22.0							1																	
2	28	18.5				1			1																	
1	35	20.0						1																		

TABLE 61

Width of leaf in millimeters in (*1* × *35*) F_3, *1916. Distribution of* F_3 *individuals grouped according to the means of the* F_3 *cultures.* **O** = *mean of group.*

Number of cultures	Mean width	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
2	8	1	7	4	4	2	9	O 6	5	3	3	2	2	1			2		1												
2	10		1	6	6	2	2	3	7	O 15	20	15	3	5	1	4	1														
15	11	3	7	9	13	3	31	36	55	85	O 95	123	44	50	43	14	8	3	1	1											
22	12		6	5	9	8	25	28	73	83	158	O 165	129	115	75	48	25	15	4	4	3										
30	13		8	2	7	10	21	33	39	98	114	240	O 152	182	129	121	34	38	16	13	6	5		1							
45	14		3	6	10	13	34	30	38	94	130	256	248	O 327	254	232	135	110	44	31	16	8	4	3				1			
48	15		4	4	12	12	21	17	21	53	83	166	194	197	O 277	329	185	177	87	64	42	27	9	5	2	1				1	
27	16		1	5	3	3	5	12	11	18	21	59	72	126	155	O 213	168	160	73	61	37	27	8	2	1						
18	17						2	1	2	12	16	34	36	71	70	120	O 110	134	52	77	40	36	11	5	2	1					
12	18						1	2	2	4	6	6	11	28	51	49	50	O 76	60	64	37	32	15	9	4	4	1	1			1
6	19							2	2	1	4	6	10	5	14	20	27	30	O 28	35	20	37	10	19	2	3	2				
1	20									1			1	1	1	1	2	2	6	O 9	3	12	4	6	1						
2	21										1		1		4		8	5	9	10	O 11	11	13	12	3	3	1				

TABLE 62

Width of leaf in millimeters in (1 × 35) F_3, 1916. Distribution of F_2 parents grouped according to the means of the F_3 cultures.

Number of cultures	Mean of F_3 cultures	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
2	8			1			1																						
2	10			1			1																						
15	11					2	1	1	3	2	4			1		1													
22	12					1	6	2	3	2	1	3	2	2															
30	13			1	2	1	2	4	3	3	5	3		3	1	1		1											
45	14						2	3	6	2	4	14	4	2	5		1	1			1								
48	15						1		4	5	7	3	3	9	5	4		4	2			1							
27	16								2	4	2	1	3	7	3	2	1		2										
18	17								1	1	1	3		4	5	1		1	1										
12	18											1		3	3	3	2												
6	19								1									1	2			1							1
1	20																			1									
2	21													1		1													

TABLE 63

Width of leaf in millimeters in (1 × 35) F_3, 1916. Distribution of coefficients of variation of F_3 cultures grouped according to the means of the F_3 cultures.

Number of cultures	Means of F_3 cultures	Average C.V. of F_3	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52	53 54
2	8	43.5													1										1
2	10	30.5								1							1								
15	11	25.6		1			2	2		2	2		1	2	1		1	1							
22	12	22.9				1	5	2	3	2	4	2	2		1										
30	13	22.2		1	1	4	5	4	5	2	2		3		1			1	1						
45	14	21.4			3	6	3	10	10	2	4	1	2	1	2			1							
48	15	20.8			10	6	8	8	4	1	3	1	3	2		1	1								
27	16	18.4	1		4	6	4	8			2	1			1										
18	17	17.4		1	2	5	2	4	3	1															
12	18	17.4			2	4	1	3	2																
6	19	18.6			1	1	1	1	2																
1	20	15.0				1																			
2	21	14.5			1	1																			

It is interesting to note in table 61 that practically all of the curves of group distribution are skew, i.e., they slope more abruptly toward the upper limit.

While the parental groups in table 62 exhibit considerable range, a comparison of tables 62 and 56 will show that this is not wider than occurs in the nutritional variations of a pure line.

Algerian macaroni (No. 1) × Algerian red bread (No. 3)

For this cross the F_1, grown in 1914, had too few individuals to give significant results. As a matter of record, however, the results obtained are given in table 64.

TABLE 64

Width of leaf in millimeters in (1 × 3) F_1, 1914.

Class	Number of plants	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	Average
Pure No. 1....	151	2	1	1	3	11	11	19	25	24	32	5	10	3	3	1	20
(1 × 3) F_1....	5	1	1		1				1			1					21
Pure No. 3....	3						1		1			1					20

From this material there were grown in 1915, 9 plant rows of No. 1, six plant rows (two being taken from one of the mother plants) of 1 × 3 and one plant row of pure No. 3.

Table 65 summarizes the results obtained.

TABLE 65

Width of leaf in millimeters in (1 × 3) F_2, 1915.

Class	Number of cultures	Number of individuals	Average width	Coefficient of variation of the population	Average C.V. of separate cultures
Pure No. 1....	9	651	17	13.0	10.3
(1 × 3) F_2....	6	406	14	27.6	25.8
Pure No. 3....	1	42	16	11.2	11.2

Distribution of coefficients of variation.

Class	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30
Pure No. 1..............	1	5	1	1	1							
(1 × 3) F_2............								1		3	1	1
Pure No. 3..............			1									

The average leaf width of the hybrids is below that of either parent. The coefficient of variation of the populations are greater than the averages of the separate cultures and the variation of the hybrids is greater than that of the most variable pure culture.

Table 66 gives the distribution of the individuals of the several populations and the distribution of the means of the separate cultures.

TABLE 66

Width of leaf in millimeters in (1 × 3) F_2, 1915.

Class	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Pure No. 1.......					2	1	2	1	2	6	28	62	75	117	130	107	78	26	11	3			
(1 × 3) F_2.......	2	1	3	7	15	13	20	30	30	33	37	49	44	32	30	17	19	9	6	4	1	3	1
Pure No. 3.......									1	1	2	7	11	8	9	1	1	1					

Distribution of means of cultures.

Class	13	14	15	16	17	18	19
Pure No. 1				4	1	2	2
(1 × 3) F_2	3		2	1			
Pure No. 3				1			

We first note that, notwithstanding the fact that there were nearly 200 more individuals in the population of No. 1 than in the hybrid population, still the range of leaf width among the hybrids extended markedly beyond the range of pure No. 1 in both directions, and this in spite of the fact that no single hybrid culture averaged greater than the narrowest-leaved culture of pure No. 1.

Now analyzing the relation of the F_2 hybrid cultures to their (F_1) parents we find that there is a possibility that there were some differences in the genetic constitution of the F_1 plants inasmuch as the narrow-leaved parents produced offspring with a lower average leaf width than did the wider-leaved parents. This is shown in table 67.

Table 67
Width of leaf in millimeters in (1 × 3) F_2, 1915.

Plant No. 1914	Width of leaf, 1914	Average width of leaf of offspring, 1915	Distribution of leaf width in offspring, 1915																						
			4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
33-1	13	13	1			3	5	4	3	9	5	+ O 6	3	7	8	4	3	1							
33-2	14	13				1	1	1	4	1	1	O 2	+ 4	1	2		1	1							
49-7	16	13			1	1	3	4	3	4	7	O 3	9	9	+ 3	1	3		1			1			1
32-1	20	15					4	2	2	5	4	4	7	O 9	7	8	7	3	+ 3		2	1	1	2	
52-2 (2nd head-row)	23	15	1	1	2	1	1	2	2	6	8	8	7	O 15	8	9	7	5	8	5	1	+ 1			
52-5 (1st head-row)	23	16				1	1		6	5	5	10	7	8	O 16	10	9	7	7	4	3	+ 1		1	

Now grouping these cultures according to their mean in 1915, table 68 gives the average and distribution of the coefficients of variation of these groups.

TABLE 68
Width of leaf in millimeters in (1 × 3) F_2, 1915.

Number of cultures	Average leaf width of culture in 1915	Average coefficient of variation	Distribution of C.V. of cultures				
			21 22	23 24	25 26	27 28	29 30
3	13	26.7			2		1
2	15	26.5			1	1	
1	16	22.0	1				

The coefficients of variation here show a strong decline in variability in the wider-leaved cultures.

In 1916 there were available for comparison 7 cultures of pure No. 1, 5 of pure No. 3 and 57 cultures of the F_3 hybrid 1 × 3. Table 69 summarizes the results obtained.

TABLE 69
Width of leaf in millimeters in (1 × 3) F_3, 1916.

Class	Number of cultures	Total number of plants	Average leaf width	Coefficient of variation of the population	Average C. V. of separate cultures
Pure No. 1	7	344	16	12.0	10.1
(1 × 3) F_3 (33-1)	9	406	12	21.3	18.1
(1 × 3) F_3 (49-7)	8	365	13	24.1	21.4
(1 × 3) F_3 (32-1)	40	1763	13	26.5	20.9
(1 × 3) F_3 (Total)	57	2534	13	25.3	20.5
Pure No. 3.......	5	243	14	12.2	11.4

TABLE 70

Width of leaf in millimeters in (1 × 3) F_3, 1916.

Class	Distribution of individuals																									
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Pure No. 1.........											14	24	47	53	78	57	40	21	9		1					
(1 × 3) F_3 (33-1)..		3		3	4	12	9	22	48	71	68	69	41	21	21	7	2	2	2							
(1 × 3) F_3 (49-7)..		4	4		2	6	6	17	23	66	38	47	38	37	30	27	9	7	4		1					
(1 × 3) F_3 (32-1)..	2	7	5	14	18	66	46	83	77	187	176	205	178	235	161	129	80	39	35	12	7					1
(1 × 3) F_3 (total)	2	14	9	17	24	84	61	122	148	324	282	321	257	293	212	163	91	48	41	12	8					1
Pure No. 3........								3	3	7	23	30	66	54	44	7	4	2								

Distribution of means

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Pure No. 1..............													1	1	4	1	
(1 × 3) F_3 (33-1).......									1	3	3		1	1			
(1 × 3) F_3 (49-7).......									1		2	3	1		1		
(1 × 3) F_3 (32-1).......								1	2	5	8	7	8	2	3	2	2
(1 × 3) F_3 (total)								1	4	8	13	10	10	3	4	2	2
Pure No. 3..............												1	3	1			

Distribution of coefficients of variation

	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37
	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38
Pure No. 1..............	5	1	1												
(1 × 3) F_3 (33-1).......	1	2	1		1		1	2				1			
(1 × 3) F_3 (49-7).......				1	3	1		2							1
(1 × 3) F_3 (32-1).......	2	9	12	6	3	2			2		1	1	1		1
(1 × 3) F_3 (totals)......	3	11	13	7	7	3	1	4	2		1	2	1		2
Pure No. 3..............	3	1		1											

A study of tables 69 and 70 will show that it is not worth while to treat separately the 1 × 3 hybrids originating from the different original pollinations, since their means and distributions were practically equal. They will therefore be treated together hereafter.

In table 69 we observed that the average leaf width of the hybrids was below both the parents. The coefficient of variation was, however, as usual, markedly higher for the hybrids. From table 70 we note that the hybrid range in leaf width extends from a single case markedly above both parents to plants with almost filiform leaves. The different hybrid groups show practically the same behavior. Whereas 3 hybrid cultures showed as little variability (coefficients of variation) as the least variable parental culture, more than half were more variable than the most variable parental culture.

There were 8 hybrid cultures whose mean leaf widths were as great or greater than the mean for the wider-leaved parent. It is, moreover, interesting to note that from the hybrids of parents differing, on the average, only 2 mm in leaf width, there have segregated out races whose average leaf width differs by 9 mm. The fact that a large part of the differences in leaf width observed in the F_2 generation were genetic, is shown in table 70 which exhibits the F_3 cultures grouped according to their parental leaf widths.

There is a distinct correlation between parental leaf width and the mean of the offspring. Whereas the means show a marked range of distribution in each of the parental groups, this range is never wider

TABLE 71

Width of leaf in millimeters in (1×3) F_3, 1916.

F_3 individual plants grouped according to the heights of F_2 parents

Number of cultures	Leaf width of parent	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
2	8	1	3		4	7	9	+ 4	O 11	4	8	5	5	2			1		1								
1	9						6	3	+ 6	5	O 4	4	4	4	2	1											
1	11									4	+ 17	O 10	7	4		2		1									
4	13					3	3	5	10	7	38	O 31	+ 34	12	20	7	4	2	1	2		1					
5	14			1	2	3	4	5	13	7	36	36	O 33	+ 33	23	20	9	5		1							
11	15		6	6	2	7	22	14	23	35	74	O 66	71	44	+ 50	32	26	8	4								
12	16	1	1	1	4		18	14	35	35	72	55	O 59	70	76	+ 54	39	12	3	3		1					
6	17		1			1	8	3	6	14	29	28	O 43	32	46	18	+ 15	10		1	1						
6	18		2		1	1	8	8	13	25	38	36	O 34	29	25	19	17	+ 4	5	3							
2	19											1	11	9	24	O 19	15	7	+ 5	3	1						
3	20				4	2	4	5	3	5	4	6	6	9	O 6	6	9	15	17	14	+ 5	4					1
2	22		1	1			1		1	5	2	2	3	6	10	O 15	12	14	9	6	4	+ 1					
1	23						1		1	2	2	2	8	3	5	O 7	4	5	1	4		1	+				
1	25												3		6	12	O 12	8	2	4	1				+		

Means of cultures, 1916

Number of cultures	Mean of group 1916	9	10	11	12	13	14	15	16	17	18
2	9	1	1								
1	11			1							
1	12				1						
4	12			1	2		1				
5	13				2	2	1				
11	12		1	2	3	4	1				
12	13		1	2	1	3	3	1	1		
6	13				3		2	1			
6	13			2	1	1	1	1			
2	16								2		
3	15			1						1	1
2	16						1				1
1	16								1		
1	17									1	

+ = leaf width of parent O = average leaf width of offspring than the fluctuations of the individuals of a pure line. The coefficients of variation (see table 72) show a distinct though irregular decline toward the wider-leaved parental groups.

TABLE 72

Width of leaf in millimeters in (1 × 3) F_3, 1916. Coefficients of variation of F_3 cultures grouped according to the leaf width of the F_2 parents.

Number of cultures	Parental leaf width	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	Average C. V. of group
2	8													1		1	35.5
1	9								1								24.0
1	11			1													14.0
4	13				2	1					1						18.8
5	14				1	1	1	1		1							20.0
11	15	1				1	2		2	3			1			1	23.5
12	16	1	1	1	1	1	2	1	3			1					19.0
6	17			1	1	1	1			1	1						19.8
6	18	1	1			1	1					1	1				19.7
2	19		1	1													12.0
3	20	1								1					1		23.3
2	22	1									1						18.5
1	23						1										19.0
1	25	1															10.0

This study of variation is made much more distinct by regrouping the F_3 cultures according to their own means in 1916, as in table 73.

TABLE 73

Width of leaf in millimeters in (1 × 3) F_3, 1916. Distribution of F_3 individuals grouped according to the means of the F_3 cultures.

Number of cultures	Mean of culture	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1	9	1	3		3	4	2	3	O 10	2	7	5	3														
4	10				1	8	15	9	19	O 27	40	13	11	4	2		1		2								
8	11		4		8	4	30	24	39	42	O 51	37	34	34	17	7	4	1	2			1					
13	12		4	5	1	6	18	12	29	45	130	O 100	93	40	46	20	12	6	3	1	1	1					
10	13	1	1	2	1	1	12	7	19	20	61	63	O 59	57	53	49	29	10	4	2		1					
10	14		2	2	3	1	6	4	6	10	41	38	71	O 63	84	57	48	18	3	5	2				1		
3	15									2	1	5	25	28	O 33	12	19	6	1	1							
4	16						1		1	2	2	3	20	20	46	O 35	27	15	7	8	1	1					
2	17							2		3		2	4	3	7	13	O 15	12	11	6	3	2					1
2	18								1					4	6	13	9	O 23	15	18	4	2					

TABLE 74

Width of leaf in millimeters in (1 × 3) F_3, 1916.

Number of cultures	Mean of F_3 cultures	Distribution of F_2 parents																	
		8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	9	1																	
4	10	1					1		1	1									
8	11		1						2	2		2		1					
13	12				1		2	2	3	1	3	1							
10	13							2	4	3		1							
10	14						1	1	1	3	2	1			1				
3	15									1	1	1							
4	16									1			2				1		
2	17													1					1
2	18													1		1			

Number of cultures	Mean of F_3 cultures	Coefficients of variation of F_3 cultures grouped according to the means of the F_3 cultures															Average C. V. of group
		9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	
1	9													1			33.0
4	10					1	1		1							1	29.8
8	11						1	1	2	1		1	1		1		26.1
13	12	1	1	2	1		2			3	2					1	21.1
10	13				1	3	1		3	1		1					21.2
10	14				3	2	2	1			1		1				19.9
3	15	1	1	1													11.7
4	16	1	1	1			1										13.0
2	17	1								1							17.5
2	18	2															10.0

A study of table 74 shows very plainly that there is a distinct and marked segregation of leaf-width factors in the F_2 which gives rise to F_3 cultures whose averages reach or exceed the parental means in both directions. As measured by the coefficient of variation, the variability of the hybrid cultures clearly decreased as the average leaf width increased. Does this mean that the wide-leaved cultures are more nearly homozygous (on the average) than the narrow-leaved segregates? If this were true it would follow that the factors tending to increase leaf width are recessive and that the genetically narrow-leaved plants were so on account of dominant inhibitors. This idea is, however, not supported by the fact that the leaf width of the F_1 plants (see tables 51 and 54) which had the maximum of heterozygosity, has leaf widths averaging as high or higher than either parent. If leaf-width inhibiting factors are dominant the maximum narrowness should occur in the F_1 plants. If on the other hand these factors exhibited imperfect dominance one would expect the medium races to have a higher variability than those approaching the extremes. Such, however, is not the case. We must therefore seek elsewhere for the explanation of this decrease in variability as the average leaf width of the cultures increases.

Inheritance of leaf width in bread wheat crosses, Sonora (No. 35) × red Algerian bread wheat (No. 3)

As previously mentioned no pure No. 35 was available for comparison with the F_1 generation in 1914. A comparison of the leaf width of pure No. 3 with the (3 × 35) F_1 hybrid plants is given in table 75.

TABLE 75
Width of leaf in millimeters in (3 × 35) F_1, 1914.

	Number of plants	18	19	20	21	22	23	24	25	26	Average leaf width
Pure No. 3	3	1		1			1				20
(3 × 35) F_1	18			4	2	4	3	4		1	22

While the numbers here given are too small to form the basis of definite conclusions, they at least indicate that the F_1 hybrids have leaves as wide as, or wider than, the parents.

These 18 F_1 plants gave rise to 18 plant rows of F_2 hybrids in 1915 and there were available for comparison with them 1 pure culture of No. 3, and 4 pure cultures of No. 35. The results may be summarized as in table 76.

TABLE 76
Width of leaf in millimeters in (3 × 35) F_2, 1915

Class	Number of cultures	Number of individuals	Average leaf width	Coefficient of variation of the population	Average C. V. of cultures	Distribution of C.V.				
						7 8	9 10	11 12	13 14	15 16
Pure No. 3	1	42	16	11.2	11.2			1		
(3 × 35) F_2	18	1620	18	13.9	13.4		1	2	12	2
Pure No. 35	4	169	20	13.6	13.0	1			1	2

The mean leaf width of the hybrids is intermediate between the parents. The average variability of the hybrids is only slightly above that of the pure cultures.

The distribution of the populations and means for this generation are given in table 77.

TABLE 77
Width of leaf in millimeters in (3 × 35) F_2, 1915.

	Distribution of individuals																					Distribution of means of culture					
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	16	17	18	19	20	21
Pure No. 3							1	1	2	7	11	8	9	1	1	1						1					
(3 × 35) F_2	1		3	2	3		7	17	74	113	191	256	259	225	213	127	70	31	22	5			2	14	2		
Pure No. 35				1			1	1	4	2	6	16	13	19	32	25	24	13	6	4	2				1	2	1

It is interesting here to note that the distribution of the means of the hybrids did not reach the extremes of the parents and that although the number of hybrids was many times that of No. 35, the range of variation of the hybrids toward wide leaves did not exceed that of its broad-leaved parent.

For the F_3 of this cross there were available 5 pure cultures of each of Nos. 3 and 35, and 80 plant rows of (3 × 35) F_3. The hybrid F_2 plants chosen for planting in the fall of 1915 included 11 of the 19 classes through which the population of F_2 was distributed. A first tabulation of the results follows:

TABLE 78
Width of leaf in (3 × 35) F_3, 1916.

Class	Number of cultures	Number of individuals	Average leaf width	Coefficient of variation of the population	Average coefficient of variation	Distribution of C. V.				
						9 10	11 12	13 14	15 16	17 18
Pure No. 3	5	243	14	12.2	11.4	3	1		1	
(3 × 35) F_3	80	3852	17	15.5	12.9	6	29	28	11	6
Pure No. 35	5	246	17	15.2	13.8			3	2	

One is surprised to find here the mean of the F_3 hybrids as high as the broader-leaved parent and the average coefficient of variation of the separate cultures of hybrids lower than that for the Sonora (No. 35).

The distribution of the individuals in the populations of hybrids and pure cultures is shown in table 79.

TABLE 79
Width of leaf in millimeters in (3 × 35) F_3, 1916.

	Distribution of individuals																				Distribution of means of cultures							
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	13	14	15	16	17	18	19	20
Pure No. 3				3	3	7	23	30	66	54	44	7	4	2							1	3	1					
(3 × 35) F_3	3	3	4	1	7	52	97	223	303	583	554	589	392	392	324	207	69	33	14	2		4	13	20	15	20	8	2
Pure No. 35					1		4	10	24	35	48	27	30	18	21	10	16	1	1					2	1	2		

It is particularly interesting to note here that there were ten cultures with means higher than the highest mean for the wide-leaved parent. We have here a suggestion that if there be some force limiting variability in the wider-leaved races it would more strongly affect these wide-leaved hybrid cultures and thus aid in reducing the average variability of the group. In this connection it may be remarked that the average coefficient of variability of these ten cultures is 11.4 percent, a figure well below the average coefficient of variability for pure No. 35, which is 13.8 percent.

It is also interesting to note that whereas in the macaroni—bread wheat crosses many cultures were grown, the average leaf widths of which were below that of the narrow-leaved parent, here we have no cultures lower, but there are eight above the wider-leaved parent.

The segregation and recombination of characters by which these markedly different races were isolated is shown in table 82 where the F_3 individuals are grouped according to the mean leaf width of the F_3 cultures.

TABLE 80

Width of leaf in millimeters in (3 × 35) F_3, 1916. Population grouped according to the leaf width of the F_2 parents.

Number of cultures	Parental width in 1915	Distribution of F_3 grouped according to leaf width of F_2 parents																					Average in 1916
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
2	14						3	6	17	+ 22	O 21	16	5	4	2								14.6
2	15	1				1	4	11	10	14	+O 13	19	12	5	3	1							14.8
9	16		1			2	9	16	56	51	84	+O 76	61	40	19	13	5	3					15.6
14	17	1		1			14	18	44	70	124	O 124	+ 115	72	47	32	14	2	3				16.1
11	18	1		3	1	1	11	16	30	41	96	65	O 82	+ 46	61	36	26	11	4				16.6
9	19						2	8	20	24	62	64	O 65	54	+ 49	38	32	6	2	2	1		17.2
15	20		1			3	6	18	25	59	102	113	O 104	71	78	+ 69	38	16	7				16.9
7	21							2	9	11	22	29	56	O 39	62	62	+ 29	9	4				18.1
6	22		1					1	6	8	26	21	49	O 33	36	43	36	+ 10	10	10	1		18.4
4	23						2		4		9	17	32	23	O 32	30	26	11	+ 3	2			18.5
1	24						1	1	1	3	14	O 10	8	5	3		1	1		+			16.1

This table shows a regular and nearly uniform correlation between the parental leaf width and the average leaf width of the offspring. The one exception at the wide extreme came from plant No. 21-5-2-1, a plant which stood at the end of the row and was very likely an extreme variant of about the 18 class (see range of this class in table 80).

TABLE 81

Width of leaf in millimeters in (3 × 35) F_3, 1916.

Number of cultures	Leaf width of F_2 parents	Distribution of means of F_3 cultures grouped according to leaf width of F_2 parents							Average coefficient of variation of F_3 cultures	Distribution of coefficients of variation				
		14	15	16	17	18	19	20		9 10	11 12	13 14	15 16	17 18
2	14	1	1						11.5		2			
2	15	1	1						15.5			1		1
9	16	1	3	4	1				13.3	1	2	3	2	1
14	17		4	5	4	1			12.5	2	5	5	1	1
11	18	1	3	1	2	3	1		13.4	1	4	3	1	2
9	19			3	3	2		1	12.6	1	4	3	1	
15	20		1	6	3	4	1		13.7		4	7	3	1
7	21				1	4	2		12.0	1	3	3		
6	22				1	2	2	1	13.2		3		3	
4	23					2	2		12.0		2	2		
1	24			1					13.0			1		

There is an indication of some decline in the coefficient of variation in the wider-leaved groups, but it is too much broken up by irregularities to be of any particular significance.

The study of variability of the F_3 is better made, however, by regrouping the F_3 cultures in accordance with their own means. This is done in table 82.

TABLE 82

Width of leaf in millimeters in (3 × 35) F_3, 1916. Population grouped according to the average leaf width of the F_3 cultures.

Number of cultures	Average leaf width of F_3 cultures	Distribution of leaf widths of individuals																			
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
4	14	1				3	12	19	31	**O** 36	40	31	15	3	1	1					
13	15			3	1	1	20	28	83	94	**O** 146	100	82	36	20	10	2				
20	16	1	2			2	14	31	59	94	209	**O** 170	164	83	70	33	23	8	1		
15	17		1				3	12	27	48	104	126	**O** 114	93	88	64	25	10	5		
18	18	1		1		1	3	6	21	27	64	95	150	**O** 118	136	129	80	26	7	1	
8	19									3	17	30	57	50	**O** 53	72	58	20	10	5	
2	20							1	1	1	3	2	7	9	14	**O** 15	19	5	10	8	2

O = means of F_3 groups.

Comparing tables 78 and 82 we note that, starting with cultures which differed on an average by 3 mm in leaf width, we have obtained cultures whose means differ by 6 mm.

TABLE 83

Width of leaf in millimeters in (3×35) F_3, *1916.* F_2 *parents of* F_3 *cultures grouped according to the means of the* F_3 *cultures.*

Number of cultures	Mean of F_3 cultures	Distribution of F_2 parents											Average C. V. of F_3 cultures	Distribution of C.V. of F_3 cultures				
		14	15	16	17	18	19	20	21	22	23	24		9 10	11 12	13 14	15 16	17 18
4	14	1	1	1		1							13.8		2	1		1
13	15	1	1	3	4	3		1					13.4		5	6		2
20	16			4	5	1	3	6				1	13.6	1	5	7	5	2
15	17			1	4	2	3	3	1	1			13.1	2	2	8	3	
18	18				1	3	2	4	4	2	2		12.7	1	9	5	2	1
8	19					1		1	2	2	2		11.2	2	5	1		
2	20						1			1			13.5		1		1	

From table 83 we observe that the range of parents which may give rise to an offspring with a given mean is not greater than that of a pure culture.

When the coefficients of variation are calculated we find an irregular but still quite definite decline toward the wider-leaved cultures as usual (see table 83).

Algerian red bread (No. 3) × early Baart (No. 34)

This cross will be of special interest for comparison with the other crosses inasmuch as the two parents had practically the same width of leaf. The number of plants grown in 1914 are too small to furnish trustworthy averages but as a matter of record they may be given as follows:

TABLE 84

Width of leaf in millimeters in (3×34) F_1, *1914.*

Class	Number of plants	Average leaf width	Distribution of leaf widths										
			14	15	16	17	18	19	20	21	22	23	24
Pure No. 3	3	19					1		1			1	
(3×34) F_1	6	20	1			1			1	3			
Pure No. 34	12	21					1	1	4	3	2		1

TABLE 85

Width of leaf in millimeters in (3 × 34) F_2, 1915.

Class	Leaf width of parent F_1	Average leaf width F_2	Distribution of individuals													Number of plants	C. V.
			10	11	12	13	14	15	16	17	18	19	20	21	22		
Pure No. 3	20	16			1	1	2	7	11	8	9	1	1	1		42	11
(3 × 34) F_2 (44-1)	14	15	1		8	4	28	23	9	10	3	3	2			91	12
(3 × 34) F_2 (44-2)	17	16			2	2	7	16	19	13	18	7	3			81	11
(3 × 34) F_2 (25-1)	20	18					1	5	6	18	22	16	18	5		91	9
(3 × 34) F_2 (28-1)	21	16			1	1	8	18	30	14	18	1				91	9
(3 × 34) F_2 (47-1)	21	18					1	2	5	16	21	25	13	5	1	89	8
(3 × 34) F_2 (47-2)	21	18					1	4	9	8	32	13	13	7	2	89	9
Pure No. 34	18	17			1	2	9	18	13	17	18	10	3	1		92	11
Averages and totals for (3×34) F_2	19	17	1		11	7	46	68	78	79	114	65	49	7	3	532	9*

* Coefficient of variation of hybrid population = 12.

TABLE 86

Width of leaf in millimeters in (3 × 34) F_3, 1916.

Class	Number of cultures	Number of individuals	Average width of leaf	C. V. of population	Average C. V. of cultures	Distribution of C. V.						
						7 8	9 10	11 12	13 14	15 16	17 18	19 20
Pure No. 3	5	243	14	12.2	11.4		3	1		1		
(3 × 34) F_3 (25-1)	50	2387	16	13.3	12.0	1	13	16	13	7		
(3 × 34) F_3 (44-2)	49	2336	15	12.9	11.8	1	11	21	14	1	1	
Pure No. 34	5	243	14	12.6	11.4			5				

These 6 F_1 plants gave rise to 6 plant rows of F_2 hybrids in 1915 and there were available for comparison 1 pure culture of each of Nos. 3 and 34. Since the F_2 cultures differed somewhat in accordance with the leaf width of the F_1 plants, the records will be given in full rather than being summarized as usual (table 85).

Here we have the average of the hybrids less variable than either parent. It should be observed that the one hybrid culture (No. 44-1) which was more variable than either parent had a mean lower than either parent and that the three cultures having means higher than either parent all had coefficients of variation well below either parent. The mean of all of the F_2 was equal to the wider-leaved parent and the total range of the F_2 was practically confined to the limits of the parental range. The means of the F_2 cultures varied on either side of the parental means but in such cases kept their total range inside of the parental range by narrowing their own variability.

In view of these rather marked discrepancies in the means of the F_2 cultures subsequent study is confined to the progenies of but two F_1 plants (44-2 and 25-1) and these are kept separate.

In 1916 there were available for study 5 plant rows of each of the parental cultures, pure No. 3 and pure No. 34, selected from these strains of the previous season and for the hybrids 50 selections from the F_2 of 25-1 and 49 selections from the F_2 of 44-2.

Here the means of the hybrids are above the means of either parent but unlike the F_2 the coefficients of variation are slightly above that of the parental cultures. In table 87 we note that some of the hybrid cultures were more and some were less variable than certain of the pure

TABLE 87

Width of leaf in millimeters in (3 × 34) F_3, 1916. Distribution of the populations and means of cultures of hybrids and parents.

	Distribution of population																		
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Pure No. 3			3	3	7	23	30	66	54	44	7	4	2						
(3 × 34) F_3 (25-1)				7	24	69	119	327	405	555	297	321	109	98	38	14	3		1
(3 × 34) F_3 (44-2)	2	1	2	15	61	188	249	447	514	451	178	154	48	20	5	1			
Pure No. 34			2	6	25	37	34	67	47	16	7	2							
	Distribution of means of cultures																		
Pure No. 3							1	3	1										
(3 × 34) F_3 (25-1)								2	13	19	13	3							
(3 × 34) F_3 (44-2)							3	13	22	9	2								
Pure No. 34						1		4											

cultures. The differences obtained are, however, not large enough to have any especial significance.

In table 87, the most interesting feature is the distribution of the means. Here we have 46, approximately half, of the hybrid cultures with means higher than either of the parents. The same was true in the F_2 cultures (see table 85), As regards height, it will be recalled that the hybrids of this class also averaged as high or higher than the taller parent. The fact that so many races had average leaf widths so strikingly above either parent would suggest recombination with the production of races beyond the extremes of the parent. This, however, is made very doubtful by a study of table 88. There the F_3 cultures are grouped according to the leaf width of the F_2 parents. Moreover, seeds were planted from each of the plants of the F_2 of the populations of the cultures concerned (25-1 and 44-2). If therefore the variations in leaf width of the F_2 plants were partially genetic and partially nutritional (environic) the averages in the F_3 groups should show a correlation with their F_2 parents.

We do not seem to have any correlation whatsoever between the leaf width of the parent and offspring. We may therefore conclude that so far as this character is concerned the F_2 plants were all genetically equivalent and that all differences such as did arise were modifications.

A study of the distribution of the means of the F_3 cultures grouped according to their F_2 parents also confirms the conclusions already drawn that the F_2 plants were all equivalent genetically so far as leaf

TABLE 88

Width of leaf in millimeters in (3 × 34) F_3, *1916.*

Number of cultures	Parental width F_2 1915	Average leaf width F_3, 1916	Distribution of individuals in F_3 cultures																			Distribution of means of F_3 cultures					
			7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	13	14	15	16	17	18
(25-1)																											
1	14	16						2	1	+ 3	7	O 12	8	12		2									1		
3	15	16				1	1	2	10	18	+ 22	O 24	26	26	8	5	1							1	1	1	
3	16	15					4	3	7	38	O 31	+ 45	9	9	1	1								3			
9	17	16				3	3	19	21	51	62	O 93	+ 63	54	17	23	8	2	1		1			1	6	2	
6	18	16				3	4	3	6	42	45	O 65	31	+ 36	17	16	9	4					1	1	2		2
10	19	16					6	18	25	76	79	O 125	48	68	+ 18	16	6	4					1	4		5	
14	20	16					5	17	38	81	126	O 145	88	90	35	+ 26	13	4	2					2	8	3	1
4	21	16					1	5	11	18	33	O 46	24	26	13	9	+ 1							1	1	2	
(44-2)																											
1	12	13					7	+ 11	O 10	12	5	1										1					
3	14	15				2	7	6	15	+ 30	O 29	25	14	5	2								2		1		
7	15	15				3	6	29	36	63	+O 83	76	18	18	3	1							3	2	2		
11	16	15			1	3	13	46	72	111	O 138	+ 91	31	19	6	2							5	5	1		
7	17	15	1			4	7	32	27	58	O 74	61	+ 33	29	8	4						1		4	2		
12	18	15				1	12	30	41	115	O 119	135	41	+ 53	17	8	3	1					2	6	3	1	
5	19	15	1	1	1	2	8	21	32	36	O 48	28	29	14	+ 10	4	1					1	1	2		1	
3	20	15					1	13	16	22	O 18	34	12	16	2	+ 1	1							3			

+ = selected F_2 parents. O = means of F_3 cultures.

width was concerned. However, both tables indicate that the strain originating from the original hybrid plant 25-1 had slightly broader leaves than that originating from the original hybrid plant 44-2.

TABLE 89

Width of leaf in millimeters in (3 × 34) F_3, 1916.
Population grouped according to the average leaf width of the F_3 cultures.

Number of cultures	Average leaf width of	Distribution of individuals																		
	F_3 cultures	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
(25-1)																				
2	14				2	3	9	10	O 27	20	18	4	3	1	1					
13	15				1	11	30	50	133	O 132	148	55	53	6	6	1				
19	16				4	7	27	42	101	163	O 227	134	117	35	28	10	3	1		
13	17					3	12	16	59	74	144	O 84	122	53	40	13	6			1
3	18						1	1	7	16	18	20	O 26	14	23	14	5	2		
(44-2)																				
3	13				5	15	33	O 26	36	21	4	3	1							
13	14			1	8	24	75	92	O 156	135	95	25	10	2						
22	15	2	1	1	2	18	73	115	187	O 239	225	88	75	16	6	2				
9	16					4	14	12	62	104	O 111	44	58	17	6					
2	17						3	4	6	15	16	O 18	10	13	7	3	1			

O = means of F_3 groups.

In order better to study the variability of the F_3 generation of this cross, the plants were regrouped according to the means of the F_3 cultures in table 89, and table 90 gives the distribution of the F_2 parents and the coefficients of variation of the F_3 cultures in the same grouping. The distribution of the F_2 parents in this arrangement appears entirely fortuitous without any correlation whatsoever with the means of the progenies to which they gave rise. These facts therefore form additional evidence that the F_2 plants were all equivalent genetically and that all variations of individuals in the F_2 or of means of cultures in the F_3 were due to non-genetic factors.

We are unable to detect any significant difference in the coefficients of

TABLE 90

Width of leaf in millimeters in (3 × 34) F_3, 1916. F_2 parents and coefficient of variation of F_3 cultures grouped according to the means of the F_3 cultures.

Number of cultures	Means of F_3 cultures	Distribution of F_2 parents										Average C. V. of group	Distribution of the coefficients of variation							
		12	13	14	15	16	17	18	19	20	21		7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22
(25-1)																				
2	14							1	1			13.5			1		1			
13	15				1	3	1	1	4	2	1	11.5		5	3	5				
19	16			1	1		5	2		8	1	12.1	1	4	7	4	3			
13	17				1		2		5	3	2	9.4		4	3	3	3			
3	18							2		1		12.3			2	1				
(44-2)																				
3	13	1					1		1			12.0		1		2				
13	14			2	3	5		2	1			11.8		3	6	4				
22	15				2	5	4	6	2	3		12.0	1	2	11	6	1	1		
9	16			1	2	1	2	3				10.8		5	3	1				
2	17							1	1			13.0			1	1				

variation of the several groups, whether they be observed from the standpoint of averages or distribution. If, however, the two groups be combined and the columns be made to include 2 mm range in leaf width as is done in table 91 (see row for (3 × 34) F_3), we see a slight but definite decline in variability toward the wider-leaved groups.

Summary; width of leaf

In the 3 × 34 cross, the parents had essentially the same leaf width. The average of the F_1 was a little below either parent, the F_2 exhibited quite marked differences in the means of the different F_2 cultures but the average of the whole F_2 population was the same as that of the wider-leaved parent. In the F_3 the leaves of the hybrids averaged wider than those of either parent and there were again considerable differences in the means of the different hybrid cultures (see table 89). The differences observed, however, are not genetic differences, as is shown by the fact that there was no correlation whatsoever between the leaf width of the F_2 selected parents and the mean leaf width of their offspring (see table 88). In other words, the progeny of the different variants of the F_2 gave results such as would come from the fluctuants of a pure race. We may therefore justly conclude that so far as leaf width was concerned, the 3 × 34 hybrids formed a pure race. This, however, does not mean that these hybrids really formed a pure race in all characters for we have already seen that they segregated in both height and date of heading. A plant may easily be homozygous for one character and heterozygous for a number of others. We may assume therefore that the 3 × 34 hybrids received the same set of leaf-width factors from both parents. In the subsequent discussions of leaf width this group will be considered as a single pure variety.

Before proceeding with the summary and discussion of the other crosses we may first seek to discover whether or not a cause such as we found to suppress variability in the tall cultures of wheats was also operative in reducing variability in the wider-leaved cultures. Table 91 brings together all available data bearing on this point. The horizontal rows contain the data from plants or groups which were supposed to be genetically equivalent so far as leaf width is concerned.

The results obtained in table 92 are remarkably uniform and exhibit without doubt some general cause suppressing variability in the broader-leaved cultures. The nature of this suppression factor is not yet determined. Three possible explanations are suggested as follows:

(1) Can it be that the coefficient of variation is not a proper measure of the variability of quantitative characters in biology?

(2) Is it possible that even pure lines of wheat are still somewhat heterozygous and that the taller cultures are more homozygous than the others?

(3) Can there be some physiological limitation of growth in the higher classes which restricts the full development or expression of the plus combinations of factors?

The writer is inclined to attribute this suppression factor to a combination of suggestions (1) and (3). If a car be moving at rate A and we apply an additional force, say $F+m$, which gives an additional speed say $A+n$, it will require more force than $F+2m$ to give it a speed of $A+2n$.

The effect of a factor, environic or genetic, for increasing size, is probably much less in a combination which tends to produce a variant above the racial mean than in combinations, the product of which falls below the mean. We should have, as it were, a telescoping of variability in cultures with higher means. It is possible therefore that a better measure of the variability of quantitative characters would be a coefficient derived by dividing the standard deviation by some fractional power of the mean, thus $C_1 = \frac{\sigma}{M^x}$ where x is a quantity less than 1.

Returning to the macaroni—bread wheat crosses we remember that

TABLE 91

Correlation of average leaf width of culture and the coefficient of variation of the same in pure lines and genetically equivalent groups.

Culture		Total number	Leaf width in millimeters						
			9 10	11 12	13 14	15 16	17 18	19 20	21 22
Pure No. 1	No. of cultures	16			2	8	4	2	
	Average C. V.				11.0	10.6	9.9	9.0	
Pure No. 3	No. of cultures	4			2	2			
	Average C. V.				11.8	10.5			
Pure No. 34	No. of cultures	6		1	4		1		
	Average C. V.			12.0	11.3		11.0		
Pure No. 35	No. of cultures	9				2	3	3	1
	Average C. V.					14.5	13.7	14.7	8.0
(1 × 35) F_2	No. of cultures	37			5	31	1		
	Average C. V.				30.6	29.1	27.0		
(1 × 3) F_2	No. of cultures	6			3	3			
	Average C. V.				26.7	25.0			
(3 × 34) F_2	No. of cultures	6				3	3		
	Average C. V.					10.7	9.0		
(3 × 35) F_2	No. of cultures	18					16	2	
	Average C. V.						13.6	12.5	
(3 × 34) F_3	No. of cultures	99			18	63	18		
	Average C. V.				12.0	11.8	10.3		
F_3 cultures from tall F_2 plants having smooth seeds (parent-like) (1 × 35) F_3	No. of cultures	36			8	12	14	2	
	Average C. V.				19.1	17.9	15.6	14.5	
F_3 cultures from tall F_2 plants having wrinkled seeds (F_1-like) (1 × 35) F_3	No. of cultures	28		3	6	16	2		1
	Average C. V.			30.0	26.5	22.8	20.5		13.0
F_3 cultures from tall F_2 plants having smooth seeds (parent-like) (1 × 3) F_3	No. of cultures	9		1	2	3	3		
	Average C. V.			19.0	16.5	11.3	10.0		
F_3 cultures from tall F_2 plants having wrinkled seeds (F_1-like plants) (1 × 3) F_3	No. of cultures	9	1	4	3	1			
	Average C. V.		20.0	27.8	26.7	25.0			

the F_1 had wide leaves and wrinkled grains. The average leaf width of the F_2 was markedly below that of either parent but there were some F_2 plants having leaf widths as great or greater than the parental means. These wide-leaved F_3 plants were of three types, viz., (1) some had wide leaves and smooth grains (parent-like), (2) some had wide leaves and wrinkled grains (F_1-like) and a few had wide leaves and partially wrinkled grains (of uncertain classification). Now since the average of the F_2 was below that of the parents and the variability was much above the parental variability, we should expect the F_1-like F_2 plants to give F_2 cultures low in mean leaf width and high in variability, whereas the parent-like F_2 plants should give F_3 cultures high in mean leaf width and low in variability. Now disregarding the wide-leaved F_2 plants with partially wrinkled seed (on account of difficulty of classification) we find the results shown in table 92.

TABLE 92

	(1 × 35) F_3			(1 × 3) F_3		
	Number of cultures	Mean leaf width	Average C. V.	Number of cultures	Mean leaf width	Average C. V.
F_3 cultures from wide-leaved smooth-seeded F_2 plants (parent-like)...........	36	16.1	17.1	9	15.4	12.9
F_3 cultures from wide-leaved wrinkled-seeded F_2 plants (F_1-like)	28	14.9	23.8	9	12.4	26.2

No better agreement of the facts with the theoretical assumptions made, could well be expected. It is, of course, not here assumed that the parent-like F_2 plants were constituted genetically exactly like one or the other of the parents or that the F_1-like F_2 plants were completely heterozygous in every particular in which the F_1 plants were heterozygous, but it is assumed that the genetic agreement is close enough to give marked similarity in form and hereditary behavior. Where a number of factors are involved, as there probably are here, it would be extremely difficult, probably impossible, to pick out plants from the F_2 by inspection, which were exactly like either the parents or the F_1, genetically. This could only be done by judging the F_2 plants by the genetic behavior of their offspring. The facts developed seem to show that the wide-leaved F_2 plants fell into two groups, the one having a complete (or nearly complete) set of the factors from one or the other of the parental races, and that the other group contained plants which were heterozygous for all (or nearly all) of the characters in which the parents differed. Again therefore we have a situation where a complete double set of one or the other of the parental races or a complete (or nearly complete) single set from each of the two parents were able to produce wide-leaved plants, but that the large majority of the new recombinations of parental characters resulted in less vegetative development.

Now referring to table 92 we find that even in the offspring of these two groups of wide-leaved F_2 plants the factor for suppressing variability was apparent, but it was not sufficient to mask the effect of differences in heterozygosity because in the one case (those of the F_1-like parents) the means tended to be below that of the standard (pure line parents). Now when we turn to the 3 × 35 cross where the F_1, F_2 and F_3 all had average leaf widths larger than the more narrow-leaved parent, the suppression factor was able entirely to offset the theoretically expected increased variability of the heterozygous cultures. If in accordance with the F_1, the wide-leaved F_3 cultures were the more heterozygous and the more narrow-leaved the more homozygous we can easily see how the suppression factor might reduce the average variability of all of the F_3 cultures to a figure equal to or below that of the most variable parent especially in a case where the average of the leaf width of the F_3 cultures was equal to that of the wider-leaved parent.

One cannot here assume the formation of a single new blended race, for table 75 shows segregation in the F_2 with the formation of many distinct races in F_3, and moreover, in spite of the suppression factor and the fact that the F_2 had a larger mean than the F_3, the average variability of the F_3 was less than that of the F_2 (compare tables 76 and 78).

According to Mendelian expectation, the parental types of individuals in F_2 and culture means in F_3 were recovered in all cases. In 1 × 35, recombination formed individuals in F_2 and a number of cultures in F_3 whose means were significantly beyond, both above and below, the range of either parent. In 1 × 3 the range of individuals in F_1 and of means of cultures in F_3 were significantly below, but not above, the parental ranges. In 3 × 35 the range of individuals in F_2 and means of cultures in F_3 were not significantly above or below the parental ranges.

In the macaroni—bread wheat crosses the average variability of the F_2 and F_3 generations were markedly above that of the parents but in the F_3 many cultures were secured which were as little variable as either parent. In no case was there a single F_2 culture, however, which had as low a variability as the most variable parental culture.

The variability of the bread wheat crosses has already been discussed with sufficient fullness.

The segregation of simple Mendelian unit factors appears to suffice to explain all of the facts so far observed in the inheritance of leaf width in the wheat hybrids here discussed. No attempt has been made to determine the number of factors but the supposition is that there are several.

GENERAL SUMMARY

Detailed summaries of the three characters, date of first head, height, and width of leaf, may be found on pages 27, 52 and 87, respectively.

The F_1 of the macaroni—bread wheat crosses developed normally and were in every case equal or superior to the mean of the parents in vegetative vigor and they were no more variable in size characters or time of maturity than were the pure races. We may therefore conclude that a single complete set of macaroni wheat characters with a complete single set of bread wheat characters (the maximum of heterozygosis between the two varieties) will produce a perfectly normal plant.

In the second generation, on the other hand, many of the seeds would not germinate and those germinating produced plants differing in vegetative growth from those which were more vigorous than either parent to such as never got beyond the rosette stage. Moreover those which made a normal vegetative development exhibited every degree of sterility from completely sterile plants to those entirely normal in seed production. It would appear, therefore, that these facts alone refute any idea of blending inheritance, for if blending had taken place in the F_1, sterile or vegetatively deficient plants would be no more likely to occur in the F_2 than in the F_1. Hence we are compelled to predicate segregation and recombination in these quantitative characters. There is nothing to indicate even partial blending in any of the factors concerned.

In the use of the coefficient of variation as an indication of heterozygosity in hybrids involving quantitative characters, care should be exercised to make due allowance for the fact that races with high means resulting from increased vegetative growth, have their variability limited or reduced by the apparent law that size factors are more effective in producing variability in combinations tending to produce a result below the mean of the hybrid population than in combinations which tend to exceed this mean.

The suppression of variability in cultures with high means applies to pure as well as hybrid cultures. It appears to be a telescoping of variability as the mean approaches the upper physiological limit of growth rate for the species concerned.

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