

A STATISTICAL STUDY OF SEVERAL MORPHOLOGICAL
CHARACTERS ASSOCIATED WITH REPRODUCTION AND YIELD IN MAIZE

By

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R. G. R.

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INTRODUCTION

The ultimate practical aim of all plant breeding research is to assist other botanical sciences in the acquisition of knowledge which will make possible, first, the prediction of plant behavior, and second, the manipulation necessary for increasing or maintaining the production of those plant parts desired by man. The accomplishment of such ends involve at least a partial understanding of both environmental forces and response capacities inherent in the plant. Whatever the basis of evaluation, the final worth of the crop is the resultant of the interaction of both types of factors. Any improvement must come as the effect of a change in one or the other or both of these complexes. Man either attempts to fit a given environment to the organism or he attempts to alter the hereditary constitution of the organism to fit the environment, or more often, he finds it profitable to resort to both procedures. Whatever the path chosen, there are many baffling difficulties to be overcome. Gains over nature are conservative, and tediously made.

Though plant breeders must ever recognize the importance of developmental conditions, they are primarily concerned with the heredity phase of crop improvement. They endeavor to isolate that hereditary pattern which will be most expressive of the quality or qualities sought. Sometimes their reward comes easily, especially in cases where the quality in question does not deeply concern the plant's fight for existence. Beginning with the variability, either exhibited naturally in a population of individuals or induced by wide crossing, the plant breeder keeps selecting a desired type from generation to generation. He labors with the hope that finally he will obtain a strain which will "breed true" for the thing desired. Barring mutations, he cannot surpass the upper limit of the initial population. He is not synthesizing; he is merely picking out a type that exists as a member of a collection of types.

If the quality sought is closely associated with the reproductive potentiality of the plant, as is the case in yield of grain in maize, selection is apt to be of little value. Of all functions that of reproduction is the most important from the standpoint of the plant. For any individual the number of vigorous zygotes produced is a measure of its efficiency; an inventory of its competing power for a place in posterity. Thus reproduction may be looked upon as the product of number of zygotes times the vigor of zygotes. Both doubtless have a

complicated mode of inheritance. It seems safe to assume that each represents the culmination of numerous correlated activities, and that each is the recipient of every character's contribution by way of organic function. Possibly each contributing character may have a simple mode of inheritance; it may be one member of an allelomorphic series; it may or may not be independent of certain other contributing characters. Whatever the peculiarities and the inter-relations of the component genetic factors, their combined effect is reproductiveness. Thus it is enlightening to look upon reproductiveness as the arithmetical product of the respective proportionate effects of all allelomorphic series concerned. Since factors of the same series, may differ in extent of contribution, unity can be the value for the "best" effect of any one series, and zero its "worst" or inhibiting effect. The fractions between 0 and 1 will denote intermediate effect. If each series is present at its maximum value, i.e. 1, then the product must be 1 if any series have the value 0, then the product must be 0 and there can be no reproduction. Any number of combinations with intermediate values may be assumed. Thus there might be a total of, say, 6 series involved giving such a result as:

$$1.0 \times 1.0 \times 0.9 \times 0.8 \times 0.3 \times 0.2 = 0.115$$

In this case there would be only 12 percent of the possible reproduction. If 0.9 is raised to 1.0 the product is raised

to 0.128; but if instead, 0.2 is raised to 0.3, also an increase of 0.1, the product is 0.173. Therefore, the factor with lowest proportionate beneficial effect has the greatest weight upon the product, i.e. upon reproduction.

Natural selection should be very effective in so far as it impinges upon characters expressive of a plant's competing power for a place in the population at equilibrium. Since reproduction is that power, those factors detrimental to it will be eliminated unless protected by linkage or kept in the germplasm by recurring mutation. The lower the reproductive value of a factor in comparison to its allelomorph the more rapid it will be crowded out of the population. The final results would appear to be the same whether the plant is self-fertilized or cross-fertilized. Inbreeding apparently only serves to make elimination more rapid.

A population of corn plants represents one or the other of two conditions with regard to genotypic constitution: (1) the population may be at equilibrium with regard to the proportion of genotypes concerned with reproduction; (2) the population may be in a state of transition due to (a) growth in a new locality, (b) a change in native environment (appearance of a new disease etc.) (c) the occurrence of a mutation, (d) recent crossing without the population, and (e) artificial selection. Since natural selection favors the genotypes of highest reproductive value, a population at

equilibrium must be at its reproductive maximum except for recurring mutation. Any artificial selection that does not sample all genotypes to the same degree will throw the population out of equilibrium.

If all allelomorphic series segregated independently the final result at equilibrium would be one reproductive genotype. The population would be a pure line with regard to reproductiveness. But, the fact that no corn variety has ever been found that will not segregate for non-productive types upon undergoing inbreeding and also under cross-breeding to a lesser extent, proves that the pure line for reproductiveness does not exist in the normal corn population. The theory of balanced detrimental is usually presented as an explanation, i.e. the beneficial factor of one series is linked with the detrimental member of another series. When either occurs in the homozygous condition the detrimental effect is expressed. Kemp (20)^{*} has shown that for such a condition the heterozygote must have a higher reproductive value than the homozygous classes. Otherwise, the detrimental would tend to pile up in the population which would result in the presence of many non-productive types as in the case of inbreeding. Therefore, since a corn population under random breeding contains heterozygotes, it is to be expected that there will be a heterogeneous expression of reproductive value among its

* Reference by number to literature cited.

members even at equilibrium.

In the foregoing vague discussion the attempt has been made to emphasize the fact that reproductive capacity, i.e. the formation of vigorous zygotes, is the plant function through which natural selection is effective. Hence, in so far as the breeder is selecting for characters associated positively with reproduction, nature is his very able assistant. In the case of corn for grain artificial and natural selection work toward similar goals. The breeder seeks high weight of grain per plant; nature seeks a large number of vigorous kernels per plant. The former is not so particular about the manner in which the total weight is divided among the kernels; on the other hand, so long as size does not reduce progeny efficiency, small kernels are preferable from the standpoint of reproduction. A further difference results in the fact that through cross-fertilization, reproduction is favored by high pollen production as well as high ovule production. It is a question of total genetic production rather than number of ovules. The ratio of pollen number to ovule number may vary widely and yet the total genetic number may remain constant. Therefore, to the extent that this ratio is above average it will be possible for a genotype of low ovule number to maintain itself. Finally, it would appear that genotypes with low total inflorescence must be relatively more vigorous in order to hold their place against the superior genetic numbers of the highly inflorescent types.

It is for the purpose of testing experimentally some of the foregoing considerations that this work has been done. An attempt has been made to measure by means of correlation the degree of inheritance of ear and tassel characters; the extent of their inter-relations and their association with yield.

REVIEW OF LITERATURE

Theoretical Approach; - Since this study is an attempt to measure the degree of relation between certain maize characters in a cross fertilized population supposedly near its equilibrium point for genotypic proportion, it seems advisable to review important concepts bearing upon the constitution and behavior of such a population.

Pearson (30), Hardy (13), Wentworth and Rennie (41), Jennings (18)(19), Robbins (33)(34), Fisher (8)(10), Wright (43), Haldane (12), and Kemp (20) have given philosophical perspective to much work in genetics. Aided by mathematical and statistical methods they have investigated factor population as a whole rather than the behavior of individual factors in segregation. Formulas have been developed showing not only the genotypic proportion at equilibrium but also the rate of its attainment under various factorial relationships, modes of breeding and selection. Although for the sake of comprehension most of this work has been concerned with a single allelomorph series of factors, enough has been done to show that the same concepts may be applied to the more complicated situations involving multiple factors, linkage, factor interaction, and mutation. It is sufficient to say that formulas showing the theoretical proportion of genotypes for any generation and at equilibrium can be obtained through the use of a few basic assumptions.

Furthermore, these formulas can be generalized sufficiently to aid in the prediction and explanation of certain character relations observed in field populations of plants.

Kemp has made a very inclusive theoretical study of (1) conditions that may induce equilibrium, (2) the reproduction behavior at equilibrium and (3) the margin between reproduction and production. Realizing that the extent to which an allelomorph occurs in the germplasm is a function of its reproductive capacity, Kemp has arbitrarily assigned each monohybrid genotype a reproductive value lying within the limits of 0 and 1. By the use of these values in appropriate equations, he is able to get the proportion of all three monohybrid types in any given generation (F_{n+1}) from the proportion found in the preceding generation. Similarly, the rate at which equilibrium is approached and the genetic situation at that point can be gotten. Conversely, from the proportion of the genotypes in a stationary population the reproductive capacity of any one type can be calculated in terms of the others.

Using the above mode of attack Kemp has been able to verify Fisher's (10) conclusion that the heterozygous type must have a greater reproductive capacity than the homozygous classes if a detrimental allelomorph is to be retained in the population without the aid of recurring mutation. There appear to be only two ways in which the heterozygous type may be more reproductive than other types: (1) there may be something

inherently beneficial in the union, or (2) there may be a linkage of reciprocally balanced factors, i.e. the beneficial member of one pair is inseparably linked with the detrimental member of the other pair. The latter postulate is most generally accepted. Such a condition can easily be imagined for corn in the case of high inflorescence.

Kemp has pointed out that other things being equal a genotype determining high inflorescence will gain the ascendancy in the population. It will displace other types with low inflorescence and will eventually be the only type represented. In fact the sparse inflorescence types long ago would have ceased to exist barring mutation or other phenomena favoring their persistence. The balanced detrimental postulate seems to offer one possible explanation. One may assume that the types with high gametic number are held in check by being encumbered with detrimentals to such an extent that their production of vigorous progeny would not surpass that of the low inflorescence types. A second explanation consists in the possibility that the population has come into equilibrium under an environment sufficiently unfavorable to prevent a complete development of all the zygotes of the prolific types. Such a condition would tend to put the non-prolific types on an equality with the prolific types with regard to progeny numbers.

In this connection Kemp has brought out the relation of production and reproduction in plants. It is shown that

production in reality is yield of plant material desired by man as economic goods, whereas reproduction is yield of viable zygotes destined to serve in the perpetuation of the plant. In crops grown for seed the two come nearest being the same in meaning. However, even here the margin between the two may be great enough to offer the plant breeder hope of increasing yields. The crop will tend to come into equilibrium at the highest reproductive capacity, which may not necessarily mean highest yield. There may be a preponderance of strains with high total inflorescence which show a wide pollen-ovule ratio. Such strains will have a high reproductive value but their yield of grain may be relatively low. Upon the basis of such reasoning the study of tassel and ear characters associated with gametic production and yield should be of scientific value.

Experimental Contributions:- The fact that artificial selection has been effective in isolating different germinal complexes is attested by the numerous distinct varieties of corn now in existence. Not only are these varieties quite distinguishable, but they can be kept so by continuous selection and adequate protection from cross-breeding with other varieties. The observation that varieties with visible differences often show unlike yielding capacities when compared under a common environment, led breeders to anticipate the association of

certain morphological characteristics with yield.

The advent of agricultural fairs caused farmers to vie with each other in growing good crops. Their efforts involved not only seed selection, but also field management and ability to pick show samples. At first each grower had his own ideal or "fancy points". As time went on an ideal type became more or less common to a community. With regard to corn the ideal type usually included ear characters, denoting high weight of grain, soundness, and symmetry. In order to facilitate judging at fairs standards reflective of a consensus of ideals were prepared.

According to Richey (31) the judges at the Chicago exposition in 1886 formulated a set of standards for use at that time. In 1891 Orange Judd prepared for the Illinois State Fair, a score card which was later modified and adopted by the Illinois Corn Growers' Association. Following this move score cards came into general use throughout the corn growing regions of the United States. Upon their adoption agronomists set out to determine whether the various points were associated with seed value as measured by progeny yield in field comparisons. The following review includes a number of the more noteworthy investigations.

As a result of conducting a large number of ear-to-row tests with sweet corn in 1907, 1908, and 1909, Pearl and

and Surface (29) decided that there is no relation between external seed-ear characters and yield in sweet corn.

Hartley (14) from a study of 1,000 ear-to-row tests involving four varieties for six years found yield to be independent of seed-ear characters.

Montgomery (37) of the Nebraska station in 1909 reported a slight yield difference in favor of long ears with medium depth of kernel.

Experimenting with Reid's Yellow Dent and Johnson County White corn for five years, Sconce (35) of Illinois found that ears with 18 and 20 rows gave better yields than those on either side of these classes.

Love (24) made correlation studies with Minnesota No. 13 and Funk's Ninety Day corn in which he found that among the characters used length and weight of seed ear gave the highest correlation with yield. The highest coefficient found (0.323 .060) was that for weight and yield in the case of Funk's Ninety Day in the year 1909. Number of rows gave small negative values in three out of four cases. In general the values were insignificant.

Love and Wentz (25) using Funk's Ninety Day corn grown over a period of five years correlated the following seed ear characters with progeny yield: length, circumference, ratio of tip to butt circumference, circumference of cob, weight, percentage of grain, average weight of kernels, number of rows,

average length of kernels and average width of kernels. In general no close associations were found. Circumference of ear was the only character that appeared to have a significant relation to yield, its coefficient varying from $0.104 \pm .067$ to $0.360 \pm .061$ for the different years. Percentage of grain was negative, though not significant, throughout the five years. Except for 1913, number of rows was positive, but in no case significant. In their conclusion the authors state that "it is evident that the points emphasized on a score card are of no value for seed ear purposes and are entirely for show purposes".

McCall and Wheeler (26) at the Ohio station correlated length, weight, circumference, and density of seed ear with yield. Their results show only negligible relations.

Williams and Welton (42) also at the Ohio station selected seed ears for extremes in such characters as length of ear, weight of ear, shape of ear, filling of tip, kernel indentation, and shelling percentage. Based on average of 8 to 10 years they got the following differences in bushels per acre: long over short ears, 1.39; tapering over cylindrical, 1.65; filled tips over bare tips, 0.34; smooth over rough, 1.76; low over high shelling percentage, 0.42.

Lacy (23) has given a summary of experiments comparing the yields of kernels taken from the butt, middle, and tip of seed ears. The results of 81 experiments conducted during a

period of 45 years are brought together in one table. If the average yield of the middle kernels for all comparisons is taken as 100, the relative yield for the butt kernels is 103; that for the tip kernels, 105. Differences for both are statistically significant. It is suggested that, due to later silking of the butt and tip portions of the ear, there is more cross fertilization in these areas. Also the extremes of the ear may dry out more rapidly thus obtaining better maturity than the middle portion.

Using 9 dent varieties each grown in ear-to-row tests from 1 to 5 years, Cunningham (4) found that ears small in circumference, ears having a low shelling percentage, and ears with a low number of kernel rows yielded slightly better than ears in the higher class for these characters. The largest average difference, 3.7 bushels per acre, was obtained in the case of 16-rowed ears over 20-rowed ears for the varieties Boone County White, Kansas Sunflower, Leaming, Legal Tender, and Hogue Yellow Dent.

Hutcheson and Wolfe, (16) of the Virginia Station grew an early maturing strain of Boone County White in ear-to-row tests for two years. Each year the progenies were separated into high and low yielding strains. The progeny ears making up both groups were measured or scored with regard to a number of score card features. Despite the fact that there was an average difference in yield between the two groups of 17.74 bushels per

acre, there was little difference between the means for the various measurements. Of the directly measurable characters, length of ear and circumference of ear were the only ones that showed appreciable association with yield. However, less tangible features which were scored in per cent consistently favored the higher yielding groups. The authors, therefore, concluded that the score card is of value in selecting high yielding strains. Their conclusion has been somewhat discounted because their scoring was done on progeny ears, the weight and score of which may have varied together on account of growth conditions.

Hughes (17) submitted 500 unselected seed ears to 25 corn judges. After being scored a portion of each ear was planted in a field test. The 50 best ears as selected by the majority of the judges averaged only 6 bushels more per acre than the remaining ears. Furthermore, it was concluded that smooth ears with large kernels were slightly better than the other extreme.

Wallace (38) using the data from the above experiment employed Wright's (43) method of path coefficient to determine (1) the weight that the average judge gave to the various score card points, and (2) the weight that each feature should receive according to its relation to the progeny yield.

The following table gives the comparison:

Character	Judges' score: card	Correlation : with yield	Score card : based on yield
Length	42.0	.048	7.7
Circumference	13.6	.062	10.0
Wt. of kernel	18.3	.311	50.0
Lack of indentation	13.3	.112	18.0
Blistering of kernel	6.4	.056	9.0
Absence of starchiness	6.4	.033	5.3
Total	100		100

From the table it can be seen that more weight should be given to weight of kernel than to length of ear as was done by the judges. Weight of kernel had the highest correlation with yield (0.311). Therefore, it is evident that a very small portion of yield variability is concomitant with that of the ear characters studied.

In a series of ear-to-row tests involving five varieties of dent corn, each of which was grown in a different locality for 3 to 4 years, Biggar (2) found no distinct relation between number of kernel rows or between shelling percentage and yield. For number of rows and yield nine correlations were negative as against seven positive. In size, the coefficients ranged from $-.226 \pm .089$ to $+.063 \pm .081$. Of 16 comparisons 10 were negative for shelling percentage and yield, the range being $-.368 \pm .082$ to $+.276 \pm .077$. Four of the negative coefficients were significant and but one of the positive coefficients. Taken as a whole

the results tend to indicate a slight negative relation between kernel number and yield.

Keisselbaeh (21) in summarizing experimental work on ear type selection to date (1922), both at the Nebraska station and at other stations, concluded that "ear and kernel characters, aside from those known to indicate soundness and special adaptations, have little significance as indicators of high producing seed ears." He also suggested that where the tendency has been to select too large and late maturing types, selection of long, slender medium smooth ears with medium shelling percentage and with kernels of medium depth, there is a tendency to increase production.

In a comprehensive summary of corn breeding work to date (1922), Richey (31) has listed in one table the results of all important experiments concerned with the relation of seed-ear characters to yield. A part of this table is given below:

Summary of comparisons between seed ears differing in some specific character. (Adapted from Richey)

Seed Ear character	Number of comparison and crop years favoring degree stated					
	Large			Small		
	Compari- son	Crop Year	Compari- son	Crop year		
Weight	35	50	3	9		
Length	43	95	10	28		
Circumference	10	16	8	31		
Shelling pct.	11	17	29	38		
No. of rows	19	19	26	26		
Indentation	3	3	11	29		

Richey concluded that although most of the differences obtained in the above experiments were small, there is every indication that selection of heavy, long, smooth ears with fewer rows and lower shelling percentage is generally desirable. As a possible explanation it was suggested "that this superiority of the smoother, fewer-rowed ears was due to their persistence in a population too closely selected in another direction, as there is good evidence that close type selection may decrease yields. The superiority also may be inherent, or may be due to better seed condition caused by better maturity and greater freedom from disease".

Myers, Love and Russell (28) concluded from ear-to-row studies that there is no practical end to be gained from selecting seed ears with certain characteristics. However, they found an interesting correlation between weight of seed kernels and per cent of mature progeny ears harvested. For Webber's Early Dent over a 3 year period, the coefficients of correlation were $+0.196 \pm 0.068$, $+0.254 \pm 0.063$, and $+0.306 \pm 0.061$; for Cornell 12 over a two year period, $+0.391 \pm 0.057$ and $+0.026 \pm 0.067$. From these results the inference may be drawn that large kernels with their greater store of food material give the seedlings a better start in the field.

Kyle and Stoneberg (22) found that prolific corn varieties had fewer kernel rows than non-prolific varieties,

and that under growth conditions suitable for both, the former outyielded the latter. The same was true for ears of low row number both within prolific and non-prolific varieties and also in several F_1 crosses. Furthermore, it was found that selection in inbred lines was more rapid toward ears with few kernel rows, than toward ears with many kernel rows. Lines of the former type on the average were more resistant to corn smut, showed fewer heritable defects, and were more vigorous in general.

Garrison and Richey (11) isolated six strains of corn differing in number of kernel rows from a selection of Boone County White. In yield comparisons including the six isolated strains, various inter-strain-crosses, and the parental selections, it was found that crosses with a lower mean number of kernel rows tended to be more productive. But, since such crosses were between strains differing most in regard to row number, it was suggested that the effect observed might have been due to difference in the degree of hybrid vigor present in the respective crosses.

Utilizing data from 3,265 ears comprising four varieties each grown from 9 to 14 years, Richey (32) has subjected the problem of ear type and yield to rigorous statistical analysis. Through the use of special methods of correction it has been possible to combine the data from different years into one statistical set. This procedure raises the number of

comparisons sufficiently to make small correlations statistically significant. Simple, partial, and multiple correlations then have been used to determine the individual effect of each ear character upon yield. Although accidental variation due to soil and other experimental conditions was responsible for the major portion of yield variability (estimated at 90 per cent), the work showed a definite positive association between weight of ear and yield, but a negative association between yield and both number of rows per unit of circumference and number of kernels per unit of length. These relations were shown to be due directly to the characters in question, and not due indirectly to their connection with other ear characters more intimately associated with yield.

The following table modified from Richey's paper serves to illustrate the above point.

Table giving a few of the character-yields correlation coefficients found by Richey

Ear Character	Variety No.	Kind of correlation coefficient		
		Simple	Partial	Variable held constant
Weight	77	0.0279 ± 0.0192*	0.0641 ± 0.0191*	No. of Rows
	119	.1605 ± .0264*	.2013 ± .0260*	" " "
	120	.1526 ± .0233*	.1554 ± .0233*	" " "
	133	.1014 ± .0269*	.1129 ± .0268*	" " "
No. of rows	77	-.0895 ± .0190*	-.1051 ± .0190*	Butt circum-
	119	-.0905 ± .0269*	-.1325 ± .0266*	ference
	120	.0070 ± .0239	-.0147 ± .0239	" "
	133	-.0350 ± .0271	-.0877 ± .0269*	" "
No. of kernels per row	77	-.1027 ± .0190*	-.1230 ± .0189*	Length
	119	.0272 ± .0271	-.0716 ± .0270	"
	120	.0653 ± .0238	-.0143 ± .0239	"
	133	.0133 ± .0271	-.0416 ± .0271	"

* three times the probable error.

This table shows that the correlation between weight and yield is positive and is increased when number of rows is held constant. Similarly the negative relation of number of rows and yield is accentuated when butt circumference is fixed. Likewise, the coefficient for number of kernels per row and yield are all negative when length ceases to be effective. Other correlations not listed here show that butt circumference and length of ear are positively correlated with yield, and that the former is positively correlated with number of rows, and the latter, similarly correlated with number of kernels per row. It appears therefore that these two characters relating to kernel number have an opposite effect on yield to that exhibited by the characters most intimately associated with them. Furthermore, Richey found that in general the use of weight, number of rows, and number of kernels per row, in a multiple system gave almost as good results as the inclusion of all eight characters studied. These findings are evidence that the total number of zygotes is negatively correlated with productiveness, although the magnitude of the relation may vary with different varieties.

The foregoing citations have been concerned mostly with determining the extent to which seed-ear characters are associated with productivity as measured by progeny yield of grain. They have not all dealt with the inheritance of ear characters except in a very general sense. Mendelian analysis

has not been attempted. It has merely been assumed that some complicated expression of Mendel's law has applied.

Emerson and East (5) made a rather detailed study of quantitative inheritance in maize, their object being to show that such inheritance is explainable on the basis of segregation of discrete factors in the germplasm. Their work included both ear characters and plant characters, among them being number of kernel rows, length of ear, size of kernel, number of nodes, length of internode, length of plant, etc. In general their method involved crossing strains which differed in magnitude of the character under study. Beginning with the F_1 , means and variability constants were obtained for progeny populations throughout several generations. By comparing frequency distribution among progenies with the parental distributions these investigators were able to estimate the number of factors involved. They found that the F_1 was usually intermediate between the parents and less variable than either parent; that the F_2 taken as a whole had about the same mean as the F_1 but showed a distribution that spread over the opposite limits set by the parents; that in the case of row number and size of seed, parental types could be recovered in the F_3 generation. It was concluded that the results secured were precisely what could be expected if quantitative differences are due to numerous factors inherited in a strictly Mendelian manner.

Although a number of studies have been conducted on the correlation between parts of the same plants, the writer has been able to find only two references mentioning correlation, in which tassel measurements have been considered.

Ewing (7) made a number of intra-plant correlations among plants of Funk's Ninety Day corn. Several correlations involving weight of grain as one variable are presented:

diameter of stalk, $+.393 \pm .020$; length of leaf, $+.292 \pm .021$; height of plant, $+.203 \pm .035$; height of seedlings, $+.219 \pm .037$; number of tassel branches $-.009 \pm .048$.

Etheridge (6) has reported a similar study. Among others, the following correlation coefficients with weight of grain as the one variable were found: days from planting to silking, $-.4181 \pm .0133$; total leaf area, $+.0702 \pm .0161$; height of stalk, $+.1109 \pm .0160$; circumference of first internode above ground, $+.1846 \pm .0155$; length of tassel $-.1251 \pm .0170$. Tassel length was obtained by taking the total length of five average laterals, multiplying their mean length by the total number of laterals, and adding the length of the central spike.

The foregoing review of literature seems to justify the following conclusions:

1. Numerous experiments have been conducted for measuring the relation between seed-ear characters

of corn and productiveness.

2. Experimental disagreement has been due to:
 - (a) the small differences involved.
 - (b) the use of different varieties.
 - (c) unlike environmental conditions.

3. The weight of evidence points to:
 - (a) A low positive correlation for those ear characters expressive of weight of ear.
 - (b) A low negative correlation for total number of kernels.

4. Investigators are almost unanimous in agreeing that physical differences in sound seed ears are of little value as an indication of their productivity.

5. The inheritance of quantitative character in maize can be explained on a strictly Mendelian basis.

6. Pollen production with reference to quantity has received very little attention.

MATERIALS AND METHODS

Seed Stock and Field Methods:- Except for the greenhouse work, data for the study were obtained from ear-to row tests with Reid's Yellow Dent corn grown in 1926 and 1927 at College Park, Maryland. No selection of seed ears was made except that due to elimination of rubbings and decayed ears at harvest time, and to elimination through germination tests. In 1926 the 100 ears used were grown on the Experiment Station Farm at College Park, Maryland. In 1927, 200 seed ears were obtained from a lot taken from the crib of Mr. Marion C. Prough of Sykesville, Maryland. It is thought that both seed stocks have been grown in the vicinity of College Park sufficiently long to be well adapted.

Each seed ear was represented by three single-row plots systematically distributed over the experimental area. Thus there were three series, hereafter designated as Series I, II, and III. Each series contained one plot planted with seed from a given ear. In 1926 each plot consisted of eight hills. In 1927, Series I and II each contained ten-hill plots while Series III contained sixteen-hill plots. Consequently for the first year 48 plants constituted a perfect stand for any one seed ear; and for the second year, 72 plants constituted

a perfect stand. Planting was done by hand in hills checked 3.5 feet each way. Four to six kernels were placed in each hill and the stand later thinned to two plants. With the exception of Series III for 1927, the plots were located on fairly uniform land used for varietal experiments in a regular rotation. Series III for 1927 was located on an area in a separate field that exhibited considerable soil variability.

At harvest time the plants on each plot were cut, tied into a bundle, tagged and shecked in the field. After the corn had cured for several weeks, the bundles were husked and the total yield of ears for each plot determined by weight. At this time, the progeny ears, previously marked for future measurement, were picked out and stored in the seed barn. The remaining ears were discarded.

Yield Corrections:- No correction was made for moisture content of the corn. The plot yields obviously in error because of injury to the corn by rodents or poor stand were discarded. The remaining plot yields were corrected for soil variability. In 1926 each series was divided into blocks composed of five contiguous plots, and correction for plot yield was made according to the following formula:

$$x = \frac{B \times p}{b} = \text{corrected plot yield.}$$

B = average yield of a block in the series

p = actual yield of an included plot

b = yield of a given block.

This method was altered somewhat for the 1927 crop. Instead of fixed blocks of five plots each, a running average of ten plots was used as indicated in the following formula:

$$x = A \left(\frac{p + A - a}{100} \right) = \text{corrected plot yield in per cent of the series mean.}$$

- A = average plot yield for the series.
- a = average of 10 contiguous plots.
- p = actual yield of plot to be corrected, a central plot in each group of ten.

According to this method the average of a group of ten contiguous plots is found and subtracted from the mean of the series. The differences than added algebraically to both plot number 5 and number 6 in that particular contiguous group. Next the group is made to move across the field by subtracting two old plots and adding two new ones. The formula is then applied again, and the two central plots corrected as before. This process is repeated across the field. At the ends, obviously, it is necessary to use a stationary group. By calculating the yields of all plots in per cent of their respective series means it is possible to average the yields of all replications, even though these plots may be of slightly different sizes and located on fields unlike in fertility. It is admitted that either of the above methods can only be applied when plots are small so as to permit the formation of a group

of sufficient size to minimize the effect of any included plot upon the group mean.

Ear Measurements:- Length of ear, average weight of kernel, average thickness of kernel, and number of kernel rows were recorded for all seed ears. No individual measurements were made for progeny ears in 1926, but in 1927 length of ear, average thickness of kernel, and number of kernel rows were measured for each individual in a random sample of 10 ears taken from Series II. In all cases measurements were made on air-dry ears that had been stored in the seed barn for several months. Length of ear was measured to the nearest tenth of an inch. Ten kernels picked systematically from the central zone of the ear were weighed in grams and their total weight divided by 10 to obtain the average kernel weight for the ear. The mean kernel thickness was calculated from the total thickness of 20 contiguous kernels in place near the middle of the cob, all measurements being made to the nearest twentieth-inch.

Tassel Measurements:- In 1926 eight progeny plants from the same seed ear were scored for tassel characters. Scoring was done by one observer while the plants stood in the field. The degree of expression of the characters, number of tassel branches, length of spiklet, number of spikelets per unit of lateral length, and length of tassel from base

to tip was used to separate the plants into five classes. In each case class I represents the lowest degree of expression, and class 5 the highest degree of expression. Average grades for the eight progeny plants were used in the correlations.

In 1927 a more exact method was utilized. Ten tassels from each plot in Series II corresponding to progeny ears reserved for measurement, were removed from the plants standing in the field. The partially dry tassels were each placed in a ten-pound paper bag from which the bottom had been removed. The bags containing the tassels, 2000 in all, were then stored in the seed barn. Later the measurements were made in the laboratory. Number of tassel branches was obtained by actual count. The total length of the lateral branches was determined by removing all branches from the main stem, placing them in length classes of one inch interval multiplying each class value by its frequency, and adding the products. Length and density of spikelets were determined on an average branch from the modal class for length. Actual measurements of several spikelets to the nearest fiftieth of an inch permitted the calculation of an average value for the tassel. Density of spikelets was determined by counting the number of spikelets in the first two inches of lateral length. Except in progeny ear-tassel correlations, averages within a progeny group of ten plants were used for all tassel characters.

Formulas:- Except where otherwise stated, the usual formulas for statistical constants have been employed. It has been assumed that the character associations studied have a linear relation. If it be otherwise, linear correlation will only serve to give results too conservative. The product-moment equation for simple correlation (r) as modified by Wallace and Snedecor (39) for machine use has been used throughout. Pearson's Tables for Statisticians and Biometricians have been helpful. General equations are listed below.

A, B and X are separate variables

Σ = summation symbol

M = mean

σ = standard deviation

E = probable error

C = coefficient of variation.

$$\sigma = \sqrt{\frac{\Sigma X^2 - \Sigma X(M_X)}{N}}$$

$$\sigma_M = \sigma / \sqrt{N}$$

$$C = \sigma / M \times 100$$

$$E_C = .6745 \times \left[1 + 2 \left(\frac{\sigma}{100} \right)^2 \right]^{\frac{1}{2}} / \sqrt{2N}$$

(Factors for this equation are given in Pearson's Table)

$$r_{AX} = \frac{\sum AX - \sum A(M_X)}{\sqrt{\sum A^2 - 2 \sum A(M_A) \times \sum X(M_X)}} \times \sqrt{\sum X^2 - \sum X(M_X)}$$

$$r_{AB.X} = \frac{r_{AB} - r_{AX} \times r_{BX}}{\sqrt{1 - r_{AX}^2} \times \sqrt{1 - r_{BX}^2}} = \text{partial correlation between A and B when X is held constant.}$$

$$E_T = .6745 \frac{1 - r^2}{N}$$

EXPERIMENTAL RESULTS

PART I. Relation of Tassel and Ear Characters

Tassel Characters and Pollen Production:- For the problem at hand it would be ideal to know the actual number of pollen grains produced by every experimental plant. This number could then be compared directly with the values for kernel number and yield. Unfortunately total pollen counts are extremely difficult to obtain for plants growing outdoors in a humid climate. A corn plant continues to shed pollen over a period of eight to sixteen days. During this time there will be, in all probability, enough damp weather to cause moulding or caking of at least a part of the pollen even though it is being collected in water-proof tassel bags. Furthermore the number of plants required in this work is so large that counting the pollen grains would be too tedious even if the pollen could be easily collected in a sound condition. Therefore, an attempt was made to determine which measurable tassel characters are closely associated with pollen production, so that measurements of these characters could be included in the field work.

One hundred plants of Reid's Yellow Dent were grown in the greenhouse in the autumn of 1927 from a composite sample of seed. As soon as the plants began to blossom, ten-pound kraft paper bags were placed over the tassels and tied in

position. After all pollen had been shed, each tassel with its bag was cut from the plant. The pollen was then carefully dusted from the bag and passed through a 100-mesh sieve in order to remove pieces of glumes and other debris. The cleaned product from each plant was placed in an uncovered Petri dish which was immediately placed in a desiccator containing concentrated sulphuric acid. The pollen was dried over the acid for 48 hours at room temperature, and under a pressure of approximately 0.5 atmosphere. It was found that after this length of treatment the weight remained about constant.

TABLE I. - Per cent moisture lost by corn pollen dried over concentrated sulphuric acid at room temperature and 0.5 atmosphere pressure.

Plant No.	Weight in Grams.				Per cent Moisture
	Green	After 24 hrs.	After 48 hrs.	After 72 hrs.	
1	2.345	2.185	2.170	2.170	7.46
2	2.610	2.420	2.420	2.375	9.00
3	2.235	2.135	2.120	2.120	4.70
4	1.150	1.120	1.110	1.095	4.78
5	1.420	1.365	1.370	1.330	6.34
6	2.520	2.330	2.330	2.325	7.74
7	1.905	1.890	1.875	1.865	2.10
8	2.635	2.485	2.480	2.460	6.64
9	2.820	2.675	2.670	2.640	6.38
10	4.160	3.915	3.915	3.980	4.33
11	2.810	2.630	2.640	2.650	5.69
12	1.965	1.885	1.880	1.910	2.80
13	3.470	3.230	3.210	3.280	5.48
14	1.825	1.630	1.650	1.635	10.41
15	3.505	3.370	3.375	3.330	5.00
16	5.505	5.145	5.165	5.095	7.45
17	- -	2.325	2.320	2.305	- -
18	1.450	1.330	1.305	1.305	10.00
19	1.450	1.280	1.255	1.270	12.40
20	2.880	2.550	2.525	2.535	12.00
21	1.490	1.335	1.330	1.330	10.74
22	1.020	0.945	0.930	0.945	7.35
23	3.000	2.670	2.680	2.665	11.17
24	2.530	- -	2.390	2.415	4.55
25	4.085	- -	3.805	3.840	6.00
26	4.305	- -	3.965	3.945	8.36
27	3.295	- -	3.085	3.080	6.53
28	3.960	- -	- -	3.575	9.72
29	3.655	- -	- -	3.295	9.85
30	2.995	- -	- -	2.790	6.85
31	5.690	- -	- -	5.140	9.67
32	3.265	- -	- -	3.090	5.36
33	2.385	- -	- -	2.210	7.34
34	2.400	- -	- -	2.215	7.71
35	4.385	- -	- -	3.955	9.81
Average				2.633	7.40

In Table I are shown the data relating to the drying of the pollen. Due to loss or spoilage only thirty-five samples of pollen could be used. Green weights and weights made after different periods of drying are shown for the different samples. It will be noted that there is very little change in weight after 48 hours of drying. In a few cases the weight increases slightly, but this may be due to an increase in pressure or a change in temperature, since these factors were not controlled accurately. The per cent of water lost varies from 2.10 to 12.40 with an average of 7.40. The range seems rather wide but this doubtless is due to the effects on the pollen caused by changes in humidity in the greenhouse and variations in exposure of the different plants. All plants did not shed pollen during the same period of time and hence all lots of pollen were not exposed to the same atmospheric conditions. The average moisture loss is somewhat higher than that reported by Vinson (37) and Anderson and Kulp (1). The former obtained a value of 3.97 per cent and the latter 4.68 per cent. Both dried the pollen at room temperature over sulphuric acid in partial vacuum.

TABLE 2. - Means and measures of distribution for tassel characters of 35 plants grown in the greenhouse.

Symbol	Character	Mean	Extremes	Coefficient of Variability
A	No. of lateral branches	20.8	12-31	24.4±2.04
B	Total length of laterals (inches)	143.8	79-207	21.9±1.86
C	Length of tassel "	16.2	12.8-18.8	8.9±0.73
D	Density of laterals, (No. per inch)	3.57	2.88-4.40	9.5±0.81
E	Size of lat. spikelets (inches)	0.39	0.328-0.443	5.9±0.49
F	Length of central spike (inches)	1.08	6.0-14.3	16.7±1.41
G	No. prs. lat. spikelets	583	224-960	31.0±2.73
H	" " central "	132	76-181	22.4±1.86
I	Total No. prs. "	716	404-1084	25.5±2.23
J	Density of central spike	11.6	7.0-19.5	22.1±1.86
K	Size of central spikelets	0.43	.37-.50	6.2 0.49
W	Dry wt. of pollen (gms)	2.633	0.945-5.095	39.0 3.59

TABLE 3. - Simple correlation coefficients between tassel characters of corn grown in the greenhouse. Number of varieties equals 35.

	B	C	D	E	F	G	W
A	+.5320*	-.2514	+.1660	+.1248	-.6422	+.2652	+.0266
B		+.2323	-.2573	-.0862	-.1980	+.7843	+.2994
C			-.2420	-.0054			+.9044
D				-.0255		-.0392	+.0667
E						-.0967	+.0716
F							-.0514
G							+.4589
H							-.0034
I							+.4562
J							-.0308
K							-.0620
W							+.3386

* Any coefficient above 0.3093 is three times its probable error.

In addition to the determination of the dry weight of pollen a number of character measurements were made on the tassels from which the pollen was shed. The measurements were made as previously described except that the values for density and size of spikelet were obtained for every branch as well as the central stem. Actual counts of number of spikelet pairs were made for all thirty-five tassels. Table 2 gives the means and the coefficients of variability for the several characters. It will be seen that length of tassel (distance from lowest branch to the tip), size of spikelet, and density of lateral spikelets have the lowest coefficients of variability of all characters measured. Doubtless these characters are least affected by environment. The total numbers of spikelet pairs range from 404 to 1084 with a mean of 716. These values roughly approximate the number of kernels for this variety under normal field conditions. Since these figures must be multiplied by 2 in order to get the total number of single tassel spikelets it is evident that the tassel spikelets outnumber the female spikelets at least two to one. Under normal growth conditions in the field this ratio is wider. In the greenhouse, the male inflorescence showed incomplete development, in that the tips of practically all the branches contained a number of sterile flowers. According to Weatherwax (40) every male and female spikelet contains initially two flowers. Both of these develop

in the male inflorescence but only one in the female inflorescence. Thus each kernel represents one spikelet. Therefore the tassel counts made on corn plants grown in the greenhouse show that with the variety Reid's Yellow Dent there are at least four times as many staminate as pistillate flowers.

Pollen weight shows unusually high variation. Unfortunately this experiment does not indicate what proportion of this variability is heritable. It is quite likely that under field conditions the variability would not have been as great.

In Table 3 a number of simple correlation coefficients between the various tassel characters are shown. The symbols are the same as those used in Table 2. Due to the small number of items most of these correlations are not statistically significant, however there are several coefficients that are significant and are of especial importance. Only those above 0.30 need be given serious consideration. The characters giving any considerable correlation with pollen weight are total lengths of laterals (+.289), number of lateral spikelets (+.459), total number of spikelets, (+.456) and the product of length of laterals times the density of lateral spikelets (+.339). Number of lateral spikelets gave the highest value with pollen weight. The inclusion of the spikelets on the central stem lowered the

correlation slightly. According to Table 2 the central spikelets make up only about a fifth of the total number of spikelets and their number is much more variable than that of the lateral spikelets. This fact probably accounts for their negligible association with pollen weight.

Aside from actual spikelet counts, the product of total lateral length and density of spikelets gives the best correlation with pollen weight. In this connection it will be noted that total lateral length is itself the product of number of laterals times average lateral length, and that this product gives a correlation of $+0.784$ with number of lateral spikelets. From these considerations it would seem that the measures of density and lateral length should give the best available criterion of pollen production. For this reason these items have been given the most weight in the field measurements to be taken up later.

Number of Kernels:- The number of kernels present on the ear represents the contribution of the female inflorescence toward the total number of zygotes with which the particular plant is concerned. Since maize is largely cross-fertilized, the pollen makes its contribution through zygotes borne on other plants. The number of kernels then may be taken as the number of maternal zygotes produced by a given

plant, but it does not indicate the maximum number possible. It merely shows the number of ovules that have been fertilized and nourished to maturity. It would seem then that kernel number per plant should vary with the season and the soil. Under favorable conditions more of the ova present could be nourished. The presence of nubbins and ears with many rows dropped before reaching the tip, probably, illustrates the plant's attempt to reduce its food requirement.

Kernel number is obviously the product of number of rows times the number of kernels per row. The latter factor is plainly dependent upon the length of the ear and the thickness of the kernel. In order to measure the extent of variability in these characters, the means and standard deviations are given for the seed ears used in 1926 and 1927, and also for the progeny of 1927.

TABLE 4. - Means and variability constants for ear characters associated with kernel number

Character	No. Items	Mean	Coefficient Variability
Length of ear (A) - inches			
Parent 1926	86	9.30 ± .062	9.2 ± 0.47
Parent 1927	153	8.51 ± .038	8.2 ± 0.31
Progeny 1927	1148	8.86 ± .030	11.7 ± 0.17
Kernel Thickness (B) -- inches			
Parent 1926	86	0.156 ± .001	8.4 ± 0.42
Parent 1927	153	0.152 ± .001	6.6 ± 0.27
Progeny 1927	1148	0.158 ± .001	9.0 ± 0.13
No. of kernel rows (C)			
Parent 1926	86	19.14 ± .19	13.4 ± 0.68
Parent 1927	153	16.94 ± .12	11.6 ± 0.47
Progeny 1927	196	19.20 ± .13	13.6 ± 0.20
No. of Kernels (X) *			
Parent 1926	86	934 ± 11.0	16.2 ± 0.85
Parent 1927	153	945 ± 7.6	14.5 ± 0.59

* Quotient of total kernel weight divided by average kernel weight of a sample.

With the exception of ear length, the means for the different ear groups are quite uniform for the respective characters. The high value for length of ear in the 1926 seed stock may be due to a more careful sorting at harvest time, resulting in an exclusion of shorter ears. The higher coefficients of variability for progeny measurements can be explained upon a similar basis. These measurements include the "field run" of ears. Hence the variability is somewhat greater than in the seed stocks where nubbins had been discarded. An inspection of the coefficients of variability shows that number of kernels is the most variable character. This is to be expected since it is the product of other characters and hence includes their errors whether heritable or temporary. For instance, discontinuation of rows through inadequate food supply or bare tips due to incomplete fertilization might be named as temporary effects upon the fluctuation of kernel number. Of the three remaining characters studied, number of rows has the largest variability, which, as will be seen later, is largely hereditary. Ear length and kernel thickness show relatively little variation. Table 5 further brings out the inter-relations of ear characters.

By studying the simple correlation coefficients in Table 5, it will be seen that the relation between the number of kernel rows and number of kernels gives the highest value, (+.72).

TABLE 5. Simple and first order partial correlation coefficients for each character associated with number of kernels

Simple Correlation		Partial Correlation	
Designation	Coefficient	Designation	Coefficient
Kernel no. X length of ear	+0.2400 ± .0411*	$r_{XA \cdot B}$	+0.4903 ± .0331
Kernel no. X kernel thickness	-.3160 ± .0393	$r_{XA \cdot C}$	+0.4943 ± .0330
Kernel no. X no. of rows	+0.7210 ± .0209	$r_{XB \cdot A}$	-.5238 ± .0317
Length of ear X kernel thickness	+0.5083 ± .0324	$r_{XB \cdot C}$	-.3674 ± .0377
Length of ear X row no.	-.1377 ± .0428	$r_{XC \cdot A}$	+0.7841 ± .0168
Kernel thickness X row no.	-.0965 ± .0433	$r_{XC \cdot B}$	+0.7338 ± .0201

*All constants are based on 239 items resulting from the combination of 86 ears for 1926 and 153 ears for 1927.

Furthermore, this relation appears to be largely independent of either length of ear or thickness of kernel, because when the latter character is held constant, relatively little change in the coefficient results. Thickness of kernel evidently has more influence upon number of kernels per row than does length of ear. Obviously, the two relations would be expected to have opposite signs. Long ears tend to have thick kernels and few rows. A comparison of the simple with the partial correlation coefficients shows that the relation between ear length and kernel number and between kernel thickness and kernel number is accentuated by holding either of the other characters constant. This fact simply emphasizes the inter-relation of the characters in question with respect to their effect upon kernel number.

Briefly, then, it may be said that the longer the ear the fewer the rows and the thicker the kernels.

Inter-Progeny Correlations:- The foregoing results have indicated that certain measureable tassel and ear characters are intimately associated respectively with male and female genetic production. The questions now arise as to whether the male and female inflorescences present a parallelism in the size of their parts, and if so, whether such a parallelism comes about through heredity or merely through temporary response to environment. In an attempt to answer these questions, correlations involving both tassel and ear characters on the same plant

plants of the same progeny (half-siblings), and on adjacent plants of different progenies have been calculated. Since no measurements for tassels on parent plants were available, it was necessary to depend upon fraternal correlations among the 1927 progenies for testing out heredity relationships. Each progeny group was separated into pairs of plants between which simple correlation coefficients were obtained for the characters in question. Table 6 gives the means and distribution constants for the measurements concerned, and Table 7 gives the coefficients of correlation.

By comparing the means for length of laterals and number of laterals recorded in Table 6 to the means for the same two characters recorded in Table 2, it is evident that the field grown plants exhibited these characters to a far greater degree than did plants from similar seed planted in the greenhouse. The former averaged 248 inches for total lateral length and 32 for number of lateral branches, whereas the latter averaged respectively 144 inches and 21 branches. Obviously environment has affected the expression of these characters markedly. Further examination of Table 6 shows that the tassel characters studied are far more variable than corresponding ear characters. This fact might suggest either that these tassel and ear characters are not analogous or that environment affects the tassel much more than it does the ear. It may be that total length of tassel branches is a product of more variables than is

length of ear. The former, of course, is the product of the number and average length of branches, each of which has an error of its own. Accordingly, the multiplication of these variables will increase the error of their product relative to either of them. On the other hand, length of ear is not made up of separate lengths of a number of branches, but more nearly represents the length of a single branch or central stem. If the ear is to be regarded as a fusion of branches of a pistillate inflorescence originally similar to the present branched condition of the tassel as suggested by Collins (3), the length of the ear should be more comparable to the length of the central staminate spike than to the sum of lateral lengths. The coefficient of variability listed in Table 2 for the length of the tassel spike is 17 as against 22 for total lateral length. The former, therefore, more nearly stimulates the error of ear length than does the latter.

In this connection attention should be drawn to the fact that the length of but one ear per plant has been measured. Some plants bore two ears, the second being little more than a nubbin. Had both ears been measured for length and the resulting values added to obtain total ear length per plant, the variability of the population for this character would have been increased. It is doubtful, however, whether variability of ear length would even then have been as great as that for total lateral length.

TABLE 6. - Means and distribution constants for ear and tassel characters on progeny plants in 1927.

Character	No. Item	Mean	Coefficient of Variability
<u>Tassel</u>			
Length of laterals(inches)	1148	248.0±1.3	26.2±0.39
No. of laterals	196	51.16±.43	27.7±1.03
Spikelet pairs per inch	1148	3.50±.03	15.6±0.23
<u>Ear</u>			
Length (inches)	1148	8.86±.02	11.7±0.17
Kernel thickness	1148	0.158±.0002	9.0±0.13
No. of rows	196	19.17±.13	13.6±0.49

Artificial selection has been concerned with uniformity of ear, but has not been concerned at all with tassel type. For this reason alone one would anticipate a more heterogenous inheritance for the latter and hence greater variability.

Much of the foregoing discussion applies alike to length and number of branches or rows respectively in the male and female inflorescences. Number of tassel branches is not strictly analagous to number of kernel rows, - probably for reasons already given. Of the characters studied density of spikelets presents the greater similarity.

A cursory examination of Table 7 shows that, with one exception, all intra-progeny correlations are small but statistically significant. The highest coefficient (+.225) is that obtained when half-siblings are correlated for density of female spikelets. According to common usage the square of a correlation coefficient can be interpreted as per cent of total variability showing concomitant fluctuation. Thus by squaring 0.225 the value of 0.0506, or 5.06 per cent is obtained. It is then permissible to say that 5.06 per cent of the variability of spikelet density is correlated with respect to plants of a common maternal inheritance. The remaining variability, 100.00 - 5.06 per cent, is due to paternal heredity and to the effect of non-heritable factors. According to Wright, (43) the maximum theoretical correlations between parent and offspring is +0.5 and between half-siblings it is +0.25 under

random fertilization in the absence of inbreeding. The extent to which actual fraternal correlations fall short of this theoretical maximum may be used as a measure of the degree of heredity for the character in question.

The intra-progeny correlations for density are all higher than those for length. Tassel-ear correlations on the same plant are respectively +0.12 for length and +0.16 for density. As they stand, these figures do not necessarily prove that these characters tend to be inherited together. Parallel development possibly could be a result of the common effect of external conditions. However, the fact that fraternal correlations show small constants of similar sign, significant in the case of density, indicates that the tassel-ear associations are hereditary though very small.

Fraternal correlations for the tassel measurements are quite significant, the coefficients being over seven times their probable errors. Ears on half-siblings, likewise, give significant coefficients, although the one for length is very much lower than those for tassels or for ear density. Since all correlations between half-siblings are based on the measurements of plants grown side by side in the same plot, it may be thought that place effect in the field has increased the size of coefficients. In order to test out this idea correlations were calculated for adjacent plants in neighboring plots. The small size of the resulting constants seem to prove that there was little effect arising from soil variability or field exposure.

TABLE 7. - Inter-progeny correlations involving length of tassel branches, length of ear, and density or number per inch of staminate or pistillate spikelets.

Combination	Coefficients for	
	Length	Density
Tassel X ear on same plant	$+.1241 \pm .0196$ *	$+.1609 \pm .0194$ *
Tassel X ear on half-sibs	$+.0282 \pm .0199$	$+.0918 \pm .0197$ *
Tassel X tassel " "	$+.1590 \pm .0194$ *	$+.1739 \pm .0193$ *
Ear X ear on half-sibs.	$+.0787 \pm .0198$ *	$+.2349 \pm .0189$ *
Tassel X tassel on adjacent plants	$-.0394 \pm .0313$	$+.0158 \pm .0314$
Ear X ear on adjacent plants	$+.0420 \pm .0313$	$+.0673 \pm .0312$

* Significant by at least odds of 45 to 1.

Parent-Progeny Correlations:- The preceding section has dealt with relationships between half-siblings or corn plants having the female parent in common. The male parent was not known because of random fertilization in the field. In the present section the relative extent of associations between the maternal ears and the corresponding progeny plants are studied. The progenies have not been treated as individuals, but, since the number of seed ears is not large enough to make small correlations significant, the values for members of a progeny group have been averaged, and the resulting mean paired with the value for the proper seed ear. This procedure gives higher correlation coefficients than does the simple pairing of each parent with one of its offspring. The increase in the size of the coefficients is due to the canceling out of much random variability when individuals are averaged. In other words the group means for the total progeny population have a smaller error than the individuals of that same population. For the above reason the coefficients of Table 8 can only be compared among themselves; they cannot be compared directly with the half-sibling correlations of Table 7.

By means of his method of path coefficients, Wright (43) has determined the maximum theoretical correlation between parent and offspring. The r value found is $+0.50$, which, when

squared, gives 0.25. It will be seen that the coefficient of correlation between parent and progeny for number of kernels per inch is given as +0.56 in Table 8. Thus the latter constant is higher than the theoretical value; possibly because of the use of averages as just explained, or probably also because of chance fluctuation. The probable error is quite large due to the relatively small number of individuals concerned, namely 153. The difference between the theoretical value and the actual value is not three times the error of the difference. It is, therefore, not possible to regard the coefficient of +0.56 as a fixed value. It must be considered as a variable fluctuating within rather wide limits. If a similar population were used in another calculation a much lower, or a much higher coefficient might be obtained as the result of chance alone. The foregoing observation, of course, applies to all 5 values listed in Table 8. It is necessary to be conservative in comparing them with a theoretical value.

The fraternal correlations given in Table 7 are based on a relatively large number, 1148, and therefore have smaller errors than the coefficients given in Table 8. Thus it is safer to use the former in measuring the degree of heredity for the characters in question.

TABLE 8. - Correlations between parent ear and progeny. Progeny measurements used represent group averages.

Character Combination	1926	1927
Parent ear X progeny tassel Kernel wt. x length of spikelet	+ .0874 ± .0722	+ .0962 ± .0540
No. of kernels per inch X spikelet per inch	+ .2709 ± .0674	+ .1219 ± .0537
No. of kernels X no. of spikelets	- -	+ .0380 ± .0545
Ear length X total lateral length		- .0016 ± .0545
Parent ear X progeny ear Kernels per inch	- -	+ .5626 ± .0373
No. kernel rows	- -	+ .4528 ± .0434
Length of ear	- -	+ .3087 ± .0493

For instance, the actual coefficient of correlation for number of kernels per inch between half-siblings is +0.22 as against +0.25 for complete hereditary determination. The squares of the above two figures are respectively 0.0484 and 0.0625. Then $\frac{.0484}{.0625} \times 100 = 77$ or the per cent of the theoretical maximum that is actually inherited. The foregoing equation can be used to calculate the coefficient that should be obtained for the same character, that is number of kernel per inch, between parent and progeny. As has been said the maximum theoretical hereditary determination for the latter combination is $(0.50)^2$ or 25 per cent of the total progeny variability. Therefore $\frac{r_{PO}^2}{0.25} = 0.77$ or $r_{PO} = 0.77 \times 0.25 = 0.44$

It seems safe to conclude that the correct correlation value for kernels per inch between maternal ears and progeny ears is of the order $+0.44 \pm .016$. This value most certainly is sufficiently large to be of importance. A similar observation holds for number of kernel rows and length of ear. These three characters are distinctly heritable and they are influenced relatively little by growth conditions. Of the three characters length of ear is limited to the greatest degree by factors external to the germplasm. This statement seems to be borne out by field observations in that ears produced on infertile soil are short but tend to have the characteristic number of rows and thickness of kernel. In other words,

the greatest reduction in weight of grain under sub-optimum growth conditions is brought about more through reduction of ear length than through either a reduction in row number or a change in kernel thickness.

The correlations between parent ears and progeny tassels are so small in proportion to their probable errors that it is not safe to draw definite conclusions from them. The most that can be said of the latter relations is that they support the fraternal correlations in indicating a small hereditary relationship between tassel and ear with regard to the expression of characters markedly concerned with gametic numbers.

Summary of Part I. - By weighing pollen collected in the greenhouse from individual corn plants and subsequently measuring the corresponding tassels it has been possible to show that total length of lateral branches and number of spikelets per inch have an important positive relation with pollen production. Also the more or less obvious relations between total number of kernels per ear and number of kernel rows on the ear, the thickness of kernels or the number of kernels per inch, and the length of ear have been pointed out. Of the three ear characters row number has the highest correlation with total kernel number. Number of kernels per inch ranks second and length of ear comes last. In general,

it may be said that the longer the ear the fewer the number of rows and the thicker the kernels.

It has been shown by fraternal and parent-progeny correlations that there is a slight tendency for tassel and ear characters to be expressed to the same extent upon the same plant; that the characters are heritable to an appreciable extent; and that total length of tassel branches and length of ear are affected more by factors external to the germplasm than the other characters studied.

PART II. Reproduction and Yield

A Method for Reducing the Variability of Yield

Data:- In order to secure statistical significance experimental work involving small differences in crop yield is always handicapped by the necessity for a large number of comparisons. Yield of plant parts is a growth effect and like growth it is easily influenced by any one of a number of those conditions external to the plant, which, when taken collectively are called environment. Field comparisons of crop plants come under that category of experimentation in which the effect of one contributing factor is studied while other contributing factors are left to vary at will. Among other variables, soil, temperature and light cannot be completely controlled over relatively large experimental areas. The best the investigator can hope to do is to sample growth conditions equally with every member of his comparison. In the present work the unit of comparison is a progeny group of corn plants. In order to facilitate the sampling of field conditions, largely a question of soil variation, each plot has been replicated twice and the replicates systematically distributed over the experimental area. As is always the case with a large number of plots much soil variability was encountered. Consequently plots planted with seed from the same

ear have not produced equal amounts of grain.. It is true that all plants from the same seed ear did not have the same genetic constitution with regard to yield. However it would appear that genetic differences among the plants of any given plot would average out, for plot yield is simply the average yield per plant times the number of plants present. If the latter assumption be granted then differences between plots for a given progeny must be due to factors other than heredity.

It would be very helpful if the effect of heredity upon yield could be separated from that due to other causes. Such an accomplishment would reduce the number of trials necessary for making significant the small relations that may exist between various characters and yield. From the standpoint of quoting per cent effect, it would be much better to be able to state that a certain parent character such as kernel row number is associated with a certain per cent of the yield variability induced by everything. If the environment were constant for all experiments this benefit would be negligible, but unfortunately this is not the case. Sometimes it represents a large part of the total yield fluctuation while at other times it is much smaller. Thus the greater part environment plays in the size of the yield standard deviation the less will be the per cent effect of heritable characters. But were the per cent effect (obtained by squaring r or R) calculated on

genetic variability alone it would not only be larger, but more nearly constant for different trials, and, in fact, possibly could be used in calculating the degree of homozygosis in a corn population.

If all plot yields in the experiment regardless of the origin of their seed are considered as units in a total population of plot yields, the standard deviation of yield for an individual plot measures in one value the variability due to (1) unlike field conditions among the population of plots, (2) environmental effects upon the somatoplasm of the seed such as chance disease infections, immaturity or cold injury, and (3) heritable differences. The effect of (2) can be almost eliminated by rigid germination tests, but (1) offers more difficulty. The first step in the control of field variation is replication of plots. Where there are as many as three plots of a kind and a sufficient total number of plots, say not less than 50, the method used in this work seems helpful.

The method rests upon the assumption that the variability due to growth conditions can be separated from heritable variability through statistical manipulation of the standard deviation. According to Yule (44) p. 211 the square of the error inherent in the variable in question plus the square of the error of observation is equal to the square

of the error measured for the variable. Thus:

$$\sigma_{x_1}^2 = \sigma_x^2 + \sigma_o^2 \quad \text{or} \quad \sigma_x^2 = \sigma_{x_1}^2 - \sigma_o^2$$

where x_1 is the observed deviation from the mean of a variable X; x , the true deviation and o the error of observation. Hence, if any two of the errors are known, the other can easily be determined. The only condition is that the position of the mean of X be not affected by the error of observation. The present method for correcting yield variability assumes that the above formula is applicable, environmental deviation being considered analogous to error of observation. In future notation σ_H will be referred to as the standard deviation of yield due to heredity. σ_E will refer to all other variability, and σ_R will denote total variability. Thus the basic equation is:

$$\sigma_H^2 = \sigma_R^2 - \sigma_E^2.$$

Obviously since σ_R can be found from the total population of plot yields, the next step is to obtain a value for σ_E . This can be done by calculating the error for each replication group, taking the average of this value, correcting it for small numbers, and treating the result obtained as a measure for environmental variability. As previously explained this operation merely assumes that differences between the yields of plots planted from the same seed ear must be due to unlike

growth conditions. On the other hand since c_R is calculated from the mingled yields of all plots regardless of replication group, it includes not only c_W , but also c_R or the differences between replication groups.

The correction for small samples in obtaining c_W is very essential. The work of Student (36) and Fisher (9) has shown that on the average the standard deviation of an individual item as calculated from a small sample, say less than 30 items, is smaller than the standard deviation calculated for population from which the sample was drawn. The smaller the sample the greater is the sample standard deviation in error with regard to the true standard deviation of the population as a whole. This effect of small samples is entirely due to chance, and due to the formula for a standard deviation. By definition (Yule (44) p. 135), the standard deviation is the least possible root-mean-square deviation. In effect this definition says that the average of the squares of deviations from a mean is less than the average of the squares of deviations from any other position in a frequency distribution. Therefore, if the group or sample mean is not the same as the population mean, the latter represents an origin different from that of the group mean. Hence the group items will deviate less from their group mean than from the population mean. However, this does not mean that the error of a sample is always less than the error of the whole population. If the group items

TABLE 9. - Means and standard deviations for number of heads calculated from small groups of coin tosses. Each toss includes ten coins and each of the fifty groups consists of four consecutive tosses.

Group No.	Mean (M _g)	$\Sigma H^2 - \Sigma H(M_H)$	σ_g	Group No.	M _g	$\Sigma H^2 - \Sigma H(M_H)$	σ_g
1	5.00	6.00	1.2248	26	4.50	15.00	1.8028
2	4.00	14.00	1.8708	27	4.00	6.00	1.2248
3	5.75	8.75	1.4790	28	6.00	14.00	1.8708
4	4.75	0.75	0.4330	29	5.00	4.00	1.0000
5	5.75	6.75	1.2990	30	6.50	11.00	1.6583
6	5.75	2.75	0.8290	31	5.25	12.75	1.7854
7	4.50	5.00	1.1180	32	5.75	4.75	1.0897
8	4.50	25.00	2.5000	33	4.25	2.75	0.8292
9	5.75	20.75	2.2776	34	5.25	2.75	0.8292
10	4.50	9.00	1.5000	35	4.50	11.00	1.6583
11	6.00	2.00	0.7071	36	3.75	4.75	1.0897
12	4.75	0.75	0.4330	37	4.00	6.00	1.2248
13	6.00	10.00	1.5812	38	6.25	2.75	0.8292
14	4.25	4.75	1.0897	39	3.50	5.00	1.1180
15	4.00	6.00	1.2248	40	5.25	0.75	0.4330
16	5.00	6.00	1.2248	41	5.25	12.75	1.7854
17	3.50	11.00	1.6583	42	5.75	2.75	0.8292
18	5.75	14.75	1.9203	43	4.75	8.75	1.4790
19	4.25	6.75	1.2990	44	5.00	6.00	1.2248
20	4.75	2.75	0.8292	45	4.50	13.00	1.8028
21	4.00	4.00	1.0000	46	5.50	5.00	1.1180
22	5.25	2.75	0.8292	47	5.50	5.00	1.1180
23	5.75	8.75	1.4790	48	5.00	2.00	0.7071
24	4.25	4.75	1.0897	49	4.50	5.00	1.1180
25	4.00	8.00	1.4142	50	5.00	2.00	0.7071

Ave. (N=25) .. 4.87 7.670 1.2924 5.100 6.540 1.2133
 Ave. (N=50) 4.985 7.105 1.2529±0.0845
 Theoretical values 5.000 1.5811
 By use of Fisher's correction 1.5702
 By use of Kemp's correction 1.5390

are close together and mainly to one side of the population mean their error will be relatively low. Such a grouping is more likely the smaller the number (n) of items per sample.

Table 9, based on data obtained from coin tosses, has been prepared to illustrate the effect of calculating standard deviations from small samples. For this table 10 coins were tossed simultaneously 200 times. The number of coins with heads up was recorded for each toss. Later the tosses were grouped consecutively into samples of four tosses each. Then the mean and standard deviation for number of heads were calculated for each group and entered in Table 9. The average mean and average standard deviation were finally compared to the theoretical mean and the theoretical standard deviation respectively. Since the probability of a head falling upward is $\frac{1}{2}$, the mean for 10 coins must be $10 \times \frac{1}{2}$ or 5, and $\sigma^2 = npq = 10 \times \frac{1}{2} \times \frac{1}{2} = 2.5$ or $\sigma = 1.5811$. By inspection of Table 9 it will be seen that the average number of heads for 50 groups is 4.985, only 0.015 less than the theoretical value of 5.0. On the other hand the average standard deviation (1.3539) is significantly lower (odds about 99 to 1 that the difference is not due to chance alone) than the theoretical value. By correction through the use of factors derived by entirely different methods the average value is made to approximate the correct value.

Fisher (9) has published tables giving factors for correcting the standard deviation obtained from groups when n equals 4 to 100. The factor is divided into the observed value thus giving the correct value in the quotient. Kemp of the University of Maryland in unpublished work has suggested another method of correction, which for the problem at hand, involves less work and apparently gives results approximating those of Fisher. See Table 9. Fisher's tables have the advantage in that correction can be made either on a single group standard deviation or on the mean of such standard deviations. Kemp's factor must be applied to the square root of the average squares of a number of group standard deviations. It cannot be applied to a single group. On the other hand, since the average value itself must be used in the corn work, the latter method saves the labor of taking the final root for the individual group standard deviations. The factor used for correction is obtained in the following way. First the assumption is made that the standard deviation of a single item in the mingled population is expressed by the formula,

$$c_T^2 = c_M^2 + c_g^2 + c_{cg}^2 \quad \text{where } M \text{ represents the}$$

group means and g , a group item. But since groups are to be averaged the last term will be included in the average of the squares of the group standard deviation and hence drops out of

the equation. Then:

$$\sigma_T^2 = \sigma_M^2 + \frac{\sum \sigma_g^2}{N}$$

Or
$$\frac{\sum \sigma_g^2}{N} = \sigma_t^2 - \sigma_M^2$$

But
$$\sigma_M = \frac{\sigma_T}{\sqrt{n}} \text{ or } \sigma_M^2 = \frac{\sigma_T^2}{n}$$

Then
$$\frac{\sum \sigma_g^2}{N} = \sigma_T^2 - \frac{\sigma_T^2}{n}$$

By arbitrarily assigning σ_T^2 the value of unity the relative value of the average group standard deviation can be obtained.

$$\sqrt{\frac{\sum \sigma_g^2}{N}} = \sqrt{1 - \frac{1}{n}} = \sqrt{1 - \frac{1}{3}} = 0.8165 = \text{the correction factor}$$

to be used as a divisor for the observed square root of the mean of the squares of the group standard deviation.

The entire method for eliminating environmental variability (σ_E) from plot yields in the present corn experiment is outlined below.

1. Find the actual standard deviation for the means of all replication groups or plots planted to the same seed ear. Let \bar{R} represent the group means; N , the number of groups; M , a mean; and Σ , summation.

$$\sigma_R^2 = \frac{\Sigma R^2}{N} - \frac{(\Sigma M_R)^2}{N}$$

3. Find the square of the numerator term in the standard deviation formula for each replication group.

Let r equal an included plot yield and n the number of plots per group. ($n = 3$ in the present work).

$$n \sigma_r^2 = \sum r^2 - \sum r(M_r)$$

3. Determine the mean of the squares of the group standard deviations

$$\frac{\sigma_r^2}{n} = \frac{\sum (\sum r^2 - \sum r(M_r))}{Nn}$$

4. Obtain σ_E , the standard deviation due to field conditions, by extracting the square root of $\sum r^2/n$ and dividing by F a correction factor for small samples. (0.8165 for $n = 3$).

$$\sigma_e = \sqrt{\sigma_r^2/n} / F$$

5. Make σ_E comparable to σ_R by dividing by n

$$\sigma_E = \sigma_e / \sqrt{n}$$

Note: Combines in one equation (2), (3), (4), and

(5), give

$$\sigma_R = \sqrt{\frac{\sum (\sum r^2 - \sum r(M_r))}{Nn^2}} / F$$

6. Calculate σ_H from the equation

$$\sigma_H^2 = \sigma_R^2 - \sigma_E^2$$

7. Substitute σ_H for σ_R in the product-moment correlation equation. Let A be any ear character correlated with progeny yield X, and let p represent the product moment. The correlation between A and X will be without correction

$$r_{XA} = \frac{P}{\sigma_X \cdot \sigma_A}$$

with correction

$$r_{XA} = \frac{P}{\sigma_H \cdot \sigma_A} \quad \text{or for machine adaptation}$$

$$r_{AX} = \frac{\Sigma XA - EX (M_A)}{(\sigma_H \sqrt{N}) \sqrt{\Sigma A^2 - \Sigma A(M_A)}}$$

Obviously by lessening the product of the variability term in the denominator of the product-moment correlation formula the size of r will be increased provided the numerator is not likewise reduced. Now one variability term in the denominator is the standard deviation of one variable and the other is the standard deviation for the other variable. In the present type of work a parent ear character represents one variable and progeny yield represents the other. If the standard deviation of the latter is reduced to represent only variability related to the seed ear then r will be increased accordingly. The product moment in the numerator owes its size only to concomitant deviations for the two variables. Unassociated deviations cancel out automatically. Since there is no reason to believe

that environment was any different for any one parent-progeny-yield pair than for another, it can be assumed that the product moment is due only to the fact that the seed ear directly influences yield or else the two vary together on account of a common determinant transmitted from generation to generation.

It is true that any somatic unsoundness in the seed ear which is independent of heredity but which may affect the vigor of the offspring, may also influence the magnitude of seed ear characters and thus augment correlation. Thus immaturity or disease infection may effect one seed ear more than another, not because the one is inherently weaker than the other, but because the one by chance happened to have a more intense exposure than the other. Nevertheless, the disorder will not only influence such ear characters as weight of kernel or indentation of kernel, but will also reduce the vigor of the seedlings. The result will be a correlation between weight of kernel or indentation of kernel and progeny yield. However, the proportionately small effect of such situations and the fact that the germination test eliminates practically all somatic unsoundness argue for the ignoring of the foregoing possibility.

Table 10 has been included to illustrate the application of the correction process to actual data. This table represents only a small part of the table actually used

TABLE 10. - A sample portion of a large table used in making variability correction in the 1927 progeny yields

Seed ear No.	Yield in lbs. per plot.			Values in per cent of respective series means coded by subtracting 70.					
	Series			Series			Total ($\geq r$)	Mean \bar{r} (R)	$\sum r^2 - P(M_r)$
	I	II	III	I (r_1)	II (r_2)	III (r_3)			
1	20.0	15.7	24.1	38.	21.	24.	83.	27.67	164.39
2	21.3	17.0	30.6	45	28	50	123	41.00	266.00
3	17.0	19.7	29.1	22	44	44	110	36.67	322.66
4	13.3	13.8	27.1	2	10	33	48	16.00	632.00
5	14.6	14.6	22.9	9	14	20	45	14.33	60.67
6	23.6	18.9	29.0	57	40	44	141	47.00	158.00
7	20.0	22.1	26.0	38	58	32	128	42.67	370.66
8	22.5	17.9	26.9	51	34	36	120	40.00	182.00
9	17.4	16.9	22.7	24	28	19	71	23.67	40.66
10	17.8	20.5	22.3	26	49	17	92	30.67	544.66
153	17.8	15.3	26.5	26	19	34	79	26.33	112.67
	2837.2	2640.2	3908.8	4587	4568	4566	13722		44,373.92
M	18.54	17.26	25.55	29.98	29.86	29.84	89.69		290.03

$$\sigma_R^2 = \sum R^2 - \sum R (M_r) / N = 85.2409$$

$\sigma_R = 9.2326 =$ observed standard deviation of a group M

$$\sigma_E = \sqrt{\frac{\sum [\sum r^2 - \sum r(M_r)]}{N_n}} / F \sqrt{n} = \sqrt{\frac{44,373.92}{153 \times 3}} \cdot .8165 \sqrt{3} = 6.9523 = \text{the standard deviation independent of seed differences.}$$

$$\sigma_H^2 = \sigma_R^2 - \sigma_E^2 = (9.2326)^2 - (6.9523)^2 = 36.9064$$

$\sigma_H = 6.0751 =$ yield standard deviation related to seed.

in calculating the results of 1927. However, it is thought that sufficient data are included to illustrate the process. It will be noted that actual yields for each series are converted into percentages of their respective series means. This step permits the combining of plots in different fields and of different sizes. It will be noted also that the percentages are coded by the subtraction of 70 throughout, which of course does not affect the size of the resulting variability constants. The value of the true mean, however, is reduced by this exact amount. Coding merely reduces the labor involved, being a process similar to that of grouping in a correlation surface.

Tables 11 and 12 summarize the yield results for both 1926 and 1927. Attention is called to the fact that the yields of 1927 are almost double those of 1926. Doubtless both season and soil contributed to the differences. Most of the plots were on better soil in 1927 and yields of corn in the locality of the experiment were generally high on account of a favorable season.

Examination of Table 12 makes patent the fact that in so far as the correction method is reliable, about one-half of the total plot yield variability encountered in this experiment was due to soil or other field conditions. The other half apparently was due to seed differences. In the year when

TABLE 11. - Average yields of undried ear corn for 86 progeny groups grown in 1926 and 153 groups grown in 1927.

	1926				1927			
	Series			Total	Series			Total
	I	II	III		I	II	III	
No. Hills	8	8	8	24	10	10	16	36
Yield in lbs.	7.61	7.63	6.83	22.06	18.54	17.26	25.55	61.35
Bu. per Acre	48.3	48.4	43.3	46.7	94.2	87.7	81.1	86.6

TABLE 12. - Yield averages and standard deviations for the means of replication groups. Each group consisted of three plots planted from the same seed ear

Year	Average Bu. per A.	σ_R Bu. per A.	σ_R percent	σ_E percent	σ_H percent	$\frac{\sigma_H^2}{\sigma_R^3}$
1926	46.7 *	2.83	6.06	4.09	4.48	0.545
1927	87.7 †	8.09	9.23	6.95	6.07	0.433

* 83 groups in 1926; 153 in 1927

† unweighted

the total variability was low the proportion of variability induced by the seed was relatively high. This fact seems to indicate that reduction of total variability came either as a result of more uniform field conditions in 1926 than in 1927, or as a result of a more efficient plot to plot correction initially applied to the yields. The experimental area in 1926 was much smaller than that of 1927 and on the whole appeared more uniform. The similarity of the series means for 1926 given in Table 11 seems to bear out this observation. But regardless of how the reduction of total variability came about it seems safe to conclude that transmitted variability tended to remain constant for the two years.

The effect of the yield variability correction upon the size of a correlation coefficient where yield is one of the variables is easily demonstrated. If X be allowed to represent yield, A some other variable, and p the product moment, $r_{XA} = \frac{p}{\sigma_X \cdot \sigma_A}$ Then if σ_X or σ_A is reduced in size r_{XA} will be increased in direct proportion to the amount of the reduction or $r \propto \frac{1}{\sigma}$

Therefore $\frac{\sigma_R}{\sigma_H}$ gives the factor by which any given coefficient must be multiplied in order to obtain correction.

In 1926, $\sigma_R/\sigma_H = 8.06/4.48 = 1.35$

In 1927, $\sigma_R/\sigma_H = 9.23/6.07 = 1.52$

in work involving a series of yield correlations it is more convenient to make the correction directly in the denominator of the correlation equation rather than to wait until an r value is obtained and then multiply by a factor.

It is demonstrated then that the method of correction raises the coefficients of correlation from 35 to 52 per cent. If the correction cannot be proved invalid the gain in the size of the correlation coefficients seems well worth the trouble involved.

Character-Yield Correlations:- Progeny yield results for two years' of work still in progress have been used in the correlations to be discussed. The respective progeny yields have been correlated with morphological ear and tassel characters previously found to be associated respectively with ovule and pollen numbers. The method developed for reducing the effect of field variability has been used in all the character-yield correlations. All r values with their errors are presented in Table 13.

Though small in comparison with their probable errors the coefficients taken as a whole do show certain rather definite indications. For instance, each parent-ear character maintains the same sign for r in the two years of the experiment. Kernel number and number of kernel rows both

TABLE 13. - Simple correlation coefficients between various plant characters and yield of ear corn.

Character	1926	1927
Parent Ear		
Length of cob	+0.1007 ± .0720	+0.0781 ± .0542
No. kernel rows	-.0598 ± .0724	-.1608 ± .0531
Kernel thickness	+.1350 ± .0716	+.0195 ± .0545
No. of kernels	-.1145 ± .0717	-.1099 ± .0538
Ave. kernel wt.	+.3581 ± .0834	+.0868 ± .0541
Progeny tassel		
Central length	-.1738 ± .0705	+0.0927 ± .0540
No. branches	-.1697 ± .0706	+0.0967 ± .0540
Density of spikelet	-.1445 ± .0713	+.1323 ± .0535
Size of "	-.0542 ± .0735	-.0838 ± .0541
Length of branches	- - - -	+0.1183 ± .0537
Length of branches x density of spikelets	- - - -	+0.1500 ± .0533
Sum of tassel char- acter values	-.2775 ± .0671	

show a negative relation with yield. On the other hand, length of ear and weight of kernel both show a positive correlation. It would appear from this that size measurements of the parent ear have an effect opposite to that of kernel number. With the data at hand it is impossible to state whether row number determines the relation shown by kernel number with yield or whether the converse is true. Kernel thickness gives a positive r value or stated differently, number of kernels per inch gives a negative value. Here again cause and effect cannot be distinguished. Kernel thickness varies directly with length and indirectly with kernel number. Its relation to yield may be due to its association with either kernel number or size of ear. When the experiment has continued long enough to reduce the error of the simple correlation coefficients, it will be enlightening to place the several variables in a multiple correlation system with yield. Then the individual effects of the different characters can be definitely measured.

The progeny tassel measurements, like the parent ear measurements, do not tell a definite story. The most outstanding observation is that the yield relations seem to be reversed for the two years. In 1926, all signs are negative, whereas, in 1927, all but one sign, that for spikelet size, are positive. Therefore, the results for

1926 check the ear correlations for both years in that high gametic number seems to indicate low yield. In 1927 total length of lateral branches and density of spikelets, characters highly suggestive of pollen production, have comparatively high positive r values. The change for the two years cannot be explained. It is suggested that the reversal of sign may be a result of the very favorable conditions in 1927. As has been pointed out, yields for 1927 almost doubled those of 1926. Possibly tassel and ear on the same plant do not show a like response to favorable growth conditions. Further work is required to make any answer definite.

Summary of Part II:- A method for eliminating or at least reducing the effect of field conditions upon the variability of plot yields in ear-to-row comparisons has been presented. Where the number of comparisons is large and where each seed lot is represented by three or more plots distributed over the experimental area, the method is applicable. The validity of the procedure rests upon the assumption that the average yield error within all replication groups of plots after being corrected for size of sample measures the variability due to soil or other field conditions, and that the error calculated from the mingled records of all plots measures the variability due to all causes. Then the difference, properly calculated, between the latter and the former represents the portion of the total yield variability due to seed differences. Under the conditions of the experiment the latter amounted to about half of the total variability. In the year when total variability was low, the per cent of transmitted variability was high, which is evidence that the latter tends to remain constant.

Correlations with correction were calculated for yield and various tassel and ear characters. The resulting coefficients are low in relation to their probable error, but taken as a whole they show significant tendencies. Number of kernels on the parent ear and characteristics contributing to number of kernels show a small negative relation to yield. On the other hand size or mass measurements such as length of ear and weight of kernel show a

positive association with yield. For 1936, tassel characters indicative of pollen production were negatively correlated with yield, but in 1927 the sign of the relation was reversed. No adequate explanation is at hand, but it is thought that the much more favorable season of 1927 had a differential effect on ear and tassel development.

SUMMARY AND CONCLUSION

The present work was prompted by the conceptions that all plant functions culminate in that very important capacity, reproduction; that through reproduction natural selection becomes effective; and that yield of grain and reproduction in maize are similar but not synonymous. An attempt has been made to determine what measurable ear and tassel characters are expressive of genetic production, the extent to which each is inherited, the degree of association between tassel and ear characters, and finally the general relations of these characteristics to yield of grain.

From the results obtained over a period of two years and involving 249 seed ears of Reids Yellow Dent corn and their respective progenies, the following conclusions have been drawn.

1. Under greenhouse conditions total number of tassel spikelets is a good criterion of pollen production. Total length of tassel branches times estimated spikelet density gives the next best measurement of pollen production.

2. Density and size of spikelet are much less variable than length or number of branches.

3. Weight of dried pollen is exceedingly variable. Quantities produced in the greenhouse showed a coefficient of variability of 39 per cent.

4. Environmental conditions greatly influence the extent of tassel development.

5. About 50 per cent of the variability for total number of kernels is correlated with number of rows. Number of kernels per inch has more influence on total number of kernels than does length of ear.

6. Long ears tend to have few rows and thick kernels.

7. Ear length is less variable than tassel length.

8. Intra-progeny correlations are small but statistically significant for density and total length of tassel. The size of the actual correlations in comparison with theoretical values shows that these characters are largely hereditary.

9. Length of tassel and length of ear on the same plant gave a correlation of $+0.124 \pm .020$; number of tassel spikelets per inch and number of kernels per inch, $+0.161 \pm .020$. These figures indicate the possibility of wide pollen ovule ratios.

10. There is less tendency for length of ear to be inherited than either number of kernels per inch or number of rows per ear. The parent-progeny correlations coefficients are respectively $+0.309 \pm .049$, $0.562 \pm .037$, and $0.453 \pm .043$.

11. Field variability tends to obscure hereditary relationships, but it can be measured through plot replication and subsequent statistical treatment.

12. Ear characters indicative of the extent of ovule production have a small but definite negative correlation with yield, whereas tassel characters expressive of pollen production may show a reversal of sign from season to season.

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