

THE INHERITANCE OF GLUME-LENGTH AND GRAIN-LENGTH IN A WHEAT CROSS.

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(With 1 Text-figure.)

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I. THE EXPERIMENTAL MATERIAL AND THE NATURE OF THE BREEDING.

THE inheritance results in wheat published by Biffen (1) in 1905, made it clear that certain simply "measurable" or "quantitative" characters behaved, in inheritance, in much the same general fashion as the "qualitative" ones. Manifestly most of the economic plant-breeding questions, e.g. "yield" inheritance, must depend upon "measurable" characters, and the investigations to be described were undertaken with the primary object of ascertaining the precise mode of inheritance of some simply measurable character. Biffen's observations on length

of glume had revealed the segregation of "long" and "short" glumes (apparently of the parental forms) in the F_2 and, in addition, of heterozygous forms of intermediate length. It seemed desirable to determine whether or not the numerical limits which characterised the parents of the cross, also characterised the apparently "parental" types found in the F_3 .

Glume-length was chosen as the experimental character partly because of the general definiteness of Biffen's results, and further, on account of its botanical suitability to the requirements of a simply measurable character. It was such that numerous and accurate measurements were obtainable, and moreover, as a general experience proved, it was less liable to wide and sudden fluctuations than were most of the other length characters of the wheat-plant.

Grain-length it was clear, bore some definite relation to glume-length [vide (1), p. 38], and as it appeared to have an economic significance, it was included as an experimental character in the investigation.

The parents (F_0) of the cross were "Polish" (*T. polonicum* L.) and "Kubanka" (a variety of *T. durum* Desf.). They had been grown for some years by Professor Biffen, and were known to satisfy the requirements of a definition of "pure line" with regard to origin, behaviour, and mode of maintenance.

The sequence of the breeding was:

1911 { Cross made, viz. ♀ Polish × ♂ Kubanka.
Parental stocks continued.

1912 { F_1 plants grown and harvested.
Parental stocks continued.

1913 { Every grain borne by the F_1 plants was sown and 530 F_2 plants thus raised. The main ear of every F_2 plant was harvested and labelled with a serial number (1—530). Of these plants only 487 set ripe grain.
Parental stocks continued.

1914 { Every grain of every labelled ripe F_2 ear (one per plant) was sown, and 5145 F_3 plants were thus raised. The main ear of every plant was harvested. The ears from those plants which sprang from the seeds of any one F_2 plant were bunched together, and the bunch was labelled with a "family number" which was the number allotted in 1913 to the corresponding F_2 parent plant.
Parental stocks continued.

The investigation began in 1913. Prior to that year the material was in the hands of Professor Biffen.

A certain amount of sterility was encountered, but as the details given below make clear, its incidence was neither selective nor sufficiently heavy to bias the numerical results recorded.

In the F_2 a few plants failed to mature by harvest time, and consequently they were not measured. These again were not selective, but included all three of the length types found in F_2 .

The F_3 plants were kept unthreshed during 1914—19, and it is hoped to raise an F_4 in 1920.

II. THE OBSERVATIONS AND THE METHOD OF MEASUREMENT.

The class-intervals of measurement are, throughout :

For glumes, 1.0 mm. ; for grains, 0.5 mm.

As a fact, the glumes were measured to 0.5 mm., but on this basis the frequency distribution, in the case of Polish, covered a range of 45 classes. Hence to facilitate statistical work and to smooth out the irregularities introduced into such a distribution by very small classes, the observations were regrouped into 1.0 mm. classes. As a result of this regrouping a non-integral ($x.5$) number of individuals is to be found as the class frequency in some parts of the tables of observations.

In all the generations one ear per plant was harvested and one glume per ear was measured. The grain situated nearest to that glume was measured also. Either glume of the median spikelet on either side of the rachis (i.e. any one of a specified set of four glumes) was selected for measurement.

The acceptance of one glume-length as a characteristic of the ear concerned, was justified by a separate investigation. It was first established that the glumes of the median group of four spikelets on an ear, were all of practically the same length. Thus the average of this set of eight glumes (from four spikelets) could be regarded as a characteristic of the ear. Next, for every F_2 plant (total 492 plants) these eight glumes (and with them the corresponding eight grains) were measured. The frequency distribution of the deviation of every single measurement from the mean of the set of eight to which it belonged, was then compiled, regard being paid to the sign of the deviation. The mean quartile deviation of the distribution was 0.401 mm. by direct calculation and 0.435 mm. when calculated from the standard deviation of the distribution on the assumption of normality. That is to say, fifty per

cent. of the single measurements deviate from the means of the sets of eight to which they belong, by no more than ± 0.4 mm. The accuracy of measurement is only ± 0.5 mm., and consequently one glume measurement per ear was considered to be justifiable.

III. THE INHERITANCE OF GLUME-LENGTH.

The symbols "*P*," "*I*," and "*K*" are used to facilitate reference.

Thus "*P*" implies "Polish" or "of Polish type."

F_0 . *P* designates a population of pure "parental" Polish type, the type which was employed as one parent in the cross.

F_0 . M_P (glume) denotes the mean glume-length of a population of parental Polish plants.

F_0 . σ_P (glume) denotes the standard deviation of the glume-length frequency distribution for such a population.

"*K*" is similarly used in the case of "Kubanka."

"*I*" implies the heterozygote form which, as later appears, is roughly-speaking intermediate between "*P*" and "*K*".

The glume-length distributions in successive generations were as follows:

F_0 .

Both parent varieties were grown and measured in 1913 and 1914. For comparative purposes the results of 1914 are by far the more useful, for they are based on much greater numbers of observations, and the F_3 was also grown in that year, the conditions being precisely similar. Summarised, the results were:

*Glume-lengths of Parent Varieties (F_0 . *P* and F_0 . *K*) of the Cross.*

Year	Variety	Mean Glume-Length	σ	No. of Observations	No. of Table containing frequency distribution of glume-length
1913	Polish	F_0 . $M_P = 28.6 \pm 0.34$	—	80	—
1914	„	F_0 . $M_P = 30.84 \pm 0.10$	3.784	600	I
1913	Kubanka	F_0 . $M_K = 11.23 \pm 0.24$	—	25	—
1914	„	F_0 . $M_K = 11.70 \pm 0.04$	1.260	400	II

That the variability of Polish is great and that of Kubanka small becomes clear from an inspection of Tables I and II.

F_1 .

During 1914–19, the F_1 measurements were lost. From memory it can be stated simply that the F_1 mean lay somewhere between the parental means—probably it was close to the arithmetic mean of the

parental values. Backhouse (2) records extensive crosses between Polish-Kubanka, and the following values are from his results :

$$F_0 \cdot M_P = 29.0 \text{ mm.}; F_0 \cdot M_K = 9.0 \text{ mm.}; F_1 \cdot M = 18-19.0 \text{ mm.}$$

Similarly from the records of Biffen [(1), p. 36] for reciprocal Polish \times Rivet crosses, the numerical intermediateness of the F_1 is quite definite.

In the cross to be described the F_1 value was thus probably

$$= (30.84 + 11.70)/2 = 21.27 \text{ mm.,}$$

but no further use is made of this speculative value.

F_2 .

Although 530 F_2 plants were raised, only 487 of them furnished grain for the raising of an F_3 . The causes and distributions of the failures are explained in the tables which follow. The frequency distributions of F_2 glume-lengths were :

Table III (p. 133). The complete F_2 of 530 plants.

Table IV. The 487 F_2 plants which matured and whose grain was sown to raise the F_3 .

Table V. The 17 F_2 plants which, although they contributed no grain for the F_3 sowings, did set one or more imperfect grains. They were unripe at harvest.

Table VI. The 7 F_2 plants which matured but were sterile.

Table VII. The 19 F_2 plants which were unripe at harvest, and which gave no evidence of being able to set grain.

It is with the plants of Table IV that further observation is concerned, for they alone gave F_3 progeny, from the examination of which they themselves could be sorted into genetic classes. Table IV (like Table III) exhibits a definite tri-modality.

Two conclusions may be drawn from the F_2 glume-length frequency distributions (Table III or Table IV) viz. :

(1) Three glume-length types appear in F_2 .

(2) None of these types corresponds exactly to the Polish parent. It appears that this parental type is represented in the F_2 by a group of plants whose mean and fluctuation ranges for glume-length have been "shifted" down towards the lower end of the scale.

In the first place an attempt was made to "dissect" the tri-modal F_2 distribution into its three constituent types by purely mathematical methods. It was assumed that the distribution of the heterozygote type of F_2 did not extend below the lowest "peak" of the total F_2

distribution (i.e. 11.5 mm. in Table IV). If this were so, then that part of Table IV lying between 11.5 mm. and 9.5 mm. (both values inclusive) was the lower half of the distribution of all the plants of Kubanka type in the F_2 . The upper half of the distribution was obtained by writing down the frequencies symmetrical about 11.5 mm. to those of the lower half. From the distribution so completed the standard deviation (σ) and number of observations (N) were found, and the mean M was, of course, 11.5 mm. The "normal" curve equivalent to this distribution was calculated [see Yule (5) for formula and tables for use in calculation]. By the same processes the normal curve for the distribution of the Polish type of F_2 was obtained. Subtraction of these two normal distributions from the total F_2 gave the distribution of the heterozygote or intermediate type. Thus calculated, the frequencies of the F_2 types were:

K	I	P
23.29 %	57.76 %	18.94 %

while the modes were:

11.5 mm.	16.5 mm.	24.5 mm.
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This theoretical "dissection" was carried out for the sole purpose of testing the reliability of mathematical analysis of the F_2 as against the far more lengthy and laborious genetic analysis by means of a complete F_3 .

Clearly, the analysis of F_2 into constituent genetic types necessitated the raising of a complete F_3 .

F_3 .

The F_3 plants were kept in "families," an F_3 family consisting of all the plants raised from the grain borne by any one F_2 "mother" plant. From the nature of the F_3 family the genetic type of the corresponding F_2 plant was judged. Thus an F_3 family in which all the plants were P , must have originated from a homozygously P plant of the F_2 ; similarly in the case of K . An F_3 family containing plants of two or more types, e.g. P , I , and K , or P and I , or I and K , or P and K , must have come from an F_2 plant that was heterozygous, i.e. an I plant.

The sorting into types of the F_3 families necessitated a definition of the three types P , I , and K (the tri-modality of the F_2 distribution pointed to the existence of only three types). Measurement as opposed to eye-judgment was intended to be the essence of this investigation, and an attempt was made to set up measurable (quantitative) type

standards. Table II suggests that an F_3 family should be regarded as K if, and only if, no plant in it was of greater glume-length than 14.5 mm. Since the accuracy of measurement was only ± 0.5 mm., and the class interval was 1.0 mm., the value of 15.5 mm. was finally adopted as an upper limit defining the K type of F_3 family.

From the records of observations, the serial numbers were noted of all F_3 families in which occurred no plant of glume-length greater than 15.5 mm. These families were inspected, and every plant of every family proved to be to the judgment of the eye—at this stage fairly practised—of K type in general appearance. Thus far, therefore, the metrical standard was applicable; moreover it harmonised with eye-judgment.

For the Polish (P) standard it was natural to turn to Table I (F_0 . P distribution) and, for the time being, ignoring the outlying observation at 12.5 mm., to adopt 19.5 mm. (20.5 – 1.0) as the lower limit for the P type. F_3 families would thus be accepted as P if, and only if, they contained no plant of glume-length less than 19.5 mm. Certain F_3 families were found which, although they failed to pass this numerical test, were obviously composed entirely of plants possessing the unmistakable Polish eye-appearance. The “shift” downwards in glume-length exhibited in F_2 had persisted in F_3 , and thus had rendered inapplicable the metrical “ P ” standard derived from the distribution of F_0 . P . A fresh metrical standard was essayed in the form of the total range of glume-length variation in F_3 families. This too failed to harmonise with facts of eye-judgment—facts so defined that they could not be ignored.

After full trial, the metrical standard was abandoned in the case of Polish, and in its stead eye-judgment was adopted. Polish and Kubanka are so well characterised in glume-form that the practised eye has little difficulty in separating the one type from the other and from heterozygotes (intermediates). The intermediates proved to be in every one of the numerous glume (and grain) characters, excellent “blends” of the parent forms.

The standards thus finally adopted were applied, every F_3 plant being twice judged. The second judgment accorded with the first and the result was:

$$F_3 = \left\{ \begin{array}{l} 114 \text{ } K \text{ families} = 1237 \text{ plants} \\ 267 \text{ } I \quad \quad \quad = 2854 \quad \quad \quad \\ 101 \text{ } P \quad \quad \quad = 1054 \quad \quad \quad \end{array} \right\} = 5145 \text{ plants.}$$

Regarding all F_2 plants as simple heterozygotes, if in their F_3 families

there occurred more than one type, and denoting the heterozygote by "I," the F_2 ratio is:

$$\begin{aligned} F_2 = K : I : P &= 114 : 267 && : 101 [= 482 \text{ plants}] \\ &= 23.65 \% : 55.39 \% : 20.95 \% . \end{aligned}$$

[N.B. 487 F_2 plants set good seed, but only 482 F_3 families were obtained at harvest.]

From the F_2 distribution it is concluded that there are three distinct F_2 types. The classification of the F_2 plants by means of the F_3 should, on the assumption of a one-factor difference between P and K , reveal a 1 : 2 : 1 ratio among these types. Actually the ratio (given above) deviates considerably from this expectation, and as Tables V, VI, and VII show, the deviation is not explicable on the basis of selective mortality or sterility. Confirmatory evidence is to be found in Biffen [(1), p. 36] with Polish \times Rivet, Backhouse (2) with Polish \times Kubanka, and Caporn (3) with Polish \times Eloboni. In all three of these cases the evidence for a one-factor difference for glume-length was very substantial, and close approaches to a 1 : 2 : 1 ratio were obtained in the F_2 . No other explanation appears to accord as closely with the results of observation above described as does that of one-factor difference; and consequently as a working hypothesis it is assumed that either P or K possesses a factor for glume-length which the other lacks, and that the heterozygote is, broadly speaking, intermediate between the parental forms.

IV. THE MEASURABLE CHARACTERISTICS OF THE P , I , AND K GLUME TYPES IN F_0 , F_2 , AND F_3 .

In F_2 and F_3 every plant was classified as P , I , or K . The next step was to evaluate the measurable characteristics—frequency distribution, mean, and standard deviation—of all three types in F_0 , F_2 , and F_3 successively. The P (and similarly K) plants of F_3 are of two kinds, the one descendants of $F_2.P$ (designated $F_3.P$ ex $F_2.P$) and the other of $F_2.I$ (designated $F_3.P$ ex $F_2.I$). For the time being the characteristics of $F_3.P$ ex $F_2.I$ and $F_3.K$ ex $F_2.I$ will not be considered. The measurable characteristics of the three types in the three generations were as follows:

M = mean glume-length; σ = standard deviation of glume-length frequency distribution and N = the number of observations in the distribution.

*K.**Measurable Characteristics of the Kubanka Glume Type in F_0 , F_2 , and F_3 .*

Year	Generation	M	σ	N	Table of Frequency Distribution
1914	$F_0 . K$	11.70 ± 0.043	1.26	400	II
1913	$F_2 . K$	11.42 ± 0.075	1.18	114	VIII
1914	$F_3 . K$ ex $F_2 . K$	11.98 ± 0.025	1.30	1237	IX

The $F_2 . K$ population was small (114 plants) and the 1913-14 seasonal difference was doubtless responsible to a considerable extent for differences in growth. From the above values it is concluded that the K type maintained its measurable characters practically constant in F_0 , F_2 , and F_3 .

*P.**Measurable Characteristics of the Polish Glume Type in F_0 , F_2 , and F_3 .*

Year	Generation	M	σ	N	Table of Frequency Distribution
1914	$F_0 . P$	30.84 ± 0.104	3.78	600	I
1913	$F_2 . P$	23.18 ± 0.186	2.75	101	X
1914	$F_3 . P$ ex $F_2 . P$	24.66 ± 0.078	3.78	1054	XI

As in the case of Kubanka, the mean of (F_3 1914) is slightly greater than that of F_2 (1913) and the difference is small enough to be attributable to season.

The differences

$$F_0 . M_P - F_2 . M_P = 7.66 \text{ mm.} = 24.83\% \text{ of } F_0 . M_P$$

and $F_0 . M_P - F_3 . M_P = 6.18 \text{ mm.} = 20.04\% \text{ of } F_0 . M_P$

are so great in comparison with the relevant probable errors that there is full justification for stating that in the $P \times K$ cross, the parental P does not re-appear in F_2 . In its place are found P plants which closely resemble $F_0 . P$ in general appearance but whose mean glume-length is more than 20% lower than that of $F_0 . P$. This "reduced" form of P in F_2 produces, when selfed, P plants of the same "reduced" glume-length in F_3 . The possibility that "minor multiplying factors" are responsible in some way for this phenomenon of "reduction" or "shift" demands, perhaps, some form of reservation. It may be that the true $F_0 . P$ type is reproduced in F_2 but in extremely small proportion. Apart from the value of a safeguarding reservation there is nothing to recommend any theory of multiplying factors in this case. On the grounds of simplicity and agreement with observation, the most acceptable theory is that of the segregation of one factor with the attendant phenomenon of "shift."

Interesting evidence of the occurrence of "shift" accompanying an otherwise apparently single segregation of one factor is to be found in the results of a number of investigations. Caporn [(3), p. 259] has remarked upon it and it is clearly shown in some of Backhouse's results [e.g. (2), p. 130, Fig. 1*a*]. In both of these cases Polish was one parent of the cross. The importance of a recognition of "gametic impurity" or "contamination" has been emphasised by Ruggles-Gates (9) and in a variety of crosses the occurrence of the phenomenon is exemplified. Among these are Punnett and Bailey (10) and (11), Castle and Phillips (12), Davenport (13), Martin Leake [(14)—leaf factor in Cotton], East (15), Balls [(17), p. 69 on seed-weight], and possibly some of the intangible facts discovered in Tomato investigations by Groth (7) might be explained as results of "shift." It is interesting to observe that the results recorded by Belling (16) constitute one of the closest studies of length inheritance and that they show complete absence of "shift."

I.

Measurable Characters of the Heterozygous Glume Type in F_0 , F_2 , and F_3 .

Year	Generation	M	σ	N	Table of Frequency Distribution
1913	$F_2 . I$	16.407 ± 0.078	1.89	267	XII
1914	$F_3 . I$ ex $F_2 . I$	17.480 ± 0.058	2.09	580	XIII

From Tables XII and XIII it appears that the frequency distribution of glume-lengths for the plants of F_2 and F_3 which are neither P nor K (and are therefore classed as I) is unimodal, and this is in accordance with the one-factor explanation which has been adopted. With regard to the relation of the mean glume-length of the heterozygote to the means of the parents, the following values are of interest.

$$(F_0 . M_P + F_0 . M_K)/2 = 21.27 \text{ mm.} \quad (F_0 . M_P \times F_0 . M_K)^{\frac{1}{2}} = 19.0 \text{ mm.}$$

$$(F_2 . M_P + F_2 . M_K)/2 = 17.30 \text{ mm.} \quad (F_2 . M_P \times F_2 . M_K)^{\frac{1}{2}} = 16.27 \text{ mm.}$$

$$F_2 . M_I = 16.41 \text{ mm.}$$

It will be observed that a modified form of the "golden mean" theory of Groth (7) and (8) appears to fit the facts of this case.

The complete F_3 progeny of the $F_2 . I$ plants should, on the hypothesis adopted, present a glume-length distribution similar to the distribution of the complete F_2 . That this is the case is shown by Table XIV. There appear to be three constituents with modes approximately at:

$$11.5 \text{ mm.} \quad 17.0 \text{ mm.} \quad 24.5 \text{ mm.}$$

On expectation, these constituents are *K*, *I*, and *P*, and in order to determine their measurable characteristics, all plants of all $F_3 \cdot I$ families (between family No. 51 and family No. 265 both inclusive) were re-measured and re-classified as *K*, *I*, or *P*. From a sample of 1190 plants thus obtained the following values were calculated :

*Measurable Characters of the K, I, and P Glume Types bred
from $F_3 \cdot I$ plants.*

Year	Generation	M	σ	N	Table of Frequency Distribution
1914	$F_3 \cdot K$ ex $F_2 \cdot I$	11.81 ± 0.053	1.35	292	XV
„	$F_3 \cdot I$ ex $F_2 \cdot I$	17.48 ± 0.058	2.09	580	XIII
„	$F_3 \cdot P$ ex $F_2 \cdot I$	21.68 ± 0.141	3.73	318	XVI

Comparison of these values with those given under *K* (p. 117) and *P* (p. 117) show that for the mean glume-lengths :

$$[(F_3 \cdot K \text{ ex } F_2 \cdot K) - (F_3 \cdot K \text{ ex } F_2 \cdot I)] = 11.98 - 11.81 = +0.17,$$

$$[(F_3 \cdot P \text{ ex } F_2 \cdot P) - (F_3 \cdot P \text{ ex } F_2 \cdot I)] = 24.66 - 24.68 = -0.02.$$

That is to say, although "shift" was first exhibited by the *P* descendants of heterozygous plants (viz. by $F_2 \cdot P$ ex F_1) it is not again exhibited by the *P* descendants of F_2 heterozygotes (viz. $F_3 \cdot P$ ex $F_2 \cdot I$). It appears that the reduced or "shifted" value of Polish glume-length cannot be further shifted by either

(α) Selfing—for $F_3 \cdot P$ ex $F_2 \cdot P$ (mean) $\simeq F_2 \cdot P$.

(β) Hybridisation, as in the zygosis performed by $F_2 \cdot I$ plants—for $F_3 \cdot P$ ex $F_2 \cdot I$ (mean) $\simeq F_3 \cdot P$ ex $F_2 \cdot P$.

V. THE INHERITANCE OF GRAIN-LENGTH.

It was originally intended to deal with grain-length entirely by measurement but the principle of metrical type-standards proved inapplicable just as it did in the case of glume-length. In fact the breakdown was more complete, for the parental (*K* and *P*) mean grain-lengths lie, comparatively, very close, and the overlap of their distributions is considerable. From the early stages of the work upon F_2 it was quite certain that "*P*" grains were never associated with "*K*" glumes or *vice versa* and after extensive trials of sorting grains into types, it was concluded that in F_2 three types only were found (*K*, *I*, and *P*), and that on any plant *K* glumes were invariably accompanied by *K* grains and similarly for *I* and for *P*. Consequently in F_2 and F_3 the classification by glumes was accepted as a classification by grains. Biffen [(1), p. 38] remarked upon the relationship between grain and glume.

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In what follows the phrase " F_2 . K grains" refers to the grains borne by those F_2 plants which have K glumes and so on, the plant categories in F_2 and F_3 being thus identical with those of the glume-classification already described. On account of shed-grain etc., the number of plants in a grain-category is sometimes slightly less than the number in the otherwise identical glume-category.

In the successive generations the grain-length distributions were:

F_0 .

Grain-Lengths of Parent Varieties (F_0 . P and F_0 . K) of the Cross.

Year	Variety	M	σ	N	Table of Frequency Distribution
1913	Polish	$F_0 . M_P = 10.8 \pm 0.102$	—	80	—
1914	,,	$F_0 . M_P = 10.2 \pm 0.019$	0.66	526	XVIII
1913	Kubanka	$F_0 . M_K = 8.2 \pm 0.077$	—	25	—
1914	,,	$F_0 . M_K = 7.7 \pm 0.017$	0.49	395	XIX

The grain-length distributions are more smooth than those of glume-length and K again shows less dispersion than P .

F_1 .

Like the F_1 glume measurements, those of the grains were lost. From memory and from previously published investigations it is concluded that the heterozygote length is roughly intermediate between the parental ones. In the F_2 the intermediate or heterozygote grain can, with practice, always be distinguished from P and K . In some five or six well marked characters, it is a very even blend or intermediate between the characters of the parent grain-forms.

F_2 .

In maize, the occurrence of "double fertilization" has been established. Assuming it in wheat, the expectation is that the endosperm of the grain (like the embryo) will be one generation ahead of the plant which bears it. Later on the question is more fully considered but for the present the grain borne by an F_x plant will be referred to as F_x grain. This convention is in no sense prejudicial and it simplifies the designation of the grains of different generations.

Table XX contains the grain-length frequency distribution for the complete F_2 . Comparison with Table XVIII (F_0 . P) and Table XIX (F_0 . K) indicates that:

(α) The F_2 distribution contains no constituent exactly like F_0 . P for the frequency at 10.2 mm. is almost zero (F_0 . $M_P = 10.2$ mm.).

(β) Similarly it contains no component exactly like

$$F_0 . K (F_0 . M_K = 7.7 \text{ mm.}).$$

(γ) The F_2 distribution is unimodal but (α) and (β) suggest that "shift" has occurred. Possibly therefore the distribution consists of three constituents which lie very close on account of shift and which, by marked overlap, produce unimodality of the whole.

If the grain be one generation ahead of the plant which bears it, the ratio in F_2 should be 3:2:3; if not a 1:2:1 is expected. The ratio is investigated in § VI below.

It is to be observed that the F_2 distribution is based entirely on measurements and consequently the phenomena of "shift," "unimodality," etc. are unaffected by the fact that in sorting it will be assumed that K (or I or P) grains always accompany K (or I or P) glumes only.

F_3 .

The measurements and numbers of plants correspond with those for glume-length in § III above. Owing to the sterility of a few F_3 plants the distribution totals differ in some cases from those for the corresponding glumes.

VI. THE MEASURABLE CHARACTERISTICS OF THE K , I , AND P GRAIN TYPES IN F_0 , F_2 , AND F_3 .

It is necessary to recall that " K grain" (or I or P) implies the grain borne by plants whose glumes have been classed by eye as " K " (or I or P). That is to say, glume-length and grain-length are assumed to be "genetic inseparable," to be governed by the same factor. Eye-impressions amply support the assumption, and its validity may now be tested. Glume-length showed segregation in F_2 , as was made clear by examination of the F_3 progenies of the F_2 plants. The vindication of the assumption necessitates a demonstration of the segregation of grain-length in F_2 similar to that given for glume-length. This is afforded by the measurable characteristics of the K , I , and P grain types in F_0 , F_2 , and F_3 , which were as follows:

K .

Measurable Characteristics of the Kubanka Grain Type in F_0 , F_2 , and F_3 .

Year	Generation	M	σ	N	Table of Frequency Distribution
1914	$F_0 . K$	7.70 ± 0.017	0.49	395	XIX
1913	$F_2 . K$	8.33 ± 0.042	0.64	112	XXI
1914	$F_3 . K$ ex $F_2 . K$	8.19 ± 0.012	0.63	1214	XXII

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Tables XIX, XXI, and XXII show that the $F_0.K$ type is not reproduced in F_2 as does the equation $F_2.M_K - F_0.M_K = 0.63$ mm. An upward "shift" in mean glume-length appears to have occurred, and the shifted value to have bred true, for despite the 1913-14 seasonal difference, $F_2.M_K$ and $F_3.M_K$ differ by 0.14 mm. only. It will be recalled that in the case of K glume-length the differences concerned were so small that they could not safely be accepted as evidence of shift.

P.

Measurable Characteristics of the Polish Grain Type in F_0 , F_2 , and F_3 .

Year	Generation	M	σ	N	Table of Frequency Distribution
1914	$F_0.P$	10.20 ± 0.019	0.66	526	XVIII
1913	$F_2.P$	8.84 ± 0.038	0.56	101	XXIII
1914	$F_3.P$ ex $F_2.P$	8.75 ± 0.026	0.83	1028	XXIV

The tables of frequency distribution and the values of M show that $F_2.P$ very closely resembles its F_3 progeny, but that both of them are definitely "shifted" down from $F_0.P$. The amount of the shift is:

$$F_0.M_P - F_2.M_P = 1.36 \text{ mm.} = 13.34\% \text{ of } F_0.M_P,$$

$$F_0.M_P - F_3.M_P = 1.45 \text{ mm.} = 14.21\% \text{ of } F_0.M_P.$$

That there is a segregation of grain types in F_2 is shown by the regularity and resemblance of the distributions etc. of $F_2.P$ and $F_3.P$ (cf. also $F_2.K$ and $F_3.K$).

I.

Measurable Characteristics of the Heterozygous Grain Type in F_0 , F_2 , and F_3 .

Year	Generation	M	σ	N	Table of Frequency Distribution
1913	$F_2.I$	8.67 ± 0.026	0.62	266	XXV

Thus the classification of the grains of the F_2 and F_3 plants by means of the glumes with which they are associated, has led to the conclusion that three grain types occur in F_2 . These types naturally have the same frequency relations as the glume types, and as pointed out in § IV above the evidence indicates that the relations are actually an experimental expression of a 1:2:1 ratio. A unimodal distribution (Table XX, i.e. grain-lengths of the complete F_2) has thus been shown to consist of three overlapping separate constituents K , I , and P , the overlap having been much accentuated by the "inwards" shift of P and K from the F_0 values.

In the glume-length results of § IV (under "I") it was shown that the progeny of the $F_2.I$ plants had a length distribution similar to

that of the complete F_2 (i.e. the progeny of F_1 , which is also " I "). Table XXVI is for the grains of the complete descendants of the $F_2 \cdot I$ plants, and its general resemblance to Table XIX furnishes an analogous proof in the case of grain-length.

In connection with glume-length a special series of measurements was made to ascertain if the means of $F_3 \cdot P$ ex $F_2 \cdot P$ and of $F_3 \cdot P$ ex $F_2 \cdot I$ were the same (and similarly for K). Some of the data of a separate investigation may be used as a similar test in the case of grain-length. In F_3 families Nos. 1-50 (both inclusive) and 450-494 (both inclusive) every grain in the ear was measured for plants ex $F_2 \cdot P$ and for all P plants ex $F_2 \cdot I$. The results were:

Year	Generation	M	σ	N	Table of Frequency Distribution
1914	$F_3 \cdot P$ ex $F_2 \cdot P$	8.532 ± 0.010	1.03	4396	XXVII
"	$F_3 \cdot P$ ex $F_2 \cdot I$	8.389 ± 0.013	0.79	1644	XXVIII

Both of the values of M are less than the value given previously for $F_3 \cdot P$, for the last named was based upon the measurement of one "outside" grain per ear. The inner grains of a spikelet being smaller than the outside ones lower the value of M .

The difference shown, viz. $8.532 - 8.389 = 0.143$ mm., is small in comparison with the relevant probable errors, but, as compared with the values of M to which it relates, it appears to be not sufficiently significant to imply any difference in type between $F_3 \cdot P$ ex $F_2 \cdot P$ and $F_3 \cdot P$ ex $F_2 \cdot I$.

The conclusions so far reached may be thus briefly stated:

(α) The one factor which governs the P - K glume difference also governs the P - K grain difference.

(β) "Shift" occurs, so that the P and K types as seen in F_2 (glume and grain) are numerically "shifted" forms of the true F_0 type.

The shifted values persist in F_3 .

(γ) In spite of the demands of the "double fertilization" theory, the grain appears in so far as its length is concerned to belong to the same generation as the plant on which it is borne, i.e. grain-length is a maternal character and segregates on the 1:2:1 basis in F_2 .

VII. CONCERNING THE APPARENT GENETIC INSEPARABILITY OF CERTAIN CHARACTERS IN THE CROSS.

The glumes of parental P plants are of a definite, recognisable, general form; their grains are equally characteristic. F_2 or F_3 plants whose glumes are P , invariably have grains which also, to the eye,

are *P*. Moreover, no plants are found, in any generation, whose glumes are other than *P* and yet whose grains are *P*. That is to say the *P*-form of glume and the *P*-form of grain appear to be inseparables, remaining associated throughout the vicissitudes attendant upon the production of F_2 and F_3 plants. Such characters may be called "genetic inseparables" [cf. "Correlation" as used by Collins (4)]. For the *K* type the same association prevails. Heterozygous plants (*I*) present an appearance best described as a skilful blend of the *P* and *K* forms. With *I* glumes, *I* grains are always found.

Glume-form or appearance, like grain-form, is the resultant of a number of characteristics and since the resultants are inseparable, so must the constituents be. Close inspection of a great number of plants (F_0 - F_3) leads to the conclusion that there is a considerable number of such inseparable constituent characters, and a list of them is given below. The simplest view of this matter is that one factor controls all the inseparables. The list is:

- (1) Length of glume.
- (2) Ribs on main lamina of glume.
- (3) Shape of tip of glume.
- (4) Curvature of keel of glume.
- (5) Consistency of material of glume (*P* is "papery," *K* is more rigid).
- (6) Length of grain.
- (7) Shape and size of cross-section of grain.
- (8) The angle at which the embryo of the grain is set into the endosperm.
- (9) Number and length of the hairs at the apex of the grain.
- (10) Distinctness of the outline of the apical pad of the grain ("Gipfel-polster"—Kcke).

For every one of these characters *I* proves to be an interparental blend.

To test the closeness of the association, the correlation between glume-length and grain-length was evaluated for F_0 . *P* and F_0 . *K*. If r = coeff. of correlation:

$$(F_0 . K) . r = + 0.348 \pm 0.044 (N = 395),$$

$$(F_0 . P) . r = + 0.392 \pm 0.037 (N = 526).$$

The values of the coefficient are, at first sight, surprisingly low. It is to be borne in mind however that circumstances of environment which affect grain-length, do not of necessity exercise a proportionate or

indeed any influence upon glume-length. Some two months before harvest the ear of the wheat plant has fully emerged from the sheath and, whereas its glumes have attained practically full development, the grain is just commencing to form—fertilization having, it may be supposed, just taken place. Two plants of the same glume-length may thus, if their post fertilization environments be markedly different, develop grains of distinctly different length, whereas under identical conditions they would, presumably, have developed grains of the same length.

Whatever may be the explanation of the low values of r , it is to be expected that if classifying by glume-length automatically ensures grain-length classification, then the value of r will be the same for P (or K or I) in F_0 , F_2 , and F_3 . As a test, r was evaluated for $F_2.P$. The first of the eight pairs of measurements made in every F_2 plant (see § II above) was used, i.e. first glume-length and first grain-length. Calculation gave:

$$(F_2.P).r = +0.301 \pm 0.090,$$

and it may be noted that:

$$(F_0.P).r - (F_2.P).r = +0.09 = \text{p. e. of } (F_2.P).r.$$

Thus r glume/grain appears to have reasonable constancy and therefore although the absolute value of r is not great, a constant relationship between glume-length and grain-length is inferred. Owing to the fact that glume development is not contemporaneous with that of grain, the relationship is liable to be concealed by environmental influences, particularly when it is expressed as a coefficient of correlation.

VIII. AN APPARENT RELATIONSHIP BETWEEN GLUME-LENGTH AND THE DEVELOPMENT OF HAIRS ON THE GLUME.

Both Polish and Kubanka are, from the point of view of ordinary descriptive botany, regarded as smooth-glumed wheats. As a fact each, and in particular $F_0.P$, exhibits a slight development of hairs on the glumes. In F_2 there were found a few plants decidedly hairy and very noticeably different in this respect from the parents. All plants more hairy than $F_0.P$ were noted and the distribution of their glume-lengths is given in Table XXIX. They numbered 56/494, but the data available do not permit of any particular construction being placed upon this ratio. It will be observed that the increased development of hairs appears to have taken place in association with glumes of lengths below the length range of $F_0.P$. This fact and the impression gained from an examination of the glume hairs of great numbers of $F_0.P$ plants, is in agreement with the finding of Backhouse (2) that "length of glume has

acted as an inhibitor of pubescence." Confirmatory evidence cannot be sought from the F_3 plants, for it is found that, comparatively quickly, glume hairs fall off or become so brittle that they are very readily rubbed off in handling, and the F_3 plants have been stored for five years.

IX. THE INHERITANCE OF SOLIDNESS OF STRAW IN THE CROSS.

When the "shift" in glume-length became apparent, it was decided to investigate some character unconnected with glume- or grain-length, to see if it manifested in F_2 any feature corresponding to the shift of glume-length. The straw was selected. P is solid, K is hollow, and it is noteworthy that in all cases in which "shift" of glume-length is observable [vide cases cited in § IV above], one parent was solid in straw and the other hollow. Absence of shift characterises one case only, viz. the Polish \times Rivet cross [Biffen (1)], and in this both the parents are solid in straw. Thus the nature of the straw might possibly be related to the shift in glume-length.

Biffen (1) for a Turgidum (solid) \times Vulgare (hollow) cross (Rivet and Red King were the varieties actually used) found a sharp 3:1 = hollow : solid in F_2 . In the cross here described it was difficult on many occasions to separate hollow and solid straws. "Intermediate-solids" were encountered and finally were included as solids. The F_2 was classified for straw by examination of its F_3 progenies, but in all three of the glume types (P , I , and K) the ratios were such as could not be ascribed to ordinary factor segregation, whether of one or more than one factor. Different ratios were found for every one of the glume-type constituents (K , I , and P) and a different one, again, for the complete F_2 .

The result is therefore negative—shift of glume-length is not connected with any simple peculiarity of straw inheritance—but the fact that unaccountably irregular ratios were obtained points to the need of a continuation of the straw investigation in subsequent generations.

X. EVIDENCE CONCERNING THE ENDOSPERM IN INHERITANCE.

That grain-length is a maternal character was one of the conclusions arrived at by a comparative study of the inheritances of glume-length and grain-length [see § VI (γ), p. 123 above]. Singleness of length-type of all grains borne by " I " plants was manifestly a *sine quâ non* of the acceptance of such a conclusion and it was thought well to re-examine the " I " grain question both theoretically and in practice.

For the cross here described F_1 data are not available but Biffen [(1) p. 38] found that all the grains borne by all the F_1 (and therefore "I") plants were identical in form and appearance and, within the limits of natural fluctuation, of one common length-type. His conclusion is thus precisely the one which has already been expressed in this paper—a conclusion which appears to be decidedly out of harmony with the double fertilization hypothesis.

As already recorded, the F_2 of the Polish \times Kubanka cross contained 267 "I" plants and their grains afford material for a more extensive inquiry than is possible with the necessarily limited number of F_1 plants in any cross. Table XXV contains the frequency distribution of the lengths of these grains, and it exhibits clear unimodality. That unimodality of distribution is unreliable as an index of singleness of grain-type has, however, already been demonstrated. By measuring the grains of the more numerous F_2 . I plants a distribution based on a greater number of observations might be obtained but it could afford no more evidence as to the existence of sub-types of length than does the F_2 . I distribution. Only by measuring a great number of grains and grouping the lengths of those which grew respectively into *K*, *I*, and *P* plants would it be possible to determine whether the same length of grain (i.e. of endosperm) was or was not associated with the *K*, *I*, and *P* types of embryo. It is proposed to make this test next year but in the meantime, metrical methods failing, the assistance of eye-judgment has been sought. Suitably devised tests demonstrated the ability of the eye to pick out infallibly the members of the three types from an artificially prepared mixture of *K*, *I*, and *P* grains. Beyond this, however, the eye could not go. Despite very extensive trials no evidence of sub-types either for length or appearance could be found among the grains borne by "I" plants. If, owing to "double fertilization," the endosperm is "hybrid" in nature, the fact appears to find no expression in the length or appearance of the endosperm both of which are such that they may be described as "maternal" characters.

The expectation derivable from an extension of the double fertilization hypothesis is of interest. Correns (6) and others assume that the secondary or definitive nucleus of the embryo sac exerts twice as much influence on the endosperm as does the single generative nucleus of the pollen grain—the reason for this being that the definitive nucleus is formed by the union of *two* of the polar cells of the original nucleus of the ovule. The male generative nucleus unites, of course, with the female definitive nucleus and from the divisions which follow this union,

the endosperm results. To express the effect of such a "double dose of femaleness":

let p = either a generative nucleus of a pollen grain which carries the "Polish" factor or one of the polar cells which unite to form the definitive nucleus of an ovule bearing the "Polish" factor. Let k be similarly used for "Kubanka."

From the gametogenesis of a heterozygous (I) plant the ♂ generative nuclei will be one half (p) and one half (k); the ♀ definitive nuclei will be one half ($2p$) and one half ($2k$). When such a plant is selfed the following endosperms will result:

$$3p, \quad 2p \mp k, \quad 2k \mp p, \quad 3k.$$

Thus four types of endosperm are expected among the grains borne by " I " plants.

An endosperm of constitution $3p$ develops, when nourished by an $F_0.P$ mother plant, into the characteristic "Polish" form of endosperm; but it may be that when nourished by the less vigorous " I " type of plant it is imperfectly weaned. Consequently its final length may be below the $F_0.P$ grain-length standard. Similarly $3k$ may be above the $F_0.K$ standard. The remaining types $2p \mp k$ and $2k \mp p$ will presumably lie between the $F_0.P$ and $F_0.K$ types and thus the expectation for the grains borne by " I " plants is four constituents whose length-modes have, owing to irregular development of the endosperms, closed inwards. The intensified overlapping would certainly produce unimodality of the whole distribution.

This theoretical consideration casts no new light upon the problem. As will be observed, it might be elaborated into an explanation of "shift"—an embryo, genetically Polish, fed during development on an " I " plant and nourished during germination by a similarly improperly weaned ($3p$) endosperm, may be expected to grow into a reduced or "shifted" P plant¹. Several experimental methods of investigating

¹ The probable validity of such an explanation of "shift" is very greatly increased by the interesting facts collected by Kidd & West [(18) especially Part IV, pp. 222—234]. A close—almost linear—relationship is claimed between the amount of food reserve available for the embryo and the adult vigour and ultimate yield of the plant resulting from the seed. If this claim be justified, it is to be expected that in the $P \times K$ cross, there will be a relationship between seed-weight and length of glume of plant resulting from the seed. That $F_2.K$ glume-length exceeds $F_0.K$ is consistent with the explanation suggested, for a $3k$ endosperm nourished by an $F_1.I$ mother plant is likely, on an average, to be heavier than if nourished by an $F_0.K$ mother plant. In the same circumstances an increase in vigour of the embryo accompanying the endosperm is perhaps a legitimate expectation.

this problem are possible but it has been decided to apply them to a cross whose parents are more widely separated in grain-length, -form, and -weight, than are Polish and Kubanka.

XI. CONCLUSIONS.

(1) In this cross, length of glume appears to segregate simply and in the F_2 the ratio long : intermediate : short = 1 : 2 : 1.

(2) The "longs" and "shorts" of F_2 although recognisably of the same form as the parents (F_0), yet differ from them in mean glume-length. The average of the longs is reduced by 24.8 % of the F_0 value. In the case of the F_2 shorts there is an increase over the F_0 shorts but it is smaller.

This change or "shift" in the longs of the F_2 is quite definite and cannot be explained by errors of sampling, seasonal variation, or any such cause.

(3) The "shifted" form of longs of F_2 breeds true as far as F_3 (it has not yet been carried further).

(4) When, in the selfing of F_2 heterozygotes, plants of parental type are again evolved, there is no evidence of super-added "shift." Likewise there is no evidence of a tendency to the restoration of F_0 values of mean glume-length, i.e.

$$(F_3 \cdot P \text{ ex } F_2 \cdot I) = (F_3 \cdot P \text{ ex } F_2 \cdot P) = F_2 \cdot P < F_0 \cdot P.$$

(5) For grain-length results are obtained analogous to (1), (2), (3) and (4). The percentage value of the "shift" is, however, less than it is for glume-length, e.g.

$$F_0 \cdot P - F_2 \cdot P = 12.5 \% \text{ of } F_0 \cdot P.$$

(6) All the available evidence supports the view that grain-length and glume-length belong to the same generation or, differently expressed, that grain-length is a maternal character. It is difficult to harmonise this view with the double-fertilization hypothesis.

(7) Numerous grain and glume characters appear to be genetic inseparables. Long-type glumes never contain short-type grains and *vice versa*. Despite the association of glume-length and grain-length, the correlation between these two variables is low. Certain reasons may be urged in explanation.

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(8) A development of hairs, far more marked than that exhibited by either parent variety, is found in certain of the F_2 plants. These plants are all of short glume type. Length of glume appears in some manner to inhibit the full development of hairs.

(9) The Inheritance of Hollow and Solid Straw is complicated and a relationship may possibly exist between "shift" in glume-length and nature of straw inheritance.

(10) The investigation is to be continued by growing on the pure F_0 types as well as the "shifted" parental forms from the F_3 . By crossing the "shifted" and F_0 types it is hoped to test the behaviour of "shifted" types in inheritance.

Table XVII (p. 131) presents diagrammatically a résumé of the measurable characteristics of the glume types in successive generations.

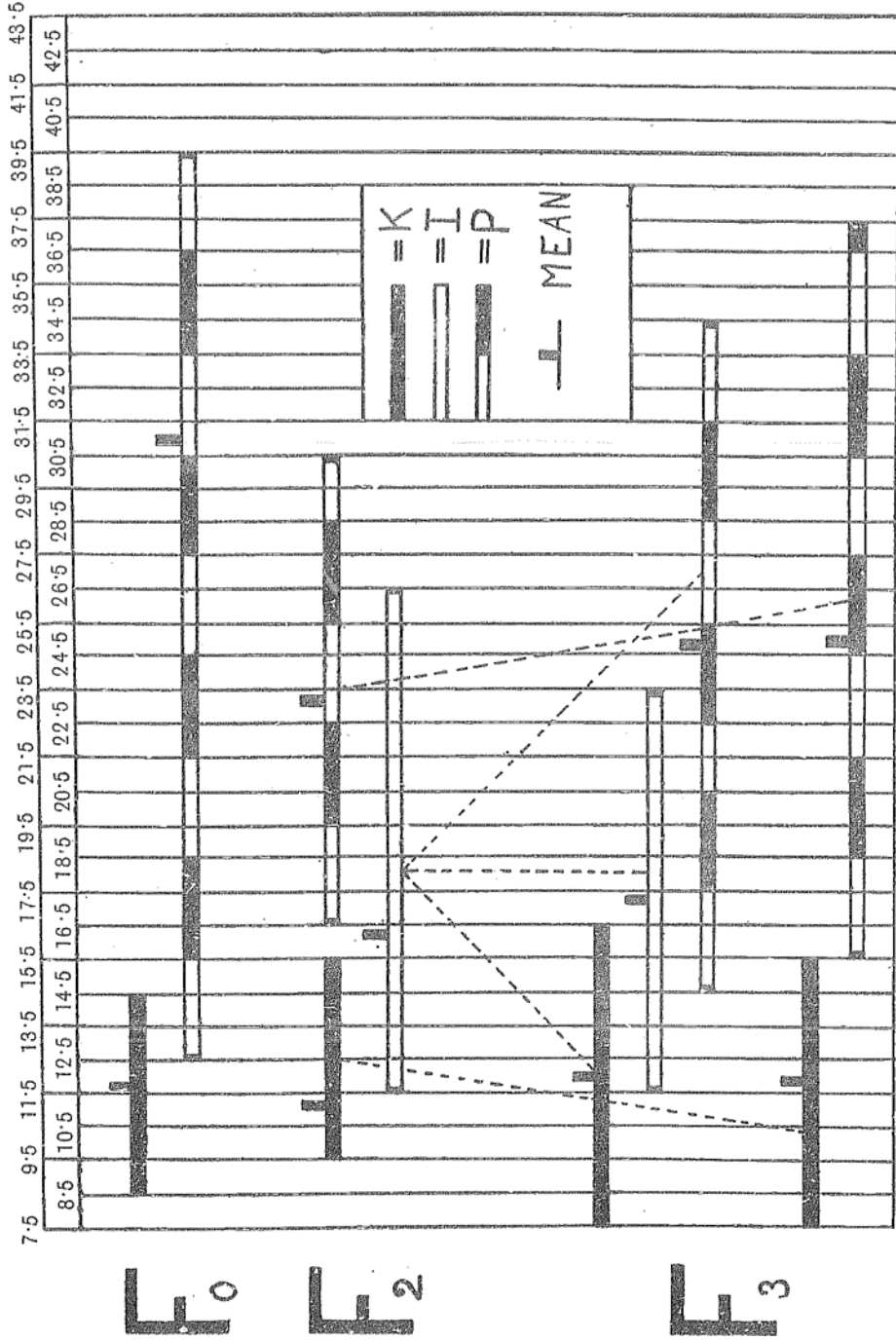
Opportunity is taken here to thank Professor R. H. Biffen, F.R.S., and Mr G. Udny Yule, M.A., C.B.E., for the help they have kindly given during the investigation.

TABLES OF FREQUENCY DISTRIBUTIONS OF GLUME- AND GRAIN-LENGTHS.

Glumes.

Table No.	Type and Generation
I	$F_0 . P$, i.e. Parent variety
II	$F_0 . K$, i.e. Parent variety
III	F_2 complete
IV	The 487 F_2 plants from which seed was obtained for F_3
V	17 F_2 plants which though fertile were unripe at harvest
VI	7 F_2 plants ripe at harvest but sterile
VII	19 F_2 plants unripe at harvest and sterile
VIII	$F_2 . K$, i.e. Kubanka type of the F_2
IX	$F_3 . K$ ex $F_2 . K$, i.e. descendants by selfing of the plants of VIII
X	$F_2 . P$, i.e. Polish type of the F_2
XI	$F_3 . P$ ex $F_2 . P$, i.e. descendants by selfing of the plants of X
XII	$F_2 . I$, i.e. heterozygote (intermediate) plants of F_2
XIII	$F_3 . I$ ex $F_2 . I$, i.e. heterozygous descendants of plants of XII
XIV	Complete descendants of the plants of XII (by selfing)
XV	$F_3 . K$ ex $F_2 . I$, i.e. K type of descendants of the plants of XII
XVI	$F_3 . P$ ex $F_2 . I$, i.e. P type of descendants of the plants of XII
XVII	Diagrammatic résumé of measurable characteristics of K , I , and P in F_0 , F_2 , and F_3 .

TABLE XVII. *A Résumé of the Measurable Characteristics of the K, I, and P Glume Types in F₀, F₂, and F₃.*



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Grains.

Table No.	Type and Generation
XVIII	F_0 . P , i.e. Parent variety
XIX	F_0 . K , i.e. Parent variety
XX	F_2 complete
XXI	F_2 . K , i.e. Kubanka type of the F_2
XXII	F_3 . K ex F_2 . K , i.e. descendants by selfing of the plants of XXI
XXIII	F_2 . P , i.e. Polish type of the F_2
XXIV	F_3 . P ex F_2 . P , i.e. descendants by selfing of the plants of XXIII
XXV	F_2 . I , i.e. heterozygote (intermediate) plants of F_2
XXVI	Complete descendants of the plants of XXV
XXVII	F_3 . P ex F_2 . P }
XXVIII	F_3 . P ex F_2 . I }

} from separate series of measurements (see § VI of text)

N.B. Table XXIX is a table of glume-lengths and refers to § VIII of the text.

Grains.

Class Means	Numbers of Tables										
	XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXV	XXVI	XXVII	XXVIII
5.5	—	2	—	—	2	—	—	—	—	20	4
6.0	—	—	—	—	5	—	—	—	10	43	19
6.5	—	9	3	2	17	—	9	—	31	123	53
7.0	—	47	11	5	56	1	36	5	82	262	94
7.5	—	111	32	10	169	2	73	16	199	509	207
8.0	4	187	89	30	399	14	167	45	589	679	324
8.5	7	36	127	36	347	20	199	68	721	864	321
9.0	37	2	151	24	189	40	274	87	691	845	343
9.5	56	1	67	4	25	23	149	40	340	585	199
10.0	165	—	7	1	5	1	95	5	138	319	76
10.5	154	—	—	—	—	—	23	—	19	112	4
11.0	81	—	—	—	—	—	3	—	2	30	—
11.5	18	—	—	—	—	—	—	—	—	3	—
12.0	1	—	—	—	—	—	—	—	—	2	—
Totals	526	395	487	112	1214	101	1028	266	2822	4396	1644

TABLE XXIX.

Class Means	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	Total
Frequencies	4	7	17	2	4	3	5	4	3	4	3	56

Glumes.

Class Means	Numbers of Tables																Totals
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	
7.5	—	—	—	—	—	—	—	—	0.5	—	—	—	—	—	1.0	—	
8.5	—	3.0	—	—	—	—	—	—	3.0	—	—	—	—	4.5	2.5	—	
9.5	—	36.0	17.0	12.5	2.5	—	2.0	12.5	60.5	—	—	—	—	34.0	22.0	—	
10.5	—	74.0	81.5	28.0	0.5	1.0	2.0	28.5	221.0	—	—	—	—	115.0	51.0	—	
11.5	—	118.5	52.0	47.5	1.5	1.0	2.0	44.0	337.0	—	—	—	1.0	217.0	89.0	—	
12.5	1.0	105.0	28.5	24.0	2.5	—	2.0	20.0	329.5	—	2.0	2.5	4.5	202.5	75.0	—	
13.5	—	51.5	29.5	23.5	—	—	4.0	184.0	—	—	19.0	19.0	18.5	153.0	36.0	0.5	
14.5	—	12.0	44.5	38.5	3.0	—	3.0	1.0	68.5	—	2.5	37.5	42.5	151.0	12.0	1.5	
15.5	—	—	47.0	46.0	1.0	—	2.0	2.0	13.0	—	9.0	44.0	69.0	186.5	2.0	1.0	
16.5	—	—	78.0	75.0	1.0	—	2.0	—	—	2.0	9.5	73.0	94.5	238.0	1.0	3.5	
17.5	—	—	46.0	43.0	1.0	2.0	—	—	—	2.0	18.5	40.5	110.0	265.0	—	3.0	
18.5	—	—	37.0	35.0	1.0	1.0	—	—	—	1.0	31.0	34.0	106.5	246.0	—	6.0	
19.5	—	—	15.5	13.5	1.0	—	1.0	—	—	6.5	49.0	7.0	61.0	181.5	—	13.5	
20.5	2.0	—	17.0	16.0	1.0	—	—	—	—	11.5	50.0	3.5	44.5	126.0	—	15.5	
21.5	0.5	—	13.5	13.5	—	—	—	—	—	12.0	86.5	1.5	18.5	114.5	—	19.5	
22.5	6.0	—	16.5	15.5	—	1.0	—	—	—	14.0	101.0	0.5	8.5	79.5	—	26.0	
23.5	16.0	—	11.5	10.5	1.0	—	—	—	—	9.0	96.5	1.0	1.0	81.0	—	17.5	
24.5	24.0	—	20.0	19.0	—	—	—	—	—	20.0	112.5	—	—	79.0	—	34.5	
25.5	14.5	—	8.0	7.0	—	1.0	—	—	—	6.0	102.0	—	—	92.5	—	40.0	
26.5	34.5	—	10.0	10.0	—	—	—	—	—	9.0	106.0	1.0	—	82.5	—	36.5	
27.5	38.5	—	5.0	5.0	—	—	—	—	—	5.0	78.0	—	—	63.5	—	33.0	
28.5	39.0	—	1.0	1.0	—	—	—	—	—	1.0	72.0	—	—	51.5	—	19.5	
29.5	48.0	—	—	—	—	—	—	—	—	1.0	53.0	—	—	30.0	—	18.0	
30.5	66.5	—	1.0	1.0	—	—	—	—	—	1.0	23.0	—	—	23.0	—	13.0	
31.5	63.0	—	—	—	—	—	—	—	—	—	18.0	—	—	13.0	—	6.5	
32.5	58.0	—	—	—	—	—	—	—	—	—	17.5	—	—	13.0	—	2.0	
33.5	69.5	—	—	—	—	—	—	—	—	—	6.0	—	—	6.0	—	4.5	
34.5	45.0	—	—	—	—	—	—	—	—	—	3.0	—	—	3.5	—	3.0	
35.5	38.0	—	—	—	—	—	—	—	—	—	1.0	—	—	0.5	—	—	
36.5	20.0	—	—	—	—	—	—	—	—	—	2.0	—	—	—	—	—	
37.5	11.5	—	—	—	—	—	—	—	—	—	0.5	—	—	0.5	—	—	
38.5	6.0	—	—	—	—	—	—	—	—	—	—	—	—	0.5	—	—	
39.5	2.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
40.5	1.0	—	—	—	—	—	—	—	—	—	1.0	—	—	—	—	—	
Totals	600	400	530	487	17	7	19	114	1237	101	1054	267	580	2854	292	318	

Means of classes are in millimetres

BIBLIOGRAPHY.

1. BIFFEN, R. H. "Mendel's Laws of Inheritance and Wheat Breeding." *Journ. Agric. Sci.* Vol. I. 1905—6.
2. BACKHOUSE, W. O. "The Inheritance of Glume-Length in *Triticum polonicum*; A Case of Zygotic Inhibition." *Journ. of Genetics*, Vol. VII. 1917—18.
3. CAPORN, A. ST CLAIR. "On a Case of Permanent Variation in the Glume-Length of Extracted Parental Types and the Inheritance of Purple Colour in the Cross *T. polonicum* × *T. Eloboni*." *Journ. of Genetics*, Vol. VII. 1917—18.
4. COLLINS, G. N. "Correlated Characters in Maize Breeding." *Journ. Agric. Research*, Vol. VI. 1, 1916.
5. YULE, G. UDNY. *An Introduction to the Theory of Statistics*, Ed. 1919, p. 303.
6. CORRENS, C. G. *Biblio. Bot.* LIII. 1—161.
7. GROTH, B. H. A. *Bulletins of N. Jersey Ag. Exp. Sta.* Nos. 228, 238, 239, 242, and 278.
8. ——. *Science*, April, 1914.
9. GATES, R. RUGGLES. "On the Modification of Characters by Crossing." *Amer. Nat.* Vol. XLIX. 1915.
10. PUNNETT, R. C., and BAILEY, P. G. "On the Inheritance of Weight in Poultry." *Journ. of Genetics*, Vol. IV. 1914—15.
11. —— and the late Major P. G. BAILEY, R.F.A. "Genetic Studies in Rabbits. I. On the Inheritance of Weight." *Journ. of Genetics*, Vol. VIII. 1918—19.
12. CASTLE, W. E., and PHILLIPS, J. C. "Piebald Rats and Selection; an Experimental Test of the Effectiveness of Selection and the Theory of Gametic Purity in Mendelian Crosses." *Carnegie Publ.* No. 195, 1914.
13. DAVENPORT, C. B. "Inheritance in Poultry." *Carnegie Publ.* No. 52, 1906.
14. LEAKE, H. MARTIN. "Studies in Indian Cotton." *Journ. of Genetics*, Vol. I. 1911.
15. EAST, E. M. "Inheritance in Crosses between *Nicotiana Langsdorfii* and *N. alata*." *Genetics*, Vol. I. 1916.
16. BELLING, J. "Inheritance of Length of Pod in Certain Crosses." *Journ. Agric. Research*, Vol. V. 1, 1915—16.
17. BALLS, W. L. *Studies of Egyptian Cotton*, 1909.
18. KIDD, F., and WEST, C. "Physiological Pre-determination; the Influence of the Physiological Condition of the Seed upon the Course of Subsequent Growth and upon the Yield." *Ann. App. Biol.* Vol. V. Nos. 3 and 4, April, 1919.