

ably primitive cottons as *G. Sturtii*, F.V.M.,\* retain the entire leaf throughout their development.

The depth of the segmentation, when present, varies within the same sub-species, as in the two forms of "Nyam-nyam kidney cotton;" possibly the Okra-leaf sport in American Uplands is another example. Such facts are suggestive of mutation, but mutations in *Gossypium* ought not to be mentioned until we know much more about natural crossing and heredity than we are likely to acquire for several years to come.

**The flower.**—In the course of an attempt to breed an uncrossable flower, to be mentioned again later, the author had had occasion to measure the various floral organs, namely, petal, style, staminal column, and filaments. The sequence of development of these in the bud begins with the petal, followed by the column and filaments, and ends with the style.

The fluctuation does not follow this order. Fifty-one plants in "77" family gave the following typical results:—

Petal ... ..	Mean, 59 mm.	<i>P.E.</i> $\pm 2.8$ per cent.
Style ... ..	" 33 "	<i>P.E.</i> $\pm 3.5$ "
Column ... ..	" 19 "	<i>P.E.</i> $\pm 5.6$ "
Filament ... ..	" 4.2 mm.	<i>P.E.</i> $\pm 7.7$ "

A portion of this increased fluctuation is probably apparent, being due to greater errors of measurement in the smaller organs, but much of the increase is certainly significant. One would rather expect the external organs to fluctuate most, but the reverse is the case.

The involucrel bracts are intermediate in their fluctuation. Their width in the same family gave a *P.E.* of  $\pm 4.0$  per cent. The ratio of width to length also gives a  $4.0$  per cent. probable error.

The measurements are taken with dividing compasses

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\* Watt, Sir G.

to the nearest millimetre except in the filaments, where half-millimetres are attempted. Three flowers are examined on every plant, and the means for all three are taken.

**First flower and maturation.**—The obvious effect of early stunting is to provide a long tail of late-flowering plants upon a graph which shows the date of the first flower. If the originally stunted plants are excluded, the *P.E.* of this date works out at a little more than four days in most families, or  $3\frac{1}{2}$  per cent. of the time elapsing between sowing and flowering.

The maturation of the flowers opening during early July at Cairo has been directly recorded by marking the flowers. The results for, *e.g.*, family “77” in 1911 gave a mean of forty-eight days with a *P.E.* of  $\pm 3.0$  per cent. The period is longer in the Delta.

**Flowering and bolling.**—The limits of the present volume do not permit of detailed discussion of the fluctuation from plant to plant in flowering and bolling curves, beyond the account of the possible controlling factors already given.

The influence of sowing-distance is shown in Fig. 44, four times the number of flowers being found on wide-sown plants as against field sowing. The point is important with regard to propagation of new varieties;<sup>32</sup> by wide-sowing we can obtain 100 bolls per plant from a strain which will only produce 15 to 20 in field crop.

The influence of defoliation by cotton-worm is peculiar, the flowering being immediately arrested, but subsequently extended much later than usual, so that a warm autumn may enable the ultimate yield to reach the normal.

A few points of interest arise with regard to the total production of flowers up to a certain date, and the bolls developed from them. The correlation between these two quantities was worked out in the wide-sown, very irregular family of “77,” for 1910, with the following results.

Total number of flowers per plant	Mean, 115	<i>P.E.</i> $\pm 29$ per cent.
"    "    bolls    "    "	"    50	<i>P.E.</i> $\pm 34$ "
Correlation between total flowers and bolls : $r = 0.85$ .		
(Imperfection of correlation is mainly due to shedding.)		
Percentage of retained flowers : Mean, 40.6 ; <i>P.E.</i> $\pm 7.5$ per cent.		

These figures demonstrate the manner in which errors accumulate during field experiments. Comparison of two rows or plots of the same variety becomes more and more erroneous as the plants grow older; comparison by the number of flowers has a lower *P.E.* than comparison by the number of bolls; this in its turn has a lower *P.E.* than comparison by weight of seed-cotton picked; this again is more precise than comparison by ginned lint. Fresh sources of error creep in at every stage, and the fact that field plots have a *P.E.* of  $\pm 6$  per cent., at least, becomes quite comprehensible.

**The boll.**—The three chief characteristics of the boll are its diameter, the number of loculi, and the shape. The first and last are determined from three full-grown bolls per plant, measured with parallel-jaw callipers, the form being expressed as a diameter in percentage of length. The number of loculi is determined by examination of not less than twenty bolls of one kind on each plant; thus forty bolls may have to be examined to obtain the critical number, if half are trilocular and half quadrilocular; such a plant receives the designating formula of 3.5. Plants whose bolls are all trilocular are designated 3.0; if all quadrilocular, 4.0, &c. For certain families the critical number has been raised to forty bolls of a kind (*e.g.*, Fig. 63).

Specimen data for these characters in Egyptian families are:—

Boll width ... ..	Mean, 25 mm.	<i>P.E.</i> $\pm 3.6$ per cent.
"    form ... ..	"    64.6    "	<i>P.E.</i> $\pm 3.8$ "
"    Loculi ... ..	"    2.81    "	<i>P.E.</i> $\pm 2.6$ "

The fluctuation of the last character is low, presumably because the number of loculi is differentiated at an early

stage of bud-development, whereas the diameter of the boll is partly dependent on the environment in which it exists during the first thirty days after the flower opens.

It may possibly be owing to this division of boll-maturation into two periods that we find no correlation of seed-weight with any of the boll-characters in pure strains, though such correlation is very evident in heterogeneous  $F_2$  families.

**Seed-weight.**—The mean weight of the seed is determined by weighing and counting samples of not less than 200 seeds. There is much to be done yet in determining the causes of fluctuation, by examining weekly pickings.

The highly irregular "77" family of 1911 had a mean at 0.097 gram, with a *P.E.* of  $\pm 8.3$  per cent.

Another family, of twenty-three very uniform plants with a mean at 0.095, had almost as much fluctuation, viz., *P.E.*  $\pm 7.0$  per cent.

The weight of a seed is completely determined by the mother plant, and not by the embryo. Thus the weights of single seeds of an  $F_1$  plant show no modality, nor does the weight of the embryo. Forty such seeds, weighed singly, gave the following fragmentary result.

Mean seed weight ...	0.180 gram	<i>P.E.</i> $\pm 5.9$ per cent.
"  testa  "  ...	0.078  "	<i>P.E.</i> $\pm 6.7$ "
"  embryo weight ...	0.102  "	<i>P.E.</i> $\pm 5.3$ "

Embryo weight = 57 per cent. of seed weight.

The difference between testa and embryo is slight, and both are equally important in causing fluctuation in seed-weight.

The causes of this fluctuation are obscure. Correlations have been plotted for all recorded characters, but with very few results. The values for "*r*" need not be given since a qualitative statement is sufficient for the available data. The only connections yet shown are: Leaf length,

some, positive; Height, doubtful, positive; Lint-length, slight, negative; Lint-weight, high, positive; First-flower, slight, negative.

None of these are very definite and the explanation lies in the fact that while height, leaf-length, and first-flower represent the mean result of a long period of environmental influence, the fluctuation in weight for any particular seed is probably fixed within a period of a few days.

The same explanation applies to the high *P.E.* of uniform families, which is nearly equal to that of the most irregular families.

Summarising, we may say that everything points to the root as the controller of fluctuation in seed-weight.

**Lint-weight and out-turn.**—We have already dealt with the correlation between weight of lint and seed, in discussing ginning out-turns. The correlation is less close in pure strains, taken plant by plant (*e.g.*  $r = 0.72$ ) than for the crop-samples there mentioned ( $r = 0.81$ ).

The fluctuation in lint-weight seems to be proportionally less than that in seed-weight; the *P.E.* being, *e.g.*,  $\pm 7.5$  per cent. as against 8.3 per cent. respectively in the same family. This statement probably requires revision for field crop conditions, since wide-sown plants give abnormally low ginning out-turns; the crop-samples gave a lower correlation between seed-weight and out-turn ( $0.220 \pm 0.094$ ) than between lint-weight and out-turn ( $0.316 \pm 0.091$ )\*.

The fluctuation in ginning out-turn for family "77" had a mean of 92 rotls, with a *P.E.* of  $\pm 3.5$  per cent. This is probably an excessively high figure, as the plants growing in the tanks gave much higher out-turns than the rest.

**Seed fuzz.**—Although this amount of "fuzz" on

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\* See Craig, J. I. (3).

the seed scarcely admits of statistical expression, it is sufficiently important to merit a comment. The cytology of the "fuzz" hairs is as yet unknown. They are certainly different from the lint hairs, but the demarcation may not be very obvious in abnormal seeds.

The presumably primitive cottons\* possess no lint, but abundant "fuzz" covers the seed-coat. Less "primitive" cottons have both fuzz and lint. In the cultivated cottons we find groups with "entire" fuzz like the primitive species, others with fuzz restricted to the hilum and raphe, and others with no fuzz whatsoever. The phylogenetic interest of the character is consequently high, especially since some evidence as to its factorial composition is available.

One of the chief features in this connection is the colour. Green, brown, and white fuzz are all known in most cultivated cottons, though—since the green is unstable—green and brown are not easily distinguished. The lint colour, on the other hand, ranges through browns and creams to white, while even the browns appear to be of various origins. There is, however, a green-linted cotton known as "Texas Wool" which appears sporadically in fields of American Upland, and breeds true to the green lint. This stock is of interest because it provides a suggestion of possible phylogenetic connection between lint and fuzz.

Apart from colour, however, we find a certain amount of fluctuation in the amount of fuzz. Within a pure strain this is very slight, but when severe constitutional changes are forced upon a semi-fuzzy stock by crossing or by a novel environment, the fluctuation may be conspicuous.

**Lint-length.**—Since data on fluctuation in lint-strength are not yet available, we can quote for lint-

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\* Watt, Sir G.

length only of those characteristics which interest the consumer of the crop.

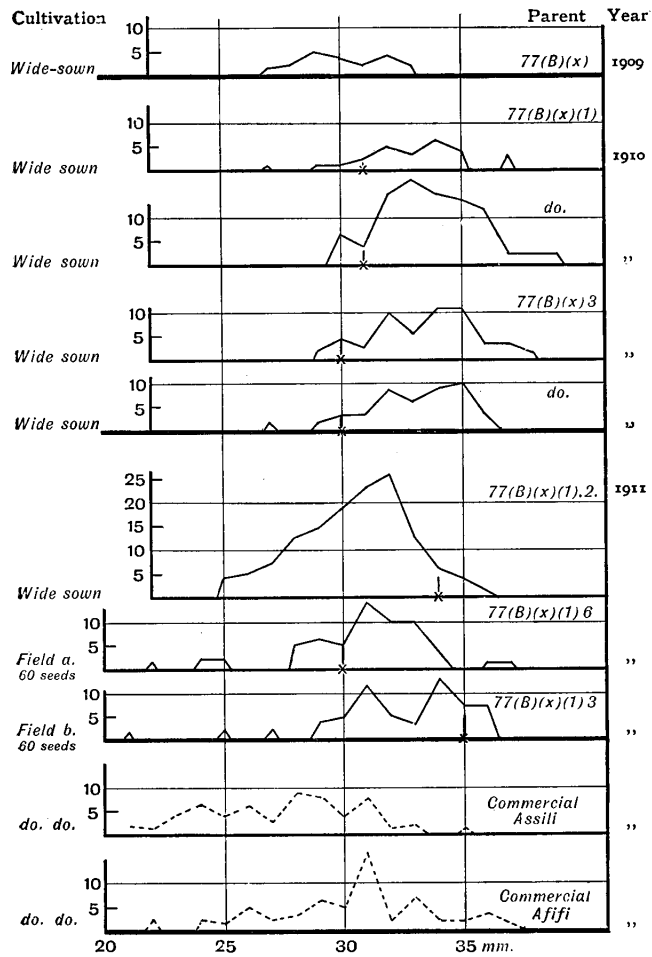


FIG. 49.—MAXIMUM LINT-LENGTH OF SINGLE SEEDS.

- × Mean length of parent plant.
- Pure strain of Afifi.
- ... Commercial "varieties."

"Field a and b" were different field plots carrying alternating rows of various cottons.

Fluctuation in this respect has been shown to vary with the season and cultivation, with the sowing distance, &c.

The extent of this fluctuation is determined on the mean maximum lint-length of five seeds taken at random from the plant, and give such results as a *P.E.* of  $\pm 2.9$  per cent. on a mean of 33.5 mm.

Taking single seeds only, we obtain such results as those shown in Fig. 49. There is a definite bi-modality in some of these graphs; probably further investigations of such modes will show us how to persuade a plant into the production of abnormally long lint as a normal product.



## CHAPTER VI

### COMMERCIAL VARIETIES

THE probable origin of the type of cotton plant grown in modern Egypt has been discussed in the historical section of this volume. Many commercial varieties have been developed within this type. Some are extinct, and are only known to the author by name; such were Gallini, Abyad, Hariri, Bamia, Hamouli, Zafiri, and Ziftawi. Others which have been subjected to examination by the author, but which have not been able to make good their footing in the market, are Brown Yannovitch, Charara, Kerki, and Bolanachi. Others again are cultivated to a limited extent, such as Sea Island (both old stock and imported seed), Sultani, and Voltos.

The main varieties at present cultivated on a commercially important scale are Yannovitch and Sakellaridis in the "fine-spinning" group; Abbassi, as the white and moderately fine type; Ashmouni, Nubari,\* Afifi and Assili in the "bread and cheese" group.

Ashmouni is the putative ancestor of all these, by way of Afifi. The origin of any one variety is most difficult to ascertain, but the majority probably arose as single-plant "selections." In the case of Yannovitch this is definitely known.

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\* Nubari is not considered as a "bread and cheese" staple at present, but its future probably lies that way. The matter is discussed in as yet unpublished reports by the author on the Lancashire cotton demand.

Lastly we have the weed cotton, so-called "Hindi." It is not a cultivated variety, but sporadic as a weed mixed with other varieties. In general appearance it could easily be mistaken for American Uplands, but the seed is devoid of fuzz. Within the Hindi type there are various sub-types; thus, of some five hundred plants grown from Hindi seed of commercial origin, only about a third were very hirsute, while others were completely glabrous.

The seven important varieties mentioned differ in age. Ashmouni, or rather the name, dates back to the 'fifties of last century. Affi was introduced commercially about 1887, Abbassi in 1893, Yannovitch in 1899, Nubari in 1907, Sakel in 1909, and Assili in 1910. These dates are, of course, approximate, being those years in which a conspicuous quantity of the lint reached the spinners.

Now with this multiplicity of varieties it might be imagined that their differentiation was easy. Such is by no means the case. All the varieties are similar in external appearance; even when grown side by side in field rows on the same plot, they cannot be distinguished with certainty. There may be far more difference between individual plants within the same variety than between two distinct varieties.

Certain physiological differences are found, however, but they are not very easily expressed in precise terms. Thus Ashmouni is the crop of Upper Egypt, Yannovitch is concentrated round a centre in the N.E. of the Delta, and Affi gave the best results in the Southern Delta. Again, Yannovitch is credited with cropping lightly, about 10 per cent. below Affi or Abbassi, and this opinion is supported by the scanty data available.

One of the cherished fables of the practician teaches that heavy crops and fine staple cannot co-exist. The inaccuracy of this belief, though long suspected, has only recently been proved by the Sakel variety. The bolling curves of Affi, Sakel, Assili, Voltos, and the pure strain

“77” are shown in Fig. 42, determined from weekly pickings of five rows apiece, with a *P.E.* of  $\pm 10$  per cent. for any point in the curves.

The total yields of these curves work out as follows :

“77” ... ..	Yield = 25.1 bolls p.p.	<i>P.E.</i> $\pm 0.6$
Assili ... ..	„ = 19.9 „	<i>P.E.</i> $\pm 0.5$
Sakel ... ..	„ = 18.5 „	<i>P.E.</i> $\pm 0.5$
Voltos ... ..	„ = 17.4 „	<i>P.E.</i> $\pm 0.4$
(Afifi ... ..)	„ = 20.0 ? „	<i>P.E.</i> $\pm 1.5$ )

Thus the three commercial varieties included in the list are practically identical with regard to yield.

We have already figured the length of the lint of “77” under these conditions, and a comparison of this pure strain with similar rows of the two varieties Afifi and Assili should be of interest, one being old and notably irregular, the other new and presumably uncontaminated. The data are plotted in Fig. 49. The *P.E.* of random single seeds in respect of mean maximum lint-length being  $\pm 6.3$  per cent., we find values of 7.8 per cent. for Assili and 7.5 per cent. for Afifi.

Thus, on the statistical evidence of lint-length, the newest “variety” is by no means uniform. This conclusion is abundantly confirmed by other evidence. Thus, the Sakel cotton contains at least two entirely distinct types of seed fuzz; the presence of these two types might possibly be unimportant, but in all probability it points to a heterogeneous origin for the original plant or plants. Such heterogeneity might occur even in the offspring of a single-plant selection, if the gametes of this plant were not uniform; in other words, if the plant was not pure-bred.

Such constitutional irregularity being manifest even in new varieties (see also Fig. 50), our next step must be to examine the cause. So soon as a family becomes heterogeneous, so soon does natural selection begin to operate. Once natural selection has begun, any sequence of alterations is possible. The usual result of such

sequences is to stimulate the belief which lies dormant in the minds of most people—practical and otherwise—namely, that all man-made plant varieties suffer from an innate perversity, due to their “un-natural” origin, which causes them to “revert” at the first opportunity, and so to revenge themselves on human interference.

Up to the present point we have considered only the zygotic constitution of the “variety,” and have merely laid emphasis on the fact that when a “variety” of cotton plants is inspected, plant by plant, the component individuals are not usually identical; we have seen, in addition, that the differences between nominal varieties are *mean* differences, which are negligible in most morphological characters, slight in physiological characters, and are definite only in respect to the nature of the commercial product—the lint hairs.

Our analysis has now to be driven much deeper. We have to investigate the origin of these zygotes to ascertain whether they are derived from identical gametes or not, and to determine what effect their constitution may have on succeeding generations.

**Gametic impurity.**—In the older writings on plant-selection we find continual references to “transmitting power,” coupled with advice to test this power by examining offspring. The reasons for this precaution are now better understood; “transmitting power” is not a mysterious vital function, but can be reduced to formulae. The causes of difference in this respect are two-fold.

In the first case, the plant originally selected may have been an extreme fluctuation and its offspring will therefore regress to the mean.

In the second case, with which we are now concerned, the original plant was heterozygous, derived from a natural or artificial hybridisation. Such hybridisation might have taken place in the previous year—the plant thus being an

$F_1$ —or more probably several years before, in which case the plant may be denoted as  $F_x$ . In this second case we are dealing with an entirely different set of phenomena, superadded to fluctuation. The segregation of the character-bearing factors in sex-cell formation, with their reunion into new combinations at fertilisation, produces a set of offspring which differ constitutionally amongst themselves. The complexity of these differences will depend on the number of characters in which the original plant was heterozygous.

An example of such a plant may be quoted from the author's records. In 1909, while examining an old field-book of 1905, a note was found which gave the names of plants in flower at a very early date. They were all Uplands with one exception. This exception was a group of plants grown from a boll of Kerki, called No. 95. The few seeds available were taken from the files and sown in 1910, since an early-maturing Egyptian stock was much needed. Only five plants were raised, of which four were slightly stunted, while the best and earliest was found in the autumn to bear an inferior and quite distinct type of lint. Whether this plant was an  $F_1$  from 1905, or an  $F_x$  from an earlier cross, our records could not disclose. The former is more probable. The remaining four were again fertilised naturally, and four families raised in 1911. They were fairly early, and—except for a few natural hybrids from crossing in 1910—were uniform in most respects excepting height. The original plants had been irregular in height, owing to stunting, but the offspring gave the following figures for height in October.

	Parent Height.	Offspring.		No. of Plants.
2	85 cm.	Mean, 117.7 cm.	<i>P.E.</i> $\pm$ 12.0 per cent.	94
3	110 "	" 138.4 "	<i>P.E.</i> $\pm$ 11.8 "	118
4	145 "	" 154.0 "	<i>P.E.</i> $\pm$ 11.5 "	145
5	80 "	" 138.2 "	<i>P.E.</i> $\pm$ 8.3 "	23

Inspection of the frequency curves showed that No. 95. C. 2 was breeding true to shortness, 95. C. 4 probably

to tallness, while 95. C. 3 and 5 were throwing out shorts.

The uniformity of the deviation, which does not reflect the heterogeneity of 2 and 3, is due to the fact that the plants were growing in pairs, and had not been checked for stunting.

Such an experience is the rule rather than the exception. Thus, a series of 75 plants of various varieties were examined in four characters, and their offspring compared with them. The results were as follows:—

*a.* Offspring like parent in thirty-eight cases; some unlike in thirty-seven cases.

*b.* Alterations in each character, twenty-five, fifteen, sixteen, and fourteen cases respectively.

*c.* Alteration of all four characters took place in two cases, of three characters in seven cases, of two in fifteen, of only one in thirteen.

There is no recorded difference between the different commercial varieties in this respect. The newest are equally heterozygous with the oldest, though with less intensity of difference.

The cause of the impurity—which soon appears even when the original strain was pure—is to be found in the act of natural cross-fertilisation, or vicinism.

The effects of this double impurity need scarcely be elaborated. It is obvious that such a welter of unequal individuals must form an excellent medium in which natural selection can work. The transference of a “commercially pure” variety to a new district will be followed by “acclimatisation”; such acclimatisation will be perfectly genuine, but it will not be due to any mysterious impress of the environment on the individuals.<sup>11, 15</sup>

Again, if such gametic contamination is continuous from year to year, and if our variety is not isolated upon an island in mid-ocean, we find a steady admixture taking place with other varieties. Such obvious contamination

as takes place through seed mixture is relatively unimportant in comparison with contamination of the ovaries by foreign pollen. We have already laid emphasis on the external similarity of the different varieties, and its bearing now becomes apparent. A field grown under the name of Affi might consist in reality of a mixture of five or six varieties with the original stock, together with all possible combinations and permutations of their multifarious gametes, but the difference would be almost

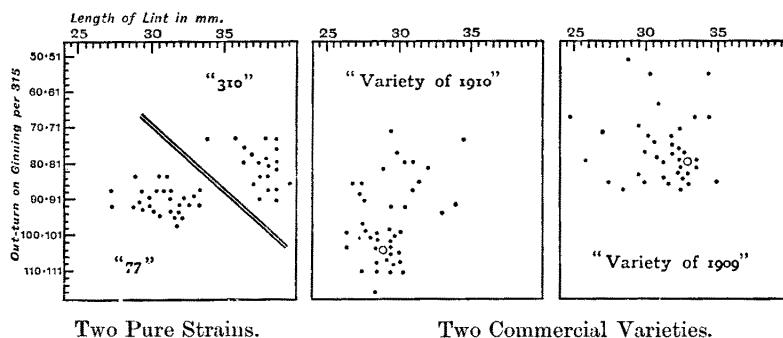


FIG. 50.—THE IMPURITY OF COMMERCIAL VARIETIES.

Target-diagram plotted from random single-plant samples in 1911.

Identical treatment, site, cultivation (wide-sown) and methods.

Compared in respect of only two important commercial characteristics.

○ = Variety-type, under given conditions.

invisible till the bolls opened. The mere fact that such a cotton as Yannovitch was a simple single-plant isolation from Affi demonstrates this statement sufficiently without resort to our detailed tables of plant to plant differences (*e. g.*, Fig. 50).

Further, although the author has quoted Egyptian illustrations, the same arguments apply to American Uplands, to Sea Islands, and to the few Indian cottons which he has studied. Mr. H. Martin Leake has demonstrated exactly similar heterogeneity in both

zygotes and gametes for Indian varieties, but the Egyptian examples are perhaps more striking, on account of their higher economic value.

Even in a uniform environment, therefore, a commercial variety of cotton must change and may deteriorate. We might almost say that the change must be in the inferior direction, since a successful new variety is mostly superior to its parent stock, and will regress if contaminated by it. A plausible fiction declares that the life of a variety of Egyptian cotton is limited to fifteen years. The kernel of truth within this dogma should now be apparent to the reader, and it should further be self-evident that the life of a variety might be prolonged indefinitely by suitable precautions.



## CHAPTER VII

### NATURAL CROSSING

WHEN the author first began his researches it was generally assumed that cotton was self-fertilised, and the only precise statement to the contrary was that of Webber, who had found 5 per cent. natural crossing between adjacent rows of distinct varieties. At the present day the seriousness of the crossing error has been demonstrated and admitted in many countries,\* but the importance of the subject does not end with this conversion.

**Field conditions.**—The author's first concern was to investigate the amount of crossing which had taken place in field crop during 1904 by examining the offspring from random single bolls of that year.<sup>5,8</sup> It was found that when a plant did not give uniform offspring, resembling itself, the difference of the offspring from the parent might be of two kinds.

In one case the offspring, or some of them, bore characters which were dominant over those of the parent; thus a 40 mm. lint might be derived from a 25 mm. lint; the presumption here was that all or some of the parent ovules had been crossed in the previous year by pollen from a long-linted plant. This was the rarer case, which in itself defines the amount of natural crossing, if we take

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\* Notably Leake, H. M. (1), (4), and Allard, H. A.

the number of such cases in proportion to the total number of plants, or bolls, originally chosen for testing. This number was 5 in 75 in the original trials, but it must be remembered that not all the vicinistic pollen parents will have characters dominant over those of the mother plant; in any one character the chances will be even for or against such recognition. These chances can be reduced by taking more than one character, but when the two intercrossed characters are identical, or nearly so, the observational errors will prevent detection. Thus, we shall not be far wrong if we double the number of cases observed when working with two pairs of characters, so that our figure becomes 10 vicinists in 75, or 13·3 per cent.

In the other case we find that some offspring bear characters which are recessive to those of the parent. A lint of 40 mm. in this case gives rise to some plants with 20 mm. lint. The presumption here is that the parent was a heterozygote, produced by natural crossing in some year antecedent to the one in which the seed was taken from the field, having been simply self-fertilised in that particular year. The number of such  $F_r$  plants in the original total is nevertheless dependent on the amount of crossing which takes place every year, and should serve as a check upon the direct observation of the former case. If now we assume simple Mendelian segregation for the characters we employ, or prove it by growing further generations from these splitting forms, we see that the number of such  $F_r$  heterozygote plants depends not only on the renewal of that number each year by fresh crossing but also on its reduction each year by segregation of homozygotes from them.

If crossing to the extent of 10 per cent. per annum were unaccompanied by segregation, we should find the number of vicinists increasing along a logarithmic curve, since some of the crossed strains would be re-crossed in

subsequent years. Thus, the years would yield:—  
A, 0 per cent., B, 10 per cent., C, 19 per cent., D, 27·1 per cent., &c.

Again, if we start with  $F_1$  plants, all being identical, allow no further crossing, and consider one allelomorphic pair only, we shall obtain the following series,  $P$  denoting homozygotes, and  $H$  denoting heterozygotes. A, 100 per cent.  $H$ . B, 50 per cent.  $H$  and 50 per cent.  $P$ . C, 25 per cent.  $H$  and 75 per cent.  $P$ ., &c. In other words, assuming the productivity of  $H$  and  $P$  to be equal, the hybrid form will decrease to infinitely small proportions. When two pairs of characters are involved, the rate of decrease of  $H$  will be slower. Instead of a 1 : 2 : 1 ratio in the year B, or 2  $H$  : 2  $P$ , we shall have the ratio of 1 : 1 : 2 : 2 : 4 : 2 : 2 : 1 : 1, or 12  $H$  : 4  $P$ , being 25 per cent. instead of 50 per cent. of homozygote forms.

Combining these two antagonistic processes, crossing and segregation, we come to the following general algebraic statement.

For  $y$  pairs of simple allelomorphs involved in a cross we obtain in  $F_2$  :—

2 $y$  homozygotes ( $P$ ) from 4 $y$  individuals.

Since crossing is renewed every year we can consider this as a general value for purification.

In each generation let  $xP$  become  $H$ , by crossing, and  $yH$  become  $P$ , by segregation.

Then the composition of the crop will be :

$$\begin{aligned} \text{1st Year : } & P \text{ only.} \\ \text{2nd ,, : } & (1-x)P + xH. \\ \text{3rd ,, : } & \{(1-x)^2 + xy\}P + \{x(2-x-y)\}H. \\ \text{4th ,, : } & \{(1-x)^3 + xy(3-2x-y)\}P \\ & + x\{3-3(x+y) + (x+y)^2\}H. \end{aligned}$$

Hence

$$\text{nth year : } H = \frac{x\{1 - (1-x+y)^{n+1}\}}{x+y}$$

When  $n$  is infinite (or practically in our case when it exceeds ten):

$$x\{1 - (1 - x + y)^{n-1}\} = x$$

and

$$H = \frac{x}{x+y}$$

In the 75 cases already mentioned, we found, dealing with two pairs of characters, that there were twenty-six cases of recessives splitting out from dominants. Thus  $H = \frac{26}{75}$  after  $n$  years

With two pairs of characters

$$y = \frac{2^2}{4^2} \text{ or } \frac{1}{4}$$

And since

$$H = \frac{x}{x+y} = \frac{26}{75}$$

$$\therefore x = 0.132.$$

Thus there was 13.2 per cent. of natural crossing as the mean value for past years.

By direct observation we found five vicinists from the previous year, implying about ten altogether, or about 13.3 per cent. of natural crossing in 1904.

The two results agree.

The absence of facilities has prevented the author from carrying this analysis further by the use of pure strains planted under field conditions, but a value of 5 per cent. to 10 per cent. for natural crossing under field conditions in Egypt has been confirmed by numerous, though non-systematic, pieces of evidence.

This value is expressed in terms of flowers crossed to total flowers ripening. The possibility of mixed pollination should not be disregarded, since we shall see that hybrid and selfed embryos may be formed side by side in the same ovary. The expression of the value in terms of ovules crossed to ovules ripening would therefore be preferable.

**Prevention.**—The evidence as to the means by which the cross-pollination takes place is not yet as full as we should like it to be, but the greater part is performed by bees. Tests for wind-blown pollen made by the author with glycerine smears on glass plates have given negative results on the breeding plot, though a certain amount of pollen must be dislodged in this way in close-sown field

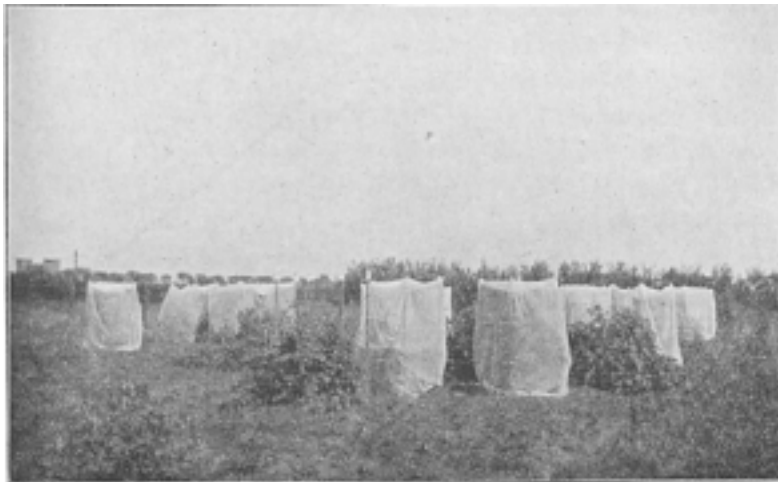


FIG. 51.—NETTED PLANTS.  
First crosses and parents.

crop.\* The remedy, therefore, seems to lie in the exclusion of bees from the flower. In most countries this can be done by covering the flowers with paper bags, but the method fails in Egypt, since about 95 per cent. of the flowers thus treated are promptly shed; this shedding appears to be due to the local interference with transpiration, and consequent over-heating of the tissues. We have therefore employed mosquito-nets, which cover the whole plant, being supported over it on four posts. (Fig. 51). Practically no vicinism then takes place, though

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\* See Allard, H. A. (2).

one or two suspicious cases have been recorded. The method has its own disadvantages, however, the first being that of expense, while the second is that some strains resent the treatment, and refuse to hold their bolls. Ratoon plants, *i.e.*, plants which have been cut back and allowed to shoot again in subsequent years, usually grow well under the nets, as also do most American Uplands, but—though erratically—many Egyptians are failures. When the method was first employed we had yet to discover the sunshine effect; this effect is precluded from its full operation by the permanent veil of netting, and netted plants consequently grow during the day, becoming abnormally tall. Improvements are being made by substituting wire gauze for mosquito net, using larger cages, and so forth, since the perfection of some preventive method of this nature lies at the very foundation of all cotton-breeding and of seed-supply.<sup>32</sup>

Another obvious possibility is the discovery, or manufacture, of a cleistogamic flower, which shall obstinately refuse to admit foreign pollen to its style. At one stage of these researches the author seemed to be well on the road to success in this direction, and the story of the ultimate failure is not without suggestiveness.

**The short-style flower.**—At the time when it was being realised that natural crossing would be a permanent source of trouble, confusion, and error, the question of floral structure naturally came under consideration. No hint of the existence of uncrossable cotton flowers\* could be found, but it seemed reasonable to expect that if we could decrease the opportunity for foreign pollen to reach the style, we might expect vicinism to diminish.<sup>13</sup>

The cotton flower has a dense brush of anthers, borne on a cylindrical column, through the centre of which the style projects. The length of this style, and the extent

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\* Compare Howard and Howard recently on the related genus *Hibiscus*.

to which it protrudes, varies in different strains and species. Most American Uplands have a much shorter style than Egyptians, and plants were noticed in  $F_2$  of Upland Egyptian crosses, whose styles did not protrude beyond the column. The inheritance was therefore investigated statistically, and from a cross of 29 mm. style with 20 mm. column, upon 24 mm. style with 13 mm. column, we bred several strains with such flowers as the one shown in the frontispiece. The plant from which this flower was photographed was an  $F_2$ , and its descendants were grown up to  $F_5$ , still breeding true to this flower form. In  $F_4$  they had a mean style length of  $18\frac{1}{2}$  mm. with a column of  $14\frac{1}{2}$  mm.: the anther filaments being  $4\frac{1}{2}$  mm. long made up the length of the brush to 19 mm., which sufficed to cover the style completely, so that it was visible only in end view, whereas the style of the Egyptian parent had projected for more than half a centimetre.

The short-style flower was thus at our disposal, but without avail. Four such plants from an  $F_3$ , similar to this respect, but otherwise differing, which had been growing close together in 1908, gave the following offspring in 1909: A. 26 plants; 7 rogues. B. 19 plants; 5 rogues. C. 47 plants; 16 rogues. D. 36 plants; 12 rogues.

The percentage of rogues due to undoubted natural crossing in the four families was thus respectively 26, 26, 34, and 33. The control families grown from long-style brothers of these, gave the same range of variation, from 25 to 35 per cent. These figures have been extended since, but without improvement, and we are driven to the conclusion that the accessibility of the style is a minor factor in natural crossing, under the conditions of our breeding plot.

The figures for the breeding plot had always been so much higher than the 5 to 10 per cent. on which we decided for field conditions, that this last reverse led the

author to reconsider the whole subject from a totally different point of view.

**The breeding plot** (Figs. 52*a* and 52*b*). We have thus far found that floral structure has no protective effect. In addition it should be noted that the geographical position of any plant on the plot seems to make but little difference; in two cases we have found natural hybrids



FIG. 52A.—THE BREEDING PLOT.

bearing a semi-red leaf, being first-crosses with a single plant of Willett's Red-Leaf, which was kept in a corner of the plot from year to year; these natural crosses had been made over a distance of 50 metres, the interval being occupied by dozens of other plants.\* Further, we have found indications that different varieties, or even different plants, growing side by side, show differences in their

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\* See, however, Leake, H. M. (4).



liability to natural crossing; we have just stated that such differences cannot be due to any obvious cause such as position or floral structure, so we are driven back upon a more abstruse explanation.

The hypothesis which has been framed to account for the facts observed is based upon an analogy drawn by Prof. Marshall Ward many years ago, between the pollen



FIG. 52B.—THE BREEDING PLOT.  
Irrigating Sudanese Tree-Cottons.

tube and the hypha of a parasitic fungus. We find in mycology that within the same strain of host-plant, different species and varieties of the same fungus possess different infection-capabilities. Conversely, the same fungus may be able to attack one strain of its host-plant with ease, while another strain may be practically immune.

Using these facts to help us in forming conceptions as to the possible behaviour of pollen, we see at once that some

such assumption as to differential susceptibility and infectivity between any style-pollen pair would lead us a long way. The method which has been employed by the author in testing this possibility, though on a very small scale as yet, is a method of mixed pollination. Equal quantities of foreign pollen and self pollen are placed on the style of a flower at the same time, as early as possible in the morning and the two sets of grains are allowed to compete with one another in the race down the style. The fact that artificial hybrids can easily be made between Upland and Egyptian in either direction shows that neither style is immune from the other pollen. Nevertheless it is quite possible that the tube from self pollen may grow faster in its own style than a foreign tube can do. Thus, on account of some effect, probably toxic, but as yet obscure, the foreign pollen-tube is beaten in the race down the style, and the majority of ovules are fertilised by the first arrivals, or self-tubes.

Using such a method, with all possible precautions to ensure equal opportunity to both sets of grains, we found that mixed pollinations of Egyptian by Upland, and the reverse, gave us ten natural hybrids in 330 ovules fertilised, or 3 per cent. of vicinism under the most favourable conditions for its manifestation. There was no significant difference between the reciprocal mixings. This figure is far below the minimum which we can possibly admit for field vicinism between plants of the same nominal variety. A new factor must therefore be involved, and we shall, in terms of our hypothesis, denote it as "relative immunity," regarding the pollen-tube of one kind as parasitic on the style of the other.

A curious side-light on this result is given by the Hindi cotton. Though the latter plant crosses readily with Egyptian under artificial treatment, and though it may amount in some fields to 15 per cent. of the crop, yet Hindi  $\times$  Egyptian hybrids are merely frequent in the

field. Certainly the error of natural crossing must be less between Hindi and Egyptian than between two Egyptians.

With a value of 3 per cent. for American and Egyptian, and of 10 per cent. for Egyptian and Egyptian, under the most favourable conditions, the occurrence of such values as 35 per cent., mentioned above, leads us to suspect that the story is not yet complete.

Before proceeding further we must define the value of our "percentage vicinism" with more exactitude. We are agreed that computation on the basis of the number of ovules is the most precise, but it remains to decide how we shall recognise those ovules. The difficulty which arises in recognition is due to the fact that all  $F_1$  hybrids, and most  $F_x$  hybrids, germinate much more energetically than their parents. In this peculiarity lies the great weakness of simple "selection methods." The precise reasons for this difference are still not clear, but knowledge of the fact is very old. It is therefore not sufficient to count the number of vicinists in a population raised from contaminated seed; we shall be nearer to the truth if we take the ratio of vicinists to the number of seeds sown, thus assuming that all the seeds which did not establish themselves were pure-bred. In inter-Egyptian crossing this factor will be insignificant as compared with its importance in crosses of Egyptian with Upland. In the latter case the author has been the victim of such absurdities as the cultivation of a family which contained 100 per cent. of vicinists; the soil tilth was not good, the weather was cool, and between the two perils of mechanical resistance and "sore-shin" not a single selfed embryo survived.

When attempting to account for amounts of real vicinism which rise as high as 30 per cent., we must consider the nature of the pollen to be found on the breeding-plot. This plot has contained cottons from Egypt, from America, from India; indigenous cottons

from Arizona, from the Sudan, &c. More than this, it has contained plants of  $F_1$ ,  $F_2$ ,  $F_3$ ,  $F_4$ ,  $F_5$ , and  $F_6$ , raised from crosses between American Uplands and Egyptian. Confining our discussion for the sake of simplicity to the  $F_1$  of such crosses, it is obvious that we possess an infinite variety of pollen grains on an acre of land. To estimate the number of allelomorphic pairs involved in the cross of "38" (King) with "89" (Charara) at fifty would be very conservative. The number of possible combinations of these pairs works out at a figure which, for our present purpose, we may consider as infinite. Now, if Mendelism is not a delusion, this infinite number of combinations corresponds with an infinite variety of nuclear composition, on the part of the male gametes. It is true that these gamete-nuclei are devoted to sexual purposes, but their relations, the vegetative nuclei of the pollen grains, are generally admitted to control the growth of the pollen-tube, and these are of identical composition with the gamete nuclei. Consequently, we may reasonably expect to find some correlation, however indirect it may be, between the gametic differences and the physiological differences in growth-rate of the pollen-tube. Such relation would imply a greater "variability" in the growth processes of pollen tubes from an  $F_1$  flower than that which we find in a pure strain. The standard deviation, or probable error, in the behaviour of  $F_1$  pollen-tubes under a given set of conditions would necessarily be much greater than that of the pollen-tubes in a pure strain, whether Egyptian or American.

Regarded in another way, this conclusion may be stated thus. If 3 per cent. of the pollen-tubes from Upland pollen fluctuate sufficiently in a positive direction to enable them to beat 3 per cent. of the Egyptian pollen-tubes in a race down an Egyptian style, then we may expect—owing to greater variability—that much more than 3 per cent. of  $F_1$  plant pollen-tubes will vary sufficiently in a

positive direction. Hence, in mixed pollination of  $F_1$  upon parent, we should find a higher percentage of vicinists.

The steps of the preceding argument were taken long before the experimental results were available. These results were as follows:—

Mixed pollination of  $F_1$  upon Egyptian . . . 20/100 or  
20 per cent.

Mixed pollination of  $F_1$  upon Upland . . . 25/65 or 28  
per cent.

Even allowing for all possible errors, and for the scanty numbers of ovules involved, the difference between 3 per cent. and 24 per cent. as values for the “prepotency” of mother-parent and of  $F_1$  pollen, under the same experimental conditions, cannot be without significance.

Hence, we conclude that some part of the  $F_1$  pollen from an inter-specific cross is prepotent over all other pollen; that self pollen is prepotent over pollen from some other species; and that pollen from other species only makes its way to the ovule with difficulty.

**Gametic differentiation.**—A conclusion which may be immediately drawn from these differences in prepotency of pollen is, that the error from natural crossing is likely to be less in the field—where it is difficult to avoid—than on the breeding-plot, where it can be avoided by appropriate, though expensive methods.

Again, it is within the bounds of possibility that immune strains might be discovered or developed. Such discovery is scarcely probable, but it may as well be borne in mind.

The chief speculation in which we may legitimately indulge relates to gametic differentiation. If our postulate as to correlation between gametic composition of the microspore nucleus and growth-processes of the pollen tube can be substantiated, it follows that those tubes which succeed during mixed-pollination must possess

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certain gametic characteristics. A detailed statistical study of the composition of  $F_x$  plants resulting from such mixed pollinations has been begun, and if we can find any constant deflection of the frequency curves from expectation, we shall have a clue as to the nature of the winning pollen-grains.

In other words, our endeavour is to ascertain whether differences which are manifest before fertilisation exist between  $F_1$  gametes. Further discussion<sup>30</sup> would be worthless at present, but any clue to gametic differentiation deserves to be followed up.

## CHAPTER VIII

### HEREDITY—I

#### i. *General*

HAVING discussed physiology, fluctuation, and natural crossing, we are now in a position to examine the inheritance of characters in crosses between two strains of cotton derived from separate reputed species.\*

The evidence to be adduced in the following pages is frequently most infirm beyond the second generation. Leaving out of account the inefficient conditions under which this part of the work has been done (Figs. 52*a* and 52*b*), the chief responsibility for this uncertainty lies with the difficulty of preparing self-fertilised seeds. When an  $F_2$  of two hundred plants is to be studied, we desire to avoid the use of nets (Fig. 51) owing to their disturbing effect upon growth; yet, if nets are not employed, we necessarily raise  $F_3$  families which are contaminated. Therefore it is better to dispense with the nets, and to rogue out the  $F_3$  vicinists; very often, however, such decisions as to vicinistic origin are based on the appearance of abnormal characters which might very well be due in reality to some rare gametic combination following self-fertilisation; we thus argue in a circle; a plant shows an unexpected characteristic, therefore it is a rogue. We have endeavoured to reduce the probability of such unjust decisions by a system of voting, whereby no plant

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\* The coming economic application of Mendel's Law to cotton will at first be made through crosses of much more nearly related forms, and hence of far greater simplicity than those which the author has chiefly investigated.



can be condemned unless it shows incredible abnormalities in several characters. Such treatment does not lend itself to precision.

A way out of the difficulty which has been employed several times has been to dispense with netting in  $F_2$ , growing the  $F_3$  from natural seed, leaving the  $F_2$  plants in the ground as ratoons, and netting any of them which appear to be important. The natural  $F_3$  is thus used for indicative, while the selfed  $F_3$  is used for critical confirmation in the following year. The method involves waste of a year, waste of labour, and waste of land, but it seems to be the only plan which gives trustworthy data.

The few crosses which have been made and studied were easily effected, taking the usual precautions.

The  $F_1$  plant was invariably netted after 1906, and the experimental error of the  $F_2$  data is therefore very low.

The  $F_3$  results, on the other hand, which are of supreme importance in disentangling the complex  $F_2$  data, are subject to the errors which we have just detailed. The same holds good for  $F_4$  and  $F_5$ —which is the highest generation we have cultivated—though by this time we usually know what plants to net, so that the data are more likely to be trustworthy; on the other hand many such families have been grown but not studied critically, through insufficient opportunity.

The elucidation of inheritance in cotton is thus no light task, and should not be undertaken without a residential laboratory, ample skilled assistance, and financial resources.

The difficulty of obtaining accurate data beyond  $F_2$  is so much the more regrettable in that the factorial analysis of cotton hybrids often requires the highest precision. We shall see that the composition of an  $F_2$  is commonly very similar to a Gaussian curve of error; this similarity is usually—probably always—fictitious, and is due to the appression of several true modes, which blend into one

another by fluctuation. Part of this blending, moreover, is not fluctuation in the ordinary sense, but rather an *autogenous fluctuation*,<sup>30</sup> provoked by correlation with other characters. Thus the modes of seed-weight in an  $F_2$  are not only subject to a *P.E.* of 12 per cent., but before this allowance can be made they have to be corrected for correlation with diameter of the boll.

A simple way of applying such correction is to dissect the frequency polygon of the family, isolating the wide-boll and the narrow-boll forms, for example, and plotting their seed-weights separately (*e. g.*, Fig. 69). Unfortunately this method reduces the size of the groups under examination, which has never been excessive to begin with, so that the precision gained in one direction is lost in another.

Again, since correlation exists between certain characters, it might be thought that the slide-rule would give the necessary correction. The difficulty here is to find out the value and nature of the correlation. The simplest Mendelian combination,  $AB \times ab$ , where the characters are simply linear measurements, gives a correlation diagram in  $F_2$ , which consists of four groups, only separable with difficulty even when correlation is perfect and linear, which—worked out in the conventional way—gives a value for  $r$  from 0.6 downwards (Fig. 53). There does not seem to be any method at present extant by which a quantitative separation of these groups can be made.\*

The difficulties enumerated, both of experiment and of computation, have prevented the author from making any exhaustive statement which can be considered as honest from the scientific viewpoint. The results are in the main indicative, and suggestive, often strongly so, but in all cases open to criticism.

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\* W.L.B. 21, and reply by Craig, J. I., *Cairo Sci. Jour.*, August, 1910.

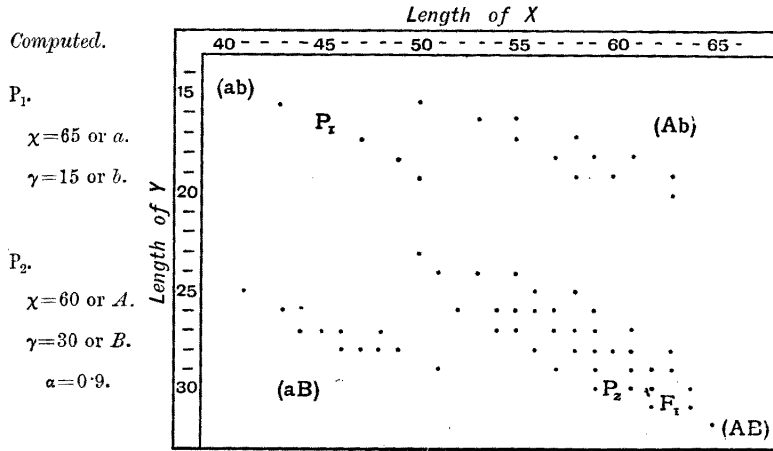
In rare cases we have been able to demonstrate the existence of Mendelian ratios in  $F_2$ , confirmed by the behaviour of later generations. In others we have failed to analyse the  $F_2$  but have dissected the  $F_3$ , where the phenomena were simpler. In others, again, such analysis has been utterly impossible, and we have been obliged to rely on the bare fact that a certain character has "bred true" in the end, though we have been unable to trace the steps of its purification. As a last infirmity, and last resort, we have fallen back on comparisons from year to year in massed data: if the graph for seed-weight in  $F_2$  shows certain modes, and if those modes reappear in the graph for all the  $F_3$  plants in the following year, we have a claim to assume that the modes are at least due to a systematic cause and not to accident.

The data to be quoted are drawn largely from crosses of Egyptian with American Upland, especially from Afifi with Truitt Big Boll (No. 252),<sup>15</sup> and from Charara with King (No. 255). Other crosses which have been made, but only partially examined through lack of space and labour, are Hindi  $\times$  Charara, King  $\times$  Russell, Russell  $\times$  Charara, and Sultani  $\times$  King. In the early stages of the work many natural hybrids were examined, which had resulted from natural crossing between Egyptian cottons, while full analysis has been made up to  $F_2$  in an inter-Egyptian cross between Afifi and another Sultani. The phylogenetic relationships of the various parents is doubtful, to say the least. The author has leaned to the designation "inter-specific," but this has been questioned, in view of the cultivated origin of the parents.\* Perhaps a description of them as "reputedly inter-specific" would best meet the case.

The cross of Afifi  $\times$  Sultani was made with the object of studying some simple examples in place of the com-

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\* See references "Egypt," in Sir G. Watt's Monograph.



Experimental.— $F_2$  of King  $\times$  Charara.

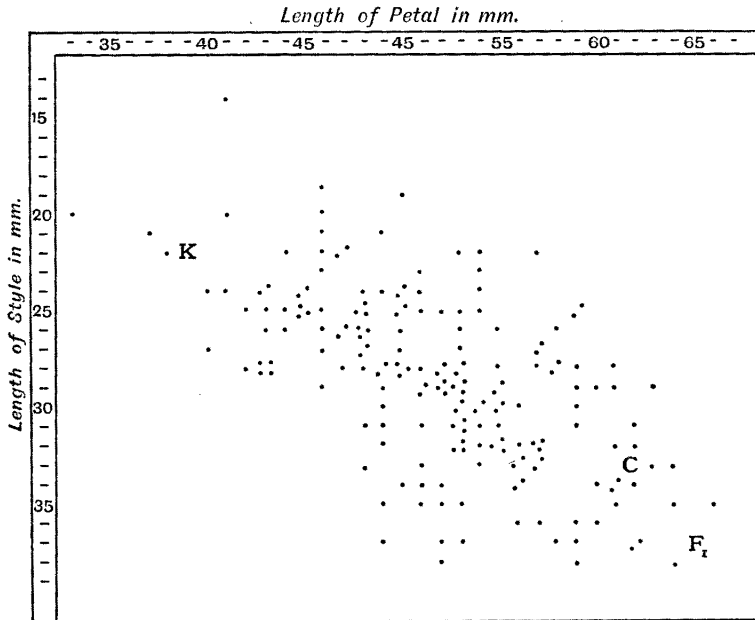


FIG. 53.—CORRELATION DIAGRAM FOR TWO PAIRS OF ALLELOMORPHS.

plexities presented by the other crosses, but it is as complex in its own way as the Upland  $\times$  Egyptian series. It seems to be quite probable that this cross was one between the old Peruvian and Sea Island stocks, and was hence not very much more intimate than the Upland  $\times$  *Ægypto*-Peruvian crosses.

The author can only reiterate his conviction that all these hybrids are subject to Mendel's Law of segregation; often obscurely—on account of defective methods—but none the less certainly. The evidence available can all be interpreted in Mendelian terms, and it is very significant that most of it should appear at first glance to be completely dissociated from the classical ratios. Mendelian students of heredity have confined themselves to the more definable characters, such as colour, partly because statistical characters take up an excessive amount of time in mere determination, and partly because the use of statistical methods is prone to provoke irrelevant criticism from mathematicians with whom the mere biologist cannot fairly compete. At the same time it is clear that the frontier of Mendel's territory is not demarcated by any special character, and—with all their experimental disadvantages—the only characters which admit of complete treatment are those which can be measured with definable precision.

There are many features of these complex results which bear a tantalising resemblance to problems of human heredity.

**Record system.**—The examples to be quoted in these pages are drawn from a systematic set of records. These records are compiled from three sources, the Field-Books, Field-Cards, and the Laboratory-Books, in which the actual observations are entered. These are then worked up at the end of the year in two ways; first in the Files, and secondly in the Ledgers. The Files consist of printed forms, one to every plant, on which are entered all particulars available; the file-sheet of the plant shown in

Fig. 54 is reproduced in Fig. 55. The Ledgers collect the data from all plants of a family under the head of each character separately; this is conveniently done in the form of frequency polygons, in which the number of each individual is written; Fig 48 reproduces a page of the ledger dealing with the height of the offspring of a plant which was brother to that shown in Figs. 54 and 55. The polygons elsewhere reproduced have had the component plant-numbers omitted in order to save space. Lastly, a Card Index of the completed ledgers enables any fact about any plant to be found immediately.

### ii. *Qualitative Characters*

Those characters which are not easily subjected to statistical expression are dealt with in this sub-chapter.

**The Leaf-spot.**—The development of anthocyanin in the leaf, which finds its fullest expression in the Red-Leaf sports, is usually noticeable at the point where the petiole begins to branch into the main veins. In Uplands, and in Hindi, this leaf-spot is conspicuous, and forms a useful diagnostic character in the seedlings for comparison with Egyptians, whose leaf-spot is fainter, smaller, and pink rather than crimson. The character varies with the water equilibrium and illumination of the plant, like all anthocyanin characters. The  $F_1$  of the “spotted by relatively spotless” cross bears an intermediate spot. In  $F_2$  the ratio of the three forms accords closely with 1:2:1. Extracted full-spot and spotless breed true, without known exceptions.

**General colour of the leaf.**—The Upland cottons possess a leaf lamina of much lighter hue than the Egyptians. This difference in colour is real, and independent of differences in hirsuteness, &c. The inheritance of the character, or character-complex, is unknown, except that large families have been found to breed true to one or the other colour after  $F_2$ .

The matter might be of importance with regard to photosynthesis.

**Colour of petal.**—The limb of the petal, apart from the colour of the basal spot, which we shall discuss shortly,



FIG. 54.—TYPICAL PLANT OF "77." JULY 10, 1909.

ranges in colour from almost pure white to a rich golden yellow. Each pure strain of cotton has a definite petal colour, which is white to creamy in Uplands and Hindi, while in Egyptian families it ranges from lemon to golden.

**FAMILY** 77(B)(x) **PLANT** (3)

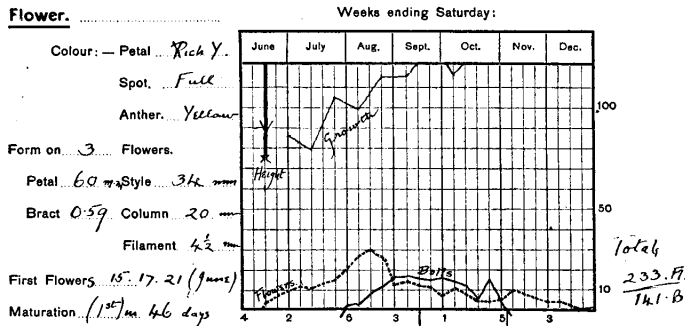
Date of Sowing . . . . . March 18<sup>th</sup> 1909  
 Seedling Condition . . . . . Good  
 Adult Condition . . . . . (Clearly comparable with adjacent  
 h.S. A 2-5. g.v.)

**Leaf.**

Spot . . . None . . . . . Hirsuteness . . . Glabrous  
 Averages: on 3 leaves: - L 168. L<sup>2</sup> 18° L<sup>3</sup> 37°

**Stem.** Height: - (1) 46 (2) 80 (3) 130 (4) 135 (5) 155 (6) 160  
 Fourteenthly (7) 165 (8) 165 (9) 170 (10) 165 (11) 170. (12) C.M.  
 Branching . . . Scarcely; Late

**Flower.**



**Boll.** Boll-Shedding 40% . . . . . First Boll July 31  
 Surface . . . Eg. . . . . Divisions, on 37 bolls: 29  
 Averages on 3 bolls: - Form 0.60 Size: 24.3 mm

**Seed.** Fuzz . . . Normal  
 Weight on 316 Seeds: - 0.103 g Out-turn 88 with

**Lint.**  
 Length 27-33 (30) . . . . . Colour . . . . . Weight 0.040 g.  
 Expert's report: -

**Notes:** - Photo July 10<sup>th</sup>

FIG. 55.



White and creamy petals are not difficult to find in Egyptian field crop, but their ancestry is dubious; some may be true Egyptians, but most are splitting-forms from Hindi  $\times$  Egyptian hybrids.

The hybridisation of these forms has not given a simple result in any cross yet made by the author. Mr. Fyson has published details from large families of Indian cottons, which indicate that the character was there controlled by a single pair of allelomorphs, but the data are not quite convincing as to this simplicity, and the same uncertainty is found by Mr. Leake (3).

The cross Afifi  $\times$  Sultani was a cross of golden petal  $\times$  lemon petal. The  $F_1$  was intermediate. In  $F_2$  we matched the offspring to the three forms, taking three flowers from each plant on different days. It should be remembered that the colour differences between these three forms are not very great, although the parents are quite distinct from one another. Many plants were matched to the same type-colour each time, but many others were matched first to one and then to another. The probability seems to be that there are more than three colour types in the  $F_2$ , just as in Tammes' work on hybrids of *Linum*, so that our matchings may mean very little.

On the simplest interpretation of the data we might imagine that the heterozygote was a simple intermediate, throwing out a 1:2:1 ratio in  $F_2$ . The figures are too discrepant to admit of this view. They tend more towards the interpretation based on two pairs of allelomorphs, giving a ratio of 9:3:3:1, where the last two are externally similar, making the ratio into 9:3:4.

The crosses of Egyptian with Upland have behaved in a similar way. The cross of yellow—whether lemon or golden—with white or cream has always given an intermediate  $F_1$ . In  $F_2$  we have obtained ratios which approached very closely to 1:2:1, but with a constant

excess of the paler parental colour-type. Testing this on the assumption of a 9:3:4 ratio, we obtained consistent results up to a certain point. Whites and some full yellows bred true, some intermediates threw out all colours like the  $F_1$ ; other intermediates threw whites only, while yet others threw only the full parental yellow, giving approximate 3:1 ratios in both cases. It seemed at one stage that the double-pair hypothesis had met all contingencies, until the following test was applied.

A family raised from an  $F_3$  plant which bore the intermediate colour had given twenty-two intermediates to seven full yellows. Six of these  $F_4$  intermediates were grown into  $F_5$ ; the obvious expectation was that four should throw out yellows, while two should breed true to the intermediate colour. The actual result was that none threw any yellows at all, but all threw whites. These whites were not, moreover, of the same colour as the parent white, but much nearer the intermediate itself. The figures for the six families, in ratio of "intermediate : new white" were (4:0), 21:5, 16:9, 26:1, 10:1, 11:3. The families were almost gametically pure in all other known respects, and all vicinists had been eradicated.

From this evidence it is plain that petal colour in crosses of Upland by Egyptian may be controlled by not less than *three* pairs of allelomorphs. The presumption is that our matching methods are not sufficiently precise, and that some form of colorimetric grading is needed. Even the inter-Egyptian cross shows the same peculiarities.

We shall see that similar evidence is to hand in the next character to be considered, together with a strong probability for gametic coupling. If the colour and marking of a flower's petal is controlled by at least five allelomorphic pairs, complicated by gametic interaction, it need not surprise us to find that the modes of seed-weight in  $F_2$ , for instance, are not very definite.

On the other hand, far more complex analyses of flower colour have been proved indisputably for such plants as *Antirrhinum*, *Matthiola*, *Lathyrus*, &c.,\* so that the indications of our fragmentary evidence may be considered as quite probable, even in a simple sap-colour.

**Petal spot.**—The Egyptian flower is characterised by a rich crimson spot at the base of the petal. This spot is not so large as in *G. herbaceum*, where it occupies the whole of the petal claw, but it is conspicuous. The typical Upland cottons and Hindi have no such spot, the petal being self-coloured. The intensity of the spot may differ within commercial Egyptian varieties, like the petal colour. Similarly, commercial stocks of, e.g., “King” Upland contain a notable proportion of plants with spots on their petals. Such differences are probably due to doubtful pedigree.

A cross between “full spot” Egyptian and “spotless” Upland gives an intermediate  $F_1$ . The  $F_1$  spot is smaller, more vague in outline, and less noticeable than the spot of the Egyptian parent. In cases where the latter had a spot which was relatively small, the  $F_1$  is proportionately inconspicuous.

In  $F_2$  the ratios are very erratic. Taking them in the order “full : intermediate : none,” we find two families from  $F_1$  sister plants giving 11 : 22 : 18, and 23 : 42 : 31. In this case the ratio approximates to 1 : 2 : 1, but it is closer to 3 : 9 : 4, and the divergence from even this is more than can be explained by errors of observation. Probably, as in the case of petal colour, there are more classes than we have admitted. This view is substantiated by the fact that we have been unable to discriminate in many cases between “Full” and “Full?”. As in the case of petal colour we find that “spotless” breeds true, while “full” may either breed true or break, and inter-

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\* See Bateson, Saunders, Baur, Wheldale, &c.

mediates break in at least two different ways. Probably there are again two allelomorphic pairs concerned.

Another series of crosses gave an entirely different set of ratios. One of these was derived from an Egyptian parent which possessed an inconspicuous petal spot, and the divergence from expectation was at first<sup>8</sup> attributed to fluctuation. The ratio in  $F_2$  was 5 : 9 : 47. The other series was not open to this interpretation, since the Egyptian parent had a fully-developed petal spot, while the  $F_2$  ratio was 27 : 41 : 112. If we assume that the petal spot in the latter cross was controlled by two allelomorphic pairs, with 3 : 1 : 1 : 3 gametic coupling, while the "full spot" class consisted of two groups which were practically indistinguishable, we obtain a theoretical ratio which is very close to actuality, viz., 25 : 40 : 115.

It is inadvisable to discuss the point more fully, since we require much larger series of numbers than those the author can present, before a decision can be taken as to the probability of this view. The consistently erratic behaviour of the spotted and intermediate forms in  $F_3$  supports such interpretation, but the figures available are not sufficient to substantiate it.

The only decisions at which we can arrive with certainty are:—that the presence or absence of the petal spot in these Ægypto-American crosses is not determined by a single pair of allelomorphs, and that there is strong evidence for complication of this mechanism by gametic coupling in some cases.

**Anther colour.**—The colour of the central brush of stamens is an important feature in the general colour-effect of the cotton flower. In Egyptians it is bright golden-yellow, in Uplands and Hindi it is whitish, or rather buff in colour, and the  $F_1$  is intermediate.

In  $F_2$  we obtain ratios which appear to be genuinely 1 : 2 : 1, and no exceptions have yet been noted in subsequent generations. The characteristic thus appears to

be under the control of a simple pair of allelomorphs, so far as evidence is available.

This presentment does not exhaust the possibilities, for a family of King Upland, grown from seed of a selected plant, showed itself to be a hybrid in this respect. The anther colour of the selected parent was pale lemon, which broke up on self-fertilisation into 24 lemon : 8 buff. The latter have since bred true, as have some of the lemons. In this case the pair was simple, with dominance of more colour over less colour.

**Hirsuteness.**—The hairiness of the plant involves a number of factors; one type of hair may be confined to the leaf-lamina, another to the veins, another to the stem, and so forth. During our studies of this character in cotton we have examined only the petiole of the leaf.

The Egyptian cottons have glabrous petioles, the American Upland petioles are more or less hirsute, and the  $F_1$  petiole is almost glabrous. The author's first published mention of this character<sup>5,8</sup> stated that the glabrous form was completely dominant. In almost all other plants the reverse is true, and further complications were expected when Mr. Holton discovered that a few long but scanty hairs were present on the  $F_1$  petiole.

Early classifications of  $F_2$  and  $F_3$  in which glabrous and intermediate were grouped together as non-hirsute, gave ratios of "non-hirsute : hirsute" as 111 : 37, 58 : 17, 43 : 9, &c. On cultivating some extracted hirsutes in  $F_4$  we found six out of seven breeding true to hirsuteness, while one broke up, giving 31 : 8, the eight being of the  $F_1$  type. Moreover, we found that the extracted forms differed in the length and density of their hairs, and that segregation in this respect was indicated within the limits of the hirsute group.

A very careful classification was then made on the  $F_2$  of another Upland-Egyptian cross, which gave the following results :—

Like Egyptian parent ... ..	48
Doubtfully Egyptian ... ..	8
Doubtfully like $F_1$ ... ..	1
Like $F_1$ (scanty hairs on dorsum) ... ..	71
Like $F_1$ , but with more hairs ... ..	6
Like Upland, but shorter hairs ... ..	10
Like Upland parent ... ..	19
Like Upland, but denser ... ..	12
Total ... ..	175

Thirty-five of these plants were grown on to  $F_3$ , but their families were not sufficiently large. One notable feature was that an “ $F_1$  type” plant gave thirteen offspring like itself, and no other forms. Other similar plants threw the glabrous type only, while others again behaved like the  $F_1$  itself. Some of the differences which had been recorded between the  $F_2$  plants seemed to be due to fluctuation, but the general trend of the evidence is to the same conclusion as in the characters already discussed, namely, gametic complexity, possibly with length and density as component factors.

It should be added that families of fifty plants have been grown in  $F_3$ , which bred true to new types of hirsuteness, such as the felty class described above “like Upland, but shorter.”

Since the hirsuteness, or rather the glabrousness, of all Egyptians is practically the same, we have no data for simpler crosses. It might be well to investigate the character in a cross of glabrous Hindi with hirsute Hindi.

**The stipule.**—During examination of Afifi  $\times$  Sultani  $F_1$  it was noticed\* that the form of the stipule was very different in the two parents. The Sultani parent had long narrow stipules, while the stipules of the Afifi parent were about four times as wide for the same length.

The  $F_1$  stipule was long and narrow like the Sultani parent.

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\* By Mr. F. S. Holton.

In  $F_2$  we found, by simple matching, that 48 plants had stipules like the Afifi, 59 like the Sultani, while 27 were recorded as doubtful.

The evidence is inconclusive, but it again points to some slight complexity, possibly a ratio of 9 : 7.

**The surface and glandulation of the boll.**—All parts of the cotton plant, other than the root, contain abundant resin glands, which produce the characteristic black speckling externally. The depth at which these glands are situated in the ovary wall is characteristic of different kinds of cotton plants. In most Egyptian bolls they are near the epidermis, which is depressed above them, forming small craters. In American Uplands we find the glands situated much further below the epidermis, which is not depressed, so that the surface of the boll is smooth, and the speckling is scarcely visible. The  $F_1$  of these two forms is intermediate, though more like the Egyptian parent.

A large number of bolls have been pickled and sectioned in the attempt to understand the inheritance of this character. It appears to be straightforward, but the evidence is not convincing. The appearance of the surface is not solely dependent on the glandulation; Egyptian bolls are bright green and shiny, while Upland bolls are of a dull, grey-green colour. Some structural differences are also shown by the microscope.

Thus the fact that an  $F_2$  was matched into 17 Uplands : 33  $F_1$  type : 14 Egyptian type, must not be taken as evidence of simple segregation. The data from  $F_3$ , &c., lead to the same uncertain views as in the more definite characters of the flower colours.

**The distribution of seed fuzz.**—The differences between various strains of Egyptian cotton in this respect range from complete nakedness to a woolly coat which covers all but the back of the seed. The former are indistinguishable from Hindi seeds, but most of them

give rise to plants which bear no sign of any Hindi ancestor.

Plants bearing seed with entire fuzz are occasionally found, but these appear to originate from crossing with Hindi.

Hindi cotton, on the other hand, always bears naked seeds, while typical American Uplands are entirely fuzzy. Naked-seeded sports occurring in the Upland crop have been discussed by Allard (1) and in the Indian crop by Fyson.

Several natural hybrids have been bred on from Egyptian cottons. In all cases they have given a simple 3:1 ratio, more fuzz being dominant over less fuzz, and expectation has been fulfilled in  $F_3$ . The cross of Affi  $\times$  Sultani behaved in the same way; some fluctuation was shown, but the groups were clearly 116:41 in  $F_2$ .

In crosses of any Egyptian with American Upland, we meet with complications. The entire fuzz is dominant, and the  $F_2$  has given such 15:1 ratios of "entire:slight" as 97:6, 180:11, &c. The naked seed breeds true in  $F_3$ , and has continued to do so till  $F_6$ , while the entire fuzz either breeds true, or breaks up. There are indications that the latter process may give either a 3:1 ratio, or a 15:1 ratio, but the figures are too small. Further, there are indications of constant differences in the entire fuzz group, some being woolly, while others are felted; if a woolly seed does not breed true, it may throw out felted seeds in a 3:1 ratio. Felted seeds, which may be regarded as a step towards the Egyptian fuzz type, do not throw woolly ones.

It would seem that two pairs of allelomorphs are here implicated, giving a 15:1 ratio in  $F_2$ . The fifteen appear to consist of 12 woolly and 3 felted. In  $F_3$  we find all the nakeds breeding true, some woollys throwing felted only, some throwing naked only, and some throwing both, while the felted forms either breed true or throw nakeds only.



An interesting proof of the tangibility of these gradations in fuzziness was afforded by a natural hybrid from Abbassi, bearing normal Egyptian slight fuzz on its seed. When selfed it threw recessive wholly naked seed derived from an unknown pollen parent. When it was crossed with American Upland we raised seven  $F_2$  families, four of which contained the typical Egyptian seed as one plant in sixteen, while three contained the naked seed in the same proportion.

The behaviour of Hindi, the seed of which is devoid of fuzz, when crossed with Egyptian (Charara) has been somewhat remarkable. In the first generation the seed was entirely fuzzy, like an Upland. This was probably a case of reversion due to the meeting of cryptomeres, and it was naturally expected <sup>12</sup> <sup>15</sup> that the  $F_2$  would show a ratio of 9 : 3 : 3 : 1, both the Egyptian fuzz and the Hindi fuzz reappearing. An unsuccessful sowing gave "14 entire : 3 Egyptian," which seemed to support this view. In the following year a family of 130  $F_2$  plants was raised, but without producing a single Hindi seed; the result was the same as if Uplands had been used instead of Hindi, namely, "123 entire : 7 Egyptian." The absence of the Hindi type in a family of this size can scarcely be accidental, and a few more crosses of this kind might throw light on the phylogeny of the Hindi cotton.

This complex inheritance is made even more interesting by the fact that a cross of the same Hindi strain with a natural hybrid of Hindi and Afifi yielded simple segregation of the naked Hindi seed in  $F_2$ .

Summarising the evidence with respect to this character we have tolerably convincing data as to the increasing complexity of inheritance when passing from varietal to reputedly inter-specific crosses, this complication taking the form of an additional pair of allelomorphs. In one case we have found reversion through the meeting of cryptomeres, and in general it would seem that the less

fuzzy cottons have been evolved from primitive cottons with entire fuzz by the loss of factors. The particular factor lost has not been the same in certain strains of Egyptian as in others, nor as in Hindi; hence we obtain reversion in some crosses, though not in others. No case of reversion in inter-Egyptian crosses has yet been noted, but it is quite conceivable.

**Colour of the seed fuzz.**—The presence and absence of colour in the fuzz-hairs appear to form a Mendelian pair. It is not easy to decide on the absence of colour, since the colouring matter is unstable, and in some cases fades very easily. There may be essential differences between green and brown fuzz, but the former fades very readily into the latter.

The quantity of fuzz on the parent is not coupled with colour. Thus, seeds which are practically naked, except for a most minute tuft of coloured hairs at the tip, will give rise, on crossing with white entire fuzz, to an  $F_1$  possessing green entire fuzz. It is interesting to note that this phenomenon, together with the  $F_2$  resulting, has been described\* as an instance of the failure of Mendel's Law; it was expected that "black seed" should form an allelomorph pair with "white seed."

**Distribution of lint on the seed.**—Parallel with the seed fuzz distribution and colour, we find characters of lint distribution and colour.

The distribution of the lint is not easily recorded, there being a large subjective error involved by the combing which is required before it can be seen. Crosses of "irregular" with "regular" give a "regular"  $F_1$ , and segregation certainly seems to occur. The most convincing example of this was an  $F_2$  from a "regular"  $F_2$  plant. The irregularly covered seeds were clearly defined, so that the curve for weight of lint per seed showed a very

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\* Cook, O. F. (1).

definite mode at the light end, consisting of eight plants as against twenty-two in the rest of the curve.<sup>15</sup> The extremes of the curve were 0.012 g. and 0.038 g. while the modes were situated at 0.018 g. and 0.032 g. respectively.

We may reason by analogy that the lint distribution will behave in much the same way as the fuzz-distribution, and may possibly be coupled with it in part.

**Colour of the lint.**—The first crosses made between Egyptians with brown lint, and Uplands with white lint, gave an intermediate  $F_1$  of creamy hue, with simple 1 : 2 : 1 ratios in  $F_2$  such as 12 : 21 : 11; the whites and browns bred true up to the  $F_5$ , while the creams broke up.

Even in these series there were manifest complications.

Thus, while never transgressing the limits of "brownness," the extracted browns were by no means uniform, some being much darker than the Afifi parent, while others were lighter. We have not yet decided whether these differences were gametic, or whether they were due to "autogenous fluctuation" with other characters.

Another cross, that of Charara  $\times$  King, where the parents were very light brown Egyptian, and white American, gave an intermediate  $F_1$  as before, but the  $F_2$  consisted of "9 brownish : 60 creamy : 109 white." This classification was made by a cotton expert, and not by the author. It is curiously reminiscent of the inheritance of petal spot, with its suggestion of gametic coupling.

The lint from  $F_3$  of this family, and from all other families grown since, has never been examined by an expert, and since this is peculiarly a case where outside judgments are best, the author prefers to leave the discussion at this stage.

**The "style" of the lint.**—At present we are completely in the dark as to the real nature of the differences between such lints as Upland and Egyptian.

We know that the lint hair of the former is shorter and of greater diameter than the lint hair of Egyptian, but there are other differences which the microscope cannot as yet determine, though to the fingers of the expert grader of lint they are far more obvious than is the colour to his eye.

The  $F_1$  of Ægypto-Upland crosses is always a superfine Egyptian. Thus, the mating of a "bread-and-cheese" Egyptian with a short-staple Upland gives a first cross bearing such lint as is required by the fine spinner. In the early stages of these researches we denoted this general peculiarity of these hybrids as "first-cross intensification," in the hope of explanation later. In many characters this explanation has been since obtained, but not in respect of the "style" of the lint. Until we know the component elements of "style" we cannot make much advance. It is safe to expect that such intensified characters will regress to the parental normal in later generations, but further knowledge might enable us to purify the particular combination of allelomorphs which leads to this immediate improvement. In point of fact we have raised families which breed true to an extremely fine and strong Sea Island type of lint, from the cross of King with Charara; the lint of the latter parent was of the Abbassi type.

From what has been said above it will be clear that the "style" of a lint sample is the resultant of an unknown number of unknown factors, both zygotic and gametic. When a set of  $F_2$  samples is placed before an expert, this becomes obvious; the expert finds one lint which resembles Afifi, except that it has the colour of Yannovitch; he next meets another which has the colour of Afifi, but which he would unhesitatingly affirm to be American Upland if the room were darkened. The task of analysing an  $F_2$  in this way is almost hopeless, however valuable the results may be for other purposes. The author is

much indebted to three Alexandrian gentlemen,\* who have assisted him in the past, by their expert opinion, given under all the difficulty involved by the smallness of the samples available, and their results, though open to these objections, are summarised thus:—

Affi  $\times$  Truitt:— $F_1$ , Yannovitch;  $F_2$  composed of 7 Affi, 24 Abbassi, 22 Yannovitch, together with 17 Hindi or Upland. Ratio, of Egyptian to non-Egyptian, being 53:17. The non-Egyptians bred true in  $F_3$ , while some Egyptians broke up. One plant from the  $F_2$ , the lint of which was described as being similar to that of the Affi cotton when first introduced in 1887, gave a remarkable series in  $F_3$ ; the limits of the brown Peruvian type of lint were never transgressed, but within these bounds we obtained almost every known modification; the old Affi, modern Affi, Ashmouni of the Fayoum, Upper Egypt Ashmouni, and—most remarkable of all—the original Jumel cotton of Mohammed Ali's time. Within the limits of this one family there was plainly an opportunity for much research.

The examination of the King  $\times$  Charara  $F_2$  was complicated by the extreme range of lint length, which ran from 18 to 40 mm. Many plants were confessedly judged as non-Egyptian because of their shortness, and hence the fact that the ratio of Egyptian: non-Egyptian was 108:71, or almost 9:7, cannot be regarded as significant.

Summarising this and similar evidence, it would seem safe to affirm that some striking feature of the lint—possibly the diameter—is inherited as a simple factor. Complications may be introduced gametically, and also by “autogenous fluctuation.” Until we can define the reasons which cause an expert to call one sample by one name and another by another, our investigation must be limited to rule of thumb.

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\* Mr. E. A. Benachi, now Minister of Agriculture for Greece, and Messrs. Marco Nacamuli and H. C. Thomas, of the National Bank of Egypt.

We have now examined the nature of the problems which the non-measurable characters present. The general trend of the evidence is to show that inheritance becomes more complex as the crossed parents are less and less closely related. The amount of labour which the author has been able to apply to these problems, under the limitations imposed by natural crossing and accidental circumstances, has not been enough to produce one clean and indisputable proof for any character. Nevertheless, he believes that the preceding discussion will be found by later workers to represent the general position of a complex subject.

## CHAPTER IX

### HEREDITY—II

#### ii. *Quantitative Characters*

ALL possible characters have been investigated quantitatively, by the methods described in the previous chapter on "Fluctuation," including flowering, bolting, and shedding.

The same difficulties already enumerated have prevented conclusions from being drawn with certainty, the chief of these being the scanty  $F_3$  data. On the other hand, we are no longer troubled by doubts as to the nature of our classification.

Presentment of all the data, the frequency polygons, correlation tables, and dissected curves, is not possible here, but it should be understood that one or more forms have been bred out pure in  $F_3$  to  $F_6$  for every character where a factorial analysis is suggested.

**Height of stem.**—The specific nature of the length of hypocotyl and first internode has already been mentioned. While the strains of Sultani and "King" Upland were being grown for this purpose, a set of  $F_2$  seedlings from these two parents was raised in the same site and soil. Data for  $F_1$  were unfortunately not available.

The plants were classified day by day, and the figures

plotted from those plants only which had all germinated on the same day, being as exactly comparable as they could possibly be, show a very definite segregation of the two parental first-internode-lengths from one another, and from a central mode. Whether the segregation is simply in a ratio of 1:2:1, or whether it is more complex, we cannot pretend to say. It is clear, however, that in commencing to analyse the height of our hybrids, we have first to take into account the internode length.

This alone is not sufficient for us. If internode-length was the only factor, then the height of the Upland would be about half that of the Egyptian, whereas the early height of the former is rather greater than that of the latter. Again, on June 18th, in Fig. 56, the same Upland strain whose internodes we measured is equal in height to the same Sultani, both being grown side by side on the breeding-plot. Hence the growth-rates must have been much the same, and the Upland merely produced more internodes in the same time. Comparing these heights with that of the  $F_1$  on June 18th, we find that the latter is nearly twice as tall. The internodes are no longer, so that the great height of the  $F_1$  must be due to a greater growth-rate.

The rate of growth, due to imperfectly known and constitutional causes, is thus the second factor in the height of the stem.

From these typical figures for June 20th, one hundred days after sowing, we might declare that tallness was dominant over shortness, whatever the components might be. If we follow the height-curve on to the end of September (Fig. 56) we shall see that this sweeping assertion would also be untrue, for the growth-rate of the  $F_1$  has slowed down, though not as much as that of the Upland, while the Sultani parent is still growing steadily.

Hence the third factor in height of stem is the amount



of change in growth-rate, or—as we have formerly interpreted this change—the liability to thermotoxy.

It was expected that a fourth factor would be found operative in  $F_2$ , &c., namely, the habit of branching, but all heights and growth-habits appear to be distributed evenly throughout all the branch-types, from plants with-

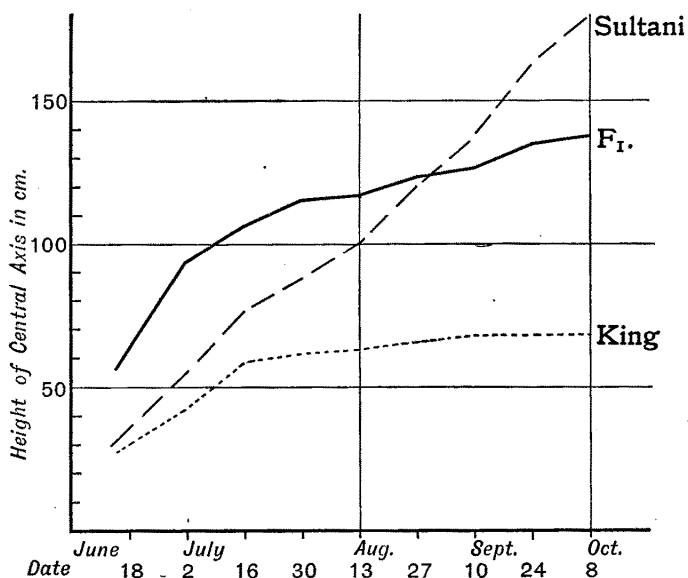


FIG. 56.—GROWTH OF STEM.

Parents  $F_1$  of an Ægypto-Upland cross. Means of families.

out monopodial branches at all,\* up to plants in which the main axis was scarcely recognisable.†

The heights of the  $F_2$  plants are therefore dependent on the three components first enumerated, but although we have described them as “factors,” they may be each the resultant of more than one factor in the Mendelian sense, as is the colour of the petal. Within the limits of

\* See Leake, H. M., (2), (3), and W. L. B. (5), (8), (15).

† Cf. Bateson, W., in *Lathyrus*.

this book we cannot compress a full set of  $F_2$  data, like the set given for fluctuation (Fig. 48), but the three main features are as follows:—

A. The internode-length of the parents reappears in  $F_2$  forming modes in the curve.

B. The early rate of growth varies in normal plants,

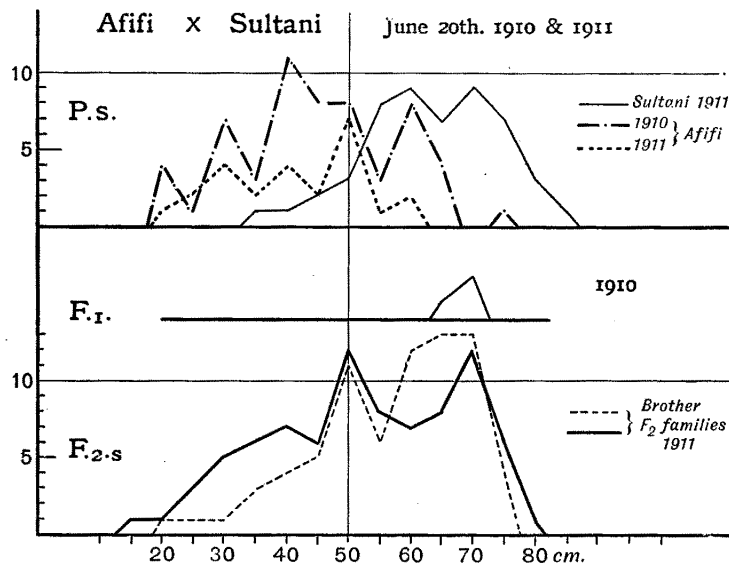


FIG. 57.—HEIGHT OF STEM IN JUNE.

Individual plants.

even if we dissect the curve of “growth-rate in June” into any component groups we may choose. Thus, taking only those plants which afterwards showed the habit of continuous growth, and omitting all but the normal seedlings, we find the growth-rate ranging symmetrically in thirty-five plants from 3·6 to 17·8 mm. per day. Moreover, on plotting these growth-rates against the ultimate height of these plants at the beginning of October—which is legitimate, since their growth curves were all “continuous”—we find a close correlation, with a value for “ $r$ ”

of not less than 0.622. The initial growth-rate of the  $F_2$  plants therefore ranges at least as high as that of the  $F_1$  and at least as low as that of either parent. (See also Fig. 57.)

C. Over and above this incomprehensible factor of "growth-rate," which needs the repetition of such experimental work as we have described under "the Individual" on every plant of a large  $F_2$  before we can interpret it, we have also the change in growth-rate, affecting the height of the plants after the end of June, or earlier, which we have endeavoured to interpret in terms of specific liability to thermotoxy. On classifying the individual growth curves in a family of 179  $F_2$  plants, we find that they were grouped as follows:—

Continuous growth, like Egyptian parent	...	...	52
Doubtfully continuous	...	...	29
Doubtfully like $F_1$	...	...	27
Semi-continuous, like $F_1$	...	...	30
Doubtfully like $F_1$ , being semi-discontinuous	...	...	30
Like American parent	...	...	9

Thus a small percentage of plants reappears in  $F_2$  with the high thermotoxic susceptibility of the American Upland parent. It might be pointed out that the figures *could* be fitted to a 9:3:3:1 ratio, two pairs of allelomorphs being involved, namely, presence and partial absence of "*x*-production" and of "*x*-removal"!

There does not appear to be any necessary correlation between any of these factors in their distribution amongst individuals. A plant with a low initial growth-rate may have the habit of continuous growth and short internodes: strains of such plants have been bred out to  $F_4$  and have remained pure. Such plants are short in the stem. Shorter still are those plants which have the discontinuous growth-habit, with short internodes and a low growth-rate. At the other extreme we meet plants with a high growth-rate, long internodes and continuous growth-habit. Con-

sequently, it is not surprising that the curve showing the height of an  $F_2$  at the end of the season exhibits continuous variation from one extreme to the other, especially since we have seen that the fluctuation in height is by no means

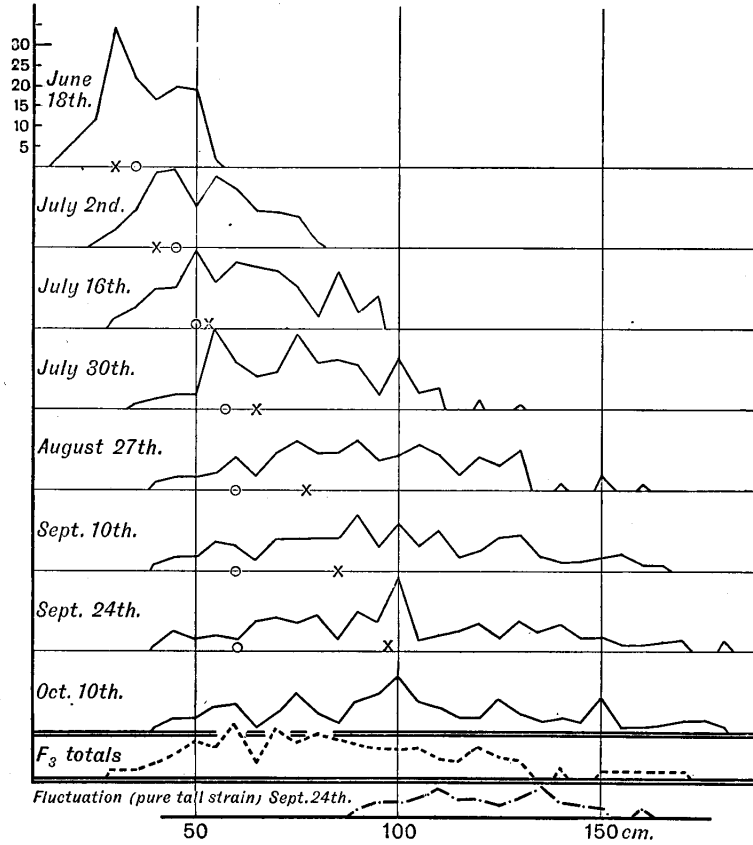


FIG. 58.—HEIGHT OF STEM IN  $F_2$  OF KING (o) by CHARARA (x).

Stunted and damaged plants excluded. Ledger page, like Fig. 48.

inconsiderable in a pure strain. There are modes in this curve, nevertheless, and the following result shows that they are not due to accident.

The  $F_2$ , the heights of which in 1909 are shown in Fig. 58, was used to provide an  $F_3$  from some thirty of its

members in 1910. Most of the plants chosen for this purpose were—for subjective reasons—short in the stem. Plotting the aggregate height of all thenormal  $F_3$  plants in 1910 against the same date in 1909, we see the same modes reappearing, in spite of the differences of soil and season (Fig. 58). These modes become less markedly coincident amongst the taller  $F_3$  plants, but the general result indicates that such modes are due to definite constitutional causes, inherent in the plants themselves.

**The form of the leaf.\***—The component characters of leaf-form appear to be the length of the mid-rib ( $L$ ), the distance from sinus to petiole ( $S$ ), and the angle of the sinus from the petiole relatively to the mid-rib ( $/s$ ).

Two other components which we have not examined in detail for more than one family are, the angle made by the first lateral vein with the mid-rib, and the presence or absence of a second lateral vein and lobe.

The three first components are concerned with the form of the central segment alone, but even in this respect we find more problems than we can solve.

Taking the length ( $L$ ) first, we have already seen that it is correlated with height of stem, in some obscure manner. King Upland, with a mean leaf-length of 75 mm., crossed with Charara, the mean leaf-length of which was about 135 mm., gave an  $F_1$  with leaves rather shorter than Charara, and this by selfing produced an  $F_2$  which ranged from 70 to 195 mm., with slight indications of modal grouping; most of the plants lay between the parental measurements (Fig. 59). This curve was dissected in various ways, thus, the plants with the “continuous” growth-habit had larger leaves than the rest, but although none of these plants had extremely small leaves, yet moderately small leaves were found as a detached group. Further dissection of this group never succeeded in

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\* See Leake, H. M. (1), (3).

producing a group of plants with leaves of identical length (*i.e.*, identical within the *P.E.* of fluctuation). Thus it seems highly probable that the length of the leaf is inherited as a separate character, although it is distorted

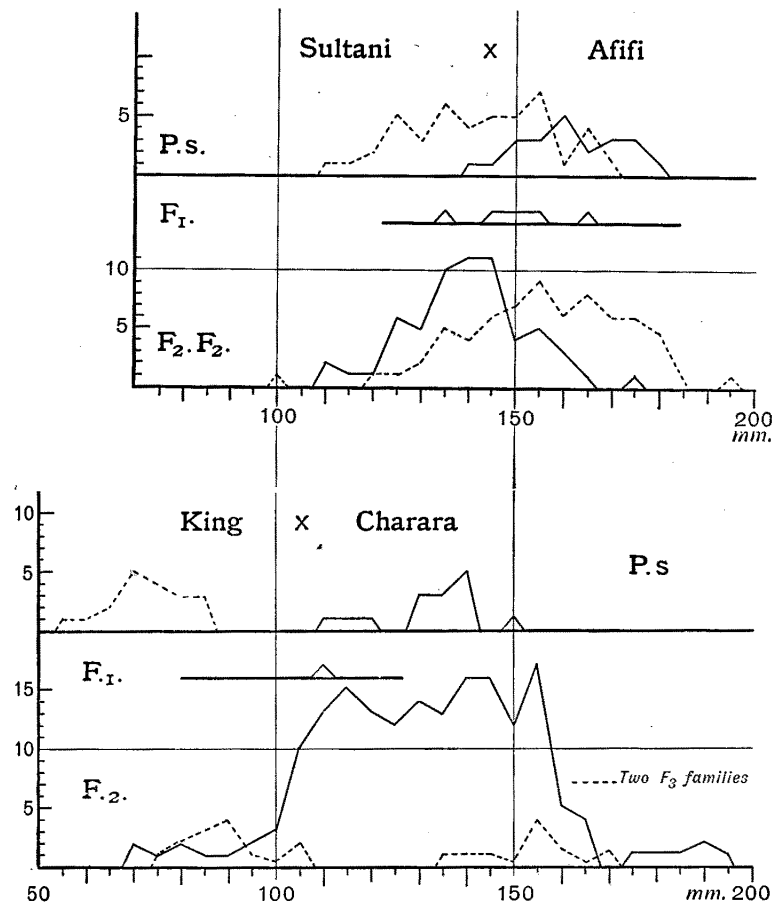


FIG. 59.—LENGTH OF THE LEAF.

from the parental length by autogenous fluctuation. The same probability is suggested by correlation diagrams for leaf-length with height, with petal length, &c.; such diagrams show a distinct indication of isolated groups, such as we shall inspect shortly in the flower measurements.

The next character "*S*," or distance from petiole to sinus, is inherited in much the same way as *L*. We can eliminate the diversities in absolute size by expressing *S* in terms of *L*, *i.e.*, plotting for the ratio *S/L*. We then find that an Upland leaf, in which *S* is relatively long, when crossed with an Egyptian in which *S* is relatively short—or, in other words, slightly and deeply dissected leaves—give rise in  $F_1$  to a leaf very like the Egyptian, but with a slightly longer *S*. In  $F_2$  we obtain the same modal curve, stretching to the parental extremes. Correlation diagrams for *L* and *S* in  $F_2$  show modal grouping and no general correlation. In other words, the length of the sinus is inherited independently of the length of the mid-rib. Now this sinus-measurement is determined by the plant at a very early stage in the primordia, since we find freshly expanded leaves showing the same form as adults; hence a factorial determination is highly probable. It is necessary to express *S* in terms of *L*, on account of the diversities of *L*. Thus, if we plot *S* simply, we find, *e.g.*, in the King  $\times$  Charara cross, that the parents are identical, while the  $F_1$  is 60 per cent. longer. It is, of course, quite possible that our use of *L* as the expression for mere size may be fallacious, but this would not affect the general argument for factorial inheritance of form.

The last component of the form of the central segment is  $\angle s$ . We have formerly seen that the position of the sinus fluctuates along the angle-lines, so that instead of using *S* and  $\angle s$  we might employ  $\angle s$  and  $\angle t$ , the latter being the angle made by the sinus with the mid-rib from the tip of the latter.

On crossing the narrow angle of Upland with the wide angle of Egyptian we obtain a wide angle in  $F_1$ . In  $F_2$  we obtain the same wide and modal curve on plotting the angle values, with some indication of simple segregation of narrow angle from wide, which is probably fallacious.

The next point to consider is the inter-relationship of

these angles, and whether a wide  $\angle s$  is necessarily linked with a narrow  $\angle t$  as in the Egyptian parent. The result of dissecting our curves in this way is very definite; there is no such linking. Thus, taking the 26 plants which had the narrowest  $\angle t$  in an  $F_2$  of 180 individuals, we find that while 24 had very wide  $\angle s$ , there were two with a very narrow  $\angle s$ , far removed from the rest. Conversely, taking out the 26 plants with the widest  $\angle t$ , we find from one to five possessing very wide  $\angle s$ , while the rest had narrow  $\angle s$ . Thus the two angles may definitely be said to be inherited factorially, and the origination of new leaf-forms in  $F_2$  need no longer be surprising.

**Flower form.**—The characters studied in the flower were the length of the petal, style, and column, measured from the apex of the ovary cavity, the length of the filaments, and the width and length of the involueral bracts. The form of the corolla has not been examined; it ranges from an open cup to a long narrow one.

The story of the inheritance of all the first four characters is much the same. In the first cross studied we found that by correcting for fluctuation, taking the petal length as the standard because it has been the same in both parents, our graphs for the  $F_2$  composition assumed the 3 : 1 form.<sup>13, 15</sup> Long was dominant over short, and all the extracted shorts tested bred true up to  $F_6$ . Here, in spite of the Ægypto-American crossing, the characters seemed to be under the control of a single pair of factors. In this way we bred out the "short-style flower" mentioned in connection with natural crossing (Frontispiece).

In the King  $\times$  Charara cross we found indications of segregation in petal length also, and it was in this connection that we developed the correlation-diagram method of seeking for segregation (Figs. 53 and 60). The method is essentially the same as the use of the slide-rule, but it enables us to deal with two variables, without correction.



If long and short petals are represented by  $A$  and  $a$ , and the style lengths similarly by  $B$  and  $b$ , and there is no mutual interaction, then we obtain

- 9 Long petals with long style,  $AB$ .
- 3 Long petals with short style,  $Ab$ .
- 3 Short petals with long style,  $aB$ .
- 1 Short petal with short style,  $ab$ .

Now if the correlation of the two dimensions within any given flower is almost perfect, we shall obtain such a correlation diagram from the  $F_2$  as that shown in Fig. 53 (upper). The  $ab$  group is almost continuous with the  $AB$  group, and is scarcely to be differentiated from it. The  $aB$  and  $Ab$  groups lie on either side of this diagonal compound scatter. Thus, on working out the value of " $r$ " for the whole table we shall obtain quite a low value, whereas it is in reality a case of almost perfect correlation. Comparing this with the observed result obtained for the King and Charara  $F_2$  as shown in the lower half of the figure, there can be no possible doubt that some such grouping is really present. The parents and the  $F_1$  are marked on the diagram as A, E, and F. The  $F_3$  data of the cross confirm this conclusion, so far as they go, and the probability is high in favour of the view that even the semi-smooth Gaussian curves of error shown by the length of petal, style, column, and filament in the  $F_2$  of this cross are (Fig. 60) essentially nothing more than simple 3 : 1 curves, which have been deformed by fluctuation, both autogenous and ordinary.

With regard to the form of the bract and its width there is nothing definite to be said. Narrow bract is dominant over wide, just as narrow leaf segments are dominant over wide segments, and narrow bolls over wide bolls. The  $F_2$  ranges from one extreme to the other in a modal curve, and pure strains have been extracted, but no details are available by which the stages of this segregation can be traced.

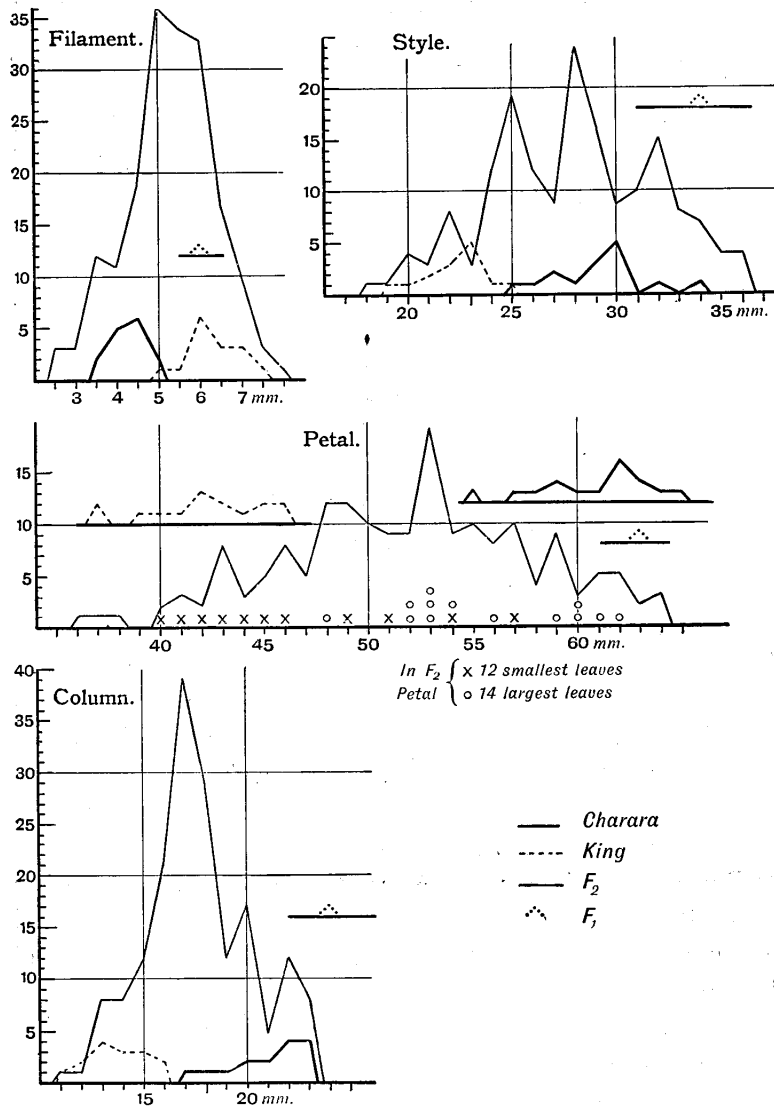


FIG. 60.—FORM OF THE FLOWER IN AN ÆGYPTO-UPLAND CROSS.

**Width and form of the boll.**—The Upland boll is usually wider and more nearly spherical than the Egyptian boll. Differences also exist within the Egyptian strains,

some approaching the long narrow boll of the Sea Island type. The form is expressed as  $\frac{\text{width}}{\text{length}}$ . A cross of Upland with a mean form of 0.75 and a width of 31 mm., upon an Egyptian with a form of 0.58 and a width of 27 mm., gives an  $F_1$  with a form of 0.60 and a width of 32 mm. In other words, the long narrow form is dominant

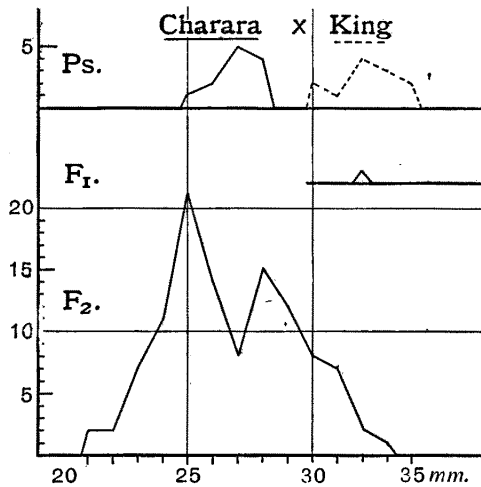


FIG. 61.—WIDTH OF THE BOLL.

though very much larger than the long narrow parent (Figs. 61 and 62).

The  $F_2$  of such a cross ranges up to the  $F_1$  width and form, but includes plants the bolls of which may be as narrow as 0.44 and 22 mm. So far as mere width is concerned, this might well be due to auto-genous fluctuation,

but the new form of the extremely narrow bolls cannot be attributed to this cause. As in the case of leaf-form, we are probably dealing with a compound inheritance, and the new forms are the result of recombinations of allelomorphs.

A side-light on this interpretation is provided by plotting the correlation table of form against width in  $F_2$ . While the general trend of the diagram indicates positive correlation between wider boll and more spherical boll, yet on comparing such a diagram with that from a pure strain, it becomes clear that the  $F_2$  family is heterogeneous.

Again, families have been raised in  $F_4$  which showed no more fluctuation in width than the parent strain, while the

form varied over double the range which could be attributed to fluctuation.

One autogenetic factor in the width of the boll is the number of boll-loculi. Without attempting to correct for any possible modality in the diagram we found the value for correlation between these two characters in  $F_2$  to be " $r$ " = 0.331 ( $\pm$  0.061). The explanation is presumably mechanical; the bolls with more loculi have more septa,

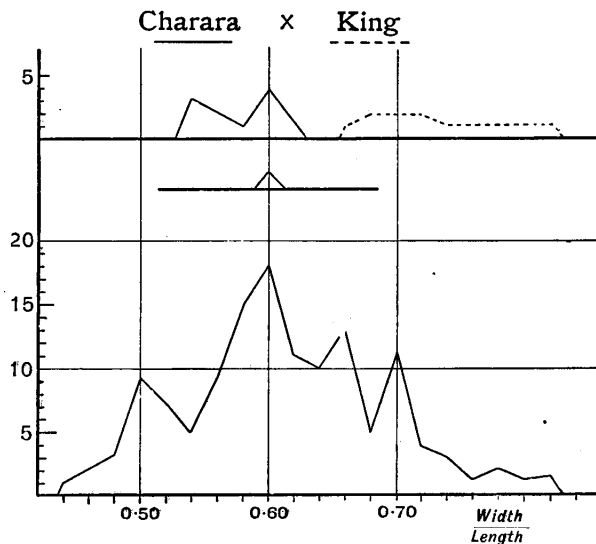


FIG. 62.—FORM OF THE BOLL.

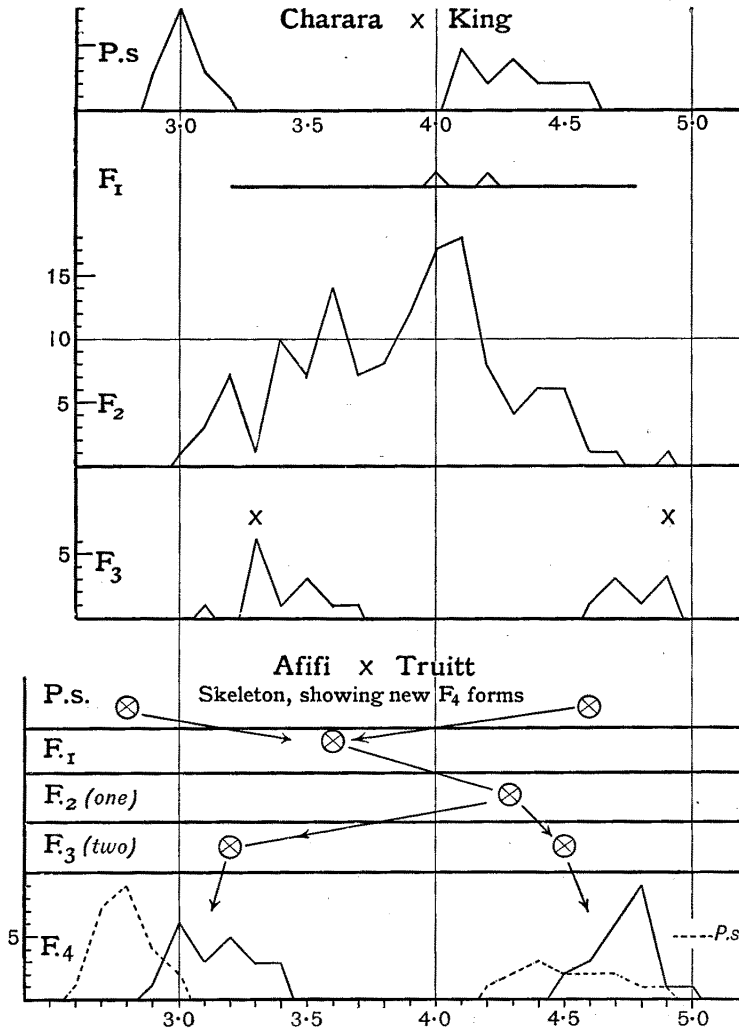
and these occupy more space, hence the boll diameter is greater.

More information on these two characters is highly desirable, because of their economic importance.

**The loculi of the ovary.**—The inheritance of this meristic character is of peculiar interest, since it is not a character of form, but of distribution, and analogous to such things as the number of ray-florets in the *Compositae*.

A cross (Fig. 63) between an Upland with its mean at 4.3 and an Egyptian with a mean at 3.0 produced an intermediate  $F_1$  with the formula 4.1. In  $F_2$  this family

gave a range of 3.0 to 4.7, with modes at 3.2, 3.6, 4.1, 4.4, and possibly elsewhere. In  $F_3$  a 4.8 bred true to



FIGS. 63 AND 64.—LOCULI OF THE OVARY.

4.8, and a 3.1 bred true to 3.2. On the other hand, 3.3 broke up into a scatter from 3.1 to 3.7, as did also a 3.6.

A 3.9 plant appeared to breed true round a mean of 4.1,

while a 3·8 scattered from 3·8 to 3·3. Similarly, a 4·0 scattered from 3·9 to 3·2, and so on. On the data available it seemed clear that the parental forms could be extracted and bred true, while the intermediate forms represented new gametic combinations which broke up in new ways, giving new forms. No large family having been raised beyond  $F_2$  in this cross, we may examine the data from another one.

The Afifi  $\times$  Truitt cross had 2·8 and 4·5 as the parental values (Fig. 64). The figure 4·5 is uncertain, because there was every indication that the American parent was heterozygote in this respect. The  $F_1$  had 3·6 loculi, and the  $F_2$  spread from 2·9 to 4·8. Only five  $F_3$  families were raised; one of these was derived from a 3·3 plant, and its twenty-one offspring ranged from 2·9 to 3·4, thus resembling the Egyptian parent closely but not exactly. Another 3·3 behaved in the same way, and repeated this behaviour in  $F_4$ . Conversely, a 4·8 gave only 4·6 to 4·9; while a 4·5 gave 4·2 to 4·6. The offspring of a 4·3 form broke up into a wide scatter from 3·3 to 4·9; several small families of these were bred on into  $F_4$ , but the largest and most interesting was one from a 4·5 plant, which consisted of twenty-nine plants, ranging only from 4·5 to 5·0, and giving a frequency polygon with the same probable error as the parent.

The inter-Egyptian cross was expected to unravel a portion of this tangle, but although the critical numbers were doubled, and the data classified to half-grades the result was much the same (Fig. 65). Sultani (3·20) crossed by Afifi (2·80) gave an  $F_1$  at 3·00. The  $F_2$  of this broke up with great symmetry over the parental extremes with a single mode at the  $F_1$  value. The spread of this curve of the  $F_2$  is too narrow to be the expression of a 1 : 2 : 1 ratio, so it is probable that at least two factors are involved even here. There is a slight indication of the possible nature of these factors, namely,

differentiation and coalescence, but it is not worth further consideration until we possess the data from later generations.

This Afifi  $\times$  Sultani cross was made principally in the hope of obtaining a simple inheritance of this particular

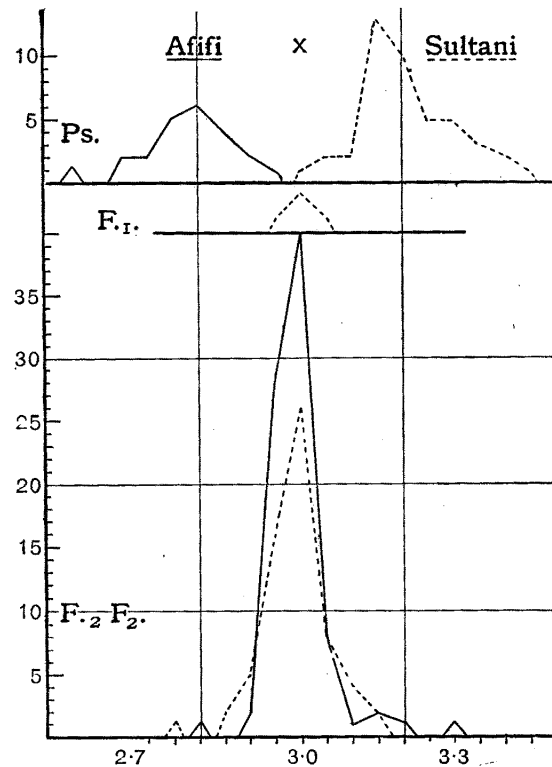


FIG. 65.—LOCULI OF THE OVARY.

character. Although it has failed to give the expected simplicity it is still less complex than the *Ægypto-American* crosses. The graphs are most strongly indicative, to the unbiased mind, of the formation of a new character in  $F_1$ , which subsequently breeds true; nevertheless, in the light of the other crosses, there can be little doubt that such is not the true interpretation.

**The weight of the seed.**—The inheritance of the mean seed-weight is particularly interesting. In the first place it fluctuates more than any other character, excepting the height, and it further shows clear evidence of autogenous fluctuation.

The first cross in which this character was carefully examined was Afifi  $\times$  Truitt (Fig. 66), where the mean seed-weights were 0.105 g. and 0.135 g. The seed-weight in  $F_1$  was 0.165 g. In  $F_2$  the weights ranged from 0.08 to 0.175 g., with two marked modes at 0.095 and 0.115. The form of this  $F_2$  graph suggested that light seed was

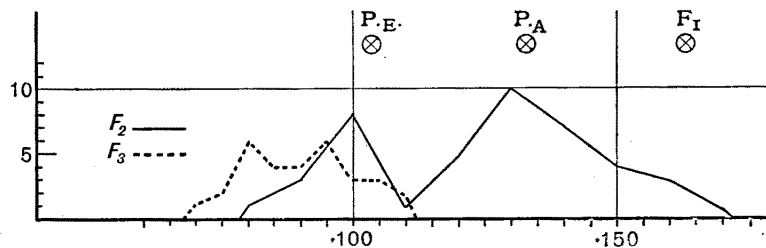


FIG. 66.—MEAN SEED-WEIGHT.

Afifi  $\times$  Truitt, showing extraction of small seed in  $F_3$ .

segregating from heavy seed, and on testing this by breeding on, we found no reason to modify this conclusion; thus, a plant with seed weighing 0.100 regressed slightly in  $F_3$  to a mean of 0.090, with a scatter from 0.070 to 0.110, and no higher probable error than the parent strain; and  $F_4$  raised from a 0.090 plant of these gave the same result, ranging from 0.065 to 0.110. The plants of the  $F_4$  had been extremely diversified in most other characters, such as height, while the  $F_4$  was almost a pure strain.

Whether the segregation was simple or compound, it was clear that the size of the seed—expressed by us as weight—was an inherited characteristic.

In another cross, namely Charara  $\times$  King (Fig. 68), the matter became more interesting, and the inheritance



obviously complex. The seed-weights of the two parents were substantially the same, being 0·085 for the American, and 0·095 for the Egyptian. The weight of the  $F_1$  seed was 0·145. Thus a very marked "intensification" had taken place, and the problem of finding the cause was set to the author. The seed-weight in  $F_2$  gave an unexpected frequency polygon; instead of a 3:1 form we obtained a modal curve, otherwise fairly symmetrical, which ranged from 0·055 to 0·170; the principal modes were situated at 0·085, 0·105, 0·120, and 0·140.

Before discussing this graph any further we may note that the  $F_3$  data were of the same nature as those described under the preceding character; the parental small seed was extracted and bred true, while larger seeds sometimes threw small ones in a way which suggested a 3:1 ratio, or less commonly bred true. In the latter case a new character, not found in either parent, had been "fixed." In the ordinary Mendelian characters such phenomena are usually due to the meeting of cryptomeres, but we shall see that our cryptomeres in this case are even less cryptic than Miss Wheldale's enzymes in *Antirrhinum*.

The attempt to dissect the  $F_2$  graph into its components led to the plotting of numerous correlation tables, and to the preparation of "dissected graphs" (Fig. 69). In the latter method, which is more rapid than the former, we take plants possessing some character in common, such as a very large boll, and mark off their position on the graph of the whole family. The mean of the special group, as compared with the general mean, serves to indicate any displacement, while the form of the "dissection" is usually less complicated than that of the general graph. On dissecting in this way for the fifteen plants which had the greatest boll-width of the whole 181  $F_2$  individuals, the mean seed-weight was raised by 0·0105 g.; moreover, though these large-boll plants constituted the greater part of the 0·140 mode, yet four of them were found in the 0·085

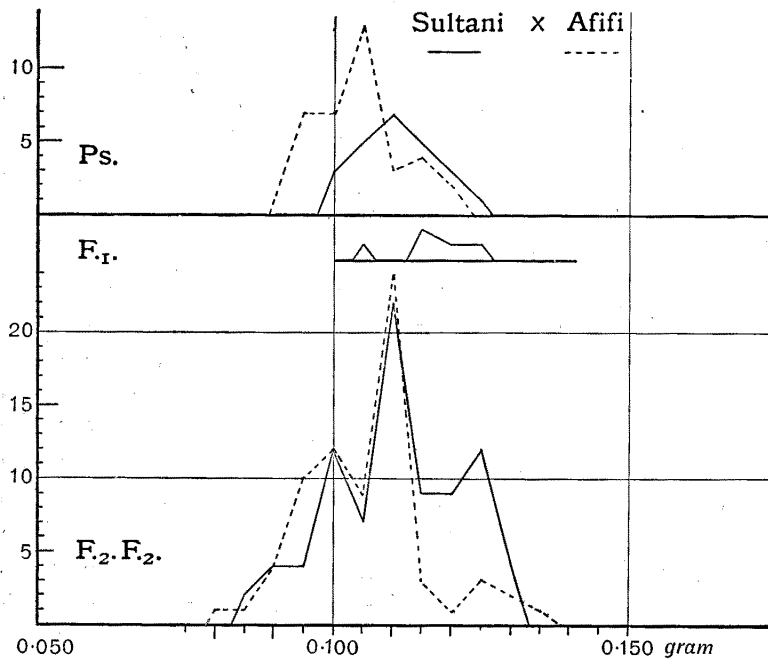


FIG. 67.—MEAN SEED-WEIGHT IN INTER-EGYPTIAN CROSS.

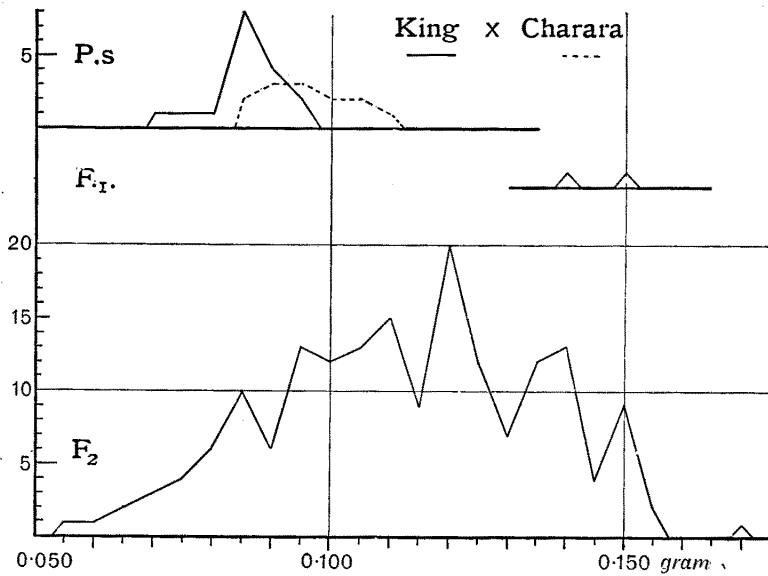


FIG. 68.—MEAN SEED-WEIGHT IN ÆGYPTO-UPLAND CROSS.

mode. This result indicated correlation of big-boll and big-seed, with segregation of big seed from small within the group. Similarly, on dissecting for the twenty-four smallest bolls, the modes were at 0.105 and 0.075. On plotting the correlation diagram it was found to give a value for " $r$ " of about 0.3, but this diagram was distinctly modal, the points being grouped, so that the true value of " $r$ " was probably very much higher.

Similar dissections were made in respect of almost every character available. In no case did the groups show uniform seed-weight within the error of fluctuation. Either the new group was evenly distributed over the graph, there being no correlation, or else it moved to one side. In the latter case, the group always assumed the 3:1 form. The most interesting of these for comparison with the big-boll dissection was the dissection for "discontinuous habit of growth"; the twenty plants which most resemble the Upland parent in this respect did not exceed 0.130, and formed two modes, one on and behind 0.085, the other on 0.105. Again, though classification according to habit of branching showed no marked shifting of the group-centre, yet the "unbranched" plants filled up the 0.120 mode, while "freely branched" occupied the mode at 0.140 (Fig. 69).

Two general conclusions result from this analysis. Firstly, that the modes in the  $F_2$  curve are genuine, and largely due to autogenous fluctuation.

Secondly, that the  $F_2$  curve consists of superposed curves having the 3:1 form, but mutually obscurant until groups of comparable individuals are taken.

Thus we have shown that light seed is segregating from heavy seed in  $F_2$ , probably as a simple pair of allelomorphs, just as in the Afifi  $\times$  Truitt series. The only serious weakness of this view lies in the fact that both the parents were light-seeded! The Upland parent, however, bore these light seeds inside a boll of 32 mm.

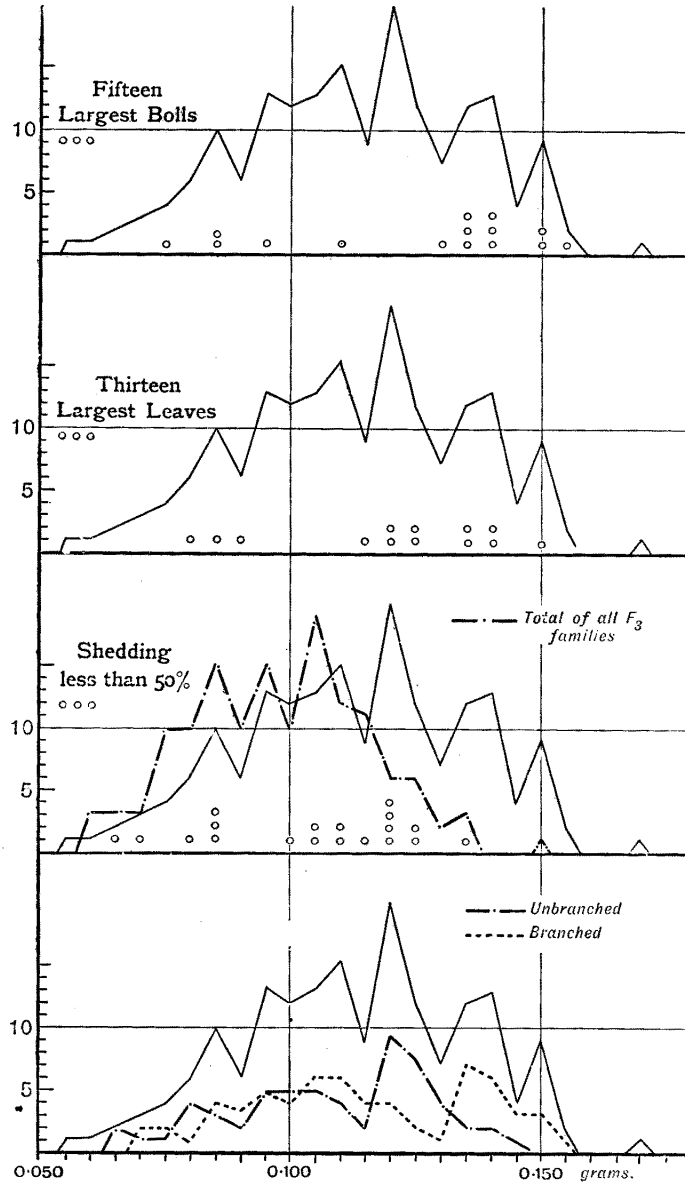


FIG. 69.—DISSECTION OF MEAN SEED-WEIGHT IN  $F_2$ .

The  $F_2$  curve of Fig. 68, dissected in respect of four correlated characters.

diameter, while the Egyptian boll was only 27 mm. in diameter. On crossing the two strains we effectively placed the Egyptian seed inside a boll whose cubic capacity had been doubled, and an increase in seed-size followed. Thus we may regard the Egyptian seed as being constitutionally large, and dominant over the genuinely small Upland seed. At gametogenesis in  $F_1$ , the two seed-weight allelomorphs separate from one another, and the 3:1 ratio appears in  $F_2$  if we clear away the lumber brought in by autogenous fluctuation.

We have discussed this masking of the difference in seed-weight, and the development of the difference under equal opportunities, in terms of boll-width alone for convenience, though other factors are also involved. The displacement of the means for such dissected graphs, when compared with the probable error of a pure strain, which is obviously too stringent a test for these heterogeneous groups, gave significant deviations in respect of "discontinuous growth"; a slight but significant deviation with respect to branching; a slight indication of connection between extensive shedding and heavy seed, which is probably indirect, since "discontinuous growth" sheds less than the other types; and a very marked relation between wide or narrow boll and heavy or light seed respectively. In the last case the figures were as follows:—

36 Widest bolls.	Mean seed-weight	+ 9.4%	( $P.E \times 3.2 = 4.3\%$ )
24 Narrowest bolls.	" "	- 13.2%	( $P.E \times 3.2 = 5.3\%$ )

The simple cross of Sultani  $\times$  Afifi showed dominance of heavy seed over light in  $F_1$  (Fig. 67), and although the difference between the two parents was very small, yet some indication of segregation is shown. This takes the form of two modes in the  $F_2$  curve, which appear in both the brother families; since the mean weights are computed, and hence do not suffer from any subjective error, this coincidence is probably significant, and due to

the superposition of a small-seed mode on the flank of a large-seed mode.

Summarising the evidence, it would seem that beneath all the complexity involved by fluctuation, by autogenous fluctuation and by correlation, there existed in all these hybrids a straightforward segregation of seed-size, controlled by a single allelomorphic pair of factors in every case.

**The mean maximum length of the lint.**—The inheritance of this character has been curiously similar to that of seed-weight, but the evidence is not so clear. The Afifi  $\times$  Truitt cross showed segregation which was ostensibly simple, long being dominant over short; the Charara  $\times$  King cross gave dominance of length in  $F_1$ , with subsequent modal composition in  $F_2$ . Sultani  $\times$  Afifi again gave dominance of length, and the  $F_2$  curve was almost symmetrical between the parental extremes (Fig. 70).

Subsequent generations have shown that pure parental length can be extracted, while new intermediate lengths may also breed true.

Dissection of the  $F_2$  revealed a similar series of phenomena to those shown by seed-weight. In this case, the most definite result was obtained by grouping to seed-weight; the 28 largest seed-weights had a mean lint-length which was 5.9 per cent. above the general mean, with modes at  $26\frac{1}{2}$  and 32 mm., the form of the dissection being that of the 3:1 type (Fig. 70). Conversely, the 27 smallest seed-weights were 5.9 per cent. below the mean general lint-length, with modes at 21 and 27 mm.

It thus seems highly probable that lint-length is also inherited simply, in spite of the seeming complication of the Charara  $\times$  King second generation.

**Miscellaneous.**—All the characteristics mentioned in the chapter on Fluctuation have been made the subject of

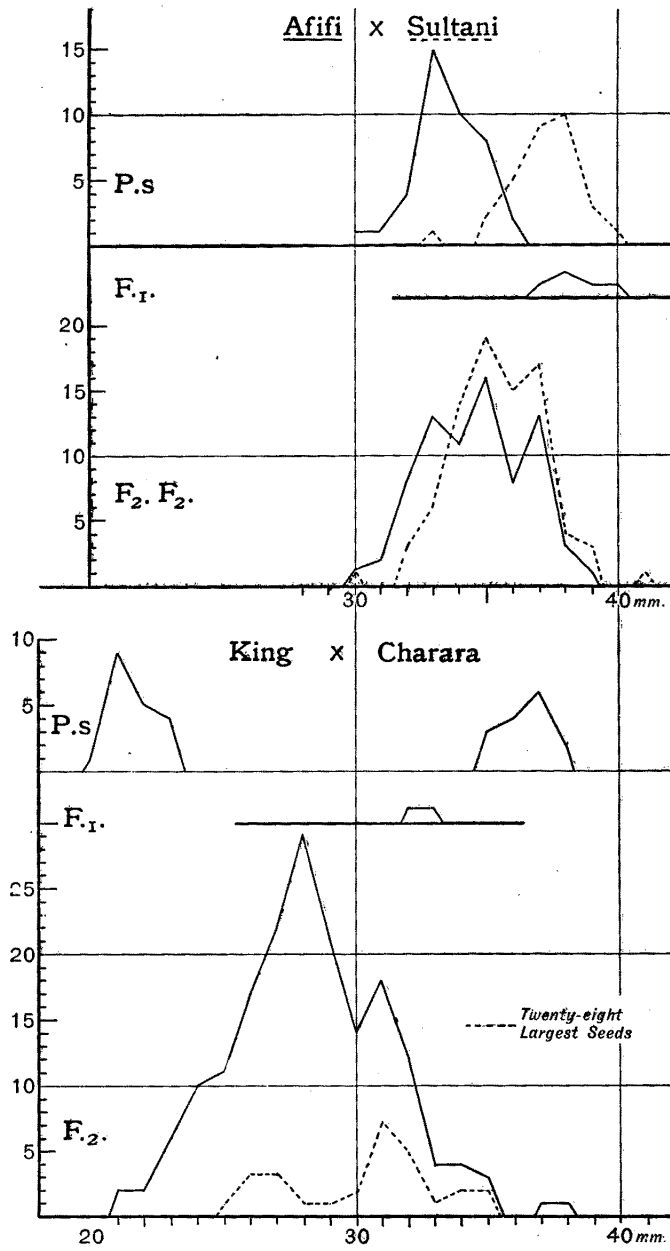


FIG. 70.—MEAN MAXIMUM LINT-LENGTH.

statistical records in the ordinary course of routine observations. Thus we possess the curves for growth, flowering, bolling, and shedding for almost every individual studied. Data for weight of lint per seed, and for ginning out-turn are also to hand, but the majority of these records are of more value as supplementary sources of information in physiology than from the standpoint of Genetics. At the same time, they are frequently of interest as showing the commercial resultant of those conflicting gametic forces whose lines we have endeavoured to trace.



## SECTION IV

### CHAPTER X

#### ECONOMICS \*

WITHIN the limits of this volume we can do no more than glance at the many matters of economic interest to which those researches are linked. Their most direct and immediate application has been found in the Sub-Soil Water controversy, from which many of the inquiries originated. No attempt has here been made to emphasise the economic importance of root asphyxiation and restriction, but the text and diagrams should show that a deep water-table is essential, and that a rise of the water-table to the roots is deadly in July, prejudicial in September, and almost harmless in December. For several years the yield per acre in Egypt had been lessening (Fig. 71), and many causes<sup>24</sup> had been invoked to account for it, but the matter was obscure until Mr. J. R. Gibson, assisted by M. Audebeau, showed that the level of the water-table had risen on the State Domains, and pointed out the probability that such a rise, produced by improvements in the system of irrigation, might suffice as a general cause.<sup>13, 15</sup> Mr. Gibson's death deprived the author of his collaboration

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\* See Todd, J. A., for discussion of the purely economic problems of cotton in Egypt and Lancashire.

in developing the biological side of this hypothesis, which —after three years of animated discussion<sup>16, 17, 18, 24, 27</sup>— has now become a factor in the administration of Egypt.\*

The original hypothesis is still unproven, and must so remain, in the absence of extensive records to show the water-levels of past years, but so strong a case has been

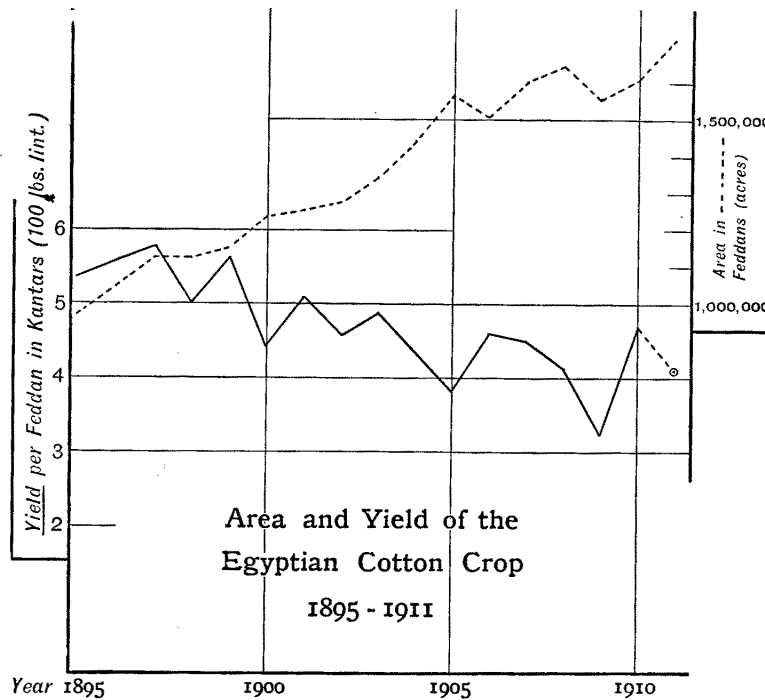


FIG. 71.—AREA AND YIELD OF THE EGYPTIAN COTTON CROP, 1895-1911.

made out for the presumption † that, when taken in conjunction with the physiological evidence summarised in the present volume, the proof may be regarded as exhaustive. The preliminary solution of one of the neatest problems ever set to agricultural science has thus been

\* Report of Cotton Commission, 1910; Reports of H.M. Agent and Consul-General on Egypt and the Sudan (Egypt No. 1) 1910, 1911, and 1912.

† Ferrar, H. T.; Lucas, A.; Audebeau, C.

achieved, on a crop which is worth twenty to thirty millions of pounds per annum.

Concurrently with the depreciation of yield, there had also been a depreciation of quality in the chief variety grown.<sup>7, 15, 32</sup> This latter trouble was partly due to the same cause, but chiefly to varietal "deterioration."

The coincidence was extremely unfortunate, for the short crops led to inflated prices,\* which were intolerable with a degrading quality; the consumers, driven to experiment with inferior cottons, succeeded beyond all expectation in the substitution of long-staple Upland, and even of ordinary Upland, for Egyptian cotton. The typical Egyptian cotton has thus lost the monopoly which it formerly enjoyed.

The remedies for these two troubles are now being applied,† to wit, drainage and restricted irrigation in the first case, together with the supply of better seed in the second. With regard to seed-supply we have seen that the problem is essentially the avoidance of natural crossing, since "deterioration" must ensue if a single foreign pollen-grain enters the pedigree. By cultivating pure lines in bee-proof cages, propagating from these in isolated sites, or in plots protected by related populations, and by *renewing continually* the seed-supply of any strain in this way from the laboratory through seed-farms, the varieties of the future will be proof against "deterioration," unless mutation takes place. It cannot be too strongly insisted upon, that any scheme for the introduction of new cottons is doomed to ultimate failure unless continual replacement of contaminated stocks is taking place every year from the original pure strain.<sup>5, 32</sup>

The demands of Egyptian cotton upon the cotton-breeder,<sup>5, 7, 15</sup> apart from this question of purifying and

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\* Todd, J. A.

† Lord Kitchener's Report on Egypt and the Sudan, 1912.

distributing the existing varieties, have sunk of late years into insignificance, through contrast with the urgent call for physiological information. Still, they are by no means trivial, and once stability is restored to the supply of Egyptian cotton, there will be room for much improvement in detail. The chief interest of the data on genetics<sup>5, 8, 15, 20, 30</sup> relates to the extension of cotton cultivation into fresh countries and climates. The reader will probably concede, whatever may be the soundness of the interpretations given, that there is no doubt as to the formal nature of the inheritance of various characters in cotton crosses, even where such inheritance appears most dependent on simple chance. Such characteristics as yielding-capacity, earliness of maturity, climatic suitability, and others of agricultural importance, are the outcome of complex and interacting combinations of allelomorphs, and must in no way<sup>19, 20, 25, 30</sup> be considered as simple things; but sufficient time and research will ultimately deduce the laws of their transmission, now that the said research has been placed on a precise basis. The outcome of such deductions must be that the colonial agriculturist of the near future will no longer carry a bag of seed, searching for a district in which it will grow to the consumer's liking, but will choose his district first, and then manufacture a cotton plant to suit it. A further impetus towards the precise study of genetics will be given by the specialisation of manufacturing processes, demanding more various types of raw material, each suited to special purposes, and therefore worked up with greater economy. The aeroplane is already beginning to affect the Egyptian fellah.

An important advantage of seed-supply projects lies in their simplicity from the viewpoint of the native cultivator, who is usually prejudiced and frequently unskilled. A change in the variety of cotton supplied to him causes no change in his habits or methods, and interferes less with

his personal freedom than any other manifestation of the "march of progress."

With regard to the general cultivation of cotton, these researches have thrown into prominence the immense importance of the root system, whereof—in a limited sense—the aerial portions are only the visible expression.<sup>7, 13, 15, 16, 26, 27, 29</sup> It seems probable that a great deal of botanical research in the coming twenty years will be subterranean. Researches have also cleared up the causes of seed-failure, have obtained some general expressions for the effect of environment on development, and by means of a system of records, which can be kept with no more trouble than meteorologists' observations, they have thrown light on the causes of variation in crops from year to year, and from place to place, in the form of certain curves of flowering, bolling, and growth, which have a precise value.

The designation of lines upon which to drive our wedges still further into the mass of available material is almost impossible, since the most valuable results are usually obtained by following out a side line, which in its turn has been detected through the accidental direction of attention to a commonplace phenomenon. Knowledge of the changes in water-content of various layers of soil can be applied directly to irrigation practice, study of the growth processes in the fruit will demonstrate the causes of fluctuation in the grade of the commercial product, and any information about the infectivity of foreign pollen may reveal the way by which the contamination of varieties can be eliminated. Lastly, it should be borne in mind that most of these researches are based on evidence collected at the apex of the Egyptian Delta, so that there is a long field of operations in which our present results may be re-examined, stretching from the Mediterranean into the heart of the Sudan.

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