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# INHERITANCE IN THE FOXGLOVE, AND THE RESULT OF SELECTIVE BREEDING.

By ERNEST WARREN, D.Sc. Lond.

In *Biometrika*, Vol. xi. pp. 302—327, 1917, the author published a preliminary report on the earlier results obtained in the breeding of foxgloves; and the present paper contains some account of the final results of the selection experiments.

In 1914 ten foxglove plants (*Digitalis gloxiniaeflora*), obtained from various sources and of different characteristics, were crossed among themselves and also self-fertilised. In subsequent years, 1915—19, new generations were obtained chiefly by the self-fertilisation of selected parents. The measurement, or when not possible the grading, of certain characters (pelorism, colour, size of flower, spotting of flower, etc.) was undertaken in all the generations in order to determine the effect of selection when selfing alone occurred in an apparently pure race.

## 1. PELORISM.

Mendelian inheritance occurred in a typical fashion. A peloric plant crossed with a non-peloric plant produced non-peloric offspring. On selfing these, or crossing them together, there resulted on the average one peloric to three non-peloric.

Of the 10 parent plants two exhibited the peloric condition in a fully developed form, and the rest were non-peloric. The character was very perfectly recessive, and by breeding, it was found that three of the remaining plants were really heterozygous, while all the others were non-peloric and homozygous.

It was soon observed that the peloric condition was by no means a clearly defined and fixed character. Pelorism in the foxglove may be regarded as an abnormal lack of power to produce internodes between the flower-buds, and consequently there may result considerable fusion of such buds with one another.

The maximum stage of pelorism is seen when the main-axis is short and abruptly ceases to grow in height. Only two or three normal flowers may be produced by the axis, and its blunt, sharply truncated end is surrounded by a whorl of bracts or sepals, petals being absent. Sometimes a ring of sessile anthers occurs (Pl. I, figs. I, II).

In typical pelorism the inability to produce internodes affects the terminal portions of all of the flower-axes of a plant, both central and side-axes. A variable number of flower-buds fuse and the corollas unite and may form a large symmetrical cup or saucer of some ornamental value, but the sepals mostly remain

separate (figs. III, IV). When numerous flower-buds fuse a dense rosette may be formed by the petals, and the result is not pleasing. The peloric or crown-flower opens early, often before any of the normal flowers. After the crown-flower has faded, the main-axis usually grows through the centre of it, and may even produce a second crown-flower (fig. VI); but in the case of the side-shoots the axis generally ends in an ovary and no further growth occurs (fig. V).

If the peloric tendency is not so well-marked, the main-axis may be only slightly affected by the suppression of several internodes, and by the partial fusion of flower-buds, at a variable distance above the lowest normal flower of the axis. Sometimes a considerable number of internodes may be unduly shortened, so as to produce excessive crowding of flowers which do not actually fuse (fig. VII), and frequently a strongly marked spiral bending of the axis occurs (fig. VIII).

At other times the suppression of the internodes may occur only high up on the flowering axis close to where it normally ceases to grow (fig. IX).

When the central axis is strongly peloric the side-axes are invariably so, and in all other cases the side-axes exhibit greater pelorism than the main-axis.

Finally, the main-axis may be quite normal and show no peloric tendency, but the side-axes may still be strongly peloric.

The last trace of pelorism in a plant is shown when only one or two of the weaker side-axes exhibit some slight sign of a peloric tendency.

It is unfortunate that it has not been found possible to devise any practical method of measuring the intensity of pelorism, and therefore the plants have been arranged in four grades.

0° grade = no peloric tendency.

1°— 25° grade = those in which the central axis is non-peloric, but the side-axes exhibit some peloric tendency.

26°— 50° grade = main-axis non-peloric, but side-axes may reach full pelorism.

51°— 75° grade = main-axis partially peloric, side-axes fully so.

76°—100° grade = plants ranging to complete pelorism in all axes.

In the generations produced from 1914—19 there were in all 128 fertilisations of different classes of individuals, recessive (peloric), homozygous dominant (non-peloric) and heterozygous dominant (non-peloric) plants, and families were raised. In the table on p. 105 the experimental and theoretical results are compared. The fertilisations of the classes  $DD \times DD$ ,  $RR \times RR$ , and  $DR \times DR$  include both selfing and crossing. The sum totals of the experimental and theoretical results are remarkably close; being, crowned, 1019 experimental and 1013 theoretical; non-crowned, 1169 experimental and 1175 theoretical.

It must be noted here that a plant was recorded as "peloric" or "crowned" if it exhibited the least tendency towards pelorism in any of the axes. Taking all the classes or groups together it may be said that the inheritance of the quality of pelorism is typically Mendelian. The group  $RR \times RR$  should include no non-crowned offspring, and the 7 which occurred were obtained by gradual selection.

The group in which the experimental result diverged the most widely from the theoretical result was  $DR \times RR$  (heterozygous plants crossed with recessives) and it would be interesting to know whether such is generally the case in Mendelian inheritance.

Gametic Nature of Pairings	Number of Families	Number of Offspring	Number of <i>Crowned</i> Offspring		Number of <i>Non-Crowned</i> Offspring	
			Experimental	Theoretical	Experimental	Theoretical
$DD \times DD$	16	266	0	0	266	266
$RR \times RR$	43	741	734	741	7	0
$DR \times DR$	38	777	187	194	590	583
$DR \times DD$	5	93	0	0	93	93
$DR \times RR$	12	156	98	78	58	78
$DD \times RR$	14	155	0	0	155	155
Totals	128	2188	1019	1013	1169	1175

*The Inheritance of the Degree or Intensity of Pelorism.*

If a peloric plant be crossed with a non-peloric homozygous dominant, the offspring are heterozygous and non-peloric, and if these are self-fertilised or crossed together the peloric character re-appears in an apparently unchanged and undiluted condition. If, on the other hand, a strongly peloric plant is crossed with a weakly peloric one the offspring are more or less intermediate, and if the offspring are selfed or fertilised together the intermediate nature of the peloric character tends to be retained.

In the accompanying table  $A, B, C, D, E$  are plants of various gametic constitution. On selfing ( $A$ ) the offspring were all fully peloric. On selfing some 5 offspring,  $A, 2-9$ , the plants produced were all essentially fully crowned.

On crossing two recessive plants ( $A$  and  $E$ ) of different peloric intensities (see bottom of table) the offspring tended to be intermediate.

On crossing ( $A$ ) with an ordinary plant ( $B$ ) the offspring were non-peloric and heterozygous. On selfing two of these plants, ( $A \times B$ ) pls. 2 and 7, the offspring were either fully peloric, or non-peloric (heterozygous and homozygous). On selfing two recessives, ( $A \times B$ ) 2, pls. 8 and 9, obtained from ( $A \times B$ ) pl. 2, the offspring were all nearly completely peloric. Thus, there was no clearly marked dilution or apparent contamination by crossing a peloric plant with a non-peloric one. When, however, the same recessive plant ( $A$ ) was crossed with a heterozygous plant ( $C$ ) having in its gametes a weak peloric tendency of about  $35^\circ$  there was much variation in the offspring, and on selfing some of these plants, ( $A \times C$ ) 1, 2, 7, 11, and raising a new generation it was obvious that considerable dilution of the peloric tendency had occurred. On crossing the same plant ( $A$ ) with a heterozygous plant ( $D$ ) having a stronger peloric tendency ( $75^\circ$ ) in its gametes it was clear that in the next generation raised ( $A \times D$ ) 6, 5, 11 less dilution had taken place than in the former case.

*Pelorism—Various Pairings.*

Parentage	Peloric Offspring				Non peloric	Offspring (selfed)	Peloric Offspring				Non-peloric
	100°	75°	50°	25°			100°	75°	50°	25°	
<i>A</i> (100° pelorism) Selfed = <i>RR</i> × <i>RR</i>	33	0	0	0	0	<i>A</i> pl. 2 (100° pelorism) <i>A</i> pl. 3           " <i>A</i> pl. 4           " <i>A</i> pl. 6           " <i>A</i> pl. 9           "	13 3 2 6 1	1 0 0 0 0	0 0 0 0 0	0 0 0 0 0	
<i>A</i> ♀ (100° pelorism) × <i>B</i> ♂ (0° pelorism and homozygous) <i>A</i> × <i>B</i> = <i>RR</i> × <i>DD</i>	0	0	0	0	13	( <i>A</i> × <i>B</i> ) pl. 2 (non-peloric and heterozygous) ( <i>A</i> × <i>B</i> ) pl. 7 (non-peloric and heterozygous) ( <i>A</i> × <i>B</i> ) 2 pl. 8 (100° pelorism) ( <i>A</i> × <i>B</i> ) 2 pl. 9           "	6 5 12 5	0 0 1 0	0 0 0 0	0 0 0 0	21 23 0 0
<i>C</i> (heterozygous) Selfed = <i>DR</i> × <i>DR</i>	1	0	2	3	13						
<i>A</i> ♀ (100° pelorism) × <i>C</i> ♂ (non-crowned and heterozygous with, say, 35° pelorism in gamete) <i>A</i> × <i>C</i> = <i>RR</i> × <i>DR</i>	4	12	3	1	7	( <i>A</i> × <i>C</i> ) pl. 1 (75° pelorism) ( <i>A</i> × <i>C</i> ) pl. 2 (50° pelorism) ( <i>A</i> × <i>C</i> ) pl. 7 (heterozygous) ( <i>A</i> × <i>C</i> ) pl. 11           "	20 6 — —	4 7 — 2	9 1 2 3	2 1 0 1	0 0 10 7
<i>D</i> (heterozygous) selfed	1	1	1	0	8						
<i>A</i> ♀ (100° pelorism) × <i>D</i> ♂ (non-crowned and heterozygous with, say, 75° pelorism in gamete)	11	2	0	0	10	( <i>A</i> × <i>D</i> ) pl. 6 (100° pelorism) ( <i>A</i> × <i>D</i> ) pl. 5           " ( <i>A</i> × <i>D</i> ) pl. 11 (75° pelorism)	17 21 27	2 0 5	2 6 1	0 0 0	0 0 0
<i>A</i> ♀ (100°) × <i>E</i> ♂ (50°)	4	1	3	0	0						

In the last generation it will be seen that there was no sharp separation of the plants into two groups attributable to the two grandparental factors. Thus, in the case of (*A* × *C*) pl. 2 (50°) the offspring are not clearly divisible into those of 100° resembling *A*, and those of 35° attributable to *C*; in other words there was no obvious segregation into two degrees of pelorism.

On the factorial and chromosome hypotheses we must suppose that the factor or factors governing the peloric character tend to become mutually changed and intermediate in nature when the male and female chromosomes containing the factors for the two degrees of pelorism lie alongside each other in the zygote.

It will be of interest to obtain a general measure of the strength of inheritance between mid-parent and offspring with respect to the transmission of the degree or intensity of pelorism. For this purpose only recessives were used, involving

30 mid-parents. Employing Prof. Karl Pearson's method the accompanying table gives the correlation surface.

*Pelorism—Correlation Table—Recessives. Mid-parent and Offspring.*

Offspring. Grade of Pelorism.

Mid-parents. Grade of Pelorism	76°—100°	51°—75°	26°—50°	1°—25°	Totals
1°—25°	6	2	23	18	49
26°—50°	58	61	68	11	198
51°—75°	64	31	15	—	110
76°—100°	143	14	11	5	173
Totals	271	108	117	34	530

The coefficient of correlation, calculated from the table, between mid-parent and offspring is .52. The result can be regarded as only a very rough approximation, since a satisfactory method of measuring pelorism has yet to be found. The figure obtained is somewhat low, but it would seem to indicate that the inheritance of the degree of pelorism is of the nature of ordinary blended inheritance.

The point of interest to notice is that the union of two peloric plants of different peloric intensities influences the gametes, while the union of a peloric plant with a homozygous non-peloric plant does not very readily affect the purity of the gametes with respect to pelorism.

*Pelorism. Effect of Selection in a homogeneous race.*

A peloric plant (C) with pelorism of about 85° intensity was self-fertilised, and the offspring, 16 in number, were as follows: 7 with 100°, 4 with 75° and 5 with 50° of pelorism.

Parentage (Self-fertilisation)	Crowned Offspring				Not crowned	Parentage (Self-fertilisation)	Crowned Offspring				Not crowned
	100°	75°	50°	25°			100°	75°	50°	25°	
C(85°) ... ..	7	4	5	0	0	C 2, 11 (75°) C 2, 2 (50°) C 2, 8 (50°)	6	13	5	0	0
C 2 (50°) ... ..	7	7	10	0	0		2	16	10	0	0
C 7 (50°) ... ..	17	11	18	2	0		1	13	11	0	0
C 7, 10 (25°) ...	0	2	18	2	5	C 7, 10, 20, 4 (0°)	0	0	0	0	6
C 7, 10, 20 (25°)	0	0	1	2	7		0	0	0	0	6

Two of these plants of 50° (*C* 2 and 7) were selfed, and the generation raised exhibited a lowered pelorism. The various selections made and the results obtained are shown in the accompanying table. It will be seen that finally on the selfing of plant *C* 7, 10, 20, 4 (0°) only non-peloric offspring were obtained.

## 2. GENERAL COLORATION OF THE COROLLA.

As described in the previous report (*loc. cit.*) the intensity of the purple coloration was measured by comparing it with a colour-scale founded on the intensity of colour by transmitted light of varying depths of a standard colour-solution.

Purple and white foxgloves exhibit the ordinary Mendelian relationship, purple being dominant. A confusing aspect of the problem is introduced by the fact that "white" foxgloves are not necessarily entirely white, since they may exhibit a faint purple coloration which on the colour-scale adopted may amount to about 5. On crossing such a plant with an ordinary purple plant segregation occurs when the heterozygous offspring are self-fertilised. Any higher coloration, say 10—15, does not exhibit segregation, but gives a blended inheritance, and such a plant is to be regarded as a very pale purple one and not "white." From certain observations that have been made it is probable that a similar condition occurs in the Blue *Agapanthus* lily, since some of the "white" plants have flowers faintly tinged with blue. It is quite likely that the phenomenon is general, and it may throw an important light on the physical theory of heredity. Possibly it may be surmised that a factor for a coloration of less than 5 units is unable to blend with, or influence, the factor controlling a higher coloration, in that we have reached the lowest dynamic unit.

Of the ten original plants, five were purple and homozygous, four were purple and heterozygous and one was white or recessive. These were very variously crossed in all manner of ways. In the accompanying table the experimental results are compared with the Mendelian expectation for the different gametic pairings.

### *General Coloration of Corolla—Breeding Results.*

Gametic Nature of Pairings	Number of Families	Number of Offspring	White		Purple	
			Experimental	Expectation	Experimental	Expectation
<i>DD</i> × <i>DD</i>	120	1620	2+3	0	1615	1620
<i>RR</i> × <i>RR</i>	17	336	330	336	6	0
<i>DR</i> × <i>DR</i>	50	785	190	196	595	589
<i>DR</i> × <i>DD</i>	11	103	0	0	103	103
<i>DR</i> × <i>RR</i>	8	76	24	38	52	38
<i>DD</i> × <i>RR</i>	8	87	0	0	87	87
Totals	214	3007	549	570	2458	2437



In the gametic group  $DD \times DD$  (homozygous purple  $\times$  homozygous purple) there were 1620 offspring. These should have been all purple, but there were two white plants which occurred in two deeply coloured families and three white plants which occurred in one pale-coloured family. I do not believe that there was contamination, and it is probable that the two former plants were sports, while the three latter plants were produced by selection.

In the group  $RR \times RR$  (white  $\times$  white) there were 336 offspring, and these should have been all white, but there were six pale-coloured plants. The difficulty in distinguishing a tinged "white" plant from a pale-coloured plant may account for this result, but I favour the view that we are here witnessing the beginning of a coloured race.

The result given by  $DR \times DR$  (heterozygous purple  $\times$  heterozygous purple) is very closely Mendelian. Out of 785 offspring there were 190 white plants while the expectation was 196.

Heterozygous plants crossed with dominants ( $DR \times DD$ ) gave nothing but coloured plants, and this was also the case with dominants crossed with recessives ( $DD \times RR$ ).

The gametic group  $DR \times RR$  (heterozygous plants  $\times$  recessives) gave a result which diverged rather widely from the expectation: there were insufficient whites, there being 24 whites and 52 purples instead of 38 of each. The numbers are somewhat small for drawing conclusions, but it is important to notice that in the character of pelorism it was the same gametic group which diverged the most widely of all the classes from the theoretical expectation. On the chromosome hypothesis it may be conjectured that possibly preferential pairing of the male and female chromosomes may explain the discrepancy.

*The Inheritance of the Intensity of Coloration.*

On crossing a purple homozygous plant with a white plant the offspring were all heterozygous and all coloured, but the intensity of the coloration was mostly reduced very considerably. On selfing these offspring the next generation yielded some homozygous dominants in which the original colour-intensity of the grandparent was regained; thus, at first sight it appeared that there had been no real dilution of the colour by crossing with the white. This was my first impression from the earlier results, but with more extended experience I found that there was certain evidence that the crossing with the white did have some deleterious action on the intensity of the coloration of the dominant grandchildren, although the coloration which appeared was much greater than a half and half blend with white.

If two homozygous dominants of marked difference in colour-intensity were crossed, the offspring tended to be intermediate. On selfing these offspring the next generation was similarly intermediate, and there was no segregation into the two different intensities of the grandparents. Thus a true blend of the two intensities had taken place.



In the accompanying table the results of some instructive crossings and self-fertilisations are given. In Series I two dominants (*E* and *F*) of different colour-intensities were selfed and the families raised showed that the parents were homozygous. On crossing (*E*) and (*F*) a family of intermediate offspring was obtained.

## Colour-Intensity—Various Pairings.

No. of Series	Gametic Constitution	Parentage	Mid-Parental Colour	Colour-Scale—Offspring										Mean of Coloured Offspring	
				Coloured plants									"WHITE"		
				125°—139°	110°—124°	95°—109°	80°—94°	65°—79°	50°—64°	35°—49°	20°—34°	5°—19°	0°—4°		
I	<i>DD</i> × <i>DD</i>	<i>E</i> (selfed) ... ..	90	—	2	0	5	8	—	—	—	—	—	—	83
	<i>DD</i> × <i>DD</i>	<i>F</i> (selfed) ... ..	68	—	—	—	6	3	—	—	—	—	—	—	64
	<i>DD</i> × <i>DD</i>	♀ <i>E</i> × ♂ <i>F</i> ... ..	79	—	—	—	4	3	5	—	—	—	—	—	71
	<i>DD</i> × <i>DD</i>	( <i>E</i> × <i>F</i> ) pl. 16 (selfed) ...	82	—	—	2	6	2	—	—	—	—	—	—	87
	<i>DD</i> × <i>DD</i>	( <i>E</i> × <i>F</i> ) pl. 9 (selfed) ...	61	—	—	—	—	1	10	1	—	—	—	—	56
II	<i>DD</i> × <i>RR</i>	♀ <i>E</i> × ♂ (WHITE) ... ..	45	—	—	—	—	11	1	4	2	—	—	—	60
	<i>DR</i> × <i>DR</i>	<i>E</i> × (WHITE) pl. 18 (selfed)	71	—	—	1	1	5	1	1	1	—	2	—	66
III	<i>DD</i> × <i>DD</i>	<i>B</i> (selfed) ... ..	95	3	0	2	3	6	1	—	—	—	—	—	102
	<i>DD</i> × <i>RR</i>	♀ <i>B</i> × ♂ (WHITE) ... ..	47	—	—	—	1	4	4	1	1	—	—	—	59
	<i>DR</i> × <i>DR</i>	( <i>B</i> × WHITE) pl. 1 (selfed)	80	—	—	—	—	1	2	—	—	—	—	—	64
	<i>DR</i> × <i>DR</i>	( <i>B</i> × WHITE) pl. 5 (selfed)	32	—	—	—	—	—	—	2	3	—	5	—	31
IV	<i>DD</i> × <i>DD</i>	<i>B</i> (selfed) ... ..	95	3	0	2	3	6	1	—	—	—	—	—	102
	<i>DR</i> × <i>DR</i>	<i>A</i> (selfed) ... ..	70	—	—	—	4	12	4	1	—	—	7	—	70
	<i>DD</i> × <i>DR</i>	♀ <i>B</i> × ♂ <i>A</i> ... ..	82	2	0	1	4	4	2	—	—	—	—	—	105
	<i>DD</i> × <i>DD</i>	( <i>B</i> × <i>A</i> ) pl. 7 (selfed) ...	130	1	1	3	12	13	—	—	—	—	—	—	87
	<i>DD</i> × <i>DD</i>	( <i>B</i> × <i>A</i> ) pl. 2 (selfed) ...	65	—	—	—	2	13	12	—	—	—	—	—	67
V	<i>DD</i> × <i>DD</i>	<i>B</i> (selfed) ... ..	95	3	0	2	3	6	1	—	—	—	—	—	102
	<i>DR</i> × <i>DR</i>	<i>C</i> (selfed) ... ..	34	—	—	—	—	—	1	9	2	—	4	—	40
	<i>DD</i> × <i>DR</i>	♀ <i>B</i> × ♂ <i>C</i> ... ..	65	—	—	—	—	2	4	2	—	—	—	—	53
	<i>DD</i> × <i>DD</i>	( <i>B</i> × <i>C</i> ) pl. 8 (selfed) ...	50	—	—	—	—	—	2	1	—	—	—	—	50
	<i>DD</i> × <i>DD</i>	pl. 4 ... ..	50	—	—	—	—	4	17	3	—	—	—	—	59
	<i>DD</i> × <i>DD</i>	pl. 7 ... ..	58	—	—	—	—	5	4	1	1	—	—	—	60
	<i>DD</i> × <i>DD</i>	pl. 6 ... ..	68	—	—	—	—	6	14	9	—	—	—	—	54
	<i>DD</i> × <i>DD</i>	pl. 1 ... ..	70	—	—	2	4	20	4	—	—	—	—	—	74

Two of these offspring were selected, (*E* × *F*) pls. 16 and 9, as widely divergent from each other as possible, and selfed. In the families obtained there was no tendency for the occurrence of segregation into the two colour-intensities of (*E*) and (*F*) respectively. There was thus a definite blend, and the means of the two families approached the respective colour-intensities of the two self-fertilised plants.

In Series II the same homozygous dominant plant (*E*), with colour-intensity of 90°, was crossed with a white plant and all the offspring were heterozygous and intermediate. On selfing one of the darker coloured offspring, no. 18, the dominant plants raised tended to be of about the same colour-intensity as the grandparent

(E). In Series III a dark-coloured homozygous dominant plant (B) was also crossed with a white plant. One of the darkest heterozygous offspring (B × White) pl. 1 was selfed and the coloured plants raised tended to be paler than the grandparent, but the family was small.

In Series IV the dark-coloured homozygous plant (B) was crossed with a dark heterozygous plant (A). From the offspring raised, two were selected and selfed, one very dark and the other moderately dark. The two families included only coloured plants, and consequently the parents may be supposed to have been homozygous. The moderately dark parent (B × A) pl. 2 failed to produce any offspring as dark as the grandparent (B).

In Series V the same plant (B) was crossed with a light heterozygous plant (C). From the offspring produced five homozygous dominants were selfed, and in the five families raised only two plants reached the colour-intensity of the grandparent (B).

On taking all these results together it may be said that there is evidence for the view that crossing a dark race of foxgloves with white plants tends to dull the colour-intensity of homozygous dominants of subsequent generations.

*General Coloration—Strength of Inheritance and Effect of Selection.*

In 1914 a dark-coloured homozygous plant ( $B_4 \text{ ♀}$ ) was crossed with a somewhat pale-coloured heterozygous plant ( $C_1 \text{ ♂}$ ) =  $DD \times DR = \text{III}$ . The offspring would consist theoretically of approximately equal numbers of dominants and heterozygous individuals. The reciprocal cross ( $C_1 \text{ ♀} \times B_4 \text{ ♂}$ ) was also made =  $\text{II}$ . Several dominants were selfed and families were raised. Out of these families certain plants were selected and selfed and new families were obtained. This procedure was continued until 1917, and the results are given in the accompanying table. The families of the different years are arranged in ascending order of the colour-intensities of the parents. On comparing the means of the families with the colour-grade of the parents (shown in brackets) it will be at once seen that small variations in the colour-intensity of the parents tended to be transmitted to the offspring. It is obvious that the table exhibits the effect of selection in self-fertilised homozygous generations.

For example we may take the following :

Homozygous plant, II. 1	had a colour of	70	and a mean of offspring	74
An offspring of above, II. 1, 4	”	74	”	82
An offspring of above, II. 1, 4, 17	”	110	”	95
Homozygous plant, III. 2	”	75	”	66
An offspring of above, III. 2, 1	”	66	”	55
An offspring of above, III. 2, 1, 18	”	80	”	85
An offspring of above, III. 2, 1, 18, 28	”	95	”	100

Reverse selection is shown also :

Homozygous plant, III. 2	”	75	”	66
An offspring of above, III. 2, 5	”	52	”	57
An offspring of above, III. 2, 5, 5	”	40	”	41
An offspring of above, III. 2, 5, 5, 12	”	30	”	32

*Inheritance of Colour-Intensity among Dominants.*

Grades of Colour-Scale (Offspring)	$DR \times DD$	Dominant Generations (Self-fertilisation)																			
	$II = C_1(34) \times B_4(80)$	Parents II 4 (50)	II 6 (6f)	II 1 (70)	II 4, 8 (45)	II 4, 6 (49)	II 6, 3 (49)	II 6, 4 (54)	II 4, 2 (61)	II 6, 11 (61)	II 6, 1 (68)	II 4, 12 (69)	II 1, 4 (74)	II 1, 2 (91)	II 1, 1 (120)	II 1, 2, 20 (53)	II 6, 11, 6 (59)	II 1, 4, 3 (64)	II 1, 1, 2 (77)	II 1, 4, 17 (110)	
30—39	2	—	1	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
40—49	0	3	3	—	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
50—59	4	8	13	1	6	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
60—69	1	12	4	9	—	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
70—79	1	1	3	14	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
80—89	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
90—99	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
100—109	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
110—119	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
120—129	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Means	53	59	54	74	51	66	54	62	66	69	64	64	82	78	70	59	65	71	81	95	
Grades of Colour-Scale (Offspring)	$III = B_4(80) \times C_1(34)$	Parents III 2 (75)	III 2, 5 (52)	III 2, 7 (52)	III 2, 13 (63)	III 2, 1 (66)	III 2, 2 (71)	III 2, 8 (72)	III 2, 5, 5 (40)	III 2, 5, 18 (52)	III 2, 7, 9 (62)	III 2, 5, 10 (72)	III 2, 1, 18 (80)	III 2, 5, 5, 12 (30)	III 2, 5, 10, 17 (37)	III 2, 5, 5, 11 (42)	III 2, 1, 18, 10 (53)	III 2, 5, 10, 22 (70)	III 2, 1, 18, 12 (85)	III 2, 1, 18, 21 (95)	III 2, 1, 18, 28 (95)
20—29	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
30—39	1	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—
40—49	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
50—59	1	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
60—69	0	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
70—79	2	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
80—89	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
90—99	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
100—109	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
110—119	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
120—129	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
130—139	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Means	67	66	57	54	60	55	71	69	41	47	62	68	85	32	43	47	44	74	75	91	100

Thus, starting with a plant of about 70 colour-intensity we arrive by selection of self-fertilised plants at mean family intensities of 100 in one direction and 32 in the reverse direction.

In another series, starting with a homozygous dominant plant of colour-intensity of about 11, I have by selection obtained plants in which the corolla exhibited no general tint. On selfing the pale plant no white plants occurred,

and the offspring were all pale-coloured; but when the intensity was decreased by selection to about 4, the "white" plants showed Mendelian segregation, for the offspring arising from the plants produced from a cross with a dark-coloured plant were sharply divisible into strongly coloured and "white" individuals.

As a further example of selection, I started with a homozygous medium-coloured (48) plant (*G*). This was selfed and a family of 31 coloured plants was raised, there were no whites. Thus, the parent plant may be regarded as homozygous. A plant (*G* 3) in this family, not far removed in colour (55) from the average, was selfed and the resulting family had a mean colour approximating to the colour of the parent. A light-coloured (27) plant (*G* 3, 20) and a dark (81) plant (*G* 3, 13) in this last family were selfed also, and the two families raised tended to resemble their respective parents. In a succeeding generation further progress was obtained in securing a dark race and a pale race. The necessary details are given in the accompanying diagrammatic table. The families printed in heavy type are those leading to a dark race, while those in ordinary type are passing into a light race.

*Formation of Light and Dark Races from a Dominant (homozygous) G.*

Parents		Offspring—Scale of Colour.								
Number	Colour	95—104	85—94	75—84	65—74	55—64	45—54	35—44	25—34	15—24
<i>G</i> (selfed) ...	48	—	—	—	1	9	15	6	—	—
<i>G</i> pl. 3 ...	55	—	—	2	1	0	4	5	3	1
<i>G</i> 3, pl. 20 ...	38	—	—	—	—	—	—	4	1	—
<i>G</i> 3, pl. 13 ...	81	—	<b>2</b>	<b>3</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>3</b>	—	—
<i>G</i> 3, pl. 20 ...	27	—	—	—	—	—	—	4	5	2
<i>G</i> 3, 13, pl. 2 ...	80	<b>2</b>	<b>6</b>	<b>2</b>	—	—	—	—	—	—

*Correlation Table—Colour-Intensity—Dominants (homozygous). Series II and III.*

Parents. Grade of Colour-Intensity	130—139	120—129	110—119	100—109	90—99	80—89	70—79	60—69	50—59	40—49	30—39	20—29	Offspring
30—39	—	—	—	—	—	—	—	—	1	4	9	3	17
40—49	—	—	—	—	—	—	2	7	26	29	10	—	74
50—59	—	—	—	—	—	—	4	31	38	23	4	—	100
60—69	—	—	—	—	—	3	18	37	31	13	1	—	103
70—79	—	—	2	2	8	19	54	50	9	0	1	—	145
80—89	—	—	—	2	5	4	3	2	1	—	—	—	17
90—99	2	5	9	7	15	8	5	5	5	—	—	—	61
100—109	—	—	—	—	—	—	—	—	—	—	—	—	0
110—119	—	—	—	2	0	1	—	—	—	—	—	—	3
120—129	—	—	—	—	—	1	5	2	1	—	—	—	9
Totals	2	5	11	13	28	36	91	134	112	69	25	3	529

In the last table, p. 113, a correlation surface is shown between parents and offspring. It is formed from the series of families given in the table preceding the last, and arising by self-fertilisation.

The constants calculated from the table are: standard deviation of weighted parents 1.7805 units, and of offspring 1.8962 units, coefficient of correlation .707.

In this table 39 families were involved, as detailed in the previous table. The starting points were four homozygous dominant plants occurring in the two families raised from the reciprocal crosses ( $C_1 \times B_4$ ) and ( $B_4 \times C_1$ ).

### 3. BROWN SPOTS.

The amount of spotting on the inside of the corolla is not closely correlated to the intensity of the general purple coloration of the flower, for even in white plants the spots may be numerous and of a deep purple colour. In coloured plants the spots were almost always dark purple. As a very rare exception in the coloured plants (4 plants in about 2500) some of the spots were russet brown, and in the case of the larger spots there was a middle area of brown bordered by a margin of purple. In white flowers the spots were fairly frequently brownish-green or brown. In such brown spotted white flowers I could never detect the slightest tinge of purple on the general surface of the corolla, while in purple-spotted white flowers a faint tinge of purple could often be seen. The brown spots of white flowers might not become visible until the flowers were on the point of fading, and in the case of any given white plant it was wholly impossible to affirm that brown spots were, or would be, entirely absent from all of the flowers.

With the exception of the four plants mentioned above there was a sharp discontinuity to the naked eye between purple spots and brown spots, intermediate conditions being absent. The brown colouring matter may be regarded as altered or decomposed anthocyanin. In purple spots a microscopic examination often showed a certain amount of decomposition; but, with the exception of the four plants, the amount was not enough to alter the colour of the spots sufficiently for detection by the naked eye. Thus, the discontinuity lies between a normal small amount of decomposition, and an abnormal entire decomposition. It may be stated that under ordinary circumstances brown or greenish spots (as seen by the naked eye) are linked to a perfectly white corolla, but purple spots occur in both purple and "white" flowers, and an apparently perfectly white corolla may also bear purple spots.

If a brown spotted plant is crossed with a purple spotted one the offspring are all purple spotted and heterozygous. The brown spotted condition is inherited in Mendelian fashion, and is recessive to purple spots.

No special crossings have been made to investigate the matter, and the results which are given below are merely picked out from the records of the numerous families which have been raised for other purposes.

In the accompanying table it is useless to include families in which there was no taint of whiteness, since all the individuals (except 4, plants out of 2500) had purple spots.

*Brown Spots—Families White or Some Taint of Whiteness.*

Gametic Nature of Pairings	Number of Families	Number of Offspring	Purple Spotted		Brown Spotted	
			Experimental	Mendelian Expectation	Experimental	Mendelian Expectation
<i>DD</i> × <i>DD</i>	13	344	344	344	0	0
<i>RR</i> × <i>RR</i>	11	169	0	0	169	169
<i>DR</i> × <i>DR</i>	13	213	166	160	47	53
<i>DR</i> × <i>DD</i>	15	137	137	137	0	0
<i>DR</i> × <i>RR</i>	1	8	3	4	5	4
<i>DD</i> × <i>RR</i>	6	70	70	70	0	0
Totals	59	941	720	715	221	226

It is obvious from the table that the brown spotted condition exhibits Mendelian inheritance.

#### 4. INHERITANCE OF CERTAIN SPORT ABNORMALITIES.

*Crenate Margin.*—In a homogeneous family of 29 plants there appeared one plant in which the free edge of the mouth of the flower exhibited a well-marked serrated condition. All the flowers of a main-axis of considerable size were similarly affected, and later, lateral flowering axes were formed, and the flowers were also serrate. The character was sufficiently marked to be noticeable at a casual glance of the plant, and since all the numerous flowers were alike in this particular, the character was clearly inherent in the plant, and was not due to a chance environmental disturbance influencing a young growing axis or certain flower-buds. The plant was self-fertilised, and it was confidently expected that the character would reappear in the offspring. Out of a family of some 20 plants 12 flowered and no sign of the peculiar serrated condition could be detected in any one of the plants. Here we have a conspicuous character in a large healthy plant affecting every flower of all the flowering axes, and yet apparently it was incapable of being transmitted to the offspring.

*Split Corolla.*—In a homogeneous family (XXXIV) of 27 plants there appeared one plant in which in the great majority of the numerous flowers the corolla was symmetrically divided into an upper, a lower and two lateral pieces by four lateral splits extending down to the base of the flower. The plant was a large, healthy one and produced a number of similar lateral axes. At least 90% of the flowers were completely split (Pl. I, fig. 10).

In a family (VIII 7) unrelated to the above there were 16 plants, and of these, four plants were similarly affected. In one of these plants practically all



(99%) of the flowers were entirely split into four pieces, while in the remaining three plants some 50—60% of the flowers were split. All the plants were large and vigorous. It was thought that very probably the character would exhibit Mendelian inheritance. The results of crossing and selfing are shown in the accompanying table.

*Inheritance of Split Corolla.*

Offspring. Percentage of Splitting	Parents															
	No Splitting	Registered Number														
	26	12	8	7	2	3	1	0	0	9	26	12	15	10	10	Mid-parental degree of Splitting
1—14	0	0	6	3	4	2	1	2	0	0	0	0	0	0	1	0
15—29	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
30—44	0	0	0	1	1	1	2	2	0	0	0	0	0	0	2	0
45—59	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0
60—74	0	2	0	1	1	3	3	2	1	0	0	0	0	0	0	0
75—99	1	1	0	2	5	4	1	1	3	0	1	0	0	0	0	0
		XXXIV (selfed)	VIII 7 (selfed)	XXXIV 4 (90%) × VIII 7, 9 (99%) = S. J.	S. J. pl. 9 (selfed)	S. J. pl. 18 (selfed)	S. J. pl. 6 (selfed)	S. J. 18 pl. 11 (selfed)	S. J. 18 pl. 4 (selfed)	S. J. 18 pl. 10 (selfed)	II 6, 1 (selfed)	XXXIV (selfed)	II 6, 1 (0%) × XXXIV 4 (90%) = R. J.	R. J. pl. 9 (selfed)	R. J. pl. 16 (selfed)	R. J. 16 pl. 14 (selfed)

The first mentioned plant (XXXIV 4) with 90% of the flowers split was crossed with an unrelated plant with some 99% of the flowers split (5th vertical column of table). Of the 17 offspring 8 plants were wholly unsplit, while the remainder exhibited the character in a very greatly weakened condition. Three of these offspring, S. J. nos. 9, 18 and 6 having 0%, 13% and 18% of the flowers split respectively, were selfed, and the families raised all contained some plants very conspicuously split, but the character was more marked in the two families raised from parents 18 and 6 which showed some degree of splitting. In a subsequent generation (S. J. 18 pl. 4 and S. J. 18 pl. 10) raised by selfing, the character became very strongly pronounced.

An unrelated non-split plant (II 6, 1) was crossed with the first mentioned plant having at least 90% of the flowers split (XXXIV 4). In the family of



12 plants raised none of the plants exhibited splitting. Two of these offspring (R. J. nos. 9, 16) were selfed and no splitting occurred in the two families. Another generation was raised from R. J. 16, plant 14 and some re-appearance of splitting was detected. The table includes all the split plants which have occurred among some 3000 plants which have been under observation.

The results obtained indicate that heredity has some influence, but the data are insufficient for determining the nature of the transmission which does not bear a Mendelian aspect.

*Creased Upper Lip.*—In a certain plant in the majority of the flowers the upper surface and lip exhibited a conspicuous pucker or crease. This plant was crossed with an unrelated normal plant with no crease. Most of the seedlings were killed by the violent elements, but four plants were raised, and in one, a number of flowers exhibited a crease, which, however, was much less developed than in the paternal parent. The data are scanty, but the hereditary transmission does not seem to be Mendelian.

*Spontaneous Appearance of White plants.*—Among the numerous homozygous dominant coloured families that have been raised a white plant appeared spontaneously on two occasions in two unrelated families. These plants, of course, bred true, and as there was no evidence of contamination of the seed the plants must be regarded as new sports.

##### 5. INHERITANCE OF SEED-LENGTH.

The mean length of the seed varied considerably in different plants. No discontinuous variation could be detected, and inheritance was of the blended type. Ten seeds were taken at random from one or more capsules of a number of plants of certain series and the means determined. The seeds of a capsule exhibited a moderate amount of variation, but they were monomorphic in varietal crossings, and not dimorphic as was noticed in an interspecific crossing. The distribution was more or less normal. Unfortunately there was very considerable variation in the mean size of the seeds in different capsules of the same plant, and consequently no very accurate determination of the strength of inheritance was possible with this character without an excessive number of measurements. As it was, the investigation entailed the measurement of about 1000 seeds.

A plant,  $C_1$  (mean seed-length 639 units), was crossed with  $B_4$  (mean seed-length 628 units) and a family was raised;  $C_1 \times B_4 = \text{II}$ . In family II twelve plants were selfed, namely II 1, II 2 ... II 12, the seeds were measured and twelve families were obtained. In family II 1 three plants were selfed and the seed-length determined, namely (II 1) 1, (II 1) 2 and (II 1) 4. The means of the seed-lengths of these three plants were compared with the seed-length of the parent II 1. Similarly, for example, in family II 1, 2 two plants were selfed, namely (II 1, 2) 5 and (II 1, 2) 20, and the means of the seed-lengths of these two plants were compared with the seed-length of the parent II 1, 2. The data are given in the accompanying table.

*Mean Seed-length, Parents and Offspring.*

Parent (selfed)		Offspring (selfed)		Parent (selfed)		Offspring (selfed)		Parent (selfed)		Offspring (selfed)	
Designation	Mean Seed-length	Designation	Mean Seed-length	Designation	Mean Seed-length	Designation	Mean Seed-length	Designation	Mean Seed-length	Designation	Mean Seed-length
II 1	606	II 1, 1 II 1, 2 II 1, 4	572 668 649	II 4	592	II 4, 8 II 4, 12	628 598	II 9	653	II 9, 3	629
II 1, 2	668	II 1, 2, 5 II 1, 2, 20	668 642	II 6	620	II 6, 1 II 6, 3 II 6, 4 II 6, 11	621 641 670 695	II 10	646	II 10, 1 II 10, 2 II 10, 5 II 10, 7 II 10, 8 II 10, 13	660 669 649 660 713 681
II 1, 4	649	II 1, 4, 3 II 1, 4, 17	655 674	II 6, 11	695	II 6, 11, 6	665				
II 2	528	II 2, 1 II 2, 3 II 2, 5 II 2, 16	624 582 637 566	II 7	547	II 7, 1 II 7, 12 II 7, 14	671 570 624	II 10, 1	660	II 10, 1, 18	642
				II 7, 1	671	II 7, 1, 7	649	II 10, 5	649	II 10, 5, 5 II 10, 5, 10 II 10, 5, 18	598 629 649
II 3	629	II 3, 1 II 3, 4 II 3, 15	686 686 672	II 8	620	II 8, 2 II 8, 3	629 624	II 10, 7	660	II 10, 7, 9	653
II 4	592	II 4, 2 II 4, 6	668 657	II 9	653	II 9, 2 II 9, 11 II 9, 10	633 620 630	II 11	615	II 11, 8	617
								II 12	679	II 12, 9	642

$C_1$  (self-pollen) seed-length = 639

$B_4$  (self-pollen) " = 628

$C_1$  ( $B_4$  pollen) " = 642, these last seeds produced fam. II.

The coefficient of correlation, calculated from the above numbers, between parents (selfed) and offspring (selfed) is .378. This is low for mid-parental correlation; but as all the generations arose by self-fertilisation we ought to have practically no correlation at all according to the pure-line hypothesis, for the two original parents ( $C_1$  and  $B_4$ ) were closely similar to each other in the character under investigation.

## 6. PURPLE SPOTTING OF THE COROLLA.

The purple spotting of the lower surface of the corolla-tube and lower lip varied greatly in the original parent plants, and the character was obviously inherited. The amount of spotting had little relationship to the intensity of the general coloration of the corolla, and "white" flowers were sometimes richly spotted with purple.

The percentage area of the lower surface covered with spots was estimated by comparing the flowers with a series of diagrams each covered with a definitely known percentage of spotting. With practice it was found that sufficiently uniform results could be obtained by this method.

In plants which had lost completely the power of producing any purple coloration whatever, the spots were brown and usually small and scanty, and among such plants an almost entire absence of spots of any kind occasionally occurred. We have already seen that with regard to the colour of the spots (brown and purple) Mendelian segregation takes place.

In the inheritance of the *amount* of purple spotting no Mendelian relationship could be detected. The smallest amount of purple spotting met with in coloured foxgloves equalled about 1%, and the maximum about 70%. It will be remembered that on crossing a dark purple plant with a plant bearing flowers very faintly tinged with purple (say, colour 4 of standard), definite segregation into "white" and purple plants occurred in the second generation following; but on crossing a plant possessing an abundance of purple spots (say, 50%) with a plant bearing very few purple spots (say, 2% or 3%) no such segregation was found, and the spotting tended to remain intermediate in amount.

In the numerous crosses that have been made for various purposes the condition of the spotting was observed, and it is undoubtedly true that the means of the spotting of the families resulting from the crosses tended on the average to approximate to the spotting of the mid-parent,  $\frac{1}{2}(\sigma + \text{♀})$ . No difference could be detected between the reciprocal crosses of two plants.

*Influence of Selection and Strength of Inheritance in Self-fertilised Generations.*

In this connection details of Series II and III may be given (see p. 120). Plant  $C_1$  with 11% spotting was crossed with pollen of plant  $B_4$  with spotting 48% = II. Seven of the offspring were selfed and the spotting of the resulting families was determined. Subsequently two other generations were raised by selfing. Plant  $B_4$  was crossed with pollen of  $C_1$  = III. Four of the offspring were selfed and subsequently three other generations were raised by self-fertilisation.

The distributions of the spotting in the families of the different generations are shown in the accompanying table. In each generation the families are arranged in the ascending order of the parental spotting (see the top and middle horizontal lines). A casual inspection indicates at once that the general trend of the family-distributions follows the gradual increase in the spotting of the parents.

As an example of selection we may take :

III 2 (9%) selfed	produced with others a plant	III 2, 5 (15%)
III 2, 5 (15%) selfed	" "	III 2, 5, 10 (22%)
III 2, 5, 10 (22%) selfed	" "	III 2, 5, 10, 17 (27%)
III 2, 5, 10, 17 (27%) selfed	produced a family with mean spotting of	39%

Thus, we have passed from a plant with 9% spotting to a plant with 27%, which on selfing produced a family with a mean spotting of 39%.

With reference to the strength of inheritance two tables are given on p. 121, one for parents and offspring, and one for grandparents and grandchildren. The respective coefficients of correlation are .560 and .395. This correlation does not arise by the mixture of two races which have been sorted out by segregation

*Purple Spotting—Families from Self-fertilised Parents. Series II and III.*

Offspring. Percentage Grade Spotting	C <sub>1</sub> (11) selfed		B <sub>4</sub> (48) selfed		II = C <sub>1</sub> (11) × B <sub>4</sub> (48)		Spotted Parents	Parents	Spotted Parents	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	
	10	37	18	17	18	19																																		20
Means	10	37	18	17	18	19	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39				
Offspring. Percentage Grade Spotting	III = B <sub>4</sub> (48) × C <sub>1</sub> (11)	III 1	III 2	III 3	III 4	III 2, 1	III 2, 2	III 2, 5	III 2, 7	III 4, γ	III 2, 13	III 2, 8	III 1, 11	III 4, x	III 2, 5, 18	III 2, 7, 9	III 2, 5, 5	III 4, γ, 30	III 4, x, 27	III 2, 1, 18	III 2, 5, 10	III 4, x, 23	III 4, x, 5	III 4, x, 22	III 2, 5, 5, 12	III 2, 1, 18, 12	III 2, 1, 18, 10	III 2, 1, 18, 28	III 2, 5, 5, 11	III 2, 1, 18, 21	III 2, 5, 10, 22	III 2, 5, 10, 17								
	0-3	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
	4-7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	8-11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
	12-15	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
	16-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
	20-23	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
	24-27	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
	28-31	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
	32-35	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
	36-39	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	40-43	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	44-47	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	48-51	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	52-55	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
56-59	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	

during the different self-fertilised generations. Inspection of the tables shows that the distributions of the various families give no indication whatever of the occurrence of segregation into little spotted and much spotted plants. The gradual rise in the degree of spotting of the different parents is followed by a gradual increase in the spotting of the respective families obtained by self-fertilisation. The fact that the correlation between the grandparents and grandchildren is less than that between the parents and offspring is further evidence that the small, apparently fortuitous, variations in spotting occurring among self-fertilised generations are inherited. This result is opposed to the pure-line hypothesis, according to which such small variations are regarded as slightly different expressions of the same identical character which remains unchanged in its essence from one self-fertilised generation to another. If such were the case

*Correlation Table—Spotting—Parents and Offspring. Series II and III.*

Offspring. Grades of Spotting.

Parents. Grades of Spotting	48-51	44-47	40-43	36-39	32-35	28-31	24-27	20-23	16-19	12-15	8-11	4-7	0-3	Totals
0-3	—	—	—	—	—	—	—	—	—	1	6	8	—	15
4-7	—	—	—	—	—	—	—	—	2	7	1	—	—	10
8-11	—	—	—	—	—	—	2	2	18	18	17	10	1	68
12-15	—	—	—	—	—	1	8	28	40	68	19	5	2	171
16-19	—	1	1	5	14	10	28	34	33	49	20	1	—	196
20-23	2	3	5	4	9	16	25	26	25	17	3	1	—	136
24-27	—	2	5	6	3	8	15	14	10	3	1	—	—	67
28-31	—	1	3	3	6	10	9	4	10	2	2	—	—	50
32-35	—	—	—	—	—	—	—	—	—	—	—	—	—	0
36-39	—	—	—	—	—	—	—	—	—	—	—	—	—	0
40-43	—	—	—	—	—	—	—	—	—	—	—	—	—	0
44-47	—	2	—	1	—	—	—	—	—	—	—	—	—	3
Totals	2	9	14	19	32	45	87	108	138	165	69	25	3	716

*Correlation Table—Spotting—Grandparents and Grandchildren. Series II and III.*

Grandchildren. Grades of Spotting.

Grandparents. Grades of Spotting	44-47	40-43	36-39	32-35	28-31	24-27	20-23	16-19	12-15	8-11	4-7	0-3	Totals
8-11	—	—	1	4	2	6	8	19	35	19	5	2	101
12-15	1	1	2	5	4	17	21	20	31	10	12	—	124
16-19	2	3	6	12	9	20	22	25	37	15	2	1	154
20-23	2	4	1	1	4	7	9	15	13	3	1	—	60
24-27	—	1	6	4	7	8	0	4	—	—	—	—	30
28-31	2	3	1	4	7	8	6	8	1	—	—	—	40
Totals	7	12	17	30	33	66	66	91	117	47	20	3	509

the small variations would be fluctuating, non-inheritable variations; but the results in the present case are definitely against a supposition of this kind.

It might be urged by some that the result is really due to the existence of genotypes, and that variations within the limits of each genotype are not inheritable. The distributions of the families in the table do not indicate the occurrence of genotypes of any considerable magnitude. If the genotypes are supposed to be very small the practical result would become indistinguishable from the inheritance of continuous variations.

#### 7. RATIO OF BREADTH TO LENGTH OF COROLLA.

The breadth was measured as the maximum horizontal width across the mouth of the corolla of a fully expanded flower in which the anthers had opened; the length was the maximum distance measured along the mid-adcauline surface with the lower lip stretched out straight in the long axis of the flower. It is convenient to express the ratio in the form,  $\frac{\text{Breadth}}{\text{Length}} \cdot 1000$ . The mean of the ratios of the four lowest flowers of an axis was taken as the mean of the plant.

The original parent plants varied widely in this ratio, and the families raised by selfing tended to have the same ratio as their parents.

A plant bearing wide flowers was crossed with one having narrow flowers, and the offspring tended to be intermediate. On selfing these offspring the new generation exhibited, of course, considerable variation, but taken as a whole the intermediate condition was retained, and there was clearly no segregation into wide flowers and narrow flowers. Thus, the different degrees of this character blend readily on crossing, and the mode of inheritance is very similar to that of the spotted condition.

The results of a multitude of crossings of plants bearing variously shaped flowers have been carefully determined and tabulated, and there is no question about the general accuracy of the statement made above. In the present place we may confine our attention to the self-fertilised generations of Series II and III (p. 123).

A plant ( $\text{♀ } C_1$ ) with relatively wide flowers (ratio 608) was crossed with a plant ( $\text{♂ } B_4$ ) having relatively narrow flowers (ratio 487). The family (= II) had flowers approximately intermediate. The reciprocal cross = III. The distributions of the families of the various generations raised by selfing are shown in the accompanying table. The families of each generation are given in an ascending order of the ratios of the parents. As in the case of the character of spotting it will be seen that there is a clearly marked tendency for the mean ratios of the families to approximate to the ratios of the respective parents. In none of the families do we find any definite segregation into plants with wide flowers and plants with narrow flowers resembling those of the two progenitors of the series.

Wide and narrow races could be raised by selection using only self-fertilisation.

Thus in family III with a mean ratio of 531 there was a single plant (III 2) with as high a ratio as 575. This was selfed and the mean ratio of the offspring







*Inheritance in the Foxglove*

was 574. In this family there was a plant (III 2, 1) with a ratio of 533 and the mean of offspring = 563. III 2, 1, 18 (ratio 551) produced a family with mean 561, and III 2, 1, 18, 28 (ratio 598) produced a family with a mean of 606.

In the reverse direction, through III 2, III 2, 5, III 2, 5, 10 and III 2, 5, 10, 22 we pass from a parent of ratio 575 to a family having a mean ratio of 477.

With the data given in the preceding table, correlation tables have been prepared for parents and offspring, and grandparents and grandchildren.

*Correlation Table—Ratios of Corolla—Parents and Offspring.  
Series II and III.*

## Offspring.

Parents. Grades of Ratios $\frac{B}{L}$ 1000	680—709	650—679	620—649	590—619	560—589	530—559	500—529	470—499	440—469	410—439	380—409	350—379	Totals
410—439	—	—	—	—	1	0	1	4	5	4	—	—	15
440—469	—	—	—	—	—	1	1	8	8	6	1	—	25
470—499	—	—	—	—	4	16	39	35	23	11	3	1	132
500—529	—	2	3	8	15	28	45	40	28	6	2	1	178
530—559	—	1	6	15	29	47	38	32	7	3	—	—	178
560—589	—	2	12	15	30	34	18	13	2	—	—	—	126
590—619	1	2	9	18	14	5	—	—	—	—	—	—	49
620—649	—	—	—	—	—	—	—	—	—	—	—	—	0
650—679	—	2	3	2	2	0	1	—	—	—	—	—	10
Totals	1	9	33	58	95	131	143	132	73	30	6	2	713

*Correlation Table—Ratios of Corolla—Grandparents and Grandchildren.  
Series II and III.*

## Grandchildren.

Grandparents. Grades of Ratios $\frac{B}{L}$ 1000	680—709	650—679	620—649	590—619	560—589	530—559	500—529	470—499	440—469	410—439	380—409	350—379	Totals
440—469	—	—	—	—	1	0	3	9	9	7	—	—	29
470—499	—	—	—	—	2	3	10	15	11	3	1	1	46
500—529	—	—	—	—	4	22	36	25	22	12	2	—	123
530—559	1	3	14	38	37	34	24	16	9	2	1	—	179
560—589	—	2	8	10	18	33	21	21	3	2	—	—	118
590—619	—	—	—	—	—	—	—	—	—	—	—	—	0
620—649	—	—	—	—	—	—	—	—	—	—	—	—	0
650—679	—	2	3	3	1	1	—	—	—	—	—	—	10
Totals	1	7	25	51	63	93	94	86	54	26	4	1	505

The coefficients of correlation are .601 for parents and offspring and .492 for grandparents and grandchildren. The latter figure is somewhat high; but taking the results altogether they are incompatible with any notion of pure-lines.

## 8. GENERAL CONCLUSIONS.

In the various characters that have been dealt with in the crossing of different strains of the garden foxglove we have seen that in pelorism, colour of corolla and colour of spots, the mode of inheritance is Mendelian with reference to the qualities: peloric and non-peloric, purple and white corolla, purple spots and brown spots. If, however, there are any marked differences in the intensities of these qualities, the mode of inheritance of the intensity of the quality was found to be of the blended type.

The other characters examined were quantitative in nature, such as degree of the development of purple spots and the ratio of breadth to length of corolla, and these characters blended completely.

When the intensity of a quality is very slight and approaching zero the difficulty arises as to which category the individual should be referred. When Mendelian inheritance is in evidence the critical point may apparently be determined by the occurrence of segregation. Thus, if a homozygous plant with a very faint tinge of purple (say an intensity of about 4) is crossed with a homozygous strongly coloured plant, segregation occurs in the so-called  $F_2$  generation, and we obtain on the average 1 faintly tinged plant to 3 much more darkly coloured plants. When, however, the pale plant has a somewhat greater intensity (say about 10), the  $F_2$  and subsequent generations are intermediate, and definite segregation does not occur. In accordance with this procedure a plant with flowers having an intensity of general coloration which did not reach 5 of the scale was classed as "white." Without employing such a line of demarcation the results obtained were wholly unintelligible.

From the strict Mendelian standpoint, in the example given above, it would probably be affirmed that the faint tinge of purple on "white" flowers is not really a fractional part of the general purple coloration of coloured plants, but is a distinct character governed by a different factor or set of factors in the chromosomes. To one who has grown the plants this view appears an artificial one. In my previous account I stated that there appeared to be a distinct gap among my plants between "white" plants and coloured plants, and that colorations of about 8—25 of the scale were extremely rare or almost absent, but I have subsequently obtained a number of plants having such intensities of coloration, passing imperceptibly down to absolute whiteness. Consequently it is quite unlikely that the faint tinge of purple on "white" flowers is anything else than the last remnant of a general purple coloration.

It is quite similar in the character of pelorism, but the difficulty in finding a suitable method of measuring this character renders the matter less obvious. Thus, it would appear that if a character is not present beyond a certain minimum or unit quantity it may be unable to blend on crossing with a plant possessing the character in a well-marked degree.

With reference to the characters which blend, the accompanying table summarizes the results obtained for parental correlation. Mid-parents and self-fertilised parents are regarded as comparable.

Character	Number of Offspring	Coefficient of Correlation. Parents and Offspring
Intensity of pelorism (homozygous recessive, mid-parents and self-fertilised parents) }	530	·520
Intensity of general purple coloration (homozygous dominants, self-fertilised parents) }	529	·707
Seed-length (self-fertilised parents) ... ..	46	·378
Spotting (self-fertilised parents) ... ..	716	·560
Ratio of Corolla (self-fertilised parents) ...	713	·601

The probable errors of these results are reasonably small and the average coefficient for the 5 characters is ·553 which is not far removed from the average coefficient found by Professor Karl Pearson for a large number of characters in a variety of different organisms.

It must be again emphasized that these results are based on self-fertilised generations of pedigree plants of known gametic constitution, and on Johannesen's theory of pure-lines these parental coefficients should be zero, or at least very small.

The evidence of the present investigation is therefore definitely against any general application of the theory of pure-lines and of genotypes of any appreciable magnitude, and further it indicates that selective breeding within self-fertilised generations of a homogeneous race is capable of modifying that race to a marked degree.

### EXPLANATION OF PLATE I.

Figs. 1 and 2.—Pelorism of maximum intensity; grade 100°. Corollas absent, sessile anthers.

Figs. 3 and 4.—Perfect pelorism, grade 100°. Corollas joined along their split edges forming a complete saucer. Stamens with filaments.

Fig. 5.—Peloric flower of side-axis; the axis terminates in an ovary.

Fig. 6.—Pelorism of grade 100°. Numerous flowers fused irregularly forming a rosette, the axis has grown through the crown.

Figs. 7 and 8.—Incomplete pelorism of main axes, grade 75°. A spiral bending often occurs.

Fig. 9.—Faintly defined pelorism. When such occurred on the lateral axes the plant was said to possess a grade of 25°. Side view, and view from above.

Fig. 10.—Flowering axis of a conspicuous sport in which practically all the corollas are completely split longitudinally into four elongated blades. Nature of inheritance obscure.

The photographs were kindly taken by Dr Conrad Akerman.