

THE INHERITANCE OF PELORIA AND FLOWER-COLOUR IN FOXGLOVES (*DIGITALIS PURPUREA*).

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[TEXT-FIG. 2].

A SERIES of experiments was commenced in 1907 in order to investigate the mode of inheritance of peloria and of colour in the Foxglove (*Digitalis purpurea*). The experiments are being continued; but, owing to the biennial nature of the plant, it must be some years before they are completed. We propose therefore to publish such results as we have already obtained, to indicate the conclusions to which they point, and to supplement the present paper by another when the behaviour of the next generation of plants shall have been determined. The mode of inheritance of peloria has a special interest owing to the fact that Darwin (1868), working with the snapdragon (*Antirrhinum majus*), obtained statistics which, as Bateson (1901) has pointed out, indicate for this phenomenon a simple Mendelian mode of inheritance. Darwin's experiments (*loc. cit.*) may be summarised briefly:—

1. Peloric flowers, *selfed*, yielded plants, all peloric.
2. Peloric \times non-peloric and the reciprocal cross gave F_1 all non-peloric. "I thus raised two great beds of seedlings and not one was peloric." The dominance of non-peloric over peloric was almost, but apparently not quite, complete, for "in a few instances the minute rudiment of a fifth stamen, which is always present, was more fully or even completely developed."

3. Darwin left the plants of F_1 to seed themselves (without precautions against crossing) and obtained an F_2 composed of 127 plants, of which 88 were non-peloric, 2 intermediate, and 37 perfectly peloric. The experiments indicate dominance of non-peloric and precise segregation in F_2 . Darwin's numbers contrasted with the numbers expected on a simple Mendelian 3 : 1 ratio are:—

Darwin's	...	non-peloric 90	...	peloric 37
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Calculated	...	non-peloric 95.25	...	peloric 31.75
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whence it is evident that the experimental results are in close agreement with those expected by Mendelian theory.

1. **PELORIA IN FOXGLOVES.** Turning now to our experiments with Foxgloves: all interested in gardens are aware that races of these plants are in cultivation which exhibit the phenomenon of peloria. In Foxgloves, peloria, at all events in the examples which we have had under observation, is confined to the terminal flower of the raceme. Whereas the lateral flowers retain their typical zygomorphic state, the terminal flower of a peloric plant is bell-shaped. Moreover, it stands up vertically and so forms a striking contrast with the pendulous, zygomorphic, lateral flowers. The peloric flower shows other indications of its monstrous nature; its corolla may be nine-lobed, the anthers as many as 8, and the stigma possessed of 5 stigmatic surfaces.

Though built on such abnormal and massive lines the peloric flowers of Foxgloves appear to be perfectly fertile with their own pollen. Thus the terminal, regular flowers of a peloric plant (plant B, Table I, p. 76) self-pollinated in 1907, gave seed from which 12 plants were raised. These 12 flowered in 1909 and were all peloric.

In the next place it is noteworthy that the typical, zygomorphic, lateral flowers of peloric plants carry, though they do not reveal, the factor which determines peloria. For example; the lateral flowers of a peloric plant (Plant A) selfed, gave an F_1 of 22 plants all peloric with respect to their terminal flowers. The question as to the significance of the facts just mentioned is one on which we are at present engaged; but with respect to which we are not at present prepared to make any statement. That peloria depends upon a recessive character is indicated by the following records:—

Plant D: non-peloric, selfed, 1907.

F_1 = 11 non peloric and 3 peloric.

Plant E: non-peloric, selfed, 1907.

F_1 = 9 non-peloric and 4 peloric.

Combining the numbers obtained in these experiments we have non-peloric, 20, peloric, 7. From which we may conclude that peloria (p) is recessive to normal (P). Crosses between peloric and non-peloric confirm this conclusion. Thus plant D (non-peloric) (Pp) \times plant E (non-peloric) (Pp) F_1 should give:—

1 PP : 2 Pp : 1 pp.

3 Dominant : 1 Recessive.

Our numbers = 35 Dominant : 11 Recessive.

Another case: plant F (peloric) (pp) \times plant E (non peloric) (Pp) should give:—

2 pp : 2 Pp.

Observed:— 16 : 24.

Peloria of Foxgloves therefore depends on a character which is recessive to normal. Inasmuch as it is characterised primarily by absence of the typical zygomorphy of normal flowers, and inasmuch as evidence is accumulating in support of the presence and absence hypothesis of the nature of dominant and recessive members of allelomorphic pairs of characters, it is not perhaps surprising to find peloria behaving as recessive to normal.

2. FLOWER COLOUR. The colour-characteristics, the mode of inheritance of which we are investigating, are white, magenta, deep magenta: red spots, brown and yellow spots, which characters are displayed by the corollas of various garden races of Foxgloves.

In Tables I and II (pp. 76, 77) are tabulated the colour-characters of the various plants under investigation and the behaviour of these characters in the F_1 generations resulting from self-fertilization of these plants, and from the cross-fertilization of plant D \times plant E and plant F \times plant E.

Inspection of Table I. shows that certain white plants breed true to whiteness (Plant E); others, e.g., plant D, when selfed, yield an F_1 composed of white and magenta-flowered plants. Similarly when E, which, so far as the comparatively small numbers in F_1 admit of a conclusion, is to be regarded as pure to whiteness, is crossed with D, whites and magentas are obtained. We therefore conclude that Foxgloves, like *Primula sinensis* (Bateson, 1909), contain a *dominant-white* factor (W), that is a factor which inhibits the expression of colour in a zygote, the contributory gametes of which carried a colour factor. Since colour appears in F_1 from plant D selfed, that plant is not pure, but heterozygous with respect to the dominant white factor, i.e., its gametic constitution is Ww. Nor may the plant D be pure with respect to magenta colour-factor (M), for, if it were, its gametic constitution would be Ww MM; it would yield gametes wM and WM and, on selfing, would produce an F_1 composed of 3 dominant white : 1 magenta, thus:—

WM.wM, male gametes.

WM.wM, female „

giving in F_1

1 WW MM : 2 Ww MM : 1 ww MM

3 white

; 1 magenta.

The result of selfing plant D,—13 white, 1 magenta,—indicates that it is heterozygous for magenta colour-factor, *i.e.*, is *Mm*. So that its full gametic composition with respect to ground colour is *Ww Mm*, and the gametes which it produces bear the characters *WM*, *Wm*, *wM*, *wm*.

Male gametes bearing these characters meeting female gametes also bearing these characters will produce zygotes, the composition of which may be indicated in the usual way (Fig. 2).

	<i>WM</i>	<i>Wm</i>	<i>wM</i>	<i>wm</i>
<i>WM</i>	<i>WM</i> <i>WM</i>	<i>WM</i> <i>Wm</i>	<i>WM</i> <i>wM</i>	<i>WM</i> <i>wm</i>
<i>Wm</i>	<i>WM</i> <i>Wm</i>	<i>Wm</i> <i>Wm</i>	<i>WM</i> <i>wm</i>	<i>Wm</i> <i>wm</i>
<i>wM</i>	<i>WM</i> <i>wM</i>	<i>WM</i> <i>wm</i>	<i>wM</i> <i>wM</i>	<i>wM</i> <i>wm</i>
<i>wm</i>	<i>WM</i> <i>wm</i>	<i>Wm</i> <i>wm</i>	<i>wM</i> <i>wm</i>	<i>wm</i> <i>wm</i>

Fig. 2.

Illustrating the Ratio of 13 White : 3 Magenta (shaded) in *F*₁ of Plant D, selfed (see Text).

Of 16 zygotes, 12 will produce white flowers because of the presence of the dominant white factor (*W*), 1 because of the absence of both magenta colour-factor and dominant white factor (*wm*). That is we shall expect a ratio of 13 white to 3 magenta. The numbers obtained in *F*₁ from plant D selfed are 13 whites, 1 magenta, and though it must of course be conceded that the number of *F*₁ plants raised is too small to provide absolute proof, yet the fairly close agreement of the numbers obtained (13 white, 1 magenta) with the numbers expected (13 white, 3 magenta) justifies the assumption that plant D is heterozygous for both the dominant-white and the magenta-colour factors.

As we shall show, the hypothesis that plant D is heterozygous for these factors permits of a reasonable interpretation of the results of other crosses.

Thus plant E, white with yellow spots, when selfed, gives an *F*₁ of 13 plants all white. Plant E, crossed with plant D, which

contains dominant white (W), yields an F_1 containing magentas as well as whites. Therefore plant E cannot be pure with regard to the dominant white factor (WW); for, if it were, all the plants of the cross $D \times E$ would be white. It must consequently be of the constitution ww or Ww . If it is the former, it cannot, since it is white, contain the magenta colour factor M. Its complete constitution with regard to these factors must therefore be $ww\ mm$. So that $D \times E = Ww\ Mm \times ww\ mm$, and the gametes produced are of the constitution:—

Gametes of plant D:— WM, Wm, wm, wM:

Gametes of plant E:— 4 wm :

giving zygotes,

4 $Ww\ Mm$: 4 $Ww\ mm$: 4 $ww\ mm$: 4 $ww\ Mm$
12 white : 4 magenta,

as compared with the actual numbers,

Obtained, 36 white : 10 magenta.

Calculated, 34.5 white : 11.5 magenta.

On the other hand, if plant E contain dominant white (W), its possible complete constitutions are:— $Ww\ MM$, $Ww\ Mm$, $Ww\ mm$.

The first two possibilities, however, are negated by the fact that E selfed gives an F_1 all white. In the case of the third $D \times E = Ww\ Mm \times Ww\ mm$, which would produce zygotes in the ratio:—

6 WM : 6 Wm : 2 wm : 2 wM
14 white : 2 magenta.

Since, however, the experimental numbers are 36 white, 10 magenta, the most probable constitution for plant E is $ww\ mm$, *i.e.*, it is recessive to both negative magenta and dominant white.

Cross F \times E. Though the number (5) of plants in the F_1 of plant F selfed is too small to throw certain light on the gametic constitution of plant F, we record our attempt to determine this constitution.

Since the F_1 of the cross $F \times E$ contains magenta-flowered plants and since plant E is recessive to both magenta colour factor and dominant white factor, *i.e.*, is $ww\ mm$, plant F must contain the magenta colour factor (M). And, since plant F is itself white, if it is carrying magenta it must also be carrying the dominant white factor (W). It cannot, however, be carrying pure W, for, if it were, the cross $F \times E$ would yield an F_1 of all white-flowered plants. Therefore the gametic constitution of plant F is $Ww\ MM$ or $Ww\ Mm$.

Assuming the constitution of plant F to be Ww MM, the cross $F \times E = Ww MM \times ww mm$.

The gametes produced by plant F = WM and wM, by plant E = wm, and the zygotes of $F_1 = 1 Ww Mm : 1 ww Mm$.
= 1 white : 1 magenta.

On the other hand, if the second alternative be adopted, *viz.*, that plant F is heterozygous for W and M, *i.e.*, is Ww Mm, then plant F \times plant E = Ww Mm \times ww mm: gametes of plant F = WM, Wm, wM and wm: gametes of plant E = wm. So that F_1 will contain:—

$$\begin{array}{c} 1 Ww Mm : 1 Ww mm : 1 ww mm : 1 ww Mm. \\ \hline 3 \text{ white} \qquad \qquad \qquad : 1 \text{ magenta.} \end{array}$$

The numbers actually obtained, *viz.*, 15 white, 25 magenta, indicate fairly conclusively that the gametic constitution of plant F is Ww MM and *not* Ww Mm. Plant F is pure for magenta factor and heterozygous for dominant white factor.

Dark Magenta Flower Colour. Plant A, (see Table I.), bearing a deep magenta (purple) coloured flower yields an F_1 composed of 11 deep magenta (purple), 6 magenta, 5 white. If we assume the presence of a darkening factor (D) which may change magenta to purple, but which is without effect on white (*i.e.*, one which is epistatic to magenta) then a fairly close fit between expectation and realisation is obtained by ascribing to plant A a constitution of Mm Dd, *i.e.*, one heterozygous for magenta colour factor M and darkening factor D. A plant of such a constitution produces when selfed an F_1 composed of:—

$$9 MD : 3 Md : 3 mD : 1 md$$

$$9 \text{ purple} : 3 \text{ magenta} : 4 \text{ white,}$$

as compared with the numbers obtained,

$$11 \text{ purple} : 6 \text{ magenta} : 5 \text{ white,}$$

calculated on 9 : 3 : 3 : 1 ratio,

$$12.4 \text{ purple} : 4.1 \text{ magenta} : 5.5 \text{ white.}$$

Spot Factor. Yellow, brown, or red spots occur generally in the corollas of Foxgloves. The spots vary considerably in size, contour and frequency. In white flowers the spots may be of any one of the three colours; and so far as our observations go, no Foxglove, no matter what the ground colour of the corolla may be, is altogether devoid of spots, which may, however, be so faint as to be only just distinguishable. It is not improbable that the colours, yellow and brown, of these spots are due to one and the same cause,

viz., the breaking down of localised groups of chromatophores : at all events yellow spots often turn brown as the flower bearing them grows older. Further, it is to be noted that, so far as we know, no flower which has a magenta ground-colour is devoid of red spots.

The distribution of red and brown spots in the F_1 generation produced by selfing plant A is noteworthy.

The numerical ratio is 17 red-spotted to 5 yellow-brown (approximately 3 : 1). The red spots, however, are confined to the flowers with magenta ground colour, the brown to the white flowers. We have ample evidence (plants D and F) that white flowers may exist with red spots. But in such cases the whites are dominant whites, and we have no evidence at present of a flower of a recessive white bearing red spots.

The behaviour of the red and yellow-brown spots appears to admit of a simple interpretation.

Reference to Table I. shows that red spots occur only in plants containing M. In the case of plant A, the presence of this magenta colour factor M is evident from inspection, since the flowers are purple. In plants D and F, however, the presence of the factor M is not directly apparent, on account of the inhibiting influence of the dominant-white factor (W), but becomes evident in the F_1 selfs and crosses. Also the plant (E), in which the factor M is absent, has yellow-brown spots. From these facts it would appear probable that the red colour of the spots is caused by the presence of the same factor (M) that is responsible for the magenta ground-colour of the corolla, and that the red spots are due to local action of magenta colour factor on the yellow-brown spot areas. If this is so, it follows that (W) the dominant white factor, which inhibits the expression of magenta ground-colour (M), is without this inhibiting effect on the M factor in the spot areas. Accepting this interpretation it follows that all white Foxgloves with red spots are dominant whites, *i.e.*, carry both W and M, also that, of white foxgloves with yellow-brown spots, all are pure recessives with respect to magenta, though some may be carrying a dominant white factor. The various theoretically possible constitutions of white Foxgloves are, therefore :—

White with red spots—WW MM, WW Mm, Ww MM, Ww Mm.
White with yellow-brown spots—ww mm, Ww mm, WW mm.

The ratios obtained by selfing and crossing which support these conclusions with respect to the nature of red and yellow-brown spots are as follows :—

Plant F (Ww MM) selfed, gives F_1 , all with red spots.

Plant E (ww mm) selfed, gives F_1 , all with yellow-brown spots.

Plant F \times E (Ww MM \times ww mm) gives F_1 , all with red spots (40 plants).

Plant D (Ww Mm) selfed, gives F_1 , 12 plants with red, 2 with brown spots.

Plant A (ww Mm) selfed, gives F_1 , 17 plants with red, 5 with brown spots.

Totals—29 plants with red, 7 with brown spots.

Calculated—27 plants with red, 9 with brown spots.

It should be noted that in the results of plant D selfed there is a distinct departure from the expected numbers, *viz.*—

Obtained=12 : 2

Calculated=10.5 : 3.5

That this is, however, attributable to the fewness of the F_1 plants is rendered probable by the results obtained by crossing plants D and E.

Plants D \times E=Ww Mm \times ww mm should yield F_1 composed of 4 Mm ww : 4 Mm Ww : 4 mm Ww : 4 mm ww, that is equal numbers of red spotted and yellow-brown spotted flowers. The numbers obtained are 21 plants with red spotted, 25 with brown spotted flowers.

The hypothesis that red spots are due to magenta factor acting on yellow-brown spot-areas provides a simple explanation of the relation between colour of spots and ground colour exhibited by the F_1 from plant A; *viz.*, 17 magenta-containing plants all with red spots and 6 white plants all with yellow-brown spots. It also explains how it is that *all* the magenta Foxgloves have red spots. It is not improbable that the view which we have expressed, namely that a dominant white factor (W) is able to inhibit ground colour and not spot colour—though both ground colour and spot colour are due to the same colour factor (M),—may prove of importance in interpreting the origin of spots and bars and stripes in animals and plants. Given localised inconspicuous areas, the addition of a ground colour factor would produce a self (uniformly) coloured surface on which spots and bars and stripes might or might not stand out conspicuously. Wash over that surface with a dominant white factor and then the general ground colour will be suppressed and conspicuous splashes of colour in spots, colours or stripes will stand out on a white ground. Finally, the suggestion may be worth making, that this differential action of a dominant white factor—inhibiting

ground colour but not colour in spot- or stripe-areas may provide a clue to the behaviour of such striped types (Darwin, loc. cit., p. 45, Vol. 2 and Bateson (1909), p. 99) as are known to produce, *occasionally*, self-coloured offspring.

TABLES I. AND II.

Showing inheritance of colour and marking of petals in the Foxglove (*Digitalis purpurea*).

TABLE I.—ALL PARENTS SELF-FERTILISED.

PARENTS.		F ₁ .		PROBABLE GAMETIC CONSTITUTION OF PARENTS			
Plant.	Characters.	Characters.	Number of Plants.	Peloric Factor.	Ground Colour.	Darkening Factors.	Dominant White Factors.
E	White with yellow spots	All white with yellow spots ...	13	Pp	mm	dd	ww
D	White with red spots	13 white (=11 red spots +1 brown spot +1 yellow spot) +1 magenta (=1 red spot) =12 red spots+2 brown or yellow	14.	Pp	Mm	dd	Ww
F	White with red spots	4 white+1 magenta (rogue)* =5 red spots	5	pp	MM	...	Ww
A	Purple=deep magenta with red spots	5 white (=5 brown spots) +6 magenta } (=17 red spots) +11 purple } =17 red spots+5 brown	22	pp	Mm	Dd	ww
B	White with purple flush and red spots	6 white (=2 red spots +2 brown spots +2 yellow spots) +5 magenta } (=6 red spots) +1 magenta flush } =8 red spots+4 brown or yellow	12	pp	?	?	?

*Since all the other evidence points to peloria being recessive, this plant, which is non-peloric, is to be regarded as a rogue.

TABLE II.—CROSSES.

PARENTS.	OFFSPRING.	
	Characters.	Number of Plants.
D × E	36 white (= 11 red spots + 12 brown spots + 13 yellow spots) + 10 magenta (= 10 red spots) = 21 red spots + 25 brown or yellow spots	46
F × E	15 white + 25 magenta = 40 red spots	40

CONCLUSIONS.

- (1). Peloria in Foxgloves is a Mendelian recessive to normal.
- (2). Peloric flowers and also the non-peloric flowers of peloric plants carry the recessive character.
- (3). The allelomorphs responsible for colour are :—
Mm ; M being magenta colour factor, dominant to m.
Dd ; D being a darkening factor dominant to d and
converting magenta to purple.
Ww ; W being a dominant white factor in the presence of
which the expression of colour due to M is inhibited
so that the flowers are white.
- (4). All flowers appear to be spotted. In the presence of the
colour factor M, spots are red : in the absence of M they are yellow-
brown. The presence of the dominant white factor W does not
inhibit the expression of the colour factor M in regard to the spots
(at least when present as a heterozygote=Ww).
- (5). The suggestion that dominant white acts differentially on
ground colour, inhibiting it generally but not in spot-areas, may
prove of service in explaining the origin of bars, spots and stripes
in plants and animals and also the behaviour of certain ever-
sporting varieties.

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