

# SOME EXPERIMENTS WITH *GERANIUM* SPECIES

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THE late W. C. F. Newton started the investigation of several interesting crosses between species of *Geranium* in 1920. Since 1927 Prof. L. Newton, J. F. S. Rudge, A. C. Fabergé and F. W. Sansome have attempted to carry on the work at the John Innes Horticultural Institution. Unfortunately the seed production under controlled conditions is meagre and the percentage of germination is low. For example, it has been usual to obtain 2-3 plants from the pollination of all the flowers on one plant during a period of 2 months. Having regard to these difficulties it has been decided to put the scanty but suggestive data on record and to discontinue the work.

## HYBRIDS BETWEEN *G. ENDRESSI* GAY AND *G. STRIATUM* L.

Table I contains the results of the various crosses made between these two species.

TABLE I

Family	Cross	Normal plants	Male sterile plants
25/22	<i>Endressi</i> × <i>striatum</i> $F_2$	2	1
26/22	<i>striatum</i> × <i>Endressi</i> $F_2$	4	—
1/23	<i>Endressi</i> × <i>striatum</i> $F_2$	4	1
2/23	<i>striatum</i> × <i>Endressi</i> $F_2$	4	—
1/25	<i>striatum</i> × <i>Endressi</i> $F_2$	1	—
2/25	<i>Endressi</i> × <i>striatum</i> $F_2$	1	—
3/25	25/22 ♂-sterile × <i>striatum</i>	—	1
4/25	1 <sup>1</sup> /23 ♂-sterile × <i>striatum</i>	—	1
5/25	1 <sup>1</sup> /23 ♂-sterile × <i>Endressi</i>	7	—
6/25	1 <sup>2</sup> /23 ♂-sterile × <i>striatum</i>	—	5
7/25	1 <sup>2</sup> /23 ♂-sterile × <i>Endressi</i>	1	—
9/26	1 <sup>1</sup> /23 ♂-sterile × <i>striatum</i>	—	2
10/26	1 <sup>1</sup> /23 ♂-sterile × <i>Endressi</i>	1	—
11/26	1 <sup>1</sup> /23 ♂-sterile × ( <i>E.</i> × <i>s.</i> ) $F_1$	1	1
12/26	1 <sup>1</sup> /23 ♂-sterile × ( <i>s.</i> × <i>E.</i> ) $F_1$	5	3
2/27	1 <sup>1</sup> /23 ♂-sterile × ( <i>s.</i> × <i>E.</i> ) $F_1$	3	1
3/27	1 <sup>2</sup> /23 ♂-sterile × ( <i>s.</i> × <i>E.</i> ) $F_1$	2	—
1/28	1 <sup>2</sup> /23 ♂-sterile × ( <i>s.</i> × <i>E.</i> ) $F_1$	10	8
2/28	1 <sup>2</sup> /23 ♂-sterile × ( <i>s.</i> × <i>E.</i> ) $F_1$	10	18
3/28	1 <sup>2</sup> /23 ♂-sterile × ( <i>E.</i> × <i>s.</i> ) $F_1$	1	4
4/28	( <i>B.</i> × <i>s.</i> ) $F_1$ × ( <i>s.</i> × <i>E.</i> ) $F_1$	4	5
5/28	( <i>s.</i> × <i>E.</i> ) $F_1$ × ( <i>E.</i> × <i>s.</i> ) $F_1$	5	—
6/28	( <i>E.</i> × <i>s.</i> ) $F_1$ × <i>striatum</i>	3	2
7/28	<i>Endressi</i> × ( <i>s.</i> × <i>E.</i> ) $F_2$	22	7

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The facts suggest that a factor carried by *G. striatum* when homozygous in the cytoplasm derived from *G. Endressii* causes the contabescence and petaloidy of the anthers. The plants carrying flowers with petaloid anthers have distinctive characteristics. The petals are smaller in size, very narrow and deeper in colour than the normal *striatum*; the stamens are white in colour and the anthers more or less petal-like. The last characteristic is variable in degree, but empty and deformed pollen sacs are a constant feature. The leaves of the plant also may show differences from the hermaphrodite plant, under dry conditions the leaves of the male-sterile plants are narrower and more liable to shrivel. The evidence regarding segregation is summarized thus:

TABLE II

	Normal	Petaloid anthers
<i>Endressii</i> × <i>striatum</i> $F_2$	7	2
<i>striatum</i> × <i>Endressii</i> $F_2$	5	—
$F_2$ ♂-sterile × <i>striatum</i>	—	10
$F_2$ ♂-sterile × <i>Endressii</i>	8	—
$F_2$ ♂-sterile × $F_1$	32	35
( <i>E.</i> × <i>s.</i> ) $F_1$ × ( <i>s.</i> × <i>E.</i> ) $F_1$	4	5
( <i>s.</i> × <i>E.</i> ) $F_1$ × ( <i>E.</i> × <i>s.</i> ) $F_1$	5	—
( <i>E.</i> × <i>s.</i> ) $F_1$ × <i>striatum</i>	3	2
<i>Endressii</i> × ( <i>s.</i> × <i>E.</i> ) $F_2$	22	7

The postulated factor carried by *G. striatum* is recessive to an allelomorph carried by *G. Endressii*.

The crosses were made primarily to test the foregoing hypothesis but some evidence regarding the inheritance of other characters was obtained.

The contrasting characters studied were:

	Pollen	Petal-veins	Stigma	Purple spot on leaf
<i>G. Endressii</i>	Blue	Dark	Red	Present
<i>G. striatum</i>	Yellow	Clear	Light yellow	Absent
$F_1$ 's	Blue	Dark	Light yellow	Faint spot

The  $F_2$  segregation was:

Dominants	Recessives	Dominants	Recessives
Blue	Yellow pollen	45	14
Dark	Light veins	52	12
Yellow stigma	Red	48	15
Purple spot	No spot	46	16

There is no sign of linkage between these characters. Other crosses were made but most of them provided little useful data concerning the segregation of these characters, since their parents were  $F_2$  plants of unknown genotype and the families were of small size.

*G. SANGUINEUM* L., *G. SANGUINEUM* VAR. *ALBUM*, *G.*  
*LANCASTRIENSE* MILL.

These three forms of *G. sanguineum* are found in the wild, and differ from one another in a number of characters. The following differences were studied in the experiments.

	Flower colour	Petal-veins	Pollen	Bud	Habit
<i>G. sanguineum</i> L.	Magenta	Dark	Blue	Revolvate	Sub-erect
<i>G. sanguineum</i> var. <i>album</i>	White	Clear	Yellow	Imbricate	Erect
<i>G. lancastriense</i> Mill	Pale	Dark	Yellow	Imbricate	Prostrate

The data obtained are shown in Table III.

TABLE III

Cross	Flower colour Dominant- magenta	Recessive (white or <i>lancastriense</i> )
$F_2$ <i>lanc.</i> × <i>sang.</i>	92	—
$F_2$ <i>lanc.</i> × <i>album</i>	73	—
$F_2$ <i>album</i> × <i>lanc.</i>	2	—
$F_2$ <i>sang.</i> × <i>album</i>	11	—
$F_1$ ( <i>lanc.</i> × <i>sang.</i> ) × <i>sang.</i>	20	—
$F_1$ ( <i>sang.</i> × <i>album</i> ) × <i>album</i>	4	—
$F_1$ ( <i>lanc.</i> × <i>album</i> ) × <i>album</i>	13	2 white
$F_2$ ( <i>lanc.</i> × <i>album</i> ) × <i>lanc.</i>	40	1 <i>lanc.</i> , 2 mericlinal
$F_2$ ( <i>sang.</i> × <i>album</i> ) × <i>album</i>	13	2 white

Only one plant of each form or  $F_1$  was used throughout the crosses in this table.

The  $F_1$  and  $F_2$  hybrids between any two of these forms were, with a few exceptions to be mentioned, all similar in flower colour, imbricate veneration of flower bud, blue pollen colour and distribution of colour in the veins. The habit varied from suberect to subprostrate in the  $F_1$  and most of the  $F_2$  plants, but the latter showed a greater range and occasionally approached the habits of *album* or *lancastriense*. Two plants in the  $F_2$  of *lancastriense* × *album* had paler magenta flowers, revolute petals and yellow pollen. One of these exceptional plants was used in breeding and gave, on crossing with *lancastriense*, one plant of *lancastriense* type, with prostrate habit, *lancastriense* petal colour, veins and pollen, and two plants which were mericlinal chimaeras for flower colour (*sanguineum*-magenta and *lancastriense*-pink (see Table III).

Table III summarizes the segregation of flower colour in these crosses. It will be seen that the recessive colours are rare in occurrence, although the total number of plants involved is rather small. The fact that recessives were only recovered after back-crossing  $F_2$  plants which were vaguely different from their sister plants is interesting. Early in the

investigation it was thought that *lancastricense* and *album* contributed complementary factors for *sanguineum* flower colour and this appears to be confirmed by the available data. The scarcity of recessives was only accounted for when it was discovered that the chromosome number of these forms was  $2n = 84$ , whereas other *Geranium* species have  $2n = 28$ . The chromosome number was ascertained by Mr Rudge. Dr Warburg, Botany Department, Cambridge University, who has made a special study of the cytology of the Geraniaceae, has confirmed this chromosome number in a private communication. It is therefore suggested that auto-hexaploid ratios are here involved. Using Haldane's formula for calculating the gametic output, we find that the segregation from hexaplex dominant  $\times$  recessive would be 399 dominant : 1 recessive; duplex  $\times$  recessive nulliplex would be 4 dominant : 1 recessive; simplex  $\times$  recessive nulliplex would be 1 dominant : 1 recessive (chromosomal or complete reductional segregation).

On this basis the  $F_2$  plants backcrossed to the recessive parent may be triplex and duplex respectively, the 42 : 1 and 13 : 2 ratios corresponding to the theoretical 40.8 : 2.2 and 12 : 3 ratios. Among the 178 plants of the  $F_2$  we should expect the following plants:

	$A_6$	$A_5$	$A_4$	$A_3$	$A_2$	$A_1$	$a$
Approx.	0.44	8.1	44	72.16	44	8.1	0.44

if the segregation of the genes followed strictly chromosome segregation in an auto-hexaploid unaccompanied by other disturbing influences. It will therefore be seen that such theoretical considerations might account for the reduced segregation of flower colour in the  $F_2$ . The occurrence of two plants, some of the flowers of which were mericlinal chimaeras for *sanguineum* and *lancastricense* may be significant. These occurred in one family where (on this theory) simplex plants were to be expected most frequently and they may indeed be simplex forms. An attempt was made to test these plants and other parts of the general problem by critical crosses but the practical difficulties mentioned earlier were too great.

The remaining characters behaved in a similar manner to that of flower colour; the important point, however, is that plants recessive for flower colour were recessive for the other characters, and the particular plants used in the  $F_2$  generations for crossing were selected because they carried recessive, or at least, different characteristics from the remaining  $F_2$  plants. Hence it is possible that there is close linkage between these characters. Naturally it was not possible to obtain definite information with this refractory material.

## SUMMARY

From the reasons stated, although there is no proof, the evidence indicates that:

(1) There is a factor carried by *G. striatum* which, in the presence of cytoplasm of *G. Endressi*, causes petaloidy of the anthers.

(2) There is autohexaploid segregation of flower colour in *G. sanguineum*.

## REFERENCE

- HALDANE, J. B. S. (1930). "Theoretical genetics of autopolyploids." *J. Genet.* **22**, 359-72.