

GENETICS OF FLOWER COLOUR IN
TRIFOLIUM PRATENSE L.

I. BASIC WHITE COLOUR (FACTOR c)

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(With Three Text-figures.)

THE flower colour of most red clover plants is reddish mauve varying in intensity within a fairly narrow range. However, a few plants with flowers of other tints, such as rose, lilac, pink and white, may usually be found in most varieties; and in recent years several new recessive flower-coloured forms, not yet found in wild or cultivated varieties, have appeared in my pedigree cultures as a result of inbreeding. It is proposed to publish in a series of papers the data on the mode of inheritance and the linkage relationships of thirteen different red clover flower colours which I have investigated. In this paper, the first of the series, the data on the inheritance of the basic white-flower colour are presented.

WHITE-FLOWERED TYPES.

Three pure white-flowered red clover forms due to different recessive factors, designated c , c_y and c_d , have been isolated. The factor pairs C/c and Cy/c_y are known to be in different linkage groups, but the linkage relationship of Cd/c_d has not yet been ascertained. The three dominant factors C , Cy , Cd are complementary, all plants carrying one or more of these genes in the homozygous recessive condition are white-flowered. The three recessive factors are epistatic to all the other flower factors, with the exception of a dominant factor C_p which gave rise to a variegated flower colour; they also completely inhibit the development of anthocyanin pigment in all the vegetative organs, so that all plants homozygous for one or more of these three factors in the recessive condition are completely devoid of any anthocyanin pigment in all floral and vegetative organs, except when the dominant factor C_p is present.

The basic flower colour factor in red clover is C . In the absence of C_p , all cc plants have pure white corollas which assume a characteristic dull greyish colour on withering; the seeds are pale ivory in colour.

Plants carrying homozygous recessive factors $c_y c_y$ together with

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a dominant basic factor **C** have white flowers tinged with yellow, which may be described as pale cream. The withered flowers are of a deep brown colour—a character by which **C-c_yc_y** plants may be readily distinguished from **cc** plants. The seeds are bright yellow and plump. Plants carrying the recessive factors **c_ac_a** are phenotypically similar to **c_yc_y** plants.

INHERITANCE OF BASIC WHITE-FLOWER COLOUR.

The first basic white-flowered plant (**cc**) used in these studies was found in a field crop of a variety known as Montgomery late. The same form has since been obtained from five different sources; twice in a Montgomery seed crop, twice in *F*₂ progenies of English broad red crosses,

TABLE I.

*F*₂ of red × basic white, **Cc** × **Cc**. Year 1927.

Family	Coloured	White	Deviation from 3 : 1	Deviation ÷ S.E.
550 (2) 1 × 2	207	100	+ 23.25	3.06
2 × 3	227	98	+ 16.75	2.14
3 × 4	167	112	+ 42.25	5.84
4 × 5	152	78	+ 20.50	3.12
551 (2) 1 × 2	322	141	+ 25.25	2.71
1 × 5	120	63	+ 17.25	2.94
4 × 30	49	25	+ 6.50	1.74
25 × 30	99	40	+ 5.25	1.03
553 (2) 4 × 24	95	46	+ 10.75	2.09
48 × 51	91	34	+ 2.75	0.56
22 × 51	195	49	- 12.00	1.77
555 (2) 1 × 4	243	110	+ 21.75	2.67
2 × 3	192	91	+ 20.25	2.78
3 × 4	190	58	- 4.00	0.59
23 × 65	88	32	- 2.00	0.42

and once in an *F*₂ family of a wild red cross. Since these plants when intercrossed in various combinations gave only white-flowered offspring, it is evident they must be of the same constitution in regard to the basic flower colour **c**. From the description given it seems that the white-flowered plants reported by Witte (1921) and Wexelsen (1932) are of the same type as my basic white.

In 1927 four unrelated red-flowered plants having the constitution **CC** were mated with the same white-flowered plant **cc**. The resulting offspring, consisting of 598 plants, were full red, the factor **C** being completely dominant to **c**. A number of *F*₁ plants from each progeny were crossed *inter se*. Of these matings four proved to be cross-incompatible and fifteen cross-compatible. The *F*₂ flower-colour results given by these families are shown in Table I.

Of the fifteen F_2 progenies, only four, namely, 551 (2) 25×30 , 553 (2) 48×51 , 555 (2) 3×4 and 555 (2) 23×65 , gave results which approximated to a 3:1 ratio. One family, viz. 553 (2) 22×51 , gave, on the basis of monohybrid segregation, a decided deficiency of whites. In the other ten families the whites were for the most part greatly in excess of expectation. In three of these the deviations were more than three times the standard errors; it is, therefore, extremely improbable that the divergence from the expected 3:1 segregation in these families was due to fluctuation in sampling. Since none of the F_2 frequencies conformed to a 9:7 distribution it is clear that the results obtained are not due to independent duplicate genes, nor can they be explained by assuming the presence of two linked flower-colour factors.

TABLE II.

 F_2 of red \times basic white, Cc \times Cc. Year 1929.

Family	Coloured	White	Deviation from 3:1	Deviation \div s.e.
677 (2) 1×2	70	30	+ 5.00	1.16
1×6	55	13	- 4.00	1.12
3×4	36	21	+ 6.75	2.07
4×6	30	12	+ 1.50	0.53
628 (2) 1×4	173	55	- 2.00	0.31
2×3	270	44	- 34.50	4.41
3×4	187	103	+ 30.50	4.14
629 (2) 1×5	233	50	- 20.75	2.85
2×5	286	44	- 38.50	4.89
3×4	194	90	+ 19.00	2.60
632 (2) 1×2	115	67	+ 21.50	3.68
1×5	95	20	- 8.75	1.88
1×6	93	56	+ 18.75	3.55
1×13	104	53	+ 13.75	2.53
2×3	151	34	- 12.25	2.08

In 1929, four other red-flowered plants were crossed with a cc plant of a different origin from that used in the 1927 crosses. All the F_1 plants were red-flowered. Twenty-nine sib crosses were made, seven of these proved to be cross-incompatible and twenty-two cross-compatible. Only fifteen of the F_2 families were scored for flower colour; the results are shown in Table II.

As seen from Table II, four of the fifteen F_2 families gave results which are in close agreement with 3:1 segregation, six families gave a great excess of whites and five families gave an equally marked deficiency of whites.

The different F_2 families within the same cross often gave widely divergent distribution. In cross 628, for example, family 1×4 gave 173 reds to 55 whites, an almost exact 3:1 ratio; family 2×3 gave

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270 reds to 44 whites, a deficiency of 34.5 whites; while family 3 × 4 gave 187 reds to 103 whites, an excess of 30.5 recessives.

In several instances F_2 families which had a common F_1 parent gave widely different flower-colour distributions. In cross 632, the F_1 plant No. 1 was mated with four sibs, Nos. 2, 5, 6 and 13. Families 1 × 2, 1 × 6 and 1 × 13 all gave a significant excess of whites on a 3:1 basis, while family 1 × 5 gave a marked deficiency of whites. In cross 628, family 2 × 3 gave 270 reds and 44 whites, a deficiency of 34.5 whites, while in family 3 × 4 there was an excess of 30.5 in the recessive class.

Most of the F_1 plants were crossed reciprocally. The distributions of reds and whites in the reciprocal crosses were approximately the same. The data below are representative of the results obtained from most of the reciprocal $F_1 \times F_1$ matings.

Family	♀ plant	Coloured	Whites	Ratio
550 (2) 1 × 2	1	90	46	1.9:1
	2	117	54	2.2:1
550 (2) 2 × 3	2	73	30	2.4:1
	3	154	68	2.3:1
551 (2) 1 × 2	1	147	60	2.4:1
	2	175	80	2.2:1
555 (2) 2 × 3	2	91	35	2.6:1
	3	152	75	2.0:1
557 (2) 1 × 5	1	103	4	27.7:1
	5	120	17	7.1:1
628 (2) 3 × 4	3	109	56	1.9:1
	4	79	47	1.7:1
628 (2) 1 × 4	1	100	30	3.3:1
	4	61	25	2.4:1
628 (2) 2 × 3	2	140	28	5.0:1
	3	129	16	8.1:1
629 (2) 3 × 4	3	108	45	2.4:1
	4	86	46	1.9:1
629 (2) 1 × 5	1	133	22	6.0:1
	5	140	28	5.0:1
629 (2) 2 × 5	2	106	18	5.9:1
	5	180	26	6.9:1

LINKAGE BETWEEN STERILITY ALLELOMORPHS (S)
AND THE FLOWER FACTORS C/c.

(1) F_2 data.

Self- and cross-sterility in red clover have been shown to be due to the action of a series of multiple allelomorphs acting as oppositional factors (Williams and Silow, 1933). The results given by the red × white crosses are in accord with expectation if it is assumed that (i) the difference between the coloured and white plants is due to a single factor, and (ii) that the colour factors are loosely linked with the sterility allelo-

morphs. It is interesting to note that a similar linkage between the incompatibility allelomorphs and the basic flower factor has been found in *Nicotiana Sanderac* (Brieger and Mangelsdorf, 1926). Evidence of linkage between sterility allelomorphs and corolla tube length, style length and pollen colour has been reported in *Nicotiana Langsdorffii* × *N. alata* crosses (Anderson and De Winton, 1931).

It is highly probable since they were totally unrelated that the original red and white plants used were all carrying different sterility factors. Assuming linkage between **S** and **C** factors, the original plants crossed may be represented as being of the constitution

$$(\mathbf{S}_1\mathbf{C}) (\mathbf{S}_2\mathbf{C}) \times (\mathbf{S}_3\mathbf{c}) (\mathbf{S}_4\mathbf{c}).$$

The F_1 offspring of such a cross should consist of the following four intrasterile interfertile groups in approximately equal numbers:

$$\begin{array}{cccc} (1) & (2) & (3) & (4) \\ (\mathbf{S}_1\mathbf{C}) (\mathbf{S}_3\mathbf{c}) & (\mathbf{S}_1\mathbf{C}) (\mathbf{S}_4\mathbf{c}) & (\mathbf{S}_2\mathbf{C}) (\mathbf{S}_3\mathbf{c}) & (\mathbf{S}_2\mathbf{C}) (\mathbf{S}_4\mathbf{c}) \end{array}$$

If an equal number of plants from each of these four groups are intercrossed in all combinations one-third of the resulting F_2 families would be expected to give reds and whites in the ratio of 3:1, one-third should give an excess of whites, and the remaining one-third a deficiency of whites.

When F_1 plants carrying different incompatible alleles were mated, as, for example, when plants of the sterility group 1 are crossed with those in group 4, $(\mathbf{S}_1\mathbf{C}) (\mathbf{S}_3\mathbf{c}) \times (\mathbf{S}_2\mathbf{C}) (\mathbf{S}_4\mathbf{c})$, and plants of group 2 with those of group 3, $(\mathbf{S}_1\mathbf{C}) (\mathbf{S}_4\mathbf{c}) \times (\mathbf{S}_2\mathbf{C}) (\mathbf{S}_3\mathbf{c})$, the resulting progenies should give normal 3:1 ratios for reds and whites, since all the gametes would be functional.

When **C** is linked with a common **S** factor, as in F_1 crosses

$$(\mathbf{S}_1\mathbf{C}) (\mathbf{S}_3\mathbf{c}) \times (\mathbf{S}_1\mathbf{C}) (\mathbf{S}_4\mathbf{c}) \text{ and } (\mathbf{S}_2\mathbf{C}) (\mathbf{S}_3\mathbf{c}) \times (\mathbf{S}_2\mathbf{C}) (\mathbf{S}_4\mathbf{c}),$$

as illustrated below, an excess of whites resulting in a narrow ratio is expected owing to the elimination of pollen tubes carrying the common factor as a result of the inhibitory action of the style.

		♂ gametes				
		Non-cross-overs		Cross-overs		
		$\mathbf{S}_1\mathbf{C}$	$\mathbf{S}_3\mathbf{c}$	$\mathbf{S}_1\mathbf{c}$	$\mathbf{S}_3\mathbf{C}$	
♀ gametes	Non-cross-overs	—	Reds Whites	—	Reds Reds	
		$\mathbf{S}_1\mathbf{C}$	—	Whites Reds	—	Reds Reds
	Cross-overs	$\mathbf{S}_1\mathbf{c}$	—	—	—	Reds Reds
		$\mathbf{S}_3\mathbf{C}$	—	—	—	Reds Reds

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Since only the non-cross-over S_3c and the cross-over S_3C male gametes are able to accomplish fertilisation, the proportion of reds and whites resulting from such a cross will depend on the intensity of the linkage between S and C ; with complete linkage equal numbers of reds and whites are expected.

Similarly, F_2 progeny resulting from crossing F_1 plants in which c is coupled with a common S factor, as in crosses

$$(S_1C) (S_3c) \times (S_2C) (S_3c) \text{ and } (S_1C) (S_1c) \times (S_2C) (S_1c),$$

would be expected to give a deficiency of whites. As illustrated below, the non-cross-over gametes give rise only to reds, the whites being derived solely from the union of cross-over gamete S_2c with the female gamete S_3c (non-cross-over) and S_1c (cross-over).

		♂ gametes			
		Non-cross-overs		Cross-overs	
		S_2C	S_3c	S_2c	S_3C
♀ gametes	Non-cross-overs	Reds	—	Reds	—
	S_1C S_3c	Reds	—	Whites	—
Cross-overs	S_1c	Reds	—	Whites	—
	S_3C	Reds	—	Reds	—

It should be explained that the F_2 crosses reported in this paper were made before it was realised that factors S and C were possibly linked. Had this hypothesis been formulated earlier the sib matings could have been arranged in such a way as to indicate the sterility groupings of the plants concerned. Though the data on this point are far from being complete, fortunately in many cases a sufficient number of sib matings were effected to allow the sterility groupings of the F_1 plants crossed to be determined with reasonable accuracy.

In cross 629 five F_1 sibs were reciprocally interpollinated in six different combinations with the results shown in Fig. 1.

	1	2	3	4	5
1	—	0	.		+*
2	0	—	+		+
3		+	—	+	
4			+	—	0
5	+	+		0	—

Fig. 1. Cross 629. Compatibility relationships of F_1 plants.

* Explanation of symbols used in Figs. 1-3:
+ = cross-fertile; 0 = cross-sterile; - = self-sterile.

As seen from Fig. 1, sibs 1 and 2 being reciprocally cross-incompatible must have been of a similar constitution as regards their sterility factors. Sibs 4 and 5 were also cross-incompatible. Since sib 1 was cross-compatible with sib 5, plants 4 and 5 must have been in a different sterility group from that of plants 1 and 2. Plant 3, being cross-fertile from plant 2 on the one hand, and plants 4 and 5 on the other, must have belonged to another group. These five plants, therefore, fell into three sterility groups, one consisting of plants 1 and 2, another of plants 4 and 5, and a third group with plant 3.

The seeds of the 2×3 cross were not sown. The flower-colour frequencies given by the other three compatible crosses are as follows:

	Coloured	Whites	Deviation from 3 : 1	Deviation \div s.e.	Ratio
1 \times 5	233	50	-20.75	2.85	Excess of whites
2 \times 5	286	44	-38.5	4.89	Excess of whites
3 \times 4	196	90	+19.0	2.60	Excess of coloured

The marked deficiency of whites in 1×5 cross suggests that the two sibs concerned were carrying a common **S** factor linked with **c**. Since sib 2 was found to be of the same sterility constitution as sib 1, cross 2×5 would also be expected to give a deficiency of whites. This was found to be the case. If we assign to sibs 1 and 2 the constitution (**S**₁**C**) (**S**₃**c**) then sibs 4 and 5 must be of constitution (**S**₂**C**) (**S**₃**c**). Since plant 3 is in a different sterility group from plants 1 and 2 and plants 4 and 5, its constitution must be (**S**₁**C**) (**S**₄**c**) or (**S**₂**C**) (**S**₄**c**); the excess of whites obtained from 3×4 cross suggests that **C** factors in these two plants are linked with a common sterility factor, viz. **S**₂. We are, therefore, able to assign to plant 3 the constitution (**S**₂**C**) (**S**₄**c**). The results of the compatibility tests and the F_2 flower-colour data are fully in accord with the expectation on the assumption that the five F_1 plants involved were of the following constitution:

F_1 plants:	(S ₁ C) (S ₃ c) 1, 2	(S ₁ C) (S ₃ c) —	(S ₂ C) (S ₃ c) 4, 5	(S ₂ C) (S ₄ c) 3
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In cross 557 five F_1 plants were cross-pollinated in six different combinations with the results shown in Fig. 2.

These five F_1 plants fall into three sterility groups, viz. one group with plant 1, another group with plant 2, and a third group with plants 3, 4 and 5. The F_2 data of the three compatible crosses are:

	Coloured	Whites	Deviation from 3 : 1	Deviation \div s.e.	Ratio
2 \times 3	175	78	+14.75	2.14	Excess of whites
2 \times 1	179	71	+ 8.5	1.24	3 : 1
1 \times 5	223	21	-40.0	5.72	Excess of coloured

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These results are in accordance with expectation assuming that constitutions of the F_1 plants were:

	(S ₁ C) (S ₂ c)	(S ₁ C) (S ₂ c)	(S ₂ C) (S ₂ c)	(S ₂ C) (S ₁ c)
F_1 plants:	3, 4, 5	2	1	—

In cross 632, eight F_1 's were interpollinated in the various combinations shown in Fig. 3.

		♂				
		1	2	3	4	5
♀	1	-	+			+
	2	+		+		
	3		+	-	0	0
	4			0	-	0
	5	+		0	0	-

Fig. 2. 557 cross. Compatibility relationships of F_1 plants.

		♂							
		1	2	6	13	5	12	3	4
♀	1	-	+	+	+	+			
	2	+	-	0		+		+	
	6	+	0	-		+			
	13	+			-	+	+		
	5	+	+	+	+	-	0		+
	12				+	0	-		
	3		+					-	0
	4					+		0	-

Fig. 3. Cross 632. Compatibility relationships of F_1 plants.

Of a total of thirteen crosses made, three were incompatible and ten compatible. F_2 flower-colour data of nine of these crosses are given below—the remaining cross, viz. 1 × 5, was not scored for flower colour.

	Coloured	Whites	Deviation from 3 : 1	Deviation ÷ s.e.	Ratio
1 × 2	115	67	+21.50	3.68	Excess of whites
1 × 6	93	56	+18.75	3.55	Excess of whites
1 × 13	98	53	+15.25	2.87	Excess of whites
5 × 4	68	31	+ 6.25	1.45	Excess of whites
5 × 13	90	40	+ 7.50	1.52	3 : 1
5 × 6	138	40	- 4.50	0.78	3 : 1
12 × 13	57	18	- 0.75	0.20	3 : 1
1 × 5	95	20	- 8.75	1.88	Excess of coloured
2 × 3	151	34	-11.75	1.99	Excess of coloured

As seen from Fig. 3, all the four possible sterility groups are represented. The compatibility relationships of the F_1 plants and the flower-colour frequencies of the F_2 families are again fully in accord with expectation if we assume that the compositions of the F_1 plants were as follows:

	(S ₁ C) (S ₃ c)	(S ₁ C) (S ₁ c)	(S ₂ C) (S ₃ c)	(S ₂ C) (S ₁ c)
F_1 plants:	1	2, 6, 13	5, 12	3, 4

In another cross, viz. 1039, seven F_1 sibs were interpollinated in eight different combinations, three of which were incompatible and five compatible. The F_2 flower-colour data of the five compatible crosses are given below:

	Coloured	Whites	Deviation from 3 : 1	Deviation ÷ s.e.	Ratio
2 × 8	63	37	+ 22.50	4.86	Excess of whites
3 × 8	74	45	+ 15.25	3.23	Excess of whites
3 × 6	83	28	- 0.25	0.05	3 : 1
4 × 5	30	8	- 1.50	0.55	3 : 1
5 × 7	213	39	- 24.00	3.49	Excess of coloured

The seven F_1 plants concerned were found to fall in three different sterility groups, with plants 2, 3, 4 in one group, plants 7 and 8 in another, and plants 5 and 6 in the third group. As in the other crosses previously discussed, the widely divergent red : white ratios given by the various F_2 families are readily interpreted on the assumption that the constitutions of the F_1 sibs crossed were as follows:

	(S ₁ C) (S ₃ c)	(S ₁ C) (S ₁ c)	(S ₂ C) (S ₃ c)	(S ₂ C) (S ₁ c)
F_1 plants:	2, 3, 4	7, 8	—	5, 6

In addition to the four crosses discussed above, a sufficient number of cross-pollinations have been made in five other red × white crosses to allow the sterility groups of the F_1 plants to be determined. The flower-colour distribution in twenty-eight F_2 families derived from these nine crosses have been correlated with the sterility groupings of the F_1 plants concerned, and, with the exception of one family which may possibly have been wrongly numbered, all the results are in accordance with the hypothesis.

It seems from all the evidence available that the number of incompatible allelomorphs in red clover is very large. I have recently carried out an extensive experiment for the purpose of ascertaining the number of sterility allelomorphs carried by a given number of red clover plants. With this object in view, twenty plants, taken at random from English broad red variety, were each crossed with a plant (S₁S₁) known from previous tests to be homozygous for sterility factors (unpublished data). A number of plants of each of the twenty F_1 families were then separated

by appropriate compatibility tests into their respective sterility groups $\mathbf{S}_x\mathbf{S}_1$ and $\mathbf{S}_y\mathbf{S}_1$, making a total of forty groups. F_1 plants representing each of these forty groups were afterwards cross-pollinated in all possible combinations. All the crosses, except two which have not yet been tested, were found to be fully cross-compatible. It is evident from these results that the twenty original broad red plants used in this experiment had thirty-nine (probably forty) different incompatibility alleles.

In view of the multiplicity of the sterility allelomorphs carried by red clover, it is extremely improbable that any of the original red- and white-flowered plants crossed were carrying like sterility allelomorphs, particularly since all the plants used were derived from different sources. On this assumption the F_1 progeny of all the original red \times white crosses must have consisted of four phenotypes:

$$(\mathbf{S}_1\mathbf{C}) (\mathbf{S}_3\mathbf{c}); (\mathbf{S}_1\mathbf{C}) (\mathbf{S}_4\mathbf{c}); (\mathbf{S}_2\mathbf{C}) (\mathbf{S}_3\mathbf{c}); (\mathbf{S}_2\mathbf{C}) (\mathbf{S}_4\mathbf{c})$$

in equal numbers. If a number of F_1 plants is mated in all combinations 25 per cent. of the crosses should be incompatible and 75 per cent. compatible, while one-third of the F_2 progenies would be expected to give a ratio of 3 reds: 1 white, one-third a marked excess of reds, and one-third a marked excess of whites.

Out of the total of ninety-two red \times white sib-matings (in ten crosses) that have been made, twenty-four proved to be cross-incompatible and sixty-eight cross-compatible, the expected being twenty-three incompatibles and sixty-nine compatibles; and of the F_2 families obtained from the compatible crosses, eighteen gave a normal 3:1 ratio of reds and whites, twenty-one gave an excess of reds and twenty-nine gave an excess of whites. Except for slight excess of F_2 families giving an excess of whites, the observed results show a close agreement with expectation.

A number of crosses, the results of which will be given in detail later, have also been made between self-fertile reds ($\mathbf{S}_1\mathbf{C}$) ($\mathbf{S}_2\mathbf{C}$) used as ♂♂ and self-sterile whites ($\mathbf{S}_3\mathbf{c}$) ($\mathbf{S}_4\mathbf{c}$) used as ♀♀. The data of F_2 progenies obtained from self-fertile F_1 derivatives of these crosses probably afford a more accurate basis for calculating the linkage intensity between \mathbf{S} and \mathbf{C} factors than the data of the F_2 progenies from sib-crosses. If we accept 0.35—the figure calculated from the data given by selfed F_2 progenies—as the mean cross-over value for \mathbf{S} and \mathbf{C} , the expected flower-colour distribution from sib-crosses in which \mathbf{C} is linked with a common \mathbf{S} factor, as in ($\mathbf{S}_1\mathbf{C}$) ($\mathbf{S}_3\mathbf{c}$) \times ($\mathbf{S}_1\mathbf{C}$) ($\mathbf{S}_4\mathbf{c}$), is 2.08 reds:1 white, and from sib-crosses in which \mathbf{c} is linked with a common \mathbf{S} factor, as in ($\mathbf{S}_1\mathbf{C}$) ($\mathbf{S}_3\mathbf{c}$) \times ($\mathbf{S}_2\mathbf{C}$) ($\mathbf{S}_4\mathbf{c}$), 4.64 reds:1 white.

All the F_2 data of sib-crosses are given in Tables III–VI. As it was not always possible from examination of the data to decide whether the divergences from expectation were due to linkage or merely to sampling errors, standard deviations of all the F_2 frequencies from 2.08:1, 3:1 and 4.64:1 ratios were calculated. The results approximating a 2.08:1 ratio are shown in Tables III and IV, those conforming to a 3:1 ratio

TABLE III.

F_2 of red \times white C linked with a common S factor as in $\frac{S_1C}{S_2c} \times \frac{S_1C}{S_3c}$.

Family No.	Observed		Deviation \div s.e. on the basis of		Calculated cross-over values
	C	cc	3:1 segre- gation	0.35 cross- over value	
550 (2) 1 \times 2	207	100	3.07	0.03	0.35
2 \times 3	227	98	2.15	0.91	0.39
4 \times 5	152	78	3.12	0.46	0.32
551 (2) 1 \times 2	322	141	2.71	0.94	0.39
1 \times 5	120	63	2.95	0.54	0.31
553 (2) 4 \times 24	95	46	2.09	0.03	0.35
555 (2) 2 \times 3	243	110	2.67	0.54	0.38
1 \times 4	192	91	2.78	0.25	0.36
557 (2) 2 \times 3	175	78	2.14	0.57	0.38
632 (2) 1 \times 2	115	67	3.68	1.24	0.26
1 \times 6	93	56	3.53	1.32	0.25
1 \times 13	104	53	2.53	0.51	0.39
4 \times 5	68	31	1.45	0.27	0.37
5 \times 13	90	40	1.52	0.42	0.38
628 (2) 3 \times 4	187	103	4.14	1.09	0.29
629 (2) 3 \times 4	194	90	2.61	0.29	0.37
677 (2) 1 \times 2	70	30	1.15	0.53	0.40
3 \times 4	36	21	2.07	0.68	0.26
829 (2) 1 \times 4	46	27	2.36	0.81	0.23
2 \times 4	142	86	4.28	1.68	0.25
3 \times 4	122	66	3.20	0.76	0.29
6 \times 7	126	52	1.29	0.94	0.42
1039 (2) 3 \times 8	74	45	3.23	1.24	0.24
1043 (1)	36	18	1.09	0.01	0.33
1371 (2) 2 \times 3	70	39	2.59	0.71	0.29
1425 (1)	113	59	2.81	0.51	0.31
1432 (1)	82	39	1.84	0.06	0.36
1491 (2) 3 \times 4	183	99	3.91	0.93	0.29
Observed total	3684	1826			
Expected (3:1)	4132.5	1377.5			

in Table V, and those in which the whites were significantly in excess of the normal 3:1 ratio are given in Table VI.

In most of the twenty-eight families shown in Table III the number of whites is greatly in excess of expectation on the basis of 3:1 segregation. As is evident from the value of $\chi^2=204.99$ (the corresponding value of P is very small), the deviation from the 3:1 ratio is well outside the range of fluctuation due to sampling. The total frequencies of 3684

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reds and 1628 whites is equivalent to a ratio of 2.2 reds:1 white. This is very close to the 2.08:1 ratio expected on the supposition that the factorial compositions of the F_1 plants crossed were $(S_1C)(S_3c) \times (S_1C)(S_3c)$ with 35 per cent. crossing-over between **S** and **C**. On this basis the value of χ^2 is 17.858 and of P is 0.92, indicating a very close agreement with hypothesis.

In this series the mean cross-over value for factors **C** and **S** is 0.32, but the value for the individual families varied from 0.23 to 0.40. Considering the small number of plants in many of the families, these variations are not in excess of those expected from random sampling.

In six other F_2 families, results of which are shown in Table IV, the whites were greatly in excess of the number expected on the basis of linkage between **S** and **C** factors, with 35 per cent. crossing-over.

TABLE IV.

F_2 of red \times white. **C** linked with a common **S** factor as in $\frac{S_1C}{S_2c} \times \frac{S_1C}{S_3c}$.

Family No.	Observed		Deviation \div s.e. on the basis of		Calculated cross-over values
	C	cc	3 : 1 segre- gation	0.35 cross- over value	
550 (2) 3 \times 4	167	112	5.84	2.73	0.19
829 (2) 4 \times 5	102	71	4.16	2.39	0.18
9 \times 12	122	84	5.07	2.54	0.18
13 \times 14	166	148	9.06	5.54	0.06
1039 (2) 2 \times 8	63	51	4.86	2.79	0.11
1371 (2) 3 \times 4	33	32	4.51	2.88	0.02
Observed total	653	498			

Applying the test of agreement between the observed distribution for these six families with the expected on the basis of simple segregation with 35 per cent. crossing-over between **S** and **C**, the calculated value of χ^2 is 66.315, the corresponding value of P is very small, clearly indicating that the deviations from expectation are highly significant. It would seem from these results that the **S** and **C** factors were much more closely linked in the plants involved in these six crosses than in the majority of the plants investigated. In family 1371 (2) 3 \times 4, which gave 33 reds to 32 whites, the calculated cross-over value for **S** and **C** is only 0.02, though the number of plants in this family is admittedly too few for determining linkage intensity. Family 829 (2) 13 \times 14 consisting of a total of 314 plants gave very similar results, 166 reds:148 whites, indicating a cross-over value for **S** and **C** of only 0.06, while the two sister families 829 (2) 4 \times 5 and 829 (2) 9 \times 12, consisting of 173 and 206

plants respectively, each gave a cross-over value of 0.18. These aberrant results for flower colour were not due to contamination, since the six families segregated in accordance with expectation for a number of other characters, *e.g.* variegation and leaf marking. It is interesting to note that ten out of twelve of F_1 plants involved in these families—the only exceptions were the two F_1 plants of cross 550—were also heterozygous

TABLE V.

F_2 data of red \times white F_1 plants carrying different sterility alleles as in

$$\frac{S_1C}{S_2c} \times \frac{S_3C}{S_4c} \text{ crosses.}$$

Family No.	Observed		Deviation \div s.e. on 3 : 1 basis
	C	cc	
550 (3) 163 \times 187	54	21	0.60
551 (2) 4 P \times 30	49	25	1.74
25 \times 30	99	40	1.03
553 (2) 48 \times 51	91	34	1.09
555 (2) 3 P \times 4 P	190	58	0.58
23 \times 65	88	32	0.42
557 (2) 1 \times 2	179	71	1.24
35 \times 93	68	29	1.11
628 (2) 1 \times 4	173	55	0.31
632 (2) 5 \times 6	138	40	0.77
12 \times 13	57	18	0.19
829 (2) 7 P \times 8 P	41	14	0.08
10 \times 12	89	26	0.59
1039 (2) 3 P \times 6 P	83	28	0.05
1042 (2) 7 P \times 8 P	127	42	0.04
1434 (1)	51	15	0.35
1491 (2) 1 \times 2	55	20	0.33
1491 (2) 2 \times 4	117	45	0.82
1509 (1)	37	10	0.59
1519 (2) 3 \times 14	171	61	0.45
5 \times 11	146	53	0.53
6 \times 7	116	43	0.59
7 \times 10	125	47	0.71
12 \times 16	37	14	0.44
2042 (1)	310	127	1.96
Observed total	2691	968	
Expected (3 : 1)	2744	915	

$$n = 25; \chi^2 = 15.7808; P = 0.92.$$

for another flower factor **P** which is known to be also very strongly linked with the sterility allelomorphs with a cross-over value of less than 1 per cent. It is possible that recessive factor **p** or another factor closely linked with it may have the effect of reducing the frequency of crossing-over.

In contrast to the results given in Tables III and IV the frequency data of the twenty-five F_2 families presented in Table V show a very close agreement with the expected 3:1 ratio. The total frequencies were

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2691 reds and 968 whites, an excess of only fifty-three whites on the basis of simple monohybrid segregation.

Test of goodness of fit applied to these data gives the value of χ^2 as 15.780, and the value of P as 0.92, indicating a remarkably close fit with expectation. On the supposition that the two F_1 plants in each cross were carrying different sterility factors, the results given by these twenty-five F_2 families are in accord with hypothesis.

All the sixteen families, the results of which are shown in Table IV, gave a marked deficiency of whites on the basis of 3:1 segregation, and

TABLE VI.

F_2 data of red \times white. Factor c linked with a common S factor as in

$$\frac{S_1C}{S_3c} \times \frac{S_2C}{S_3c} \text{ crosses.}$$

Family No.	Observed		Deviation \div s.e. on the basis of		Calculated cross-over values
	C	cc	3 : 1 segre- gation	0.35 cross- over value	
550 (3) 187 \times 209	78	12	2.55	1.09	0.27
553 (2) 22 \times 51	195	49	1.77	0.98	0.41
557 (2) 1 \times 5	223	21	5.91	3.72	0.18
5 \times 92	192	46	2.02	0.65	0.39
25 \times 93	122	30	1.49	0.71	0.39
628 (2) 2 \times 3	270	44	4.49	1.71	0.28
629 (2) 1 \times 5	233	50	2.85	0.01	0.35
2 \times 3	286	44	4.89	2.08	0.27
632 (2) 1 \times 5	95	20	1.88	0.33	0.35
2 \times 3	151	34	2.08	0.24	0.37
836 (1)	142	26	2.85	0.75	0.31
1039 (2) 5 \times 7	213	39	3.49	0.92	0.31
1430 (1)	86	16	2.17	0.54	0.31
1431 (1)	38	8	1.19	0.05	0.35
1372 (2) 5 \times 6	117	14	3.73	2.11	0.22
1519 (2) 8 \times 15	44	6	2.12	1.06	0.24
Total	2485	459			

in the majority of cases the departure from expectation is significant. The total observed distribution in the sixteen families is 2485 reds and 459 whites, the expected being 2208 reds and 736 whites. Applying the test for goodness of fit to these data we find that χ^2 is 156.478 and that P is very small, indicating that the deviation from expectation is highly significant. On the assumption that the two F_1 plants involved in each cross had a common S allelomorph linked with c , as in cross $(S_1C)(S_3c) \times (S_2C)(S_3c)$ with 35 per cent. crossing-over between S and C factors, the ratio expected is 4.64 reds:1 white, which agrees fairly closely with the observed ratio of 5.37 reds:1 white. As may be seen from the calculated deviation \div s.e. in Table VI, the observed frequencies of each family show a

much closer agreement with expectation on the basis that **c** is linked with a common **S** allelomorph with 0.35 cross-over value for these two factors than with the 3:1 ratio, and with the exception of family 557 (2) 1 × 5, which gave a very wide ratio of 10.5 reds:1 white, the data of each family show a reasonably close agreement with hypothesis. Excluding the 557 (2) 1 × 5 data the value of χ^2 for the other fifteen families is 17.565, and of *P* is 0.29, indicating that the departure from expectation on the basis of 35 per cent. crossing-over is not significant. Taking the total data of the sixteen families, the calculated mean cross-over value for **S** and **C** factors is 0.31, and if 557 (2) 1 × 5 data are excluded the mean cross-over value for the remaining fifteen families is 0.32, which is precisely the same value as that given by

$$(\mathbf{S}_1\mathbf{C}) (\mathbf{S}_3\mathbf{c}) \times (\mathbf{S}_1\mathbf{C}) (\mathbf{S}_1\mathbf{c})$$

crosses (see Table III).

(2) *Back-crosses.*

A number of F_1 and F_2 plants heterozygous for the basic flower-colour factor have also been back-crossed to parental and other related whites, and to unrelated whites. Unfortunately many of these crosses were made in only one direction, with reds as females in some crosses and whites as females in others, but in a few instances both red and white plants were crossed reciprocally.

The results obtained from these back-crosses are interesting in that they afford confirmatory evidence of the occurrence of linkage between **S** and **C** factors.

When F_1 plants resulting from mating a homozygous red ($\mathbf{S}_1\mathbf{C}$) ($\mathbf{S}_2\mathbf{C}$) with a white plant ($\mathbf{S}_3\mathbf{c}$) ($\mathbf{S}_1\mathbf{c}$) are back-crossed with their white parent plants, *e.g.* ($\mathbf{S}_1\mathbf{C}$) ($\mathbf{S}_3\mathbf{c}$) × ($\mathbf{S}_3\mathbf{c}$) ($\mathbf{S}_1\mathbf{c}$), the proportion of reds and whites in the resulting progeny is expected to vary according to the direction of the cross. When F_1 plants are used as ♀♀ equal numbers of reds and whites are expected, but when the white parent is used as ♀ a deficiency of whites is expected owing to the elimination of the pollen tubes carrying the \mathbf{S}_3 factor with which the **c** factor is coupled.

When heterozygous reds are back-crossed to related whites other than their immediate parent, *e.g.* red F_1 × white F_2 daughter plants and F_2 plant × a white sib, the progenies of the red plants used as females should give a normal 1:1 segregation, but the reciprocal crosses may give 1:1 segregation or an excess, or a deficiency, of whites according to the factorial constitution of the plants crossed.

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Heterozygous reds \times unrelated whites and the reciprocal crosses would be expected to give reds and whites in equal numbers, provided the plants crossed have no **S** allelomorphs in common.

(i) *Heterozygous reds \times whites.* The data obtained from back-crosses in which only the red plants were used as females are summarised in Table VII.

As shown in Table VII, twelve families resulting from red F_1 plants $\text{♀} \times$ white parents $\text{♂} \text{♂}$ gave a total of 703 reds and 785 whites, an excess of forty-four whites on the basis of 1:1 segregation. Applying the test of goodness of fit to this series, we find that the value of $\chi^2 = 18.82$, and the value of $P = 0.10$, indicating that the difference between the observed distribution and expectation is not significant.

TABLE VII.

Back-crosses Cc ♀ \times cc ♂.

Cross	No. of ♀	No. of families	C	cc	Deviation from 1 : 1 ratio	χ^2	P
$F_1 \times$ original white parent	630	3	247	322	+ 37.5	3.9066	0.27
	631	4	183	189	+ 3.0	2.8850	0.56
	627	4	239	244	+ 2.5	11.7880	0.02
	677	1	34	30	- 2.0	0.2500	0.63
Total	12	12	703	785	+41.0	18.8296	0.10
$F_1 \times$ white F_2 daughter	—	4	159	173	+ 7.0	1.7540	0.78
Red $F_2 \times$ white F_2 sister	—	3	102	107	+ 2.5	2.5620	0.47
$F_1 \times$ unrelated white	—	8	623	631	+ 4.0	9.8118	0.29
Total	15	15	884	911	+13.5	14.1278	0.50

Another series of back-crosses (also shown in Table VII) in which four F_2 plants were pollinated by F_2 white-flowered daughter plants gave 157 reds and 173 whites. The agreement between the observed and expected frequencies is again fairly close; in this case the value of χ^2 is 1.754 and of P is 0.78.

$F_2 \times$ white sib-crosses also gave approximately equal numbers of reds and whites (120 reds:107 whites). The heterozygous reds \times unrelated white crosses also gave, in accordance with expectation, approximately equal numbers of reds and whites.

(ii) *Whites \times heterozygous reds.* The data of white \times heterozygous red crosses are given in Table VIII.

The data of four small families resulting from white F_2 daughter \times red F_1 crosses are shown in Table VIII. Each cross gave a very marked deficiency of whites, and though the number of plants was too small to allow definite conclusions to be drawn, the results are such as would be

expected from $(S_1c)(S_3c) \times (S_2C)(S_3c)$ crosses with about 27 per cent. crossing-over between **S** and **C** factors.

As expected, the unrelated white $\times F_1$ red crosses gave approximately equal numbers of reds and whites.

TABLE VIII.

Back-crosses cc ♀ × Cc ♂.

	Cross No. of female plants	Observed		Deviation ÷ s.e. on the basis of		Calculated cross-over value
		C	cc	1 : 1	0.35 cross-over value	
White F_2 daughters × red F_1 plants	550	17	5	2.56	1.2	0.27
	551	32	13	2.84	0.9	
	555	48	17	3.84	1.5	
	632	65	25	4.22	1.4	
	Total	162	60			
Unrelated whites × red F_1 plants	553	44	46	0.21	—	—
	556	29	26	0.40	—	—
	557	46	32	1.58	—	—
	629	31	23	1.09	—	—
	Total	150	127			

TABLE IX.

Reciprocal back-crosses (S₁C)(S₃c) × (S₃c)(S₄c).

Cross No.	Plants mated	Probable composition	♀ plant	Red	White	Excess of whites on 1 : 1 basis	Devia- tion ÷ s.e.	Cross- over values
2138 (1)	Red F_1 × white parent	$S_1C \times S_3c$ $S_3c \times S_4c$	Red	288	316	+ 14.0	1.14	0.37
			White	344	201	- 71.5	6.13	
2136 (1)	Red F_1 × white parent	$S_1C \times S_3c$ $S_3c \times S_4c$	Red	108	120	+ 6.0	0.79	0.36
			White	113	62	- 25.5	3.86	
982 (1)	Red F_1 × white F_2 daughter	$S_1C \times S_3c$ $S_3c \times S_4c$	Red	61	60	- 0.50	0.09	0.38
			White	46	28	- 9.0	2.09	
1460 (1)	Red F_1 × white F_2 daughter	$S_1C \times S_2c$ $S_3c \times S_4c$	Red	32	46	- 7.0	1.58	
			White	59	68	- 4.5	0.79	
1042 (2) 2 × 7	Red F_2 × white F_2 sister	$S_1C \times S_3c$ $S_3c \times S_4c$	Red	33	47	+ 7.0	1.57	0.32
			White	60	28	- 16.0	3.41	
1042 (2) 2 × 8	Red F_2 × white F_2 sister	$S_1c \times S_2c$ $S_3c \times S_4c$	Red	22	29	+ 3.5	0.98	
			White	59	47	- 6.0	1.16	
1458 (1)	Red F_1 × unre- lated white	$S_1C \times S_5c$	Red	99	98	- 0.5	0.07	
2108 (1)	Red F_1 × unre- lated white	$S_3c \times S_6c$	White	108	107	- 0.5	0.07	

(iii) *Reciprocal back-crosses.* The results from reciprocal back-crosses are shown in Table IX. The two families 2138 (1) and 2136 (1) were obtained by reciprocally back-crossing two red F_1 plants with their white parent plants. In cross 2138 (1) the F_1 plant used as ♀ gave 288 reds and 316 whites. This is clearly a 1:1 segregation, the deviation

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from expectation being only 1.14 times the standard error. From the reciprocal cross with the white parent plant as ♀ the results were 344 reds and 201 whites, a deficiency of 71.5 whites on the basis of 1:1 segregation, and since the deviation in this case is more than six times the standard error the departure from expectation is very significant. Cross 2136 (1) gave similar results; the F_1 used as ♀ gave 108 reds and 120 whites, while the reciprocal cross gave 113 reds and 62 whites. These results are fully in accord with hypothesis. The calculated cross-over value for **S** and **C** factors in cross 2138 (1) is 0.37, and in cross 2136 (1) the cross-over value is 0.36.

In crosses 982 (1) and 1462 (1) (Table IX) two F_1 plants were back-crossed reciprocally with two white-flowered daughter plants. In cross 982 (1) the red F_1 used as ♀ gave 60 reds and 61 whites, while the white plants used as ♀ gave 46 reds and 28 whites, but in family 1460 (1) the reciprocal crosses gave results strongly suggesting normal 1:1 segregation. On the basis of these results the plants used in cross 982 (1) may be assigned the constitutions (**S₁C**) (**S₃c**) × (**S₃c**) (**S₄c**) and in cross 1462 (1) (**S₁C**) (**S₃c**) × (**S₂c**) (**S₄c**).

In the two F_2 crosses, 1042 (2) 2×7 and 1042 (2) 2×8 , the same red F_1 plant, namely, No. 2, was reciprocally crossed with two different white sibs. As expected, the red-flowered plant, No. 2, used as ♀ gave a normal 1:1 ratio in both crosses, as did also white sib No. 8 when used as ♀, but a big deficiency of whites occurred when white sib No. 7 was used as the ovule plant, the data being 60 reds to 28 whites. It is fairly evident from these results that sibs Nos. 2 and 8 had no sterility factors in common and that the **S** allelomorph with which factor **c** is coupled in No. 2 plant was also carried by No. 7 sib.

The reciprocal crosses resulting from mating an F_1 with an unrelated white gave normal 1:1 segregation. This is in accord with expectation on the assumption that the two plants involved had different **S** allelomorphs.

(3) F_2 data of self-fertile plants.

In 1927 a self-fertile mutant was discovered in F_2 progeny of a Montgomery cross. Several self-fertile derivatives of this mutant which were known to be heterozygous for the self-fertility factor, but homozygous for the flower factor **C**, were crossed on to various self-sterile cc plants. These crosses may be represented as follows:

$$(\mathbf{S}_3\mathbf{c}) (\mathbf{S}_4\mathbf{c}) \text{ ♀} \times (\mathbf{S}_1\mathbf{C}) (\mathbf{S}_1\mathbf{C}) \text{ ♂}$$

The F_1 progeny from the crosses consisted of self-fertile plants (**S₁C**) (**S₃c**)

and (S_1C) (S_4c) and self-sterile plants (S_1C) (S_3c) and (S_1C) (S_4c) in approximate equality. A number of the self-fertile plants in each F_1 progeny were self-pollinated. The flower-colour data of the F_2 families derived from the self-fertile F_1 plants are given in Table X.

If S and C are independent factors the selfed F_2 families would be expected to give a 3:1 segregation for flower colour, but on the other hand, if S and C are assumed to be completely linked then only reds would be expected in the F_2 , since the gametes carrying c factor would be non-functional. If it is assumed that S and C factors are linked, then the occurrence of whites in F_2 progenies must be due entirely to crossing-over between these two factors.

TABLE X.

F_2 selfings of self-sterile white ♀ × self-fertile red ♂.

Parents: $\frac{S_2c}{S_3c} \times \frac{S_1C}{S_1C}$. Self-fertile F_1 plants: $\frac{S_1C}{S_2c}$ or $\frac{S_1C}{S_3c}$.

Cross No.	No. of F_2 families	Observed		Deviation from 3:1 s.e.	Deviation ÷ s.e. on the basis of		Calculated cross-over values
		C	cc		3:1	0.35 cross-over value	
977 (1)	3	231	43	- 25.50	3.57	0.88	0.32
1376 (1)	3	355	95	- 17.50	1.91	1.88	0.42
1519 (1)	3	569	95	- 71.00	6.36	2.31	0.29
1520 (1)	18	1574	363	- 121.25	6.36	0.19	0.37
1522 (1)	3	386	66	- 47.00	5.11	1.74	0.29
1523 (1)	2	105	25	- 7.50	1.42	0.45	0.39
1524 (1)	1	25	5	- 2.50	1.05	0.15	0.35
1529 (1)	3	85	22	- 26.75	5.75	0.76	0.41
1532 (1)	1	57	16	- 2.25	0.65	0.94	0.44
Total	37	3387	730	- 296.75	—	—	0.35

All the thirty-seven selfed F_2 families scored for flower colour gave a deficiency of whites on the basis of 3:1 segregation, and in most of the families the departure from expectation was clearly significant. The observed total for all the families was 3387 reds and 730 whites, a deficiency of 296.75 whites on the basis of 3:1 ratio. Applying the χ^2 test to the whole series we find that this deviation is eleven times the standard error, therefore the odds that the difference between the observed and expected is not due to fluctuation in sampling are enormous.

The results given by these selfed F_2 families afford additional evidence of linkage between S and C factors. The calculated cross-over values for S and C in the different families range from 0.29 to 0.44, the mean cross-over value for the thirty-seven families being 0.35.

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SUMMARY.

1. In red clover the basic dominant flower-colour factor (**C**) is a simple dominant to the pure white factor (**c**).
2. The basic recessive factor (**c**) is epistatic to all the other known flower-colour factors (with the exception of **Cp** gene), and to the anthocyanin factors.
3. The factor pair **C/c** is linked with the incompatible allelomorphs **S_i**, **S₁**, **S₂**, etc.
4. The mean cross-over value for **S** and **C** factors is about 35 per cent.

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