

REDUPLICATION SERIES IN SWEET PEAS. II.

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THE present note is supplementary to a paper on the same subject published in an earlier number of this Journal¹. It is concerned with the work of the two seasons 1914—15, and although, owing to various circumstances, the results are not so full as I had hoped, they serve nevertheless to determine several points of interest. These supplementary data relate only to the **BEL** series in which the characters dealt with are blue (**B**) as opposed to red (**b**), erect standard (**E**) as opposed to hooded (**e**), and long pollen (**L**) as opposed to round pollen (**l**). The axil-sterility-cretin series (**DFN**), which in some respects is the more interesting, I hope to deal with later when the experiments in progress are more complete.

(1) An important point which had to be left undecided in the previous account was the relation between **E** and **L** in plants homozygous for **B** or **b**. Data for determining this point are now available, and are set out in detail in Table I (p. 192). As stated in the earlier account it was anticipated that the intensity of the coupling between **E** and **L** would be very close to that obtaining between **B** and **L**, and this anticipation is borne out by the figures. From the mating **EL** × **el** 1118 plants were recorded in 1914 for shape of standard and pollen, and the four classes were distributed as follows²:

	Erect standard Long pollen	Erect standard Round pollen	Hooded standard Long pollen	Hooded standard Round pollen
	EL	El	eL	el
	765	62	71	220
Expectation on 7:1:1:7 basis	773	65.5	65.5	214

¹ *Journal of Genetics*, Vol. III, 1913, p. 77.

² I am much indebted to Mr Bateson for his kindness in growing more than one half of these F_1 plants under glass at the John Innes Horticultural Institution. The 16 plants so treated gave rise to families 129—144 of Table I and were all reds. It is interesting that although they were growing in close contact with various purples not a single purple rogue appeared among the 560 plants belonging to these F_2 families. The pods all set under glass and were subsequently placed out in the open to ripen off.

(3) In my earlier paper the figures were given for two classes of families derived from parents which were heterozygous for all three of the factors **B**, **E**, and **L**, and it was pointed out that the values both of the **BL** series and of the **EL** series were somewhat widely removed from the normal 7:1 basis¹. In the case of the families resulting from the mating **BEL** × **bel** the inference rested on some 700 plants only. I am now able to add more than 1000 records to this material, of which the full details are set out in Table III (p. 193). If each pair of factors be considered separately their relations are as follows:

(α)	BL : Bl : bL : bl :: 1203 : 105 : 115 : 380
	Exp. on 7:1:1:7 basis 1245 : 106 : 106 : 346
(β)	BE : Be : bE : be :: 1296 : 12 : 10 : 485
	Exp. on 127:1 basis 1345 : 7 : 7 : 444
	Exp. on 63:1 basis 1337 : 14 : 14 : 438
(γ)	EL : El : eL : el :: 1199 : 107 : 119 : 378
	Exp. on 7:1 basis 1245 : 106 : 106 : 346

The two series (α) and (γ) are evidently closely represented on a 7:1 basis, while the series which best fits (β) is that of 63:1. In my earlier account when fewer data were available the figures for the **BL** and the **EL** series pointed to the ratio 13:3:3:13, and it was suggested that the normal coupling was distributed in some way not understood when the plant was also heterozygous for the third factor. The progeny of the **BeL** × **bEl** cross also pointed to a disturbance of the normal intensity of the coupling for the **BL** series, though in this case in the direction of increased instead of diminished intensity.

The more ample data now available from F_2 families of the **BEL** × **bel** cross suggest that this was a mistaken view, and that the normal value, 7:1:1:7, of the **BL** and of the **EL** series is maintained in the F_2 generation from the mating **BEL** × **bel**, in spite of the fact that the F_1 was heterozygous in all three factors.

On the other hand the much larger numbers available for the **BeL** × **bEl** cross certainly suggest a more intense form of coupling for the factors **B** and **L**, viz. a 10:1:1:10 series instead of 7:1:1:7. It is difficult not to believe that this is significant and that a disturbance of the usual 7:1:1:7 series is brought about through the operation of some undetected cause. At present, however, we are without any clue

¹ *Journal of Genetics*, Vol. III. 1913, pp. 81—84.

and the point must remain unsettled. It is possible that some light may be thrown upon the matter by an examination of F_2 families from the crosses $BEI \times beL$ and $BeL \times bEL$. Experiments are in progress, but several years must elapse before sufficient data can be accumulated.

With regard to the BEL series the position is as follows: When in a homozygous condition for the third factor both B and L and E and L exhibit coupling which in each case is closely on a 7:1 basis. Under similar conditions B and E exhibit coupling of a much higher intensity which can be nearly represented as on a 127:1 basis. The repulsion series obtained under similar conditions are in accordance with the above inferences as to the values of the coupling series.

Further, in the mating $BEL \times bel$ the value of the three series seems to be unchanged, for although the BE series is here nearer 63:1 than 127:1 the numbers are too small to attach much weight to them where the coupling is so high.

On the other hand the figures for the mating $BeL \times bEl$ suggest a coupling value for B and L which is nearer 10:1 than 7:1, and it is possible that in certain types of mating the normal coupling values may be modified.

A paper has recently appeared by Bridges¹ in which he endeavours to shew that the facts of linkage in the sweet pea and in the primula can be explained as well on the chromosomal 'crossing-over' hypothesis as on the hypothesis of reduplication. In so far as the values of the EBL sweet pea series are concerned this would appear to be true, and now that the value of the EL coupling has been determined a more detailed consideration of it in this connection may be worth while.

In this determination of the coupling values in the gametic series Bridges makes use of Yule's Coefficient of Association². Using the data given in the present paper, I have calculated the Coefficient of

¹ *Am. Nat.* 1914, p. 524.

² For a zygotic series of the form $AB : aB : Ab : ab$ this coefficient is given by the formula:

$$\frac{(AB \times ab) - (aB \times Ab)}{(AB \times ab) + (aB \times Ab)}$$

It is evident that as the coupling becomes more intense the expression $(aB \times Ab)$ diminishes in value as compared with $(AB \times ab)$, and the coefficient approximates more nearly to unity.

Association (α) between E and L and (β) between B and L in the case of the zygotic series derived from the mating $EBL \times ebl$ (Table III): also (γ) the coefficient for E and L in families homozygous for B or b (Table I) and (δ) that for B and L in families homozygous for E or e (p. 186). They are as follows:

For E and L	For B and L
(α) .9454	(β) .9485
(γ) .9491	(δ) .9538

It will be noticed that for each of the pairs (α) (β) and (γ) (δ) the Coefficient of Association for B and L is greater than that for E and L. On the chromosome hypothesis this of course means that the locus for E is further removed from that for L than is the locus for B. The linear arrangement for the three loci is therefore that shewn below:



This conclusion, though subject to some uncertainty owing to paucity of data, Bridges had already arrived at (*loc. cit.* p. 528)¹. It is evident also that the pair of values (γ) (δ) also bears out his interpretation. For although the Coefficient of Association is in each case rather higher here, the alteration is in the same sense. The coefficient for B and L (δ) remains above that for E and L (γ) and is thus consonant with the view that the locus for E is further removed from L than is that for B.

But the facts are also in harmony with Trow's hypothesis². Here we should find a 7 : 1 coupling between B and L or between E and L in families homozygous with respect to the third factor of the series. Both of these coupling values are close to a 7 : 1 : 1 : 7 series. Again, in

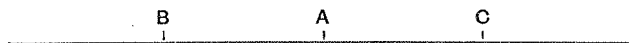
¹ The data used by Bridges in his calculations differ of course from those used here in not being so full. He has also made use of certain data previously published which I have not used. In calculating the BL relation for example he has incorporated the figures from $BeL \times bEl$ cross, *Journ. Gen.* 1913, Table VI, with those given in Tables I, II, and V. As I am inclined in this cross to suspect some disturbing feature not yet identified, I have omitted this block of data. And here I may point out that in Table IV, p. 531, of his paper Bridges has overlooked the fact that the families given on p. 17 of Report IV to the Evolution Committee were not all heterozygous. Some were homozygous for purple and others for red, and consequently the figures in line 2 of his Table IV, p. 531, are not correct. So also the figures in line 3 of the same Table are vitiated by the fact that here again he has included homozygous families as well as heterozygous ones. However the argument as to the independence of the factors is but little affected by the necessary corrections.

² *Journal of Genetics*, Vol. II. 1912-13, p. 313.

the EBL \times ebl families one of these couplings should be close to 7 : 1, while the other, the secondary reduplication, should be somewhat less, viz. about 6.4 : 1. In this case the secondary reduplication is evidently that between E and L¹.

In series where three factors are concerned, such as the EBL series, both the chromosome hypothesis and the reduplication hypothesis are in accordance with a different value for the coupling or linkage between each three different pairs of factors. Clearly this must be so for the fundamental conception underlying each interpretation is a linear one; in the one case a linear arrangement of factors along the chromosomes—in the other a linear sequence of segregating divisions in the reduplicational series.

Though data such as those just treated of do not appear to offer much hope of discriminating between the rival hypotheses, there is nevertheless one point in connection with them which should be borne in mind. On the chromosome hypothesis there is only one set of positions which allows of two of the coupling values between three factors A, B, and C to be equal, viz. when two loci are equidistant from the third, thus :



The coupling or linkage values between A and B, and between A and C, are here of the same value, but when this is so it follows of necessity that the value for B and C must be considerably *lower* than either of the other two. If a three-factor case were found of such a nature that two of the values were equal and the third definitely higher, such a case might serve as a criterion between the two hypotheses. At first sight such a case appears to be that of the sweet pea just considered. It will not however serve as a critical case owing to the high coupling value between B and E. Where the third value is very high, as here, the other two values must on the chromosome hypothesis, as well as on the reduplication hypothesis, be very close together and the method employed is not sufficiently refined to distinguish in such cases between equal values and values which are very close together. What is required is a case where all the values are relatively low.

¹ Where three factors come into play simultaneously I have regarded two of the reduplication series as "primary," that is to say as having the same value that they would have were each of the two pairs of factors in question alone involved. Though the figures appear to fit in best with this assumption it is of course by no means the only one possible, and Bailey has suggested that in such a case all three of the series are to be regarded as secondary, all reacting upon one another (*Journal of Genetics*, Vol. III, p. 221).

Such a case is probably to be found among primulas in connection with the three pairs of characters magenta (M) and red (m), short style (S) and long style (s), green stigma (G) and red stigma (g). Altenburg¹, has recently published the results of a back cross of the nature **MmSsGg** (ex **MSG** × **m~~s~~g**) × **mmssgg** where the numbers are considerable. His figures, which confirm those previously obtained by Gregory² on a smaller scale, may be tabulated as follows:

(a)	MS	Ms	mS	ms
					1697	234	195	1558
Expectation on 7:1:1:7 ratio					1612	230	230	1612
(β)	MG	Mg	mG	mg
					1243	688	565	1188
Expectation on 2:1:1:2 ratio					1228	614	614	1228
(γ)	SG	Sg	sG	sg
					1102	790	706	1086
Expectation on 5:3:3:5 ratio					1151	691	691	1151

The figures, though rather irregular, are in fair accordance with the expectations demanded on Trow's hypothesis, the secondary reduplication **S** and **G** being of the form 5:3:3:5, derived from the two primary reduplications 7:1:1:7 and 2:1:1:2 in the way indicated by him³. The figures as they stand offer of course no criterion between the rival hypotheses, for the critical experiment is yet to be made. This must consist in the cross between **SsGg** plants (ex **SG** × **sg**) and the double recessive **ssgg**, where all individuals used are homozygous for either **M** or **m**. On the chromosome hypothesis the linkage values should remain the same as those given above (γ); on the reduplication hypothesis we should expect to find the linkage higher, probably of the form **2SG** : **1Sg** : **1sG** : **2sg**. It is to be hoped that this critical experiment may be made at the earliest opportunity, and in numbers sufficient to yield an unequivocal result.

¹ *Genetics*, Vol. I. 1916.

² *Journal of Genetics*, Vol. I. 1910—11.

³ *Journal of Genetics*, Vol. II. 1912—13, p. 315.

TABLE I.

Families shewing coupling between erect standard and long pollen.

(Nature of mating EL × el.)

Reference Number	Erect		Hood		
	Long	Round	Long	Round	
1914, 54	19	2	—	3	
55	16	2	1	4	
57	53	3	4	15	
58	26	5	2	12	
129	13	3	2	5	
130	48	—	5	14	
131	23	1	1	17	
132	29	3	7	8	
133	19	2	1	3	
134	12	—	2	3	
135	10	—	1	1	
136	11	1	—	4	
137	10	1	—	3	
138	29	6	6	8	
139	28	3	4	8	
140	29	—	2	7	
141	19	—	—	5	
142	37	—	5	7	
143	21	2	1	5	
144	46	4	5	10	
145	15	1	2	7	
146	71	6	5	23	
157	32	4	2	7	
158	51	2	4	13	
159	98	11	9	28	
Totals	...	765	62	71	220

Families 54, 55, 145, 146, 157—159 were homozygous for B; the rest did not contain B. Families 55, 131, 138, 139, 141, 143 also contained whites which are included in the totals given.

TABLE II.

Families heterozygous in colour and pollen.

(Nature of mating BL × bl.)

Reference Number	Purple		Blue		Red		Rosy-mauve		White	
	Long	Round	Long	Round	Long	Round	Long	Round	Long	Round
1915, 43	58	4	24	1	7	22	7	5	18	12
44	63	7	26	1	11	16	2	11	28	10
45	21	2	5	—	2	7	—	2	—	—
46	32	2	10	—	8	7	—	2	10	3
48	48	2	6	—	2	12	—	2	2	4
153	66	—	13	5	9	24	2	5	30	9
154	37	4	10	1	5	7	2	5	21	6
Totals	325	21	94	8	44	95	13	32	109	44

TABLE III.

Families heterozygous in standard, colour, and pollen.

(Nature of mating EBL × ebl.)

Reference Number	Purple				Red				White			
	Erect		Hood		Erect		Hood		Erect		Hood	
	Long	Round	Long	Round	Long	Round	Long	Round	Long	Round	Long	Round
1914, 160	27	—	—	—	—	—	5	7	31	1	3	6
161	67	6	1	—	—	—	8	27	—	—	—	—
162	54	4	—	1	—	1	4	12	13	—	1	3
1915, 77	138	7	1	—	—	—	5	41	—	—	—	—
78	106	4	1	—	1	—	6	33	42	1	4	6
90	18	2	—	—	—	—	3	10	4	—	—	2
91	10	1	—	—	—	—	—	—	1	—	—	—
92	67	3	—	—	—	—	5	30	23	1	1	9
93	16	3	—	—	—	—	1	9	4	—	—	1
94	10	—	1	—	—	—	1	3	—	—	—	—
95	7	—	—	—	—	—	—	6	3	—	—	1
96	20	2	—	—	—	—	—	4	15	—	1	4
97	18	2	—	—	—	—	2	1	11	1	2	1
98	17	2	—	—	—	1	—	5	3	—	—	2
99	18	2	1	—	—	1	1	12	14	1	3	6
100	44	3	—	—	—	—	3	8	7	—	1	4
101	45	2	—	1	—	—	—	12	—	—	—	—
102	3	—	—	—	—	—	2	3	1	—	—	—
103	12	1	—	—	—	—	1	3	4	—	—	—
104	7	1	—	—	—	—	1	3	—	—	—	—
106	15	—	—	—	—	—	—	5	3	1	—	1
J. G. 1913, Tab. V	477	55	2	3	2	4	64	139	147	15	17	32
Totals	1196	100	7	5	3	7	112	373	326	21	33	78