

## REDUPLICATION SERIES IN SWEET PEAS.

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## INTRODUCTION.

THE present paper aims at bringing together some of the results of work done with sweet peas during the seasons 1908-13, and especially that part of it which concerns the phenomenon of the reduplication of terms in the gametic series. Some of the results have already been published in two short papers (Bateson and Punnett, (4) and (5))<sup>1</sup>. The work is far from completion, but as the subject is beginning to excite greater interest it has seemed advisable to collect together and publish these records for the use of other students. Many new points

<sup>1</sup> These figures refer to the list of literature at the end of this paper.

have arisen, especially during the present summer, and several years must necessarily elapse before they can be settled satisfactorily.

The work recorded in the following pages deals with the inheritance of six factors, viz.:

B	the factor for blue as opposed to red.
E	„ „ erect standard as opposed to hooded.
L	„ „ long pollen „ „ round.
D	„ „ dark axil „ „ light axil.
F	„ „ fertile anthers „ „ sterile.
N	„ „ normal flower „ „ cretin.

As pointed out elsewhere ((4), p. 4) the relation between the factors B, E, and L is such that a plant which is heterozygous for any pair of this series shews coupling or repulsion according as the mating is  $AB \times ab$ , or  $Ab \times aB$ . Until the present summer (1913) the experimental evidence was in favour of regarding this generalisation as true also for the series D, F, N, and to some extent it certainly is true. But, as will appear later, there are grounds for supposing that under certain conditions, hitherto undetermined, a simple Mendelian relation, without coupling or repulsion, is to be found for this trio of factors. In this connection it is interesting to recall Baur's work with *Antirrhinum* (1) suggesting that in this genus coupling may result from the cross  $AB \times ab$ , while for the same pair of characters the mating  $Ab \times aB$  may give an ordinary Mendelian result. In considering the data given in the present paper, those relating to the B, E, L series will be taken first.

#### A. THE B, E, L SERIES.

(1) *The relation between B and L in plants homozygous for E or e.*

(a) Nature of mating  $BL \times bl$ .

This was the reduplication series first discovered, and the nature of the  $F_2$  generation can be explained on the hypothesis that  $F_1$  plants made in this way produce a series of gametes of the form  $7BL : 1Bl : 1bL : 7bl$ . To the evidence already given, derived from  $F_2$  families ex Emily Henderson long pollen  $\times$  E. H. round pollen ((2), p. 36), can now be added 4 further  $F_2$  families (Table I, A), 40  $F_3$  families (Table I, B), and 14 families (Table I, C) derived from various crosses inside the E. H. strain. The entire material was homozygous

for E. As Table I shews the results from these three sources are all in accordance and confirm the original view that the results are probably the outcome of a gametic series of the form  $7BL : 1Bl : 1bL : 7bl$ . That the reduplication is of the same form in both ♂ and ♀ gametes is supported by some experiments made in pollinating red round-pollened plants with  $F_1$  plants ex  $BL \times bl$ . 112 plants were raised in this way and consisted of

Purple long	50,	<i>Expectation being</i>	<i>49.</i>
„ round	7,	„	„
Red long	8,	„	„
„ round	47,	„	„

The figures make it evident that the ♂ gametic series is of the form suggested, and as the  $F_2$  results can only be explained on the supposition that this series of ♂ gametes fertilizes a similar series of ♀ gametes there is every reason for supposing that the series is of the same form in both. This will be assumed throughout the various cases discussed.

It is assumed therefore that the reduplication between B and L is on the 7 : 1 basis inside the E. H. strain, and though in some families the two forms Bl, bL are in excess while in others they are deficient these will be regarded as chance results. Further there is some evidence to shew that the nature of the reduplication may remain unchanged when the E. H. strain is crossed with some other strain. Eight such families are given in Table II and shew that the expectation on the 7 : 1 basis is closely realised. These families also afford evidence that the form of the colour-pollen reduplication is unaffected by the presence of sterility in the families.

There are however other cases in which the reduplication departs considerably from the 7 : 1 basis. These are families derived from plants which are also heterozygous for E. To these we shall return later (p. 81).

(β) Nature of mating  $Bl \times bL$ .

Four families containing 419 plants were raised from this form of mating and the numbers of the four classes were

Purple long	Purple round	Red long	Red round
226	95	97	1

It has been pointed out elsewhere ((5), p. 297) that this result is in harmony with the supposition that the gametic series was

$$1BL : 7Bl : 7bL : 1bl.$$

The four families consisted of hooded plants only and were not of the pure E. H. strain. One small family however was raised from a cross between a blue round and a red long in the E. H. strain. The  $F_2$  ('11, 43) consisted of 8 blue long, 3 blue round, and 5 red long and there is little doubt that if larger numbers were available the series would resemble that just dealt with.

(2) *The relation between B and E in families homozygous for L or l.*

( $\alpha$ ) Nature of mating  $BE \times be$ .

25 families have been raised from plants of this type of mating and as is shewn in Table III the distribution of the four classes among the 2712 plants accords well with the view that the gametic series is  $127BE : 1Be : 1bE : 127be$ . All the plants were homozygous in L.

( $\beta$ ) Nature of mating  $Be \times bE$ .

Many of the families in which this form of mating occurred were also heterozygous in pollen, and these will be found recorded in Table VI. The result however was the same throughout. No red hooded plant was ever found, and the other three classes occur approximately in the ratio 2 blue erect : 1 blue hood : 1 red erect. The total numbers (including those in Table VI) are

Blue erect	Blue hood	Red erect
2969	1379	1441

This result points to the  $Be$  and  $bE$  types of gamete being considerably more numerous than the other two, and it is not incompatible with the view that the series is  $1BE : 127Be : 127bE : 1be$ . But as only one hooded red is to be looked for in 65,536 plants it is not proposed to investigate this particular case any further.

(3) *The relation between E and L in plants homozygous for B or b.*

( $\alpha$ ) Nature of mating  $EL \times el$ .

At present there are no records of such a cross though a number of such families are expected in 1914.

( $\beta$ ) Nature of mating  $E1 \times eL$ .

Four such families were raised in 1908 and as is shewn in Table IV

they consisted of the three classes erect long, erect round, and hooded long approximately in the ratio 2 : 1 : 1. It is probable that the relation between E and L is similar to that existing between B and L, and between B and E, but at present the exact nature of the series must be left undecided.

(4) *The relations between B, E, and L in plants which are heterozygous in all three factors.*

As previously pointed out ((4), p. 7) there are four ways of mating to produce such plants, viz.:

- ( $\alpha$ ) BEL  $\times$  bel,
- ( $\beta$ ) BeL  $\times$  bEl,
- ( $\gamma$ ) BEl  $\times$  beL,
- ( $\delta$ ) bEL  $\times$  Bel.

Owing to misadventure an  $F_2$  generation has been raised from the first two crosses only and we may now proceed to consider the results separately.

( $\alpha$ ) Nature of mating BEL  $\times$  bel.

The appearance of a single red hooded round plant in 1910 (cf. (5), p. 297) made this mating possible and an  $F_2$  generation was raised in 1912. Details of 13 such families are given in Table V. The results are evidently complex but some attempt at analysis may be made by considering separately each pair of the three factors concerned. The figures then become

- (a) BL : Bl : bL : bl :: 479 : 58 : 66 : 143,
- (b) BE : Be : bE : be :: 532 : 5 : 6 : 203,
- (c) EL : El : eL : el :: 479 : 59 : 66 : 142.

In each case the nature of the gametic series is evidently  $n : 1 : 1 : n$  where  $n > 1$ . Since for any two of the factors the nature of the original cross was AB  $\times$  ab the "coupling" form of the series in each case was to be expected. But it is equally evident that the value of  $n$  in cases (a) and (b) is different from what it would have been had the plants been heterozygous for the two factors in question alone. The experimental numbers in (a) are not on the 7 : 1 system but the results are given far more closely by the gametic series 5BL : 1Bl : 1bL : 5bl. On this supposition expectation would be 501 blue long : 57 blue red :

57 red long : 129 red round—numbers not far removed from those actually found. The value of  $n$  for the EL series must also be very close to its value in the BL series.

Again in the BE series the figures obtained are much more closely in accordance with the supposition that the value of  $n$  is 63 instead of 127 which was found to be the case where the plants were homozygous for L (cf. p. 80). Apparently what may be termed the normal linkage ratios are upset, but this point will be considered later (p. 91).

It may however be suggested that it is possible theoretically to construct a gametic series which would give a close approach to the figures obtained. Such a series is:

103 BEL	}	giving the zygotic figures in the proportion	}	BEL 43283
23 BEI				BEI 5361
1 BeL				BeL 310
1 Bel				Bel 207
1 bEI				bEI 207
1 bEL				bEL 301
23 beL				beL 5267
103 bel				bel 10609

In such a series the gametic relations for the separate pairs of factors are:

B and L—13BL : 3BI : 3bL : 13bl,

B and E—63BE : 1Be : 1bE : 63be,

L and E—13LE : 3Le : 3lE : 13le.

As the subjoined figures shew the theoretical results accord fairly closely with the actual numbers.

	Blue				Red			
	Erect		Hood		Erect		Hood	
	Long	Round	Long	Round	Long	Round	Long	Round
	477	55	2	3	2	4	64	139
<i>Expectation</i>	493	61	3.5	2.5	3.5	2.5	60	120

At present however I do not wish to lay stress on this approximation as I am unable to picture clearly how such a gametic series comes to be formed.

(β) Nature of mating BeL × bEl.

Details of a number of  $F_2$  and  $F_3$  families ex Blanche Burpee

(hooded white long)  $\times$  E. H. round were given in *Report IV, Evol. Comm. Roy. Soc.* 1908, p. 14. The general result shewed "coupling" between B and L, together with "repulsion" between B and E, and between L and E, a result which from the nature of the mating was to have been expected. It was pointed out in an earlier account (*R. E. C.* iv. p. 11), that the two classes purple round and red long were less numerous than was expected on a 7 : 1 basis, and at the time an explanation was suggested on the grounds of some of the families being on a 7 : 1 basis and others on a 15 : 1 basis. The recent publication of Trow's Paper (16) on reduplication series has put the matter in a new light and we shall return to this case later in discussing his suggestion (p. 91). For the moment we may turn to Table VI which adds further data by the inclusion of a number of  $F_2$  and  $F_3$  families derived from the cross white hooded Bush long (BeL)  $\times$  white erect Cupid round (bEI). The  $F_2$  families were given in the earlier account ((3), p. 12) and were there regarded as a case of coupling on a 15 : 1 basis. Fuller experience however has led to the conclusion that they should be classed with the material derived from the original cross Blanche Burpee  $\times$  Emily Henderson. Three further families ('08, 89, 93, 114) have been added derived from other material in which the mating was of the nature BeL  $\times$  bEI.

Consideration of each pair of the three factors taken separately shews their relations to be as follows:

$$(\alpha) \quad \text{BL} : \text{Bl} : \text{bL} : \text{bl} :: 3006 : 164 : 212 : 843,$$

$$(\beta) \quad \text{BE} : \text{Be} : \text{bE} : \text{be} :: 2146 : 1024 : 1055 : -$$

$$(\gamma) \quad \text{EL} : \text{El} : \text{eL} : \text{el} :: 2200 : 1001 : 1018 : 6.$$

Evidently ( $\beta$ ) and ( $\gamma$ ) are "repulsion" forms of reduplication in which the zygotic series  $2n^2 + 1\text{AB} : n^2 - 1\text{Ab} : n^2 - 1\text{aB} : 1\text{ab}$  is derived from a gametic series  $1\text{AB} : (n-1)\text{Ab} : (n-1)\text{aB} : 1\text{ab}$  ((5), p. 295). An approximation to the value of  $n$  in such cases is most readily obtained by dividing the last term in the zygotic series into one of the two middle terms. This gives the approximate value of  $n^2 - 1$  from which the value of  $n$  may be readily deduced.

In the case of ( $\gamma$ )  $\frac{n^2 - 1}{1} = \frac{1018}{6}$  whence  $n^2 - 1 = 169$  and  $n =$  approximately 13. Hence the zygotic series ( $\gamma$ ) is given most nearly by a gametic series  $1\text{EL} : 12\text{El} : 12\text{eL} : 1\text{el}$ .

In ( $\beta$ ) there is no individual lacking both B and E, and all that can be stated of  $n$  is that it is almost certainly  $> 32$ .

The zygotic series ( $\alpha$ ) is evidently a "coupling" form of reduplication, and is most nearly approached by the gametic series 10 : 1 : 1 : 10, on which the expectation of the 4 forms is 2984 : 184 : 184 : 873. It is clear that in this case, as in the BEL and bel cross, the normal value of the pollen-colour reduplication series is upset, and that instead of being on a 7 : 1 basis it approximates to a 10 : 1 basis. It is possible that this upsetting of the normal value may be true also of the standard-pollen, and of the standard-colour series, but at present the point must remain undecided. For we do not know the normal value of the standard-pollen series, and in the case of the standard-colour series the data are insufficient for determining even its approximate value.

#### B. THE D, F, N SERIES.

##### (1) *The relation between D and F in plants homozygous for N.*

###### ( $\alpha$ ) Nature of mating FD $\times$ fd.

Evidence has already been given ((3), p. 16) for regarding the reduplication in this case as on a 15 : 1 basis, and to the figures previously set out we can now add a few more families (cf. Table VII). As the figures shew, the numbers of the two classes, dark sterile and light fertile, are rather below expectation. Certain of the families (marked \* in Table VII) were also heterozygous for B and L and it is possible that this may have influenced the result. Certainly when these families are deducted the discrepancy in the remainder between reality and expectation is not so marked (cf. Table VII).

###### ( $\beta$ ) Nature of mating Fd $\times$ fD.

The experimental data for this mating are given in Table VIII. So far no light axilled sterile has occurred among 2252 plants, though 2 such plants were to be expected if the gametic series is on the 1 : 15 basis. At present therefore the value of the reduplication is undecided.

##### (2) *The relation between F and N.*

Details of 9  $F_2$  families derived from the mating Nf  $\times$  nF have been given elsewhere ((5), p. 295) and it was clear that the nature of the gametic series produced by the  $F_1$  plant was 1Nf : 3Nf : 3nF : 1nf. In the same paper it was suggested that the value of the reduplication affecting two factors might be the same for both the "coupling" and



the "repulsion" series, and the low value of  $n$  in the present case offered the most favourable opportunity hitherto met with for testing this point. Accordingly large numbers of pollinations from normal fertile plants (NF) were made on to sterile cretins (nf). In not a single instance however was the operation successful and it was found subsequently that the cretin, whether producing pollen or not, is always sterile on the female side. The pods, and even the seeds, may sometimes undergo swelling but in none of the numerous cases examined was a viable seed produced. The (NF  $\times$  nf) plant had therefore to be sought for in another direction.

Since the gametic series produced by the plant formed from the two gametes Nf  $\times$  nF is of the nature 1NF : 3Nf : 3nF : 1nf such plants should give rise to the following zygotic forms:

NNFF.....	1	NNff ...	9	nnFF ...	9	nnff ...	1
NNFf .....	6	Nnff ...	6	nnFf ...	6		
NnFF .....	6						
(Nf $\times$ nF) ...	18						
(NF $\times$ nf) ...	2						

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normal fertile 33 :	normal } sterile }	15 :	cretin } fertile }	15 :	cretin } sterile }	1
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Hence out of 33 normal fertiles in such a family there should be 5 distinct classes distributed in the following proportions:

- 1 (NNFF) giving only normal fertiles.
- 6 (NNFf) giving normal fertiles and steriles only.
- 6 (NnFF) giving normal and cretin fertiles only.
- 18 (Nf  $\times$  nF) giving all 4 classes with "repulsion" between N and F.
- 2 (NF  $\times$  nf) giving all 4 classes with "coupling" between N and F.

30 such normal fertiles from  $F_2$  families were grown on to give an  $F_3$  generation in 1912. The expected 5 classes were all found, and as shewn below (and also in Table IX) the proportions in which they occurred accorded closely with expectation.

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Type of $F_2$ plant	Number found by experiment	Number expected
NNFF ...	2	·9
NNff ...	5	5·5
NnFF ...	7	5·5
(Nf × nF) ...	14	16·3
(NF × nf) ...	3	1·8
Totals ...	30	30

In one family where coupling occurred ('12, 76) the numbers were sufficiently large to indicate the nature of the reduplication. There is little doubt that it is on the 3 : 1 basis for although there was an unexpectedly large number of cretins the proportions accord fairly well with expectation<sup>1</sup>.

	Normal fertile	Normal sterile	Cretin fertile	Cretin sterile
'12 ; 76	90	20	30	34
<i>Expectation</i>	111·5	19	19	24·5

It should be mentioned that the plants in this family were all light-axilled. There are good grounds then for asserting that for the factors N and F reduplication is on the 3 : 1 or on the 1 : 3 basis according as to whether the original mating is NF × nf or Nf × nF.

Yet it is probable that the case is not so simple as it appears at first sight. Reference to Table IX shews that in two families, viz. '12, 71 and '12, 91, the proportions in which the four forms occur afford a distinct suggestion of a 9 : 3 : 3 : 1 ratio. And if these two families are taken together the figures 42 NF, 13 Nf, 14 nF, 5 nf make a very close approximation to this ratio.

The possibility that, where the factors N and F are concerned, there may be other sorts of families than those shewing the 3 : 1 or the 1 : 3 reduplications is to some extent supported by the results of growing on a further generation from the  $F_3$  family '12, 76. Unfortunately these did not set seed freely and only 11  $F_4$  families were obtained. In all of them the number of individuals was relatively small, and in two cases it was too small to give more than a qualitative result. There are however 8 families in which all the four classes occurred, and in which there are over 30 plants per family. Reference to Table X shews that these families<sup>1</sup> fall into two distinct groups:—

<sup>1</sup> I do not feel clear as to the nature of Fam. '13, 47 and have therefore not included it in the present argument. It may be a family on the 3 : 1 : 1 : 3 basis but the numbers are too few for certainty.

(a) Fams. 38, 39, 40, 41. These four families are evidently of the same nature as the parent family '12, 76. The three classes normal sterile, cretin fertile, and cretin sterile are much in the proportions that would be expected on a 3:1:1:3 reduplication system, but the number of normal fertiles is much below expectation. These four families added to the parent family ('12, 76) give the numbers:

	Normal fertile	Normal sterile	Cretin fertile	Cretin sterile
	165	58	58	78
Expect. on 3:1:1:3 basis ...	<i>346</i>	<i>59</i>	<i>59</i>	<i>76</i>

The italicised figures shew that the three last classes are closely in the ratio 7:7:9, as expected on the 3:1:1:3 system, but that the normal fertiles are only about one half as numerous as would be expected. That there is something militating against the formation of normal fertiles in such families is borne out by the following consideration. Of the 11  $F_4$  families grown from '12, 76, 10 contained all four classes of plant, while one family had cretins but no steriles. Now the normal fertiles from a family producing gametes on the system 3 NF:1 Nf:1 nF:3 nf should be of five kinds, and in every 41 plants these five kinds should be present in the following proportions:

- 9 NNFF giving normal fertiles only.
- 6 NNff „ normal fertiles and steriles only.
- 6 NnFF „ normal and cretin fertiles only.
- 18 NnFf „ all four classes with coupling.
- 2 NnFf „ „ „ „ repulsion.

Hence out of 41 such plants only 20, or not quite one half, should give the four classes. But of the 11 plants tested (Table X) no less than 10 gave all four classes. It would appear then that for some reason or other the classes NNFF, NNff, NnFF are not produced in the expected numbers, though why this should be so is at present quite obscure.

(b) Fams. 43, 45, 46. These three families are distinctly different from those just considered and the combined figures

	Normal fertile	Normal sterile	Cretin fertile	Cretin sterile
	75	23	21	5
Expect. ... ..	<i>69.75</i>	<i>23.25</i>	<i>23.25</i>	<i>7.75</i>

support the idea that we are here dealing with a 9:3:3:1 ratio. As already mentioned it is not impossible that in Fam. '12, 71 (Table IX) this type of family has been encountered once before.

(3) *The relation between N and D in plants homozygous for F.*

Hitherto the opportunity of studying this particular case has been limited to a single family. This family ('13, 119) was from a normal fertile belonging to Fam. '12, 88 (Table IX) and proved to be heterozygous in N and D but homozygous for F. It contained 100 plants and was composed of

	Normal dark	Normal light	Cretin dark	Cretin light
	48	22	27	3
Expect. on 1:3:3:1 system ...	51.6	23.4	23.4	1.6

The figures are in consonance with the idea that the reduplication for N and D is on a 1:3 basis, and this is borne out by the behaviour of these two factors in relation to one another among plants which are heterozygous for N, D, and F (see p. 89).

(4) *The relations between D, F, and N in plants heterozygous for all three factors.*

As in the case of the B, E, L series there are four ways theoretically possible by which plants heterozygous for three factors can be produced, viz.:

- (a)  $DFN \times dfn.$
- ( $\beta$ )  $DfN \times dFn.$
- ( $\gamma$ )  $DFn \times dfN.$
- ( $\delta$ )  $dFN \times Dfn.$

Of these four ways I have hitherto been able to study two, viz. ( $\beta$ ) and ( $\gamma$ ).

( $\beta$ ) *Nature of mating,  $DfN \times dFn.$*

The details of four such families raised from the same parents and comprising in all 442 plants are set out in Table XI, and may be considered together. The proportion of dark axils to light axils, of fertiles to steriles, and of normals to cretins is closely 3:1 in each case.

And if the figures are arranged for the three different pairs of factors the result is what might have been anticipated from the nature of the mating, viz. coupling between D and N, and repulsion between D and F and between N and F respectively,

## FAMILIES 48—51.

		Expectation on 3:1:1:3 system.	
ND	282	284	
Nd	49	48	
nD	52	48	
nd	59	62	
		Expectation on 1:3:3:1 system.	
NF	225	228	
Nf	106	103.5	
nF	101	103.5	
nf	10	7	
		Expectation on 1:7:7:1 system.	Expectation on 1:15:15:1 system.
DF	220	222.7	221.4
Df	114	108.8	110.1
dF	106	108.8	110.1
df	2	1.7	.4

The numbers shew that the reduplication series in the first two cases is approximately on a 3:1 basis while that for D and F fits most closely a 1:7:7:1 series. In the last case however the df class appears so rarely that the precise nature of the reduplication must for the present remain undecided. It is not impossible that it may be on a 1:15 basis which is rather to be expected in view of the fact that the coupling series for these two factors is on the 15:1:1:15 system.

It may be noted that the 3:1 basis for the relation between N and D from this mating is in accordance with the 1:3 basis for the relation between these two factors when the nature of the mating is Nd × nD.

(γ) *Nature of mating, DFn × dfN.*

The material for the study of this mating (Table XI) consists so far of two  $F_2$  families, '13, 52 and '13, 53, and of four  $F_4$  families, '13, 113, 114, 117, 123, all derived from an original cross of the same type. All six families appear to be of the same sort, and I have assumed the nature of the mating in the  $F_4$  families is what is known to be the case in the two  $F_2$  families.

In families derived from this type of mating I had anticipated

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coupling between D and F, together with repulsion between N and F and between N and D. The figures here given shew that the first part of the anticipation was realised.

	Families 52, 53, 113, 114, 117, 123.	Expectation on 15 : 1 : 1 : 15 system,
DF	172	170.4
Df	6	7.3
dF	4	7.3
df	58	55.0

There is coupling between D and F and this is not far removed from the expected 15 : 1 : 1 : 15 system. But there is no repulsion evident between either N and F, or between N and D.

	Families 52, 53, 113, 114, 117, 123.	Expectation.
ND	131	135
Nd	49	45
nD	47	45
nd	13	15
NF	130	135
Nf	50	45
nF	46	45
nf	14	15

Instead of this the figures accord closely in both cases with an ordinary 9 : 3 : 3 : 1 ratio. The possibility of a similar ratio has already been referred to in the case of other families where these factors are concerned (p. 86) and it is hoped that a further study of this interesting case may give us the clue as to the relation between normal and reduplicated gametic series. But it is evident that several years must elapse before the necessary experiments can be completed.

## PRIMARY AND SECONDARY REDUPLICATIONS.

In an interesting paper which has just appeared (16) Trow discusses the problems offered by reduplicated series of gametes, and draws a distinction between what he has termed primary and secondary series. Starting with the case where there are three factors A, B, C such that any two may form a reduplicated series, he has shewn theoretically that if the reduplication between A and B is of the form  $m : 1 : 1 : m$ , and between A and C is of the form  $n : 1 : 1 : n$ , then the secondary form of reduplication, derived from these two primary ones and expressing the relation between B and C, is of the form  $nm + 1 : m + n : m + n : nm + 1$ . The only experimental data with

which he has hitherto been able to test his hypothesis have been provided by a case among Gregory's primulas, the three factors concerned being M (= magenta), S (= short style), and G (= green stigma). The experimental evidence points to the MS reduplication being on the 7 : 1 basis and the MG reduplication on the 2 : 1 basis. The secondary reduplication between S and G should consequently be of the form  $(7 \times 2) + 1 : 7 + 2 : 7 + 2 : (7 \times 2) + 1$ , i.e. 5 : 3 : 3 : 5, and the experimental data are in fairly close accordance with this expectation (cf. Trow (16), p. 316). The data given in this paper from the two sweet pea crosses BEL × bel, and BeL × bEl afford further cases for testing Trow's hypothesis.

(1) *The BEL × bel cross.*

It has been pointed out above (p. 82) that the three reduplication series here are approximately of the following values :

$$(\alpha) \quad B \text{ and } L—13 : 3 : 3 : 13,$$

$$(\beta) \quad B \text{ and } E—63 : 1 : 1 : 63,$$

$$(\gamma) \quad E \text{ and } L—13 : 3 : 3 : 13.$$

If we consider  $(\alpha)$  and  $(\beta)$  as the two primary reduplications then the value of  $(\gamma)$  should be

$$\left(\frac{13}{3} \times 63\right) + 1 : \frac{13}{3} + 63 : \frac{13}{3} + 63 : \left(\frac{13}{3} \times 63\right) + 1,$$

i.e.  $4.1 : 1 : 1 : 4.1,$

a result which is closely in accordance with the experimental numbers. A feature of interest in connection with this case is that it demonstrates that when the value of one primary series is considerably greater than the other, the value of the secondary series will be very close to that of the lower primary series.

(2) *The BeL × bEl cross.*

In this case the relations between B and E, and between L and E, are of the nature of "repulsion." Nevertheless, as Trow has pointed out, even if these be regarded as the two primary series the secondary series (between B and L here) should be of the nature of "coupling." The facts (p. 83) point to the reduplication between L and E being near 1 : 12 : 12 : 1. That between B and E is evidently much higher though how much so we have no direct means of telling. But we have already seen that the "coupling" between B and E is on the 127 : 1 basis in families homozygous for L and on the 63 · 1 basis in the



BEL × bel cross. Also there is evidence for supposing that the “repulsion” reduplication is of the same value as the “coupling” reduplication between two given factors. We shall assume then for argument that the reduplication between B and E is of the value 1 : 63 : 63 : 1. For B and L (p. 84) the experimental data are closely approached by a series 10 : 1 : 1 : 10. We have therefore the 3 series :

$$(\alpha) \quad \text{B and E—} 1 : 63 : 63 : 1,$$

$$(\beta) \quad \text{E and L—} 1 : 12 : 12 : 1,$$

$$(\gamma) \quad \text{B and L—} 10 : 1 : 1 : 10.$$

If we treat  $(\alpha)$  and  $(\beta)$  as the primary series the value of  $(\gamma)$  deduced theoretically should be

$$(63 \times 12) + 1 : 63 + 12 : 63 + 12 : (63 \times 12) + 1$$

$$\text{i.e.} \quad \dots\dots\dots 10 \cdot 01 : \dots\dots\dots 1 \dots\dots\dots : \dots\dots\dots 1 \dots\dots\dots : 10 \cdot 01, \dots\dots\dots$$

which is a remarkably close approximation to the experimental proportions.

It will be noticed that in each of the above cases we have chosen as our two primary series those in which the reduplication values are highest. This was also done by Trow in his analysis of Gregory's primulas. It is only in this way that the hypothesis will work, for, as can be readily shewn, the value of the reduplication in the secondary series must always be less than in either of the two primary series from which it is derived.

Let A, B, and C be the three factors concerned, and let the reduplication series for

$$\text{A and B} = p : 1 : 1 : p \quad \dots\dots\dots(\alpha),$$

$$\text{A and C} = p + x : 1 : 1 : p + x \quad \dots\dots\dots(\beta),$$

where  $p > 1$  and  $x$  is positive.

Then the series for

$$\text{B and C} = p(p + x) + 1 : 2p + x : 2p + x : p(p + x) + 1 \dots\dots\dots(\gamma).$$

It is required to shew that

$$\frac{p(p + x) + 1}{2p + x} < \frac{p}{1},$$

$$\text{i.e.} \quad p^2 + px + 1 < 2p^2 + px,$$

$$\text{i.e.} \quad 1 < p^2.$$

which is evident since on hypothesis  $p > 1$ .



*Hence in a series of three reduplications, two primary and one secondary, that one is to be regarded as the secondary in which the value of the reduplication is lowest.*

In this connection the two groups of families recorded in Table XI are also of interest. In Group A from the mating  $DfN \times dFn$  there is repulsion between D and F, coupling between D and N, and repulsion between N and F. The first repulsion is not improbably on the 1:15:15:1 system or something near it (cf. p. 89), while the second repulsion and the coupling are not far removed from the 1:3:3:1 and the 3:1:1:3 systems respectively. The figures are in general accordance with Trow's hypothesis, but the numbers are not large enough to determine more precisely the values of the reduplication systems, or to decide which of the two lower series is the secondary one.

In the families of Group B in Table XI, where the nature of the mating is  $dfN \times DFn$ , there is coupling between D and F but no repulsion between N and D or between N and F. Here again the experimental facts are in accordance with Trow's hypothesis, for where one of the primary series shews no reduplication it follows that no reduplication will be exhibited by the secondary series.



CONCLUSION.

Finally attention may be drawn to some points in connection with the value of the reduplication in the various cases discussed above. Where only two factors are concerned we have regarded the reduplication as of the form  $(n-1):1$  where  $n$  is some power of 2, and we suggested in a previous paper how such a series might be brought about through alternating periclinal and anticlinal cell divisions ((5), Fig. 4). The experimental data hitherto obtained from sweet peas fit in with this view, but, as pointed out some years ago ((2), p. 9), they are also in accordance with the form of the reduplication being  $n:1:1:n$  where  $n$  again is some power of 2. It is only in cases where  $n$  is very small that we can hope to distinguish between the two without growing an impracticably large number of plants. At present the  $NF \times nf$  mating is the only one from which we can look for a critical result on this point, and the available evidence suggests that the reduplication here is  $3NF:1Nf:1nF:3nf$  (cf. p. 86), i.e. that it is on the  $(n-1):1$  basis rather than on the  $n:1$  basis<sup>1</sup>. It may

<sup>1</sup> What is evidently a case of reduplication on the 3:1 basis has been recently discovered by Collins in maize ((6), p. 579), the cross in question being one between an

be pointed out however that this scheme is not incompatible with the  $n : 1$  basis. The form of the series, whether  $(n - 1) : 1$  or  $n : 1$ , might depend upon whether the first division in the quadrant were a periclinal or an anticlinal division. In the one case (Fig. 1) we should get the  $(n - 1) : 1 : 1 : (n - 1)$  series, and in the second case (Fig. 2) the

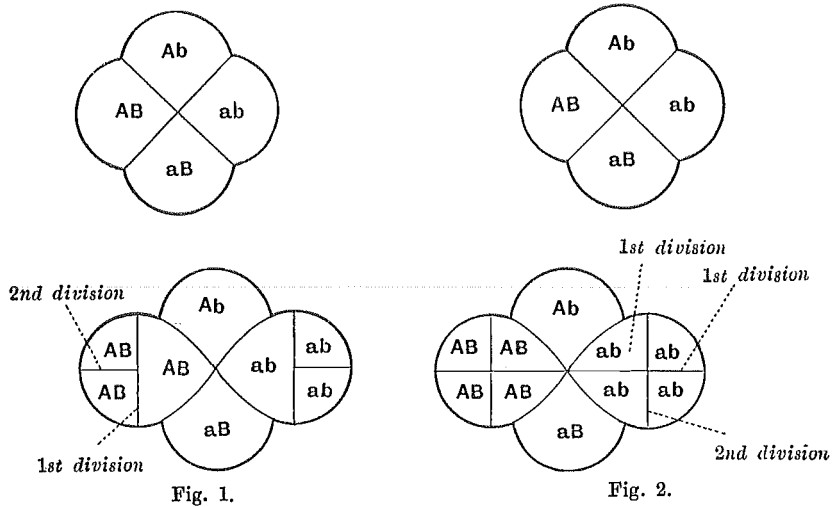


Fig. 1.

Fig. 2.

$n : 1 : 1 : n$  series. Further possible ratios also depend upon whether the first division in the other two quadrants is periclinal or anticlinal. Indeed it is obvious that there are numerous possibilities which may perhaps repay discussion when more experimental data are available. All that can be stated positively at present is that the cases hitherto worked out in the sweet pea fit in with the hypothesis that the number of cells in the reduplicated series is some power of 2 where only two factors are concerned. But where three factors are concerned this is certainly not true. The value of the primary reduplications is evidently altered, and there would seem to be some process whereby these reduplications react upon one another. Where so many points remain

American variety with coloured aleurone and horny endosperm, and a Chinese variety with white aleurone and waxy endosperm. By means of other statistics Collins is at pains to prove that the reduplication phenomena in maize are of a highly irregular nature. Much stress however cannot be laid upon these results as the author is evidently dealing with dominant as well as recessive whites in his experiments though this point does not appear to be specifically recognised by him. It is probable that a more careful genetic analysis of the whites which he uses would help to clear up the apparent irregularities in his results.

doubtful, as at present, it is difficult to suggest any scheme by which this result could be brought about, and the problem must at present be left in the hope that fresh data may eventually lead to its solution.

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TABLE I

*Families from Emily Henderson, heterozygous in colour and pollen.*A.  $F_2$  families ex E. H. long  $\times$  E. H. round.

Reference Number	Purple		Picotee		Red		Tinged-white		White	
	Long	Round	Long	Round	Long	Round	Long	Round	Long	Round
'08, 119	12	3	4	—	3	2	1	3	24	10
„ 120	22	7	9	—	2	6	—	4	34	13
'09, 6	33	2	9	—	3	11	—	5	37	10
'10, 58	62	4	21	2	7	15	—	6	73	16
Totals	129	16	43	2	15	34	1	18	168	49
			Purple		Red		White			
			Long	Round	Long	Round	Long	Round		
Above 4 families	...	...	172	18	16	52	168	49		
Report III, p. 36	...	...	1528	106	117	381	1190	394		
Totals	...	...	1700	124	133	433	1358	443		
Expectation among coloured			1652	140	140	458				

B.  $F_3$  families heterozygous in colour and pollen.

Reference Number	Purple		Red		White	
	Long	Round	Long	Round	Long	Round
'04, 152	46	4	2	10	30	4
'04 F, 82	40	4	1	9	38	10
„ 102	20	—	1	2	7	3
„ 105	47	4	8	8	39	17
„ 106	12	—	1	7	5	3
„ 128	17	—	—	4	—	—
'05, 280	31	4	3	8	18	4
„ 286	8	1	1	2	7	1
„ 291	13	3	—	8	8	3
„ 292	31	4	1	10	17	2
„ 293	10	—	1	5	11	3
„ 296	20	—	2	4	15	3
'05 F, 23	23	3	5	6	11	—
'06 F, 401	128	14	8	38	102	29
„ 402	42	7	1	12	14	3
„ 404	17	3	—	4	17	5
„ 409	48	9	7	16	—	—
„ 410	60	6	3	14	—	—
„ 406	74	6	5	39	31	15
„ 412	21	2	—	7	6	—
„ 413	79	7	5	23	21	6

B.  $F_3$  families heterozygous in colour and pollen (*continued*).

Reference Number	Purple		Red		White	
	Long	Round	Long	Round	Long	Round
'06 F, 417	50	5	4	7	28	3
„ 425	17	1	3	7	2	3
„ 428	69	5	1	18	39	18
„ 431	28	1	2	7	21	8
„ 432	15	3	3	2	19	5
„ 433	27	1	2	5	7	1
„ 437	64	2	3	16	—	—
„ 440	36	3	1	13	7	3
„ 441	84	6	5	27	75	19
„ 444	44	1	4	9	32	12
„ 448	23	4	2	5	9	2
„ 449	32	2	6	5	16	3
„ 450	23	—	—	4	—	—
„ 451	21	1	1	11	7	—
„ 452	20	1	—	6	4	1
„ 453	30	—	1	8	24	11
„ 455	47	6	2	14	9	5
„ 462	26	1	—	11	12	6
„ 463	37	1	1	10	12	4
Totals ...	1480	125	96	425		
Expectation	1470	125	125	406		

## C. Families from various crosses inside the Emily Henderson strain.

Reference Number	Nature of cross	Purple		Red		White	
		Long	Round	Long	Round	Long	Round
'06, 359	$F_2$ ex Pic. long $\times$ E. H. round	41	2	3	20	19	3
„ 391	$F_2$ ex Pur. long $\times$ E. H. round	96	9	7	28	36	7
'07, 164	$F_2$ ex P. L. round $\times$ Pic. long	32	6	5	8	—	—
„ 165	„ „ „	19	2	2	3	—	—
„ 166	„ „ „	16	—	3	9	—	—
„ 167	„ „ „	18	1	3	3	—	—
„ 168	$F_2$ ex Red round $\times$ Wh. long (ex Pur.)	22	3	1	8	11	2
„ 170	„ „ „	12	2	4	12	7	1
„ 171	„ „ „	20	—	1	9	5	1
„ 172	„ „ „	18	2	1	5	4	—
„ 173	„ „ „	13	1	—	4	3	1
'08, 121	$F_2$ ex Pur. long $\times$ T. W. round	68	6	8	16	—	—
„ 122	„ „ „	213	19	17	61	—	—
„ 125	$F_2$ ex Pic. long $\times$ T. W. round	147	10	10	35	—	—
Totals ...	...	735	63	65	221		
Expectation	...	749	63	63	209		

*Reduplication Series in Sweet Peas*

		Purple		Red	
		Long	Round	Long	Round
Total from Families	A	1700	124	133	433
"	B	1480	15	96	425
"	C	735	63	65	221
Totals	...	3915	312	294	1079
Expectation	...	3871	328	328	1073

TABLE III.

*Families shewing coupling between purple and the erect standard.*

(Nature of mating BE × be.)

Reference Number	Purple		Red	
	Erect	Hood	Erect	Hood
'08, 84	139	—	2	44
'09, 2	67	1	—	22
'10, 36	6	—	—	2
" 37	3	—	—	3
" 38	6	—	—	2
" 39	17	—	—	6
" 40	9	—	—	2
" 41	11	—	—	2
" 46	22	—	—	5
" 55	158	—	1	56
'10 F, 1	206	—	2	37
" 2-3	178	4	—	45
" 4	74	—	1	29
" 5	59	—	—	17
" 13	60	—	—	18
" 14	138	1	—	36
" 15	125	—	1	50
" 18	57	—	—	11
" 19	71	1	—	29
" 20	62	1	—	21
" 21	48	—	—	20
" 22	171	2	—	63
" 23	123	—	—	38
" 24	168	2	2	71
" 25	58	—	1	25
Totals	2036	12	10	654
Expectation on } 127 : 1 basis }	2023	11	11	667

TABLE II.

*Sterility families homozygous in axil heterozygous in pollen.*

Reference Number	Purple		Red		Sterile		White		
	Long	Round	Long	Round	Purple	Red	Long	Round	Sterile
'05, T. L. 2	55	11	8	9	12	7	48	17	20
„ „ 5	75	9	7	13	19	7	48	23	20
'06, 340	28	4	3	16	20	—	28	8	9
„ 360	33	3	3	11	15	3	31	9	10
'07, 90	154	11	6	40	45	23	54	15	22
'08, 98 <sup>1</sup>	63	4	7	15	22	6	—	—	—
„ 100	64	5	6	18	29	11	16	8	13
'09, 3	25	2	2	10	11	2	5	—	5
Totals ...	497	49	42	132	173	59			
<i>Expectation on</i> <i>7:1 basis</i> }	498	42	42	138					

TABLE V.

*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
'12, 21	20	3	—	—	—	—	7	10	—	—	—	—
„ 22	71	7	—	—	—	1	9	19	20	—	2	5
„ 23	60	4	—	—	—	—	10	16	20	1	3	5
„ 24	60	7	—	—	—	—	3	20	—	—	—	—
„ 26	58	4	—	—	—	—	7	11	25	3	1	3
„ 27	26	2	1	1	—	—	1	5	10	—	1	1
„ 28	13	1	—	—	—	—	3	2	1	1	2	3
„ 30	34	4	—	1	1	—	9	14	6	1	1	1
„ 31	14	4	—	—	—	—	3	9	19	—	—	4
„ 32	46	3	1	—	—	1	4	14	6	2	3	3
„ 33	46	9	—	1	1	2	5	14	31	4	3	1
„ 34	17	4	—	—	—	—	1	4	9	3	1	5
„ 35	12	3	—	—	—	—	2	1	—	—	—	1
Totals	477	55	2	3	2	4	64	139	147	15	17	32

<sup>1</sup> A sister plant of '08, 98, and '08, 100, gave a remarkably aberrant result. This was '08, 99 in which there were 182 plants. Of these 180 were fertile and only 2 were sterile. As in the sister plants the coloured were all deep purples and Miss Hunt and there is no reason to suspect any error. This almost complete absence of steriles is quite unlike anything else we have encountered and we are unable to offer any explanation.



TABLE IV.

Families shewing repulsion between erect standard and long pollen.

(Nature of mating  $E1 \times eL.$ )

Reference Number	Red. Erect		Red. Hood	
	Long	Round	Long	Round
'08, 94	46	21	30	—
„ 95	33	11	10	—
„ 96	46	15	16	—
„ 97	34	24	10	—
Totals ...	159	71	66	—
Expectation ...	148	74	74	—

TABLE VI.

Families heterozygous for pollen, colour, and hood.

(Nature of mating  $BLE \times bLE.$ )

	Reference Number	Purple				Red		White			
		Erect		Hood		Erect		Erect		Hood	
		Long	Round	Long	Round	Long	Round	Long	Round	Long	Round
$F_2$ ex Bush $\times$ Cupid	'07, 80	15	2	3	—	—	10	12	3	9	—
	„ 81	17	—	13	—	3	10	15	3	4	—
	„ 82	6	1	6	—	—	1	2	4	1	—
	„ 83	9	2	4	—	—	5	9	3	4	—
	„ 84	4	1	3	—	1	4	6	—	2	—
	„ 85	19	—	11	—	—	10	11	3	6	—
$F_3$ ex Bush $\times$ Cupid	'08, 101	24	2	16	—	3	14	26	17	12	—
	„ 126	11	—	6	—	4	4	—	—	—	—
	„ 127	38	4	17	—	5	6	6	5	3	—
	„ 128	16	—	8	—	2	11	6	2	1	—
	„ 133	68	—	30	—	12	25	48	31	37	1
	„ 134	30	2	12	2	1	13	11	5	6	—
	„ 135	102	15	51	—	15	49	85	42	49	—
	„ 136	58	8	23	1	7	28	46	21	25	1
	„ 137	22	4	6	—	3	12	11	5	4	—
	„ 139	41	3	22	—	7	19	28	14	10	—
	„ 159	37	4	16	—	8	13	44	14	10	1
	'09, 4	46	4	17	1	4	25	54	19	14	2
	'08, 89	101	7	56	—	14	39	45	24	15	1
„ 93	66	9	42	—	8	23	37	11	14	1	
„ 114	73	4	51	—	1	23	—	—	—	—	
Rep. IV, p. 14	1185	86	605	2	114	499	279	115	128	1	
Totals ...	1988	158	1018	6	212	843	781	341	354	8	



TABLE VII.

*Families heterozygous for sterility and axil.*

(Nature of mating FD × fd.)

Reference Number	Dark axil		Light axil	
	Fertile	Sterile	Fertile	Sterile
'09, 1	49	2	2	11*
„ 2	62	1	1	18
'10, 62	114	2	3	30*
'11, 67	69	3	3	24
'12, 102	24	—	—	5*
„ 104	32	—	—	11*
„ 108	7	—	—	1*
„ 109	14	—	—	7*
Totals ... ..	371	8	9	107
From Report IV, p. 16	627	27	17	214
Totals ... ..	998	35	26	321
Expectation on 15 : 1 basis	993	42	42	303

	Dark axil		Light axil	
	Fertile	Sterile	Fertile	Sterile
*These six families ...	240	4	5	65
Expectation 15 : 1 basis	226	9.5	9.5	69
The rest ... ..	758	31	21	256
Expectation 15 : 1 basis	767	32	32	235

TABLE VIII.

*Families heterozygous for axil and sterility.*

(Nature of mating Fd × fd.)

Reference Number	Dark axil		Light axil	
	Fertile	Sterile	Fertile	Sterile
'08 84	95	45	44	—
„ 95	31	12	21	—
„ 97	37	29	31	—
„ 106	53	17	22	—
„ 107	214	95	102	—
„ 108	43	22	29	—
„ 109	81	50	58	—
„ 110	72	27	39	—
„ 111	110	55	49	—
„ 112	177	73	99	—
'10, 56	27	17	18	—
„ 60	126	59	69	—
'12, 48	49	28	27	—
Totals ... ..	1115	529	608	—

\* Families also heterozygous for B and L.

TABLE IX.

$F_3$  families from  $F_2$  normal fertiles ex  $F_1$  plants heterozygous for sterility and cretinism.

(Nature of  $F_1$  mating =  $Nf \times nF$ .)

Reference Number	Normal		Cretin		Reference Number	Normal		Cretin	
	Fertile	Sterile	Fertile	Sterile		Fertile	Sterile	Fertile	Sterile
'12, 70	37	22	34	1	'12, 72	×	× <sup>1</sup>	—	—
" 71	22	9	9	2	" 75	×	×	—	—
" 77	×	×	× <sup>1</sup>	—	" 81	×	×	—	—
" 79	×	×	×	—	" 97	33	12	—	—
" 80	8	6	1	—	" 98	×	×	—	—
" 82	12	9	8	—					
" 86	17	10	6	—					
" 87	49	11	16	1	'12, 74	66	—	22	—
" 88	11	7	6	—	" 78	16	—	4	—
" 89	×	×	×	—	" 83	×	—	×	—
" 90	24	11	13	—	" 84	42	—	14	—
" 92	11	7	5	—	" 85	36	—	8	—
" 93	×	×	×	—	" 94	×	—	×	—
" 99	12	7	3	—	" 95	×	—	×	—
'12, 76	90	20	30	34	'12, 73	×	—	—	—
" 91	20	4	5	3	" 96	22	—	—	—

TABLE X.

$F_4$  families from  $F_3$  parent, '12, 76 (Table IX).

Reference Number	Normal		Cretin	
	Fertile	Sterile	Fertile	Sterile
'13 38	16	8	9	12
" 39	27	17	9	14
" 40	20	7	4	9
" 41	12	6	6	9
" 43	20	7	4	1
" 45	37	9	10	2
" 46	18	7	7	2
" 42	29	—	19	—
" 44	(all four classes present)			
" 47	23	4	5	4
" 136	6	1	1	1

<sup>1</sup> The cross × denotes that the type of plant indicated occurred in these families though the actual numbers were not determined. In all such cases at least 30 individuals were examined. The sign — denotes that the class of individual under which it is placed was not found.

TABLE XI.

	Reference Number	Normal				Cretin			
		Dark		Light		Dark		Light	
		Fert.	Ster.	Fert.	Ster.	Fert.	Ster.	Fert.	Ster.
A. $F_2$ ex	'13, 48	102	49	31	—	27	6	24	2
$DfN \times dFn$	„ 49	20	17	5	—	4	—	10	—
	„ 50	14	13	5	—	3	1	6	—
	„ 51	40	27	8	—	10	1	17	—
		176	106	49	—	44	8	57	2
B. $F_2$ and	'13, 52	12	1	1	6	7	—	—	1
$F_4$ ex	„ 53	17	2	—	12	6	1	—	3
$DfN \times DFn$	„ 113	25	—	2	9	15	—	—	1
	„ 114	31	1	1	6	7	—	—	4
	„ 117	22	—	—	4	3	—	—	3
	„ 123	19	1	—	8	8	—	—	1
		126	5	4	45	46	1	—	13