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SEGREGATION IN TETRAPLOID BLACKBERRIES

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1. INTRODUCTION

Modern blackberry breeding is largely confined to improvements at the tetraploid level, and is particularly concerned with the production of early thornless types. The thornless character is controlled by a recessive gene which was originally given the symbol *A/a* by Crane and Darlington (1932); but following the usage by Lewis (1939) of *S/s* (= spineless) for the character in *Rubus idaeus* this latter symbol has now been generally adopted.

This character is particularly convenient for a study of tetraploid segregation in F_2 progeny, since differences between the alleles *S* and *s* can be readily distinguished during the cotyledon stage of recently emerged seedlings. At this stage, the *S* plants have glands along the edges of the cotyledons, whereas the homozygous recessive *s* plants possess naked cotyledons. The amount of mis-classification is very low, being confined largely to seedlings with abnormal cotyledons and to very late germinators. Large populations can, therefore, be raised and classified.

Darlington and Crane (1932) examined the F_2 progeny from a cross

between *R. rusticanus* (var. *inermis*)—with an unreduced egg cell ($n = 14$)—and *R. thyrsiger* ($2n = 28$) for segregation of the thornless character. Their results, based on a total segregating population of 872 seedlings, gave ratios similar to that expected for so-called “chromatid” segregation ($20.8 : 1$) instead of the $35 : 1$ predicted if “chromosome” segregation was operating.

In view of the relative ease with which large F_2 populations could be raised, it was decided to carry out a series of crosses designed to determine not only the F_2 ratios, but also to see whether these ratios varied with the parents used.

Throughout these experiments the commercial tetraploid variety Merton Thornless ($2n = 28$), which is nulliplex for the recessive *s* gene, was used as the female parent. The three cultivated tetraploid thorned blackberries used as the pollen parents were Himalaya Giant (*R. procerus*), Edward Langley (*R. calvatus*) and Cut-Leaf (*R. laciniatus*). These three species are almost certainly SSSS in constitution, as F_1 progenies with Merton Thornless were all thorned.

2. ANALYSIS AND RESULTS

A preliminary analysis of the F_2 ratios obtained for the thornless gene in the three crosses showed significant total deviations from both a $35 : 1$ and a $20.8 : 1$ ratio. In order to test the consistency of the segregations within and between crosses (groups) it was necessary therefore to use the test devised by Brandt and Snedecor (see Mather, 1951). The resulting χ^2 values clearly showed that heterogeneity was present both within and between groups (table 1). By considering each of the three groups individually, the heterogeneity within groups was shown to be mainly attributable to the cross involving *R. laciniatus* (table 2). Whilst the omission of families 82 and 88 satisfactorily removed the heterogeneity from within this group, there was still heterogeneity between groups at the 5 per cent. level of significance. Inspection of table 3 indicates that the heterogeneity between groups is due chiefly to differences between *R. calvatus* and *R. procerus* with respect to the *S : s* ratio, since *R. laciniatus* has an intermediate value.

After omitting families 82 and 88, it was found that overall there was no longer a significant deviation from a $20.8 : 1$ ratio, although the cross involving *R. calvatus* did in fact differ from such an expectation at the 5 per cent. level of significance (table 4). The production of more thornless individuals than expected on the basis of a $35 : 1$ ratio can only be due to a higher frequency of formation of recessive gametes, which in turn will depend on two factors; the mean equational separation of the locus under consideration and the non-disjunction of adjacent chromosomes. The product of these, which estimates the amount of double reduction (α), can be calculated from the expectation of each of the two classes (see Mather, 1936; Fisher and Mather, 1943). Higher values of α indicate that recessive gametes were produced more often, resulting in the formation of a larger number of thornless individuals (table 3).

Turning to the two anomalous families, 82 and 88, both of which showed such a marked deficiency of thornless plants, the values of α obtained for each family separately were negative and therefore meaningless. These two families would seem to pose a different problem from the remainder and therefore can be legitimately omitted from the present consideration.

TABLE 1
Tetraploid segregations in Rubus

Merton Thornless × <i>R. procerus</i>			Merton-Thornless × <i>R. calvatus</i>			Merton Thornless × <i>R. laciniatus</i>		
Family no.	No. of <i>s</i> plants	Total	Family no.	No. of <i>s</i> plants	Total	Family no.	No. of <i>s</i> plants	Total
59	14	417	75	1	77	82	1	228
60	24	622	77	2	121	88	6	475
66	13	328	69	6	213	80	2	98
63	13	315	73	4	138	54	13	504
62	11	230	72	29	987	84	7	253
64	4	83	74	8	269	79	16	497
67	4	82	71	3	88	86	8	242
52	9	172	68	4	87	78	11	332
65	19	352	76	25	455	85	8	201
53	14	255	56	18	298	55	17	371
57	12	197	...	...	...	83	9	173
61	7	113	...	...	...	87	20	316
51	2	30	...	...	...	81	16	228
58	19	248	...	...	...	...	...	...
Total	165	3444	...	100	2733	...	134	3918

Grand totals	.	.	.	399	10,095
				Within groups	Between groups
χ^2	.	.	.	56.62	9.93
Degrees of freedom	.	.	.	34	2
Probability	.	.	.	0.01-0.001	0.01-0.001

TABLE 2
Test of within group heterogeneity for the 3 F₂ progenies

Group	χ^2	Degrees of freedom	Probability
<i>R. procerus</i>	10.42	13	0.7-0.5
<i>R. calvatus</i>	14.44	9	0.2-0.1
<i>R. laciniatus</i>	35.28	12	< 0.001
<i>R. laciniatus</i> (with families 82 and 88 omitted)	17.17	10	0.1-0.05

TABLE 3
Values of α for the 3 F₂ progenies

Group	Ratio <i>S</i> : <i>s</i>	α
<i>R. procerus</i>	19.87 : 1	0.1565 ± 0.0249
<i>R. calvatus</i>	26.33 : 1	0.0735 ± 0.0282
<i>R. laciniatus</i> (except families 82 and 88) .	24.31 : 1	0.0962 ± 0.0259

A comparison of the values of α obtained in this experiment with those obtained by Catcheside (1956, 1959) showed them to be intermediate between the sugary-1 locus in tetraploid maize at the lower end and the r locus in tomato at the upper end of the range.

3. CONCLUSIONS

If families 82 and 88 are omitted, the results of these experiments support the earlier work of Crane and Darlington in so far as the ratios obtained approximate more closely to the 20.8 : 1 predicted on the basis of "chromatid segregation".

Taken as a whole the F_2 progenies are homogeneous within crosses, provided families 82 and 88 are excluded. The reasons for these two families being so deficient in thornless individuals cannot be determined exactly at present, but it could be attributable to inviability, linkage to a lethal, or visual mis-classification due to the dark colour of *R. laciniatus* and its hybrids masking the manifestation of the glands on the cotyledons.

TABLE 4

χ^2 analysis for a 20.8 : 1 ratio after omission of families 82 and 88

(a)	Item	D.F.	χ^2	P.
	<i>R. procerus</i> . . .	1	0.33	0.70—0.50
	<i>R. calvatus</i> . . .	1	5.37	0.05—0.02
	<i>R. laciniatus</i> . . .	1	2.99	0.10—0.05
	Total . . .	3	8.69	...
(b)	Overall ratio . . .	1	3.67	0.10—0.05
	Heterogeneity . . .	2	5.02	0.10—0.05
	Total . . .	3	8.69	...

The fact that the *R. calvatus* and *R. laciniatus* groups (except families 82 and 88) have similar values of α clearly indicates that the meiotic behaviour of the chromosomes is the same in these two crosses, at least as far as the present data go. The *R. procerus* group, on the other hand, gives a significantly higher value for α . This can mean either that chiasmata form more often between the centromere and the s gene, or multivalent formation is more regular and more nearly complete in this cross. Discrimination between these two alternatives, however, rests ultimately on cytological analysis. If the former proves to be correct then genetic control of the distribution and frequency of chiasma will have been demonstrated. Genotypic control of chiasma distribution and frequency has been found by Rees (1955) in rye. He was able to show that significant differences existed between various inbred lines, but not generally between sub-lines within these lines. However, the demonstration of genotypic control in *Rubus* depends on the assumption that for all species the physical distance between the s gene and the centromere is the same; an assumption which will hold only in the absence of an inversion carrying the s gene.

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GENIC CONTROL OF ANEUPLOIDY IN *PENNISETUM*

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1. INTRODUCTION

Perennial *Pennisetum dubium* is an irregular high polyploid in which chromosome numbers vary from 14 to 84 in root tips, 47 to 74 at MI and 9 to 37 at MII. This variation, which occurs from cell to cell in the same root tip or anther, has been shown to be the result of various mitotic and meiotic abnormalities which are under genetic control. The single perennial hybrid plant, produced from crosses between this species and the regular annual diploid *P. typhoides* ($2n = 14$), has only 21 chromosomes (Gildenhuys and Brix, 1958).

The mitotic behaviour of the 21 chromosomes of this sterile hybrid is nearly normal, but when attempts were made to double the complement by colchicine treatment, abnormalities occurred which give further evidence of genetic control of aneuploidy.

Although many different techniques were employed in attempting to double the chromosome number of the hybrid, none was successful. This was unexpected, since neither Krishnaswamy and Raman (1954) nor ourselves, using different techniques, had great difficulty in obtaining amphidiploids from the hybrid *P. typhoides* ($2n = 14$) $\times$ *P. purpureum* ($2n = 28$). When it became evident that the hybrid between *P. typhoides* and *P. dubium* was reacting differently to colchicine from that between *P. typhoides* and *P. purpureum*, identical treatments were applied to each hybrid to try to determine the nature of the difference between the two.

2. METHODS

Two or three cuttings, each consisting of two to three nodes, were taken from the lower part of mature tillers. These cuttings were totally immersed in a 0.01 per cent. aqueous solution of colchicine for 3 days and then washed and placed in a