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Genetics of resistance to *Amphorophora rubi* (Kalt.) in the raspberry

II. THE GENES A_2–A_7 FROM THE AMERICAN VARIETY, CHIEF

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1. INTRODUCTION

In Britain the rubus aphid, *Amphorophora rubi* (Kalt.), is the vector of the raspberry diseases mosaic 1 (veinbanding), mosaic 2, leaf mottle, leaf spot, and yellow blotch (Cadman, 1951, 1952*a*, 1952*b*, 1954; Cadman & Harris, 1952). On the American continent this aphid has been shown to transmit black raspberry necrosis, leaf mottle, yellow mosaic, and rubus yellow net (Stace-Smith, 1954, 1955*a*, 1955*b*). In addition, a limited number of raspberry viruses are carried by *Aphis idaei* v.d.G. Clearly, effective resistance to aphids could be of considerable value in the raspberry.

In Part I of this series the resistance of the raspberry variety, Baumforth A, to *A. rubi* strains 1 and 3 was shown to be controlled by a single dominant gene A_1 linked with the normal allele of a semi-lethal gene, *fr*, the crossover value being approximately 3·3% (Knight, Keep & Briggs, 1959).

2. STRAINS OF *AMPHOROPHORA RUBI* ON EUROPEAN RASPBERRIES

In the course of the work reported in Part I of this series and in the present paper, the existence on European raspberries of several distinct strains of *A. rubi* was recognized (Briggs, 1959). These are listed below for convenience of reference.

European raspberry strain 1 is delineated by Briggs by reason of its inability to breed on plants carrying A_1 or on 87/6, a seedling of Chief. In relation to the work reported in this paper the strain can now be more closely defined as being unable to breed on plants carrying any of the following genes: A_1, A_5, A_6, and A_7.

European raspberry strain 2 breeds on plants carrying A_1 but not on 87/6. The resistance of 87/6 to this strain is shown in this paper to depend on the series A_2, A_3 and A_4. A_2 alone confers full resistance; A_3 and A_4 are dominant complementaries which together confer full resistance, as does the combination $A_1 A_3$.

European raspberry strain 3 is capable of some reproduction on 87/6 but is unable to breed on plants carrying A_1. In terms of the genes described in this paper, strain 3 aphids are not affected by any of the genes A_2–A_7 individually, but when all six of these genes are present the aphids cease to thrive, although some are capable of reproduction and growth to maturity on such plants.

3. DESCRIPTION OF RASPBERRY VARIETIES USED

Chief.—According to Brooks & Olmo (1949) the American raspberry variety Chief arose from a self of Latham, although from the data given later in this paper

Chief must have been an outcross and not a self. Latham was bred from the cross King × Loudon, the latter deriving from Turner × Cuthbert, both of which, according to Hedrick (1925), probably arose from varieties being grown in England at the beginning of the nineteenth century. Hedrick's illustration of the other parent of Latham, King, shows it to have been a typical American variety. Latham, the immediate parent of Chief, was thus a hybrid between *Rubus idaeus* subsp. *strigosus*, the American red raspberry, and *R. idaeus vulgatus*, the European raspberry. It is shown later in this paper that Chief is resistant to strains 1 and 2 of *A. rubi*. This variety was shown to be susceptible to *A. rubi* in America by Schwartze & Huber (1937).

87/6.—Family 87, an open-pollinated progeny of Chief, was raised by N. H. Grubb at East Malling in 1950 from seed supplied by Dr G. L. Slate of the New York State Agricultural Experiment Station, Geneva. 87/6 is a clonally propagated single plant selection from this family.

Baumforth A L3/1.—An obsolete variety of unknown origin carrying the gene A_1 for resistance to strains 1 and 3 of *A. rubi*. Certain characteristics of this variety suggest that it derives, at least in part, from *R. idaeus strigosus*.

P1.—A basic inbred line deriving from Grubb's 30/8 (Grubb & Wood, 1954), itself an F_2 seedling of a hybrid between a self of Pyne's Royal and a self of Lloyd George. For convenience 30/8 and successive selfed selections in this breeding 'line' have been called P1. These successive selections have all proved to be susceptible to strains 1, 2, and 3 of *A. rubi*.

4. RESISTANCE TO *A. RUBI* STRAIN 1

Chief and its derivative 87/6

In 1950 Briggs and Taylor tested ninty-eight seedlings of Chief by mass inoculation with adult individuals of *A. rubi* reared from a batch collected in the field at East Malling. Chief itself was not available for testing at that time and this seed, kindly supplied by Dr G. L. Slate of Geneva, New York, was of open-pollinated origin. None of these seedlings became colonized in this test although other seedlings growing in the same frame and obtained from open-pollinated Devon showed nearly 100% infestation.

During the three years 1952 to 1954, eleven clonally propagated plants of this same family derived from Chief were tested by Briggs and Keep. One of these plants (87/6) had been more extensively tested than the others and this was selected by the present writers for further work.

In 1955, six clonally propagated plants of 87/6 were put into a replicated test against controls of P1; Baumforth A, Landmark, and other types were included. Ten adult apterous strain 1 aphids were placed on each plant and counts made 14 days later showed a total of 1,311 aphids on P1, 2 on 87/6, 4 on Landmark, and 1 on Baumforth A.

Chief was not available for testing until 1955, when a single plant of this variety was inoculated with twenty *A. rubi* apterae (strain 1) of all ages; none were present 15 days later. A further 100 aphids were put on, and again none remained after

6 days. Finally, approximately 500 apterae of all ages were used: 2 days later, 1 remained, and this was no longer present on the next examination made a week later. Plants of a number of susceptible varieties were included in this same test, and these were colonized freely.

87/6 selfed

A self-bred progeny of 87/6 was grown in 1955 and the young seedlings (Family 135) all proved resistant. A second self-bred progeny of 87/6 was grown and tested in 1957 (Family 205) and in this larger family segregation into two classes 'resistant' and 'susceptible' occurred and there were no cases in which the classification was in doubt (Table 1).

Table 1. *Classification of the selfs of 87/6*

Family no.	Observed		Expected 63:1				Expected 15:1			
	Res.	Sus.	Res.	Sus.	χ^2	*P* (approx.)	Res.	Sus.	χ^2	*P* (approx.)
135	43	0	42·33	0·67	0·68	0·45	40·31	2·69	2·87	0·10
205	117	5	120·09	1·91	5·10	0·03	114·37	7·63	0·96	0·30
Totals	160	5	162·42	2·58	5·78	0·06	154·68	10·32	3·83	0·15

The data in Table 1 give slightly better agreement with a 15 : 1 interpretation than with 63 : 1, where the total χ^2 is calculated for the two separate families. If these two families are taken together as a single sample, χ^2 figures of 2·31 for a 63 : 1 expectation and 2·92 for a 15 : 1 are obtained, corresponding with probabilities of 0·15 and 0·08 respectively. Thus, although on this basis the data are in somewhat better agreement with a hypothesis of control by three dominant genes, the possibility of digenic control is not excluded.

87/6 × P1

In 1955, reciprocal crosses of 87/6 by the susceptible variety P1 were grown and tested for resistance. There were two 'doubtful' cases in Family 137. Both of these plants were included in the 'resistant' group, since although in each case an aphid deposited nymphs on them, these nymphs remained on the plants for only a few days. Apart from these two cases the phenotypes were again clear (Table 2), and the distributions agreed closely with a three-gene interpretation. In Family 137 the observed distribution was 45 : 5, but in the course of progeny testing it was found that one 'resistant' plant had been misclassified since it gave only susceptible progeny. The figures in Table 2 were therefore altered to 44 : 6.

Table 2. *Classification of progenies of 87/6 × P1*

Family no.	Parentage	Observed		Expected 7:1		χ^2	*P* (approx.)
		Res.	Sus.	Res.	Sus.		
136	P1 × 87/6	42	8	43·75	6·25	0·56	0·5
137	87/6 × P1	44	6	43·75	6·25	0·01	0·9
Totals		86	14	87·50	12·50	0·57	0·75

The distributions in Table 2 agree much more closely with a three-gene interpretation ($P = 0{\cdot}75$) than with a two-gene hypothesis ($\chi^2 = 6{\cdot}67; P = 0{\cdot}04$). If the two families are treated as a single unit, χ^2 becomes 0·21 and P is 0·65 on the 7 : 1 basis whereas the divergence from a 3 : 1 ratio is highly significant ($\chi^2 = 6{\cdot}45; P = 0{\cdot}01$).

First backcross to P1

Ten resistant plants in Families 136 and 137 (Table 2) were crossed with the inbred parent line P1. Five of the progenies were tested in 1957 (Table 3). Four of these families gave clear 1 : 1 ratios indicating the presence of a single dominant resistance gene in each case, and the fifth gave a 3 : 1 ratio indicating the presence of two such genes.

Table 3. *Classification of first backcross to P1*

Family no.	Parentage	Observed Res.	Observed Sus.	Expected Res.	Expected Sus.	χ^2	P (approx.)
Families carrying one major resistance gene (1:1)							
209	P1 × 136/9	24	23	23·5	23·5	0·02	0·9
215	137/6 × P1	24	26	25·0	25·0	0·08	0·8
217	137/35 × P1	25	20	22·5	22·5	0·56	0·5
208	P1 × 136/6	41	37	39·0	39·0	0·21	0·7
Totals		114	106	110·0	110·0	0·87	0·95
Family carrying two major resistance genes (3:1)							
206	P1 × 136/2	40	17	42·75	14·25	0·71	0·4

Five additional backcross progenies were grown but these were discarded because of contamination with a new strain of *A. rubi*. Owing to a shortage of aphids hatched from eggs in the insectary, aphids were collected from the field and used for testing at the beginning of the 1957 season. To conserve aphids, adults which had deposited five young on a seedling under test were moved to another seedling. Moreover, the aphids which had passed through all stages on such seedlings and become adult (the normal criterion of susceptibility) were then transferred to other seedlings and used for testing for resistance. These conditions imposed a strong selection pressure in favour of any race of *A. rubi* able to colonize plants carrying resistance genes from 87/6. This selection sieve resulted in the expansion of a strain of aphids which, unknown to the writers, must have existed at a low level in the field population, and, in consequence, families which on sample tests early in the season had shown promise of giving clear ratios, gradually 'dropped back' in their ratios as determined on subsequent samples (due to the expansion of the 'new' strain), until they appeared to comprise only susceptible plants. This new race of *A. rubi*, named strain 3 by Briggs (1959), thus vitiated most of the work on the first backcross progenies. By the time the contamination had been detected and eradicated, it was too late in the season to repeat the full series of tests with uncontaminated strain 1 aphids, and such tests had to be limited to the five families classified in Table 3.

Baumforth A × 87/6

Seedlings of a cross between Baumforth A and 87/6 were tested in 1956 (Table 4). Baumforth A is known to be of $A_1\,a_1$ genotype, so that this hybrid population would be expected to give a 7 : 1 or 15 :1 ratio according to whether 87/6 is heterozygous for two or for three dominant resistance genes.

Table 4. *Classification of Baumforth A × 87/6 F_1*

Family no.	Observed		Expected 15:1				Expected 7:1			
	Res.	Sus.	Res.	Sus.	χ^2	P (approx.)	Res.	Sus.	χ^2	P (approx.)
163	91	9	93·75	6·25	1·29	0·25	87·50	12·50	1·12	0·3

The distributions in Table 4 lend themselves equally to interpretation on either a two-gene or a three-gene basis. It is shown in the next section that these genes are distinct from A_1.

Evidence for independence of A_1 *from the strain 1 resistance genes in 87/6*

The gene A_1 confers near immunity to strain 3 aphids; since, however, plants of 87/6 can be colonized by this strain, it is almost certain that 87/6 does not carry A_1. Moreover, as previously noted, first backcross progenies on test in 1957 proved entirely susceptible to strain 3. Since ten progenies were involved, the chances of one or more of them carrying A_1, had this been present in 87/6, would have been of the order of 999 : 1.

Discussion

The distribution in the self-bred progenies of 87/6 (Table 1) and in the F_1 of Baumforth A × 87/6 (Table 4) are equally open to interpretation of control of 87/6 resistance by two or by three genes. The segregation ratios of the F_1's of 87/6 × P1 (Table 2), on the other hand, strongly support the three-gene hypothesis and differ widely from expectation on a digenic basis. The five first-backcross progenies (Table 3) gave 1 : 1 and 3 : 1 ratios only. The absence of 7 : 1 ratios in these families does not preclude the three-gene hypothesis, since in a sample of only five progenies the chance of finding one segregating for all three genes is only about 50%.

In view of the 7 : 1 ratios given by 87/6 × P1 and the reciprocal cross (Table 2) a three-gene interpretation is considered valid, and these genes have been designated A_5, A_6 and A_7.

The discovery of strain 3 of *A. rubi*, against which these genes are ineffective, made it imperative for plant breeding purposes to concentrate on the gene A_1, since this gives near immunity to both strains 1 and 3. All further work on the isolation and utilization of A_5, A_6 and A_7 was therefore discontinued.

5. RESISTANCE TO *A. RUBI* STRAIN 2

In Britain, the only form of *A. rubi* so far found capable of colonizing plants carrying the gene A_1 is that designated 'strain 2' by Briggs (1959). When this strain was discovered by the writers in 1955, sources of resistance to it were at once sought amongst the range of raspberry varieties and *Rubus* spp. carried at East Malling. Both Chief and its self-bred derivative, 87/6, proved resistant; P1 proved fully susceptible.

87/6 selfed

A self-bred progeny of 87/6 (Family 205) was tested with strain 2 aphids in 1957 and clear-cut segregation was obtained (Table 5).

Table 5. *Classification of the selfs of 87/6*

Family no.	Observed		Expected (57:7)		χ^2	P (approx.)
	Resistant	Susceptible	Resistant	Susceptible		
205	88	10	87·28	10·72	0·06	0·8

Although the distribution in Family 205 agrees closely with expectation on a 57 : 7 basis, it does not differ significantly from 15 : 1 ($\chi^2 = 2{\cdot}6$; $P = 0{\cdot}1$). A 57 : 7 ratio suggests control by three dominant genes, two of which are complementary.

87/6 × P1 and the first backcross to P1

F_1 families of 87/6 × P1 and the reciprocal were not tested with strain 2 aphids in the insectary, since these families were already planted out in the field by the time strain 2 became available in sufficient quantity for resistance testing. A rough test was accordingly made by topping young canes of each plant and testing these tops in the insectary, keeping the cut ends immersed in water. This rough test was not expected to give an accurate ratio, but merely to give an indication of possible resistant plants amongst which selections for backcrossing to P1 could be made. Five plants, thought to be resistant, were selected in this way and backcrossed to P1. The classification of their progenies is shown in Table 6.

Table 6. *Classification of first backcross*

Family no.	Parentage	Observed		Expected		χ^2	P (approx.)
		Res.	Sus.	Res.	Sus.		
				1:3			
215	137/6 × P1	14	36	12·50	37·50	0·24	0·6
216	137/33 × P1	7	18	6·25	18·75	0·12	0·7
Totals		21	54	18·75	56·25	0·36	0·85
				1:1			
217	137/35 × P1	19	26	22·50	22·50	1·08	0·3
				5:3			
206	P1 × 136/2	8	5	8·13	4·88	0·01	0·9
208	P1 × 136/6	50	29	49·38	29·63	0·01	0·9
Totals		58	34	57·51	34·51	0·02	0·99

Second backcross to P1

Three plants in Family 215 and three in Family 217 (Table 6) all resistant to strain 2 were again crossed as males with susceptible derivatives of P1 (Family 166). One of these plants (No. 217/2) gave a hybrid progeny all of which were susceptible, indicating either that the parent plant was misclassified or that a berry from the maternal parent had been picked and sown in error. The numbers in Tables 6 and 9 have accordingly been adjusted by transferring one $S^1 R^2$ plant to the $S^1 S^2$ phenotype ($S^1 R^2$ denotes susceptibility to strain 1 aphids and resistance to strain 2, etc.). These second backcross families gave reasonably close approximations to the 1 : 3 and 1 : 1 ratios expected (Table 7), except for Families 402 and 404 in which there were a large number of plants whose classification was doubtful. In Family 402, the thirty-two plants in the 'resistant' group included twelve plants which had been graded as 'doubtfully resistant' and in several of the others the resistance was far from sharply defined; this difficulty of classification was undoubtedly due to the plants having become somewhat pot-bound whilst awaiting their time for testing. Similarly, the forty 'resistant' plants in Family 404 included eight plants regarded as 'doubtfully resistant'. That some plants became pot-bound was due to the need to make maximum use of the available bench space in order to get through a crowded programme. Hence 'potting on' into larger pots was often of necessity delayed, especially where tests with more than one strain of aphid were required.

In addition to the progenies involving Families 215 and 217, eight plants of Family 208 were used as males in backcrossing to P1. The response of these eight plants to strain 2 was uncertain, owing to an error in labelling in the field, and two of the progenies proved to be entirely susceptible. Three progenies gave 1 : 3 ratios and three gave 1 : 1 ratios (Table 7).

Table 7. *Classification of second backcross*

Family no.	Parentage	Observed Res.	Observed Sus.	Expected Res.	Expected Sus.	χ^2	*P* (approx.)
				1:3			
402	166/9 × 215/3	32	68	25·00	75·00	2·61	0·1
403	166/10 × 215/6*	3	14	4·25	12·75	0·49	0·5
404	166/90 × 215/5	40	57	24·25	72·75	13·64	0·001
398	P1 × 208/9	13	52	16·25	48·75	0·87	0·4
399	P1 × 208/10	7	28	8·75	26·25	0·46	0·5
400	P1 × 208/11	8	11	4·75	14·25	2·96	0·1
Totals		103	230	83·25	249·75	21·03†	0·001†
				1:1			
406	166/9 × 217/4	33	45	39·00	39·00	1·85	0·2
407	166/10 × 217/7	44	38	41·00	41·00	0·44	0·5
393	P1 × 208/3	18	17	17·50	17·50	0·03	0·85
395	P1 × 208/2	20	15	17·50	17·50	0·71	0·4
396	P1 × 208/7	11	19	15·00	15·00	2·13	0·15
Totals		126	134	130·00	130·00	5·16	0·4

* Plant No. 215/6 subsequently proved to be triploid.

† Omitting Family 404 the total χ^2 is 7·39 and $P = 0·2$ approx.

Self-bred progenies from the first backcross

Self-bred progenies of first backcross plants Nos. 215/3, 215/8, 217/4 and 217/7 (Table 6) gave reasonable approximations to expectation on a 9 : 7 and 3 : 1 basis (Table 8) confirming the 1 : 3 and 1 : 1 ratios obtained in Table 7. Eleven plants of Family 208 were selfed also. The response of these plants to strain 2 aphids was uncertain (as noted earlier) and the progenies from three of them were all susceptible; of the remaining eight plants, three gave 9 : 7 ratios and five gave 3 : 1 ratios (Table 8).

Table 8. *Classification of F_2 of first backcross*

Family no.	Parentage	Observed Res.	Observed Sus.	Expected Res.	Expected Sus.	χ^2	P (approx.)
				9:7			
388	215/3 Self	20	13	18·56	14·44	0·26	0·6
389	215/8 Self	14	13	15·19	11·81	0·21	0·6
382	208/9 Self	32	22	30·38	23·63	0·19	0·7
383	208/10 Self	24	14	21·38	16·63	0·73	0·4
384	208/11 Self	30	25	30·94	24·06	0·07	0·8
Totals		120	87	116·45	90·57	1·46	0·9
				3:1			
391	217/4 Self	9	8	12·75	4·25	4·41	0·04
392	217/7 Self	45	18	47·25	15·75	0·42	0·5
376	208/2 Self	24	8	24·00	8·00	—	—
377	208/3 Self	45	12	42·75	14·25	0·47	0·5
378	208/4 Self	28	7	26·25	8·75	0·47	0·5
379	208/5 Self	16	5	15·75	5·25	0·02	0·9
381	208/7 Self	38	17	41·25	13·75	1·02	0·3
Totals		205	75	210·00	70·00	6·81	0·5

Discussion

The 57 : 7 ratio obtained in the self-bred progeny of 87/6 suggests that control of resistance to strain 2 aphids in this variety depends on three genes, one being a strong dominant capable by itself of conferring full resistance and the other two being dominant complementaries. The backcross ratios (Tables 6 and 7) of 1 : 3, 1 : 1 and 5 : 3 support this interpretation, which is further confirmed by the 9 : 7 and 3 : 1 ratios obtained in F_2 progenies of the first backcross (Table 8).

These genes are shown in the next section to be distinct from A_5, A_6 and A_7, and they have been called A_2, A_3 and A_4 respectively, A_2 by itself conferring full resistance and A_3 and A_4 being dominant complementaries.

6. TESTS OF INDEPENDENCE OF THE STRAIN 1 RESISTANCE GENES A_5–A_7 FROM THE STRAIN 2 SERIES A_2–A_4

In testing for independence of the strain 1 resistance genes from those affecting strain 2, many of the insectary tests in 1957 were invalidated because of contamination of the strain 1 aphid stock with strain 3 aphids. This point has already been discussed; it threw much of the work out of phase so that it was not always possible to test the *same* plants in each family with both strains 1 and 2. Data from the families in which the same plants were tested with both strains, are given in Table 9.

Table 9. *Classification of selfs and backcrosses for resistance to* A. rubi *strains 1 and 2*

	Family numbers										
	205			208			215			217	
* Phenotypes	Observed	Expected (3591:441:57:7)	Expected with linkage	Observed	Expected (5:3:5:3)	Expected with linkage	Observed	Expected (1:3:1:3)	Expected with linkage	Observed	Expected (1:1:1:1)
R^1R^2	87	85·92	86·08	33	24·69	28·63	12	6·25	11·25	13	11·25
R^1S^2	9	10·55	10·39	7	14·81	10·86	12	18·75	13·75	12	11·25
S^1R^2	1	1·36	1·20	18	24·69	20·74	2	6·25	1·25	6	11·25
S^1S^2	1	0·17	0·33	21	14·81	18·76	24	18·75	23·75	14	11·25
Totals	98	98·00	98·00	79	79·00	78·99	50	50·00	50·00	45	45·00
χ^2		4·39	1·58		11·32	2·68		12·08	0·72		3·44
P (approx.)		0·2	0·7		0·01	0·5		0·01	0·85		0·3

* Superscripts denote strains of *A. rubi* to which the plants are resistant (R) or susceptible (S).

Family 205 = 87/6 selfed ($A_2a_2A_3a_3A_4a_4A_5a_5A_6a_6A_7a_7$) (Tables 1 and 5).
208 = P1 × 136/6 (sus. × $A_2a_2A_3a_3A_4a_4A_5a_5$) (Tables 3 and 6).
215 = 137/6 × P1 ($A_3a_3A_4a_4A_5a_5$ × sus.) (Tables 3 and 6).
217 = 137/35 × P1 (A_2a_2 + a het. gene of A_5–A_7 group × sus.) (Tables 3 and 6).

The linkage ratios are calculated assuming 10% recombination between one of the complementary genes, A_3A_4, and A_5.

Family 205 (the self-bred progeny of 87/6) was shown to segregate for genes A_5, A_6 and A_7 (Table 1) and also for A_2, A_3 and A_4 (Table 5). The figures in Table 9 show reasonably good agreement with expectation on the basis that there is no interaction (apart from linkage) between these strain 1 and strain 2 resistance genes.

The first backcross families 208, 215 and 217 all gave 1 : 1 ratios when inoculated with strain 1 aphids (Table 3); they gave 5 : 3, 1 : 3 and 1 : 1 ratios respectively when tested with strain 2 (Table 6). From Table 9 it is clear that Family 217 agrees well with expectation on the basis that it carried the dominant gene A_2 together with a single gene of the A_5–A_7 group.

Families 208 and 215 agree less well with expectation, Family 215 which carries the complementaries A_3 and A_4 unaccompanied by A_2 (Table 6) being particularly skew. Evidently one of the genes of the A_5–A_7 group is linked with either A_3 or A_4, the distributions in Family 215 suggesting a crossover value of about 10%. For convenience this linked gene is considered to be A_5.

7. TESTS OF INDEPENDENCE OF A_1 FROM THE A_2–A_4 SERIES

In 1956, a family derived from crossing Baumforth A with 87/6 was tested with strains 1 and 2 of *A. rubi* (Table 10). The variety Baumforth A is known to be of $A_1 a_1$ genotype (Knight, Keep & Briggs, 1959) and hence to be resistant to strains 1 and 3 but susceptible to strain 2.

Table 10. *Classification of Family 163, Baumforth A × 87/6 F_1*

Phenotypes	Observed	Expected 83:37:5:3	Expected with linkage
R^1R^2	73	64·84	65·47
R^1S^2	18	28·91	28·28
S^1R^2	6	3·91	3·28
S^1S^2	3	2·34	2·97
Totals	*100*	*100·00*	*100·00*
χ^2		6·45	6·86
P		0·09	0·08

The 'expected' figures in Table 10 are based on the assumption that the genotypes A_2, A_3A_4 and A_1A_3 are resistant to strain 2 aphids. The 'expected' figures for linkage are calculated on the basis of a 10% c.o.v. for A_3 or A_4 with A_5.

Support for the assumption that A_1 interacts with one of the two complementaries, A_3A_4, is given by the results from Family 279, which was tested in 1958. This family was obtained by crossing 136/6, known to be heterozygous for $A_2A_3A_4$ (Table 6), with 130/42, a homozygous A_1A_1 plant (Table 11).

Table 11. *Strain 2 tests on* $A_2a_2A_3a_3A_4a_4 \times A_1A_1$

	Observed		Expected (3:1)			
Family	Res.	Sus.	Res.	Sus.	χ^2	P (approx.)
279	56	15	53·25	17·75	0·57	0·45

Had there been no interaction between A_1 and one of the two complementaries A_3A_4 this family would have given a 5 : 3 ratio of resistant to susceptible plants, when tested with strain 2 aphids. The interaction of A_1 with one of these genes has converted this ratio to 3 : 1 and the distribution of 56 : 15 obtained differs significantly from expectation on a 5 : 3 basis ($\chi^2 = 8{\cdot}11$; $P = 0{\cdot}007$). There is no means of distinguishing the action of A_3 from that of A_4 other than definition in terms of this interaction with A_1. For convenience of definition, A_3 is regarded as this interacting gene.

From the existing data it is impossible to determine whether A_5 is linked with A_3 or with A_4. It is only possible to distinguish A_3 from A_4 in the presence of A_1, and since A_1 confers resistance against both strain 1 and strain 3, the presence or absence of A_5 is then not detectable. This question could be determined by crossing $A_1a_1A_3a_3$ plants with A_5a_5. This would give 2 $R^1R^2R^3$: 2 $R^1S^2R^3$: 2 $R^1S^2S^3$: 2 $S^1S^2S^3$ (using superscripts of R and S to denote resistance or susceptibility to strains 1, 2, and 3). By crossing a number of these $R^1S^2S^3$ plants with A_1A_1 and testing with strain 2 aphids, it would be possible to detect whether or not there was an excess of $A_3 A_5$ plants amongst them, since $A_1 A_3$ is resistant to strain 2 whereas $A_1 a_3$ plants are susceptible. Such a method of proving which of the two genes is linked with A_5 would, however, involve an unjustifiable amount of work in view of the fact that *A. rubi* strain 3 has superseded strain 1 for plant breeding purposes.

8. GENERAL DISCUSSION

Origin of the resistance genes found in Chief

Slate (1935) and Brooks & Olmo (1949) state that Chief was selected from the self-bred progeny of the American variety Latham. In 1958 a self-bred progeny of Latham was grown; 20 of these plants were tested with strain 1 aphids and 2 showed weak resistance while 18 were more or less fully susceptible. A further 20 plants tested with strain 2 aphids, showed 1 resistant, 2 weakly resistant and 17 fully susceptible. From this it seems unlikely that Latham carries any major genes for resistance to either of these strains of *A. rubi.*

Since six dominant resistance genes have been located in Chief it follows that this variety cannot be a self-bred seedling of Latham but that it must have been an outcross, an explanation much more in keeping with the fact that Chief proved to be heterozygous for all six of these genes.

Economic significance of the individual resistance genes

The discovery, in 1957, of *A. rubi* strain 3 showed the genes A_5, A_6 and A_7 to be of little commercial importance. Since A_1 confers strong resistance to strain 1 and strain 3 aphids, this gene was chosen as the main basis of raspberry breeding designed to achieve field immunity.

Strain 2 aphids can colonize plants carrying A_1 with or without A_5, A_6 and A_7. However, adequate resistance to this aphid strain can be achieved by using A_2 alone, A_3 combined with A_4, or A_1 combined with A_3 (Table 12).

Table 12. *Interaction of resistance genes and aphid strains*

	Response to *A. rubi*		
Raspberry genes	Strain 1	Strain 2	Strain 3
A_1	R	S	R
A_2	S	R	S
$A_3 + A_4$	S	R	S
A_5	R	S	S
A_6	R	S	S
A_7	R	S	S
$A_1 + A_2$	R	R	R
$A_1 + A_3$	R	R	R
$A_1 + A_4$	R	S	R

For plant breeding purposes, the simplest control of these three strains of *A. rubi* will be achieved by using the combination $A_1 A_2$ or $A_1 A_3$. A programme involving A_1 and A_2 would require testing of progenies with both strain 2 and strain 3 aphids; the use of the combination $A_1 A_3$ would require tests with strain 2 aphids only.

Both the combinations $A_1 A_2$ and $A_1 A_3$ will be used until field tests are available on a sufficient scale to show whether there is any difference in resistance.

Minor-gene resistance

The method of breeding raspberries resistant to *A. rubi* has been based on the use of major resistance genes from Baumforth A and Chief. Nevertheless, in the course of the search for genes of suitably large effect, a number of instances were found of resistance apparently controlled by minor genes. The system of testing for resistance was designed for classifying seedlings as either more or less immune or fully susceptible, but intermediate levels of resistance are shown by the general behaviour of the aphids. Adults are more restless and tend to leave partially resistant seedlings after depositing only a few nymphs. These nymphs may linger for variable periods on such plants, often feeding on the stem and lower leaves rather than on young leaves. Occasionally they grow to maturity, but the unsuitability of the host plant is usually evident from the smallness of the resulting adult.

Tests with strain 1 aphids on self-bred progenies of Reid's AR1 showed a continuous range, as indicated by aphid behaviour, from a few plants with full resistance to others showing full susceptibility. Some derivatives evinced a measure of resistance to strain 2 and strain 3 aphids, but there was no correlation between resistance to these two aphid strains. Moreover, field counts on a self-bred progeny of Reid's AR1 showed no significant differences between populations on plants previously classified in the insectary as 'resistant', 'intermediate' or 'susceptible' to strain 1 aphids.

Numerous field counts on Norfolk Giant have shown it to be partially resistant. Selfs of Norfolk Giant, tested in the insectary with strain 1 aphids, gave a response similar to that of the Reid's AR1 progeny, both in the insectary and in the field. Similarly, self-bred progenies deriving from Baumforth B showed a continuous range from resistance to susceptibility when tested in the insectary with strain 3 aphids, suggesting that this variety, also, carries minor resistance genes.

Relative value of major- and minor-gene resistance

In breeding for resistance to pests and diseases it is often suggested that plant breeders should use resistance controlled by minor-gene complexes rather than oligogenic resistance, on the ground that the more complex the resistance, the less is it likely to succumb to new biologic strains of the pest or pathogen. This, though true of certain pests and diseases, is by no means universally applicable. Thus the high resistance of the raspberry variety Lloyd George under field conditions in North America has been shown by Schwartze & Huber (1939) to be simply inherited and this resistance has been maintained there for about 30 years without breaking down.

In the raspberry, resistance to *A. rubi* can be controlled by major genes or by minor ones, but our evidence to date suggests that minor genes confer *resistance*, rather than immunity, and mere resistance, unless it approached immunity, would be valueless in preventing virus infection and spread in a crop. Moreover, minor-gene resistance to one strain of *A. rubi* does not necessarily confer resistance to another.

There can be little doubt that resistance to *A. rubi* belongs to the group of resistances best achieved by the use of major genes. This is fortunate because few raspberries would tolerate the repeated selfing required in integrating minor-gene complexes, and the difficulties involved in handling such complexes over and above those controlling yield and fruit quality would be considerable. Moreover, the method of testing would have to be more sensitive, thus inevitably restricting the number of plants that could be handled.

SUMMARY

The American raspberry variety Chief is shown to carry three dominant genes, A_5, A_6 and A_7, each capable of conferring strong resistance to *Amphorophora rubi* strain 1.

Chief also carries three genes, A_2, A_3 and A_4, for resistance to *A. rubi* strain 2. A_2 is a dominant gene conferring full resistance by itself; A_3 and A_4 are dominant complementaries, neither gene by itself having any effect on resistance. A_5 is linked with either A_3 or A_4 with a crossover value of 10%.

The gene A_1 from Baumforth A, which confers resistance to strains 1 and 3, when combined with A_3 gives resistance to strain 2 also. Thus the three strains of *A. rubi* at present recognized on raspberries in Britain can be controlled by using either the combination A_1A_2 or A_1A_3.

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