THE CHROMOSOME NUMBERS OF SEEDLINGS FROM THE CROSS *SOLANUM DEMISSUM* × *TUBEROSUM* BACKCROSSED BY *S. TUBEROSUM*

By J. P. COOPER* and H. W. HOWARD

Plant Breeding Institute, School of Agriculture, University of Cambridge

(With Nineteen Text-figures)

I. Introduction

In breeding potatoes resistant to blight (*Phytophthora infestans* de Bary), the wild, Mexican hexaploid ($2n=72$) species *Solanum demissum* Lindl. has usually been used as the source of resistance, e.g. Black (1943, 1945*a*, *b*), O'Connor (1933), O'Connor & Salaman (1931), Reddick (1940, 1943), and Salaman (1931, 1934, 1937, 1938, 1941). Used as the female parent, *S. demissum* crosses fairly easily with the cultivated, tetraploid ($2n=48$) species *S. tuberosum* L.; and the F_1 hybrid can be backcrossed by *S. tuberosum*. As the blight resistance of *S. demissum* is due to dominant factors (Black, 1943, 1945*a*, *b*), it is theoretically an easy task to produce more or less cultivated types, which are also blight resistant, by repeated backcrossing by *S. tuberosum* plus selection for blight resistance and for cultivated characters such as short stolons, good yield of large tubers, not too late maturity, shallow eyes, and good cooking quality.

Also it is to be expected theoretically that, as a result of this repeated backcrossing by the tetraploid species, most of the seedlings in the later progenies will themselves have either the tetraploid chromosome number of $2n=48$ or of $2n=48$ plus 1 or 2 at the most. The present investigation shows that it is possible to get blight-resistant seedlings with a chromosome number of $2n=49$, but on the other hand even in the fifth backcross generation one line contained seedlings which had chromosome numbers of $2n=51$ and $2n=52$.

II. Material

The seedlings, whose chromosome numbers are given in this paper, all belong to the breeding material of the Plant Breeding Institute, School of Agriculture, Cambridge. They are all descended, see Fig. 1, from seedlings bred by Dr R. N. Salaman at the Potato Virus Research Station, School of Agriculture, Cambridge, and handed over by him on his retirement in the autumn of 1939 to the Plant Breeding Institute. The breeding work between 1940 and 1947 has been carried out by Dr G. P. Carson and H. W. Howard, and the blight testing has been done by Dr S. Dickinson. Only those parts of the breeding work and of the blight testing directly relevant to the cytological results are given in this paper, and it is hoped to publish accounts of these two subjects later.

III. Methods

Chromosome counts have been made entirely on root tip material. Root tips from plants growing in pots were fixed in CRAF solution (Randolph, 1935) and embedded in wax by the chloroform method. Sections were cut at about $16\,\mu$ and the slides stained by Newton's

* Present address: Department of Agricultural Botany, University of Reading.

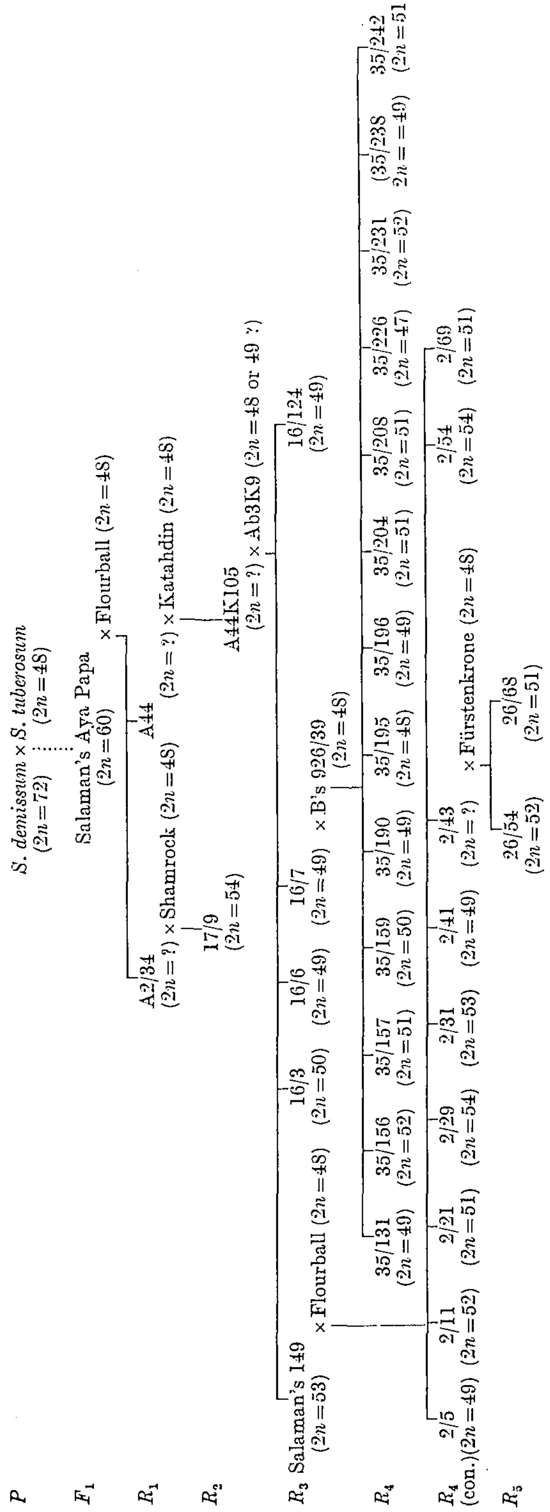


Fig. 1. Parentage of the blight-resistant seedlings whose chromosome numbers have been counted.

iodine-gentian violet schedule. Counts of about four plates were made for each seedling, and in nearly every case the different counts agreed: there was never a disagreement of more than one chromosome. Meiosis was studied in pollen mother cell squashes stained by either aceto-carmine, acetic-lacmoid or Feulgen methods.

IV. Salaman's Aya Papa

As can be seen from Fig. 1, all the seedlings are descended from Salaman's Aya Papa which has a chromosome number of $2n = 60$ (see Fig. 3) and which has been shown by Hawkes & Howard (1941) to be almost certainly an F_1 hybrid from the cross *S. demissum* ($2n = 72$, see Fig. 2) × *S. tuberosum* ($2n = 48$, see Fig. 4). Salaman's Aya Papa was found by Miss C. O'Connor to be resistant to both the A and B strains of *Phytophthora infestans* (see Salaman, 1941) and Dr Dickinson has confirmed that it is resistant to these two strains.

2 3 4

Figs. 2–4. Somatic plates. Fig. 2, *S. demissum*, $2n = 72$; Fig. 3, Salaman's Aya Papa, $2n = 60$; Fig. 4, *S. tuberosum*, variety Bankhead's 926/39, $2n = 48$.

V. First and second backcross generations

No plants of the first backcross generation were available for chromosome counts, and there was only one plant (17/9) of the second backcross generation available. This plant had a chromosome number of $2n = 54$ (see Fig. 5). It is, however, possible to state that the other plant of the second backcross generation shown in Fig. 1, A44K105, probably had a chromosome number of at least $2n - 53$ from the results of chromosome counts for family 16 in the third backcross generation (see § VI of this paper) but not necessarily as is shown by the results for family 35 (see § VIII of this paper).

VI. Third backcross generation

There were in Salaman's material as received by the Plant Breeding Institute only two clones, number 55 and a seedling 23.9 (which was renamed 149 in 1940), which were resistant to both A and B strains of blight, and which were at the same time more or less 'cultivated' for the characters short stolons and large tubers. All other 'double resisters' had rather long stolons and rather small tubers, though they were not by any means as 'wild' as *S. demissum* itself or as Salaman's Aya Papa (F_1 *S. demissum* × *S. tuberosum*). Dr Salaman also handed over a quantity of true seed which included some from the cross A44K105 × Ab3K9 from which the two clones 55 and 149 had been obtained. From this seed the Plant Breeding Institute family 16 was grown.

The pedigree of A44K105 is shown in Fig. 1. The other parent of family 16 is Ab3K9 which was a more or less cultivated type bred by Dr Salaman. It came from the cross (Abundance × 417.23.14) × Katahdin, 417.23.14 itself being a *demissum* × *tuberosum* derivative in the 5th generation (cf. pedigree given in Salaman (1937) and Salaman (1938), p. 125). The chromosome number of Ab3K9 is not known, but it was probably $2n=48$ or 49 since it was both pollen fertile and more or less of the cultivated type.

The chromosome numbers of seedlings of family 16 are given in Table 1. These plants are, however, not a random sample as they had been selected for blight resistance and also for cultivated characters such as short stolons. It will be seen that no plant had a chromosome number less than $2n=49$, and that Salaman's 149 had $2n=53$ (this high number is confirmed by counts for family 2 which came from the cross 149 × Flourball). The seedlings of family 16, which were not discarded and whose chromosome numbers have been counted, were all of a more cultivated character than Salaman's 149; and this is presumably correlated with their having only one or two extra *demissum* chromosomes as compared with five extra for 149.

Table 1. *Family* 16 *from the cross* A44K105 × Ab3K9

		Blight resistance*		
Seedling no.	Chromosome no.	A strain	B strain	C strain
Salaman's 149	$2n=53$	R	R	R
16/3	$2n=50$	R	R	S
16/6	$2n=49$	R	R	R
16/7	$2n=49$	R	R	R
16/124	$2n=49$	R	R	R

* Tests by Dr Dickinson in 1945 (R = resistant; S = susceptible). For a short account of the A, B and C strains see (Black (1945*a*) or Black in Williams (1945).

VII. Fourth backcross generation (family 2) and fifth backcross generation (family 26)

Family 2 was grown from the cross Salaman's 149 × Flourball. The chromosome numbers of several seedlings of this family are given in Table 2, and are illustrated in Figs. 8–10.

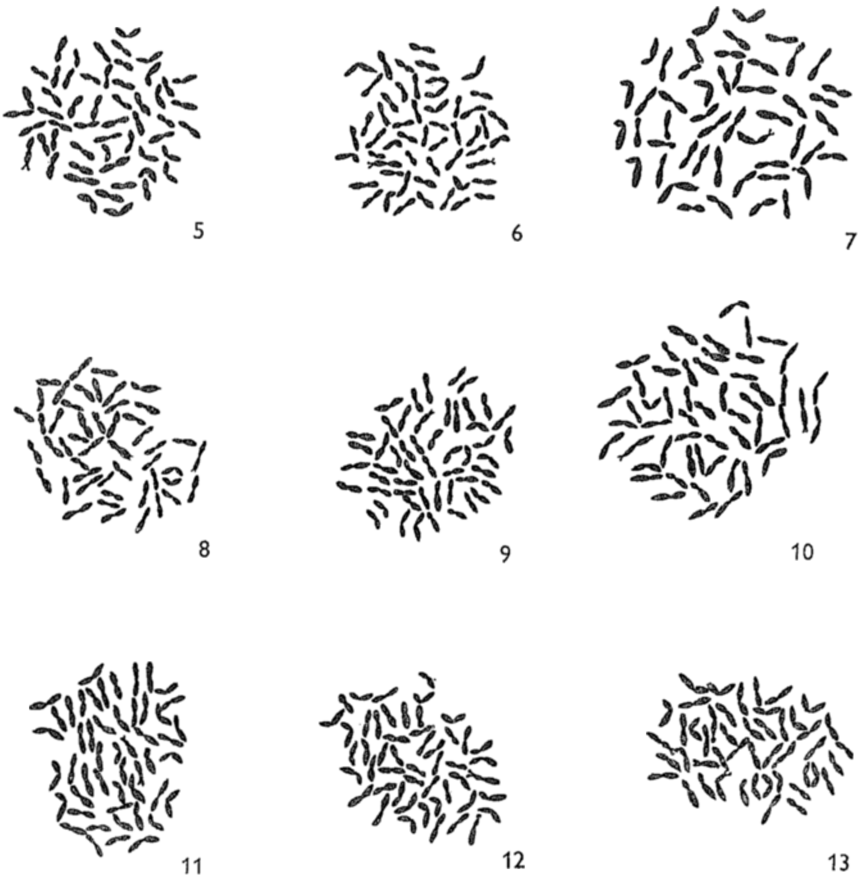
Table 2. *Family* 2 *from the cross* 149 × *Flourball and family* 26 *from the cross* 2/43 × *Fürstenkrone*

		Blight resistance*		
Seedling no.	Chromosome no.	A strain	B strain	C strain
2/5	$2n=49$	R	R	S
2/11	$2n=52$	R	R	S
2/21	$2n=51$	R	R	R
2/29	$2n=54$	R	R	S
2/31	$2n=52$ or 53	R	R	S
2/41	$2n=49$	R	R	R
2/56	$2n=54$	R	R	S
2/69	$2n=51$	R	R	S
26/54	$2n=52$	R	R	R
26/68	$2n=51$	R	R	S

* From Dr S. Dickinson's tests in 1945 (R = resistant; S = susceptible).

Also included in Table 2 are two seedlings of family 26 which came from the cross 2/43 × Fürstenkrone. It will be noticed that, as in family 16, there are no plants with the tetraploid chromosome number of $2n=48$, and that most plants have from 51 to 54 chromosomes. There has thus been little loss of the extra chromosomes during one generation of backcrossing by *S. tuberosum*. The plants examined were, however, again not a random sample as they had been selected as in family 16 both for blight resistance and for cultivated characters.

Two plants, 2/29 and 2/56, had 54 chromosomes, i.e. one more than their parent, Salaman's 149. These may be bad counts, but plants were also obtained in family 35, see next section of this paper, which had higher chromosome numbers than either of the parents.



Figs. 5–13. Somatic plates. Fig. 5, 17/9 ($2n=54$); Fig. 6, S's 149 ($2n=53$); Fig. 7, 16/7 ($2n=49$); Fig. 8, 2/5 ($2n=49$); Fig. 9, 2/21 ($2n=51$); Fig. 10, 2/29 ($2n=54$); Fig. 11, 35/159 ($2n=50$); Fig. 12, 35/131 ($2n=49$); Fig. 13, 35/226 ($2n=47$).

The two plants of family 26 were regarded in 1943 as being promising breeding material, but it is interesting to note that, even if we disregard the susceptibility to the C strain of blight, of 26/68, they have not proved such good parents as 16/7. Thus, though they are the products of two more generations of backcrossing than 16/7, the fact that they have three and four extra *demissum* chromosomes as compared with only one extra in 16/7 makes them not so good parents for the cultivated characters.

VIII. Fourth backcross generation (family 35)

This family, which, when it was grown in the field in Northern Ireland in 1945, contained some of the most cultivated type blight-resistant seedlings obtained by that time from the Cambridge material, came from the cross 16/7 × Bankhead's 926/39. The latter seedling is a pollen fertile, and wart resistant, early maincrop type raised by Mr J. Bankhead of the Plant Breeding Station, Northern Ireland Ministry of Agriculture, Stormont, Belfast from the cross (Kerr's Pink × Arran Signet) × (McGill and Smith seedling 6264 × Pepo). Bankhead's 926/39 has the regular tetraploid chromosome number of $2n=48$ (see Fig. 4).

Seedlings of family 35 were raised in the two years, 1943 and 1944. Those of the year 1944 were used in this investigation since they had been less selected for both blight-resistance and cultivated characters. As can be seen from Table 3, the chromosome numbers of three types of seedling were counted—seedlings resistant to both the B and C strains, seedlings resistant to the B strain but susceptible to the C strain, and seedlings susceptible to both B and C strains. Attempts were made to count the chromosome numbers of a fourth type of seedling—susceptible to the B strain but resistant to the C strain—but no satisfactory plates were obtained.

Table 3. *Family* 35 *from the cross* 16/7 × B's 926/39

		Blight resistance*	
Seedling no.	Chromosome no.	B strain	C strain
35/157	$2n=51$	R	R
35/159	$2n=50$	R	R
35/204	$2n=51$	R	R
35/208	$2n=51$	R	R
35/131	$2n=49$	R	S
35/190	$2n=49$	R	S
35/196	$2n=49$	R	S
35/231	$2n=52$	R	S
35/242	$2n=51$	R	S
35/156	$2n=52$	S	S
35/195	$2n=48$	S	S
35/226	$2n=47$	S	S
35/238	$2n=49$	S	S

* From Dr S. Dickinson's tests in 1945 (R = resistant; S = susceptible).

It can be seen from Table 3 that no seedling resistant to the B strain of blight has a chromosome number of less than $2n=49$, which is the number found in the blight-resistant parent (16/7). Also, rather surprisingly, seven of the thirteen seedlings have a chromosome number higher than that of either parent. This might be due to bad fixation and consequent difficulty of being sure of the exact chromosome number. This, however, seems unlikely to be true in every case; and a possible explanation of the occurrence of these seedlings with chromosome numbers higher than either parent is given in the next section of this paper.

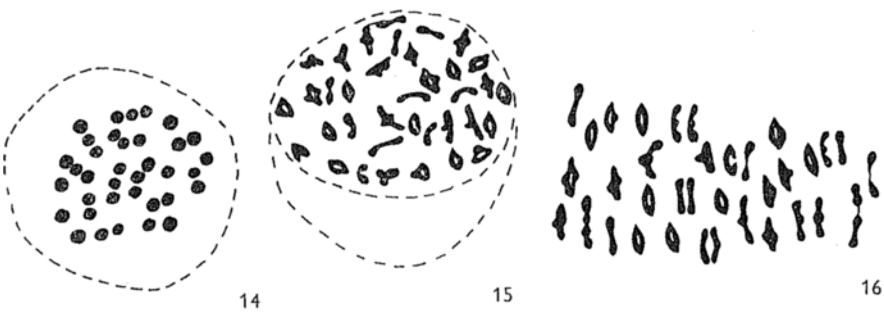
IX. Observations of meiosis

(1) *S. demissum.* Meiosis in *S. demissum* ($2n=72$) has not been examined in any detail by previous observers. Smith (1927) and Longley & Clark (1930) each show single figures for meiosis in this species, and in both cases 36 bivalents are shown. Examination of slides made on the Cambridge material (Figs. 14–16) also suggest that quadrivalents do

not occur with a frequency of more than one per nucleus, and even the quadrivalents observed may be 'false' unions of 2 bivalents. Thus *S. demissum* would appear to behave as an allohexaploid and be similar to allotetraploid *S. acaule* ($2n=48$) which Lamm (1945) found to form 24 bivalents and no quadrivalents.

(2) *S. tuberosum.* Meiosis in cultivated potato varieties has been studied by many workers. *S. tuberosum* has usually been considered to be an autotetraploid and to form a high frequency of quadrivalents, e.g. Cadman (1943) and Lamm (1945). It has, however, been suggested by Dr P. T. Thomas (see *John Innes Horticultural Institution Annual Report for* 1945, p. 11) that in cultivated potatoes there is an average of less than 2 true quadrivalents per nucleus, and that the cultivated potato is an allotetraploid hybrid between related species whose chromosomes are structurally similar.

(3) F_1 *S. demissum* × *S. tuberosum.* Miss Mary Adams in Salaman (1928) concluded that in the F_1 hybrid there were formed 24 bivalents and 12 univalents. Becker (1939) and Schnell (1948) suggested that more than 24 bivalents and less than 12 univalents are formed. Our own observations suggest that in most cells there are not more than 7



Figs. 14–16. Meiosis in *S. demissum*, pollen mother cell squashes. Fig. 14, polar view of first metaphase, 36 bivalents; Fig. 15, late diakinesis, 36 bivalents or 34 bivalents and one quadrivalent; Fig. 16, side view of first metaphase, bivalents spread out by squashing, 36 bivalents or 34 bivalents and 1 quadrivalent.

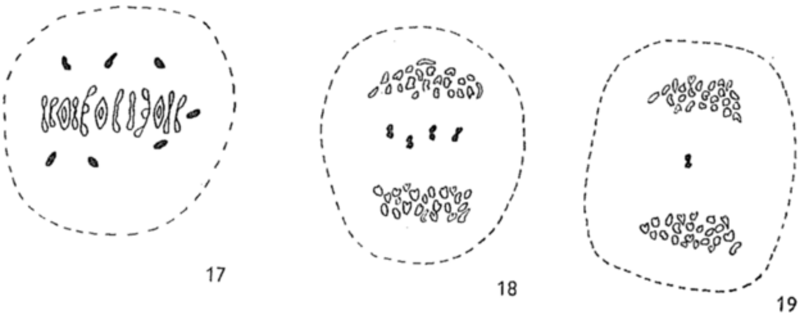
univalents, see Fig. 17, but the fixation was not good enough to count the number of bivalents and trivalents. Trivalents were, however, seen and one cell contained at least 3. Lamm (1945) also was unable to make detailed observations of meiosis in pentaploid ($2n=60$) *S. curtilobum*, but in the triploid species *S. chaucha* found as an average 4·1 bivalents, 7·9 trivalents and 4·1 univalents per cell. It therefore seems very likely that the F_1 *S. demissum* × *S. tuberosum* forms much less than 12 univalents per nucleus. Also Thomas (see *John Innes Horticultural Institution Annual Report for* 1945, p. 11, and Black (1949, p. 299)), has found that the tetraploid hybrids, *S. demissum* ($2n=72$) × *S. Rybinii* ($2n=24$) and (*S. demissum* × *S. Rybinii*) × *S. tuberosum* ($2n=48$), had a meiotic behaviour very similar to *S. tuberosum* itself. This again suggests that all five sets of 12 chromosomes each in the F_1 hybrid *S. demissum* × *S. tuberosum* would be similar enough to pair, and hence a relatively low frequency of univalents would be found in the hybrid. Also a certain amount of pairing could take place between the chromosomes of the three sets of *S. demissum* as Bains & Howard (1950) and Dodds (1950) have found that in haploid *S. demissum* 2 to 7 bivalents per nucleus are formed.

(4) *The third generation backcross hybrid*, 16/7. Family 35 (see § VIII) from the cross 16/7 × B's 926/39 was peculiar in that some seedlings had a higher chromosome number

than either of the parents. A possible explanation of this was obtained from studying meiosis in 16/7. As is shown in Table 4, and Fig. 18, there appears to be a rather high frequency of univalent formation in 16/7 which may mean that gametes are usually produced with more than 24 chromosomes. Observations on Gladstone semi-bolter ($2n=48$) are given for comparison.

Table 4. *Observations at first anaphase*

Gladstone semi-bolter		16/7	
No. of cells	No. of univalents	No. of cells	No. of univalents
18	0	11	0
5	1	11	1
2	2	2	2
0	3	2	3
0	4	2	4
0	5	0	5
0	6	1	6



Figs. 17–19. Meiosis, pollen mother cell squashes. Fig. 17, Salaman's Aya Papa, first metaphase, 7 univalents in black and bivalents and trivalents in outline and not all drawn; Fig. 18, 16/7, late anaphase, 4 lagging univalents; Fig. 19, Gladstone semi-bolter, late anaphase, 1 lagging univalent.

X. Inheritance of blight-resistance

Black (1943, 1945*a*, *b*, 1949) has discussed the inheritance of blight resistance. He postulates four genes—**Ra** which confers immunity from strain A; **Rb** which confers immunity from strains A and B; **Rc** which confers immunity from strains A and C; and **Rbc** which confers immunity from strains A, B and C. In the Cambridge material two of these genes are found. The first, which corresponds to Black's **Rb**, gives resistance to strains A and B and the second, which corresponds to Black's **Rc**, gives resistance to strains A and C. Thus in the Cambridge material four types of seedling are obtained—resistant to the A, B and C strains; resistant to the A and B strains but susceptible to the C strain; resistant to the A and C strains but susceptible to the B strain; and susceptible to all three strains.

Table 5 gives some of the results for blight testing. No data are given for the A strain since all seedlings resistant to either the B or C strains have always been found to be resistant to the A strain also. It can be seen from the second part of the table that two types of seedling have been bred from: seedlings resistant to the B and C strains (16/7, 2/41, 26/54) and seedlings resistant to the B strain but susceptible to the C strain (2/5, 26/68). The results give very good evidence for the independence of the two genes for resistance to the B and C strains respectively—there are 158 recombinations out of 315 plants in progenies segregating for both genes. It also appears from the first part of the table that Salaman's 149 may have two genes for resistance to the B strain while 16/7 and other seedlings have only one gene.

On the whole the segregations for resistance *v.* susceptibility to the C strain give good 1 : 1 ratios. On the other hand, in many cases there is a very marked deficiency of seedlings

Table 5. *Number of seedlings resistant to the B and C strains of blight in families from crosses of the type resistant × susceptible*

(*a*) Tested for the B strain only*

Female parent (resistant)	Male parent (susceptible)	Family no.	Year of test	No. of seedlings	
				Resistant	Susceptible
Salaman's 149	Flourball	2	1941	58	13
16/7	B's 926/39	35	1943	46	72
16/7	B's 926/39	35	1944, 1945	50	75
16/7	(Natural berry)	40	1943	28	40
16/7	Centifolia	42	1943	26	27
Total for 16/7	—	—	—	150	214
2/29	Fürstenkrone	30	1942	9	9
2/43	Fürstenkrone	26	1942	39	35

(*b*) Tested for the B and C strains in 1945

Female parent (resistant)	Male parent (susceptible)	Family no.	No. of seedlings*				Segregations	
			BC	Bc	bC	bc	B : b	C : c
16/7	Katahdin	68	0	3	5	7	3 : 12	5 : 10
16/7	Clarke 616†	69	2	5	8	12	7 : 20	10 : 17
16/7	Clarke 650†	70	3	1	12	9	4 : 21	15 : 10
						Totals	14 : 53	30 : 37
2/5	Clarke 464†	64	0	11	0	6	11 : 6	0 : 17
2/5	Clarke 786†	65	0	41	0	6	41 : 36	0 : 77
						Totals	52 : 42	0 : 94
2/41	Flourball	60	3	4	5	2	7 : 7	8 : 6
2/41	Clarke 650†	61	5	3	8	4	8 : 12	13 : 7
2/41	B's 926/39	62	0	2	1	1	2 : 2	1 : 3
2/41	Clarke 655†	63	5	6	4	4	11 : 8	9 : 10
						Totals	28 : 29	31 : 26
26/54	Clarke 650†	54	14	8	19	32	22 : 51	33 : 40
26/54	Clarke 786†	55	6	9	23	18	15 : 41	29 : 27
26/54	Clarke 464†	58	4	6	14	14	10 : 28	18 : 20
26/54	B's 926/39	59	1	1	11	11	2 : 22	12 : 12
						Totals	49 : 142	102 : 99
26/68	B's 926/39	56	0	4	0	31	4 : 31	0 : 35
26/68	Clarke 650†	57	0	9	0	27	9 : 27	0 : 36
						Totals	13 : 58	0 : 71

* Blight tests by Dr S. Dickinson (BC = resistant to B and C strains; Bc = resistant to B strain, susceptible to C strain, etc.).

† Clarke 464, 616, 650, etc.—pollen fertile seedlings bred by Mr John Clarke, breeder of the Ulster series of potato varieties, from crosses between different commercial varieties.

resistant to the B strain. This would be expected if the gene for resistance to the B strain was on a chromosome which normally did not pair and formed a univalent at meiosis. The cytological data given earlier give some support to this suggestion. Black (e.g. 1949) has also found deficiencies of seedlings resistant to the B strain.

It must, however, also be pointed out that the results for resistance *v.* susceptibility to blight need some consideration before they can be taken as being absolutely accurate. It is possible to score a susceptible plant as resistant, since in some tests a plant escapes infection. Thus, for family 35 of 1944 (see § *a* of Table 5), the original results in 1944 were 62 resistant : 63 susceptible—a good fit to a 1 : 1 ratio. However, on retesting the 62 resistant plants in 1945, 12 were found to be susceptible. The ratio thus becomes 50 : 75 which differs significantly from 1 : 1 at $P = 0{\cdot}05$. On the other hand, there are no reasons for suggesting that an excess of susceptibles would ever be obtained due to wrong scoring. The results in § *b* of Table 5 have been checked in 1946.

XI. Discussion

One feature of the chromosome counts needs emphasizing from the plant-breeding aspect. This is the slow progress of the families derived by backcrossing by *S. tuberosum* ($2n = 48$) to give seedlings with the true tetraploid chromosome number of $2n = 48$. It is quite possible that, unless a seedling has a chromosome number of $2n = 48$, it will not be equal in cultivated characters to existing commercial varieties. This suggests that the breeding method adopted recently by Black (see Black, 1949) of crossing *S. demissum* ($2n = 72$) by *S. Rybinii* ($2n = 24$) to get a hybrid with a chromosome number of $2n = 48$ and of then crossing this hybrid with *S. tuberosum* will be a more useful and quicker method of breeding blight-resistant potatoes than that of backcrossing the hybrid ($2n = 60$) from the cross *S. demissum* ($2n = 72$) × *S. tuberosum* ($2n = 48$).

The abnormal segregations in the Cambridge material for resistance to the B strain of blight are easily explained on the cytological data if we assume that the gene for resistance is carried on a chromosome which usually does not form a half of a bivalent at meiosis. It is also possible that a similar explanation may explain some of Black's results, and that there is no need to postulate that 'incompatibility factors derived from the wild species employed in the breeding work had a selective influence on the union of gametes, and hence on the distribution of resistants and susceptibles in the progenies' (Black, 1949).

XII. Summary

1. Chromosome numbers of seedlings in the second, third and fourth backcross generations from *Solanum demissum* ($2n = 72$) × *S. tuberosum* ($2n = 48$) backcrossed by *S. tuberosum* have been counted. The majority of seedlings had from 49 to 54 chromosomes.

2. A third generation backcross seedling with $2n = 49$ when backcrossed by *S. tuberosum* produced offspring with more than 49 chromosomes.

3. *S. demissum* ($2n = 72$) does not form more than one quadrivalent at meiosis. The F_1 *S. demissum* × *S. tuberosum*, which has a chromosome number of $2n = 60$, forms less than 12 univalents at meiosis.

4. In the Cambridge material there are two genes for blight resistance. One gives resistance to the B and A strains of blight and the other resistance to the C and A strains of blight. In many families there is a deficiency of seedlings with the gene for resistance to the B and A strains.

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