Studies on Self-Sterility in *Raphanus sativus* (L.) var. *radicula* (DC)

by

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There are at present three systems of incompatibility distinguished in flowering plants, i.e. sporophytic heteromorphic, gametophytic homomorphic, and sporophytic homomorphic (Lewis 1954a, b, Bateman 1954a, Crowe 1954a). Of these the first two have been explained and the results reported by various workers are not contradictory. The third system sporophytic homomorphic — has been distinguished on the ground of the results obtained by Hughes and Babcock (1950) with *Crepis foetida*, by Gerstel (1950) with *Parthenium argentatum*, by Crowe (1954b) with *Cosmos bipinnatus*, and by Bateman (1954b) with *Iberis amara*. This system is considered typical for the *Compositae*, *Cruciferae*, and some other families. However, the results of some experiments on incompatibility in *Cruciferae* cannot be explained conformably with the assumptions, made by the authors mentioned above. Thus, the problem of the genetic basis of incompatibility in *Cruciferae* still remains unsolved.

The genetic aspects of incompatibility in *Raphanus sativus* were studied by A. Gavin Brown (unpublished, quoted after Bateman, 1955), Sampson (1957b), and Tatebe (1957b), whereas the physiological aspects of this problem were investigated by Oelke (1957). When in 1957 I started my experiments with *Raphanus sativus* only the first of these reports had been published, but later when also the other reports became available I reached the conclusion that the opinions on the genetic aspects of incompatibility in *R. sativus* were still highly contradictory and that further researches would thus be useful and might help to elucidate the problem.

MATERIAL AND METHODS

For experiments various varieties of radish (*Raphanus sativus* L. var. *radicula* DC) grown out of foundation seed were used. The varieties were as follows: "Saxa", „Czerwona z białym końcem“, „Sopel Lodu“,

"Early Scarlet Globe Short Top Radish" and "Early Scarlet Globe Medium Top Radish". The seeds of the last two varieties were obtained from the collection of the University of Wisconsin Experimental Station, Madison, U. S. The "Saxa" variety — developed by the Freege Co., Cracow — had a relatively short vegetation period, the thick part of its root was round and the skin red. The variety „Czerwona z Białym Końcem“ — developed by the Ulrich Co., Warsaw — had a longer period of vegetation, started flowering much later, and was much more sensitive to the photoperiod. When this variety was sown out late it flowered in the middle of August and some plants had no flowers. The thick part of the root in this variety was round with red skin changing to white at the lower end. The vegetation of the „Sopel Lodu“ variety — developed by the Freege Co., Cracow — was longer than that of the "Saxa" but shorter than that of the „Czerwona z Białym Końcem“ variety. The edible part of the root in the „Sopel Lodu“ radish was oblong with white skin. Crosses between the first two of these varieties, the two red ones, and the white „Sopel Lodu“ radish had the thick part of the root elongated with a pale purple skin, and were easily distinguishable. Both "Early Scarlet Globe" varieties resembled the "Saxa" radish.

The „Czerwone z Białym Końcem“ and both "Early Scarlet Globe" varieties were used only for experiments on pseudocompatibility.

Experimental plants were grown in field cultures. In studies on incompatibility this might be a source of error, since in cold weather pseudocompatibility may increase. To reduce the possibility of error pollinations were made only on warm days between 8 a.m. and 4 p.m. when the temperature was not below 18—20°C. Seeds were sown out late, at beginning of May and consequently the radishes flowered in the hottest part of the year, from July to the middle of August.

The shoots chosen for experimental pollinations were covered by cellophane bags. The bags were taken off about a week after flowers had been pollinated. In every combination the number of pollinated flowers was 8—10, seldom less. Flowers selected for pollination were not castrated. Similarly, cross-pollinations marked out to obtain plants for further experiments were made on uncastrated flowers.

The results of pollinations were estimated from the setting of seeds. The selfs and crosses which did not lead to the setting of seeds or produced three or less seeds per flower (flower fertility) were considered as incompatible. The criteria of classifying the partially sterile crosses as compatible or incompatible will be outlined more fully further on in the paper.

In order to compare the speed at which pollen grains germinated and

the early stages in pollen tube growth on pistils after self- and cross-pollination in plants manifesting pseudo-compatibility the following experiment was carried out. On a plant eight branches were selected and on each of these branches several (5—19, but usually 8—12) flowers were castrated. When 24—48 hours later the buds opened, on four branches the flowers were self-pollinated and on four they were cross-pollinated with a compatible pollen. After four hours all stigmata were cut out on one branch with self-pollinated and one branch with cross-pollinated flowers. The stigmata were cut out with a razor blade cleaned every time with a wad dipped in alcohol to prevent any pollen reaching the cut end of the style. After the operation each branch was again covered by a clean bag. Six hours after pollination the stigmata were amputated on the next pair of branches, and eight hours after pollination the third pair of branches was submitted to the same operation. The fourth pair of branches was left for control. Some weeks later the number of seeds that had set was counted and flower fertility was determined by calculating the ratio of the number of seeds to the number of pollinated flowers.

With the same purpose in mind the experiment was repeated according to a different procedure. On each of four chosen branches of a plant several buds were castrated and when the buds opened all the castrated flowers were self-pollinated. Then on one branch immediately after self-pollination the flowers were additionally pollinated with foreign pollen. The flowers of the other three branches were additionally cross-pollinated successively 4, 6, and 8 hours after the original self-pollination. The foreign pollen for the additional pollinations was chosen so as to ensure the recognition whether the progeny originated from self- or cross-fertilization. Plants of the "Saxa" and „Czerwona z Białym Końcem" varieties were pollinated with pollen of the "Sopel Lodu" variety (only plant C3/6 was additionally pollinated with pollen of *Raphanus raphanistrum*). Plants of the „Sopel Lodu" variety were additionally cross-pollinated with "Saxa" pollen. The seeds obtained in this manner were sown out and the percentage of crosses in the progeny was counted.

RESULTS

Original populations. Eleven plants of the "Saxa"* variety were crossed in all possible combinations. The results are assembled in Table 1.

Some of the plants were mutually sterile in both directions: Sa2, Sa3, and Sa5, Sa10 and Sa11; Sa6 and Sa8 etc. However, these plants were

* The particular plants of this population were marked with the letters Sa and a number: Sa2, Sa3, etc.

not phenotypically identical: Sa2 and Sa5 as ♀ were sterile with regard to Sa7 and Sa10, while Sa3 was fertile; but neither Sa2 nor Sa5 were identical since Sa5 was sterile with Sa10 in both directions and Sa2 only as ♀. Sa10 as ♂ was sterile with regard to Sa2 and Sa5, while in the same combination Sa11 was fertile. Also the behaviour of Sa6 and Sa8 as ♂ with regard to Sa12 was different, the former was sterile and the latter fertile. This means that among 11 experimental plants there was not one pair which would be phenotypically identical. Different results in reciprocal crosses were frequent.

In some instances selfs and crosses regarded as incompatible had an average flower fertility almost as high as crosses considered as fertile. The principles on which crosses were classified as fertile or sterile were twofold: 1) The average fertility of flowers in self-pollination was

Table 1
Effects of crosses within „Saxa,, variety population sample

No. of plant ♀	3	2	5	7	10	11	16	12	14	6	8
3	S	S	S	F	F	F	F	F	F	F	F
2	S	S	S	S	S	F	F	F	F	F	F
5	S	S	S	S	S	F	F	F	F	F	F
7	F	F	F	S	S	F	F	F	F	F	F
10	F	F	S	S	S	S	S	S	S	F	F
11	F	F	F	S	S	S	F	F	F	F	F
16	F	F	F	F	S	F	S	F	F	S	S
12	F	F	F	F	F	F	F	S	F	S	F
14	F	F	F	S	F	F	F	F	S	F	F
6	F	F	F	F	F	F	F	F	F	S	S
8	F	F	F	F	F	F	F	F	F	S	S

compared to the lowest fertility of sterile crosses. E.g. in the case of plant Sa16 the average number of seeds per flower from self-pollination was 1.3, whereas this average in crosses with plant Sa8 was only 0.3. Since before pollination the flowers were not castrated and self pollen was always present on stigmata, it seems reasonable to suppose that plant Sa16 manifested pseudocompatibility in different degrees, possibly because of weather conditions. This means that all the crosses with Sa16 as ♀ in which the average flower fertility did not exceed 1.3 can be regarded as sterile. In the case of plant Sa16, not only the cross Sa16 × Sa8 but also the crosses Sa16 × Sa6 and Sa16 × Sa10 were classified as sterile, since flower fertility in these crosses was 1.2. 2) When after self-pollination no seeds were set or flower fertility was very low, cross-pollinations were classified as fertile or sterile according to the difference between

th average flower fertility of that cross and other crosses. E.g. plant Sa2 was completely self-sterile and in crosses with Sa3, Sa5, and Sa10 its flower fertility was 1.0, 0.3, and 2.8 respectively, while in other crosses flower fertility was 4.1 to 7.7. In this case the difference between the plants regarded as sterile and those regarded as fertile was relatively well marked.

In the Sa population of 11 plants seven after self-pollination produced less than 0.5 seed per flower, one produced 2.8 seeds per flower, and the others were intermediate.

In the case of the "Sopel Lodu" * variety only six plants were crossed in all combinations (Table 2). Three of the plants — L7, L15, and L14 —

Table 2
Effects of crosses within „Sopel lodu” variety population sample

No. of plant ♂ ♀	3	15	7	14	17	16
3	S	S	F	F	F	F
15	S	S	S	S	F	F
7	S	S	S	S	S	—
14	F	S	S	S	F	—
17	F	F	—	F	S	F
16	F	F	F	F	S	S

were mutually sterile, but they were not phenotypically identical, since only L15 as ♂ was sterile with L3 and only L7 as ♀ was sterile with L17. These results are thus similar to the results for the previous population: self-sterile plants cannot be ranged to the same phenotype because their behaviour with regard to other plants differs and, the differences between reciprocal crosses are frequent.

Pseudocompatibility in the case of this variety was also manifested but the differences between compatible and incompatible crosses were more pronounced. The average flower fertility from compatible crosses ranged 4.6 to 9.0 and from incompatible crosses 0 to 2.8.

Selfs. The family Sa11 — S₁ (the first self generation of plant Sa11) consisted of nine individuals of which two (no. 4 and 7) manifested some degree of pseudocompatibility. The results of crosses within this family are assembled in Table 3.

Among these plants four phenotypes were distinguished: plants (1)

* The particular plants of this population were marked with the letter L and a number: L3, L7 etc.

and (2) belonged to the first, plants (3), (6) and (8) to the second, plant (9) to the third, and plants (4), (5) and (7) to the fourth. As ♀ plant (9) behaved in the same manner as plants (3), (6) and (8), but as ♂ it was fertile with regard to plants (4), (5) and (7), whereas plant (3) in the same combination was sterile. This means that plants (6) and (8), which were

Table 3

Family Sa11-S₁. Effects of crosses with five plants from the same family

No. of plant ♀	♂	2	3	9	5	7
1		S	F	F	F	F
2		S	F	F	F	F
3		F	S	S	S	S
6		F	S	S	S	S
8		F	S	S	S	S
9		F	S	S	S	S
4*		F	S	F	S	S
5		F	S	F	S	S
7*		F	S	F	S	S

* Plants with some degree of pseudocompatibility.

not crossed as ♂ with the fourth group, had the same phenotype as either plant (3) or plant (9). Regardless of this possibility the fact remains that in the family composed of the first self generation four phenotypes were to be distinguished.

The family Sa11—2, S₂ (the second self generation of plant Sa11 derived from no. 2 in the first self generation) consisted of 25 individuals. Crosses obtained within this family and the few crosses with plants from the family Sa16×Sa11 (Table 4) manifested the phenotypic uniformity of this S₂ generation.

In 21 of these plants flower fertility in self-pollination did not exceed 0.4 seed per flower and only in one plant flower fertility amounted to 2.2 seeds per flower.

The family Sa6—S₁ (the first self generation of plant Sa6) consisted of 8 individuals. The results of self-pollination and cross-pollinations within this family are assembled in Table 5.

Although the results are certainly strongly obliterated by pseudocompatibility manifested by half of the plants in the group, it seems that the data are sufficient to distinguish five phenotypes in this family:

(1) and (3); (4) and (7); (5) and (9); (6); (8). Some seeds were set by plants (1), (3), (8), and (9) from self-pollination. However, no seeds were set by the same plants from some cross-pollinations carried out at a different

Table 4

Family Sa11(2)S₂. Effects of crosses with two plants from the same family and three plants from the Sa16×Sa11 family

No. of plant ♀	♂	Sa11 (2)-S ₂		Sa16×Sa11		
		16	7	30	17	2
1		S	—	—	—	—
2		S	—	—	—	—
3		S	S	S	f*	—
4		S	—	—	—	—
5		S	S	—	F	—
6		S	S	—	—	—
7		f	S	S	F	—
8		S	S	S	F	—
9		S	S	—	—	—
10		S	S	—	—	—
11		S	S	—	—	—
12		S	S	—	—	—
13		S	S	—	—	—
14		S	—	—	—	—
16		S	S	—	F	F
18		—	S	S	F	—
19		—	S	—	F	—
20		—	S	—	—	—
21		—	f	S	—	—
22		—	S	S	F	—
23		S	S	—	—	—
24		S	S	S	—	—
25		—	S	—	—	—
27		S	S	—	—	—
28		S	—	—	—	—

* 2—3 seeds per flower.

time than the self-pollinations, though the cross pollinated flowers had not been castrated beforehand. This means that their own pollen was not always capable of fertilizing these flowers.

The family Sa10 — S₁ (the first self generation of plant Sa10) consisted of four plants only. The results of crosses carried out within the family, listed in Table 6, indicate that it can be divided into three phenotypes. Plant (5) manifested a certain degree of pseudocompatibility, whereas the other plants were completely self-sterile.

Table 5

Family Sa6-S₁. Effects of crosses with four plants from the same family

No. of plant ♀	♂	4	7	9	8	Selfs
1		F	F	S	F	f*
3		F	F	S	F	f
4		S	S	F	F	S
7		S	S	F	F	S
5		—	F	S	S	S
9		f	F	S	S	f
6		S	S	S	—	S
8		f	F	F	f	f

* f—some degree of pseudocompatibility.

In the first self generation of plant Sa16 only two individuals survived, of which one manifested complete male sterility.

Crosses. The F₁ generation of the Sa11×Sa16 cross consisted of 34 individuals. In self-pollination only two of these plants (no. 23 and 25) developed some seeds, the other 32 plants were completely self-incom-

Table 6

Family Sa10-S₁, Effects of crosses within the family

No. of plant ♀	♂	1	2	3	5
1		S	S	S	S
2		F	S	S	F
3		F	S	S	F
5*		S	F	F	S

* Plant with some degree of pseudocompatibility

patible. The results of crosses within this family and of this family with four plants from the family Sa11—S₁ and with one fertile individual from the family Sa16—S₁ are listed in Table 7.

The Sa11×Sa16 family comprised fourteen distinct phenotypes, of which nine were represented by single plants and five were composed of 8, 6, 5, 3, and 3 individuals. The results of crosses with plants Sa11—

Table 7

Family Sa11 $\times$ Sa16. Effects of crosses with three plants from the same F_1 family, four plants from Sa11-S₁ family and one plant from Sa16-S₁

No. of plant ♀	Sa11 $\times$ Sa16			Sa11-S ₁				Sa16-S ₁
	2	8	25	3	2	5	7	2
1	F	S	F	F	S	F	F	F
3	F	S	F	F	—	F	F	F
5	F	S	F	F	S	F	F	F
6	F	S	F	F	S	F	F	F
7	F	S	F	F	S	F	F	F
8	F	S	F	F	S	F	F	F
9	F	S	F	F	S	F	F	F
15	F	S	F	F	S	F	F	F
18	F	S	S	F	S	F	F	F
19	F	S	S	F	S	F	F	F
20	F	S	S	F	S	F	—	F
24	F	S	S	F	S	F	F	F
28	F	S	S	F	S	F	F	F
36	F	S	S	F	S	F	F	F
11	F	F	—	S	S	S	S	F
13	F	F	—	S	S	S	S	F
33	F	F	F	S	S	S	S	F
30	F	F	S	—	S	S	S	F
22	F	F	S	S	F	S	S	S
27	F	S	S	S	F	S	S	F
34	F	S	F	S	F	S	S	F
10	F	S	F	S	S	S	S	F
25*	F	F	S	F	F	F	F	S
17	F	S	S	S	S	S	S	F
2	S	—	—	F	S	—	—	F
4	S	S	S	F	S	F	F	S
12	S	S	S	F	S	F	F	S
23*	S	S	S	F	S	F	F	S
31	S	S	S	F	S	F	F	S
35	S	S	S	F	S	F	F	S
26	S	S	F	F	S	F	F	S
14	S	F	S	S	F	S	S	S
21	S	F	S	S	F	S	S	S
39	S	F	S	S	F	S	S	S

* Plants with some degree of pseudofertility.

S₁ (5) and (7), (they probably had exactly identical genotypes), were always the same, though crosses were not carried out at the same time, which increases the reliability of the results.

The F₁ generation of the Sa16 × Sa11 cross was composed of 32 individuals. In this family, similarly as in the preceding one, pseudocompatibility was very rare. In 22 plants self-pollination produced less than 0.5 seed per flower and only plant (24) developed 2.3 seeds per flower from self-pollination. However, plant (24) was also classified as self-incompatible, because as ♀ in crosses defined as incompatible its flower fertility ranged 1.1 to 0.12, whereas in two compatible crosses its flower fertility was 7 and 4. In nine instances of crosses defined as compatible the average flower fertility was two to three. The nine crosses were regarded as compatible because the setting of seeds by the plants used for the crosses was generally low. If these nine crosses were defined as incompatible the number of phenotypes in the family would increase.

Crosses within the Sa16 × Sa11 family and with two plants from the Sa11 — 2, S₂ (Table 8) led to the discrimination of seven phenotypes.

The number of individuals of each phenotype was as follows: 6, 6, 2, 1, 1, 6, and 10. Crosses with the plant (no. 16 and 7) from the Sa11 (2) — S₂ family gave in all cases exactly the same results, though the cross-pollinations were not all made at the same time. This in a way is a test confirming the accuracy of the experimental results.

Pseudocompatibility. In all the populations and families of this investigation pseudocompatibility was manifested to a greater or smaller degree. In some of the populations and families already mentioned the extent of pseudocompatibility was estimated by counting seeds produced by self-pollination.

In order to obtain more data on the extent of pseudocompatibility in some other families and populations flower fertility in flowers self- and cross-pollinated was compared.

The family Sa16 (2) — S₂ consisted of 41 individuals. In 22 of these plants flower fertility after self-pollination was less than 0.5 seed per flower, in 10 it ranged 0.5 to 0.9, in 8 it ranged 1 to 1.4, and in one plant flower fertility from self-pollination was 3.7.

The family C3 — S₁ was derived from the fully self-fertile plant C3 („Czerwona z Białym Końcem“ variety). The results of self-pollinations showed that of 18 plants two were completely self-sterile, 12 manifested pseudocompatibility in various degrees (unfortunately seed counts were not made), and four produced as numerous seeds from self-pollination as from cross-pollination.

In the family Sa2 × Sa11 consisting of 28 individuals the extent of

Table 8

Family Sa16 × Sa11. Effects of crosses with six plants from the same F₁ family and with two plants from Sa11(2)-S₂ family

No. of Plants ♀	Sa11 × Sa16						Sa11 (2)-S ₂	
	2	10	4	13	21	17	16	7
13	S	S	F	—	—	—	F	F
14	S	S	F	—	—	—	F	F
16	S	S	F	—	—	—	F	F
22	S	S	F	—	—	—	F	F
26	S	S	F*	—	—	S	F	F*
27	S	S	F	S	—	—	F	F
1	S	F	S	S	—	—	S	S
3	S	F*	S	—	—	—	S	S
5	S	F*	S	—	F*	—	S	S
12	S	F*	S	—	—	F	S	S
23	S	F*	S	S	—	F	S	S
24**	S	F	S	S	—	F	S	S
2	S	F	S	F	F	—	S	S
31	S	F*	S	F*	—	F	S	S
9	S	F	F	—	—	—	S	S
6	S	F	—	—	—	—	F	F
10	F	S	S	S	—	—	S	S
17	F	S	S	—	—	—	S	S
21	F	S	S	—	—	—	S	S
28	F	S	S	—	—	—	—	S
29	F	S	S	—	—	—	S	S
32	F	S	S	S	—	—	S	S
4	F	F	S	F	F	—	—	S
8	F	F	S	F	—	—	S	—
11	F	F	S	F	—	—	S	S
15	F	F	S	F	—	—	S	S
18	F	F	S	F	—	F	S	S
19	F	F	S	F	—	F	S	S
20	F	F	S	F	—	F	S	S
25	F	F	S	F	—	—	S	S
30	F	F	S	F	—	F	S	S
33	F	F	S	F	—	—	S	S

* 2-3 seeds per flower.

** Plant with higher degree of pseudocompatibility.

pseudocompatibility was small. The average fertility of self-pollinated seeds was 0 to 0.4 seed per flower and only one plant produced an average of 4.8 seeds from every self-pollinated flower.

In the family $Sa2 \times Sa16$ consisting of 26 individuals self-fertility of flowers in 14 plants was 0 to 1.4. In three plants self-fertility of flowers ranged 5.5 to 5.9 and was approximately the same as from cross-pollination. The self-fertility of the remaining individuals was intermediate.

The family $Sa16 \times Sa2$ was only self-pollinated, but the seeds were not counted. Out of 14 plants 5 were completely self-sterile, 6 produced seeds from self pollination in the same way as from free pollination, and the remaining three plants were intermediate.

Various degrees of pseudocompatibility were also manifested by 24 plants of the „Early Scarlet Globe Short Top Radish“ and 18 plants of the “Early Scarlet Globe Medium Top Radish”. In half of the plants of

Graph 1. The extent of pseudofertility in the samples of populations and the families of radishes studied

both varieties the average fertility of self-pollinated flowers ranged from 0 to 0.4, while in the other half different numbers of seeds were set after self-pollination. The highest self-fertility of flowers manifested by one plant was 6.2 seeds per flower.

Graph 1 illustrates synthetically the extent of pseudocompatibility in all the families and populations examined for this property. In spite of the different origin of the plants (selfs, controlled crosses, the progeny of freely pollinated plants) the sample as a whole is sufficiently large to illustrate the extent of pseudocompatibility in the radish varieties covered by the experiments. As is to be seen from the graph in more than 60 per cent of plants the setting of seeds from self-pollination averaged 0 to 0.4 seed per flower and in 20 per cent the setting of seeds averaged 0.5 to 1.4 seed per flower. In other plants the setting of seeds after self-

pollination was 3—4 and even to 6 seeds per flower, it was thus difficult to decide which of these plants were self-compatible and which were self-incompatible, all the more so as in crosses the average flower fertility also varied over a wide range. It is to be stressed that plants with a varying degree of pseudocompatibility were derived only from some families and populations. Other families consisted on the whole only of plants manifesting a very low degree of pseudocompatibility.

The results obtained in experiments with the cutting off of stigmas 4, 6 and 8 hours after self- and cross-pollination are assembled in Table 9a and illustrated by Graph 2.

The variance analysis shows that the fertility of self pollinated flowers (in all plants and for all times of stigma amputation) differed signi-

Graph 2. Fertility of selfed and crossed flowers from which stigmas were removed at 4, 6 and 8 hours after pollination, or remained unremoved

ficantly from the fertility of cross-pollinated flowers. Similarly significant are the differences in the average flower fertility of both these series jointly for various times of stigma amputations (Table 9b).

The earlier the stigmas were amputated the less seeds were set. This means that if the time was too short only few pollen tubes could penetrate to the style below an amputated stigma. It seems, therefore, either that even compatible pollen grains did not germinate simultaneously on a stigma or that the initial rate of growth of pollen tubes was not the same. On the other hand, there are no statistically significant differences between the fertility of self- and cross-pollinated flowers in which the stigmas were cut off after the same time from pollination. Probably the reason for the lack of statistical differences in this case was the very low

Table 9 a

Effects of removing of stigmata 4, 6 and 8 hours after self and cross-pollination on flowers fertility

Plant number	self-pollination										cross-pollination										mean fertility of plants
	stigma removed after pollination — hours					unremoved		mean fertility of plants	stigma removed after pollination—hours					unremoved							
	4		6		8	no of flow.	seed per flow.		4		6		8	no of flow.	seed per flow.						
	no of flow.	seed per flow.	no of flow.	seed per flow.	no of flow.				seed per flow.	no of flow.	seed per flow.	no of flow.	seed per flow.								
L1	11	0.0	9	0.0	16	3.0	5	1.0	1.0	9	1.3	10	4.6	13	5.3	5	5.7	4.23			
L12	10	0.0	10	0.0	10	2.7	10	6.0	2.2	10	0.0	10	1.0	10	3.1	10	4.4	2.13			
L13	6	0.0	6	0.0	7	0.0	5	1.5	0.4	6	0.1	5	4.0	5	7.2	5	7.3	4.63			
L12(1)	10	0.0	6	0.0	5	0.2	4	1.5	0.4	10	0.0	7	0.0	9	2.7	7	4.3	1.74			
Sa11	11	0.0	10	0.0	10	0.0	10	0.4	0.1	10	0.1	10	1.7	10	3.2	6	5.3	2.58			
Sa6	8	0.0	6	0.0	6	0.0	14	0.1	0.02	7	0.0	8	0.5	12	0.6	9	4.0	1.27			
C1	6	0.0	6	0.0	7	0.0	7	0.7	0.2	6	0.0	6	0.0	8	4.0	6	8.5	3.13			
C2	5	0.0	8	0.0	9	0.0	8	2.4	0.6	5	0.0	7	3.3	6	3.2	7	7.8	3.58			
C3	10	2.3	10	6.2	10	8.1	10	8.7	6.3	9	1.2	10	3.8	10	6.1	10	6.0	4.28			
C3(5)	15	0.0	11	0.1	7	0.0	10	0.5	0.15	10	0.9	13	2.1	10	3.1	16	4.2	2.56			
C3(6)	13	1.3	10	2.0	14	2.2	9	5.3	2.7	19	2.8	14	7.0	19	8.3	15	8.3	6.59			
C5	10	0.0	10	0.0	10	0.0	10	2.0	0.5	10	1.0	10	3.8	10	3.6	10	5.2	3.40			
C15	10	0.0	15	1.0	9	1.0	10	0.0	0.5	9	1.0	10	2.7	10	4.1	6	5.0	3.20			
Mean for „hours,,		0.28		0.71		1.33		2.31	1.10		0.64		2.65		4.19		5.84	3.33			

 $t_{.05}$ Sx for the differences between mean plants fertility = 2.16 $t_{.05}$ Sx for the differences between mean fertility of selfed and crossed plants = 1.31

flower fertility when stigma were cut off 4 and 6 hours after pollination. This refers to both series, i.e. both to self- and cross-pollinated flowers.

In the case of individual plants there are statistically significant differences in the fertility of self-pollinated flowers between plant C3 and all the other plants, as well as between C3 (6) — a plant in the self progeny of plant C3 — and plants L13, L12 (1), Sa11, Sa6, C1, and C15. There were, moreover, statistically significant differences between the fertility of the majority of plants pollinated with foreign pollen. However, the differences

Table 9b

Mean fertility of selfed and crossed flowers with stigma removed at 4, 6 and 8 hours after pollination compared with fertility of flowers with stigma unremoved

	Stigma removed after pollination—hours			unremoved
	4	6	8	
Flower fertility	0.92	3.36	5.52	8.15

$$t_{0.05} Sx = 1.46$$

probably consisted in the maximum possible fertility of the particular plants and not in the speed with which pollen germinated and the rate of initial pollen tube growth. Consequently there is no need to discuss them here.

The results of additional pollinations with foreign pollen of self pollinated flowers are listed in Table 10. In spite that all the plants in these experiments manifested pseudocompatibility in various degrees, after additional pollination with foreign pollen all or nearly all their progeny always consisted — except for the progeny of the cross Sa16 × Sa2 (4) — of crosses, even when the additional pollinations with foreign pollen had been made eight hours after the original self-pollination. This means that even in seemingly self-fertile plants the pollen from self-pollination developed more slowly than foreign pollen. Very interesting results in this respect were obtained with plant C3 (6) in which after self-pollination fairly numerous seeds were set and the pollen germinated rapidly (Graph 2).

DISCUSSION

Bateman's (1955) interpretation of his own results from researches on *Iberis amara* (1954) as well as of the results obtained by Riley (1932, 1936) on *Capsella grandiflora*, by Kakizaki (1930) on *Brassica oleracea* var. *capitata*, and by A. Gavin Brown (unpublished, quoted by Bateman, 1955) on *Raphanus sativus* is based on the assumption that

Table 10
Effects of self pollination and additional pollination with foreign pollen

Mother Plant	Pollinated with foreign pollen after selfing (hours)	Progeny			
		Hybrids	Selfs	Total	Percent of Hybrids
C3 (1)	0	43	—	43	100
	2	72	—	72	100
	3	27	1	28	96.4
	4	51	1	52	98.0
C3 (3)	0	28	—	28	100
	2	42	1	43	97.6
	3	40	—	40	100
	4	36	2	38	94.7
C3 (6)	0	50	5	55	90.9
	2	79	4	83	95.1
	3	57	—	57	100
	4	67	4	71	90.4
Sa10 (5)	0	79	—	79	100
	4	22	3	25	88.0
	6	49	5	54	90.7
	8	31	—	31	100
Sa6 (8)	0	37	2	39	94.8
	4	30	7	37	81.1
	6	17	—	17	100
	8	57	5	62	91.9
L12 (5)	0	6	—	6	100
	4	19	—	19	100
	6	17	—	17	100
	8	15	1	16	93.7
L14 (2)	0	5	—	5	100
	4	49	—	49	100
	6	42	—	42	100
	8	38	—	38	100
Sa16 × Sa2 (2)	0	78	—	78	100
	4	134	7	141	95.0
	6	71	3	74	95.9
Sa16 × × Sa2(14)	0	89	2	91	97.8
	4	79	4	83	95.1
	6	59	1	60	98.3
	8	45	18	63	71.4

incompatibility in crosses is caused by one locus with a series of alleles, while the pollen reaction is determined sporophytically. The results obtained later in experiments with *Brassica oleracea* (Thompson 1957, Sampson 1957a) and with *R. sativus* (Sampson 1957b) are

explained according to the same assumption. It seems that the results of this investigation demonstrate beyond any doubt the sporophytic determination of the pollen reaction. This is indicated both by the differences in the fertility of reciprocal crosses and the differences in the phenotypes of mutually sterile plants. However, there remains for consideration the problem whether all the results here reported can be explained on the assumption that in *R. sativus* there is one locus of incompatibility.

When that part of Table 1 which lists the results for the three plants Sa7, Sa10, and Sa11 is considered the mutual fertility or sterility of these individuals can be explained by assuming only one locus of incompatibility and the following genotypes (the additional assumption is that in the determination of the pistil reaction S_4 dominates over S_2 , and S_3):

Genotype	♂	S_2S_4	S_1S_2'	S_2S_3'
♂	No. of plant	Sa7	Sa10	Sa11
S_2S_4	Sa7	S	F	F
S_1S_2	Sa10	S	S	S
S_2S_3	Sa11	S	S	S

When, however, also plant Sa16 is included in these considerations it becomes impossible to define what must be its genotype if it is to be sterile in both directions with plant Sa10 and fertile with the other plants. Obviously it is absolutely impossible to explain all the results obtained for the eleven plants of the "Saxa" variety on the assumption of only one locus of incompatibility.

The results of crosses among the six plants of the „Sopel Lodu“ variety can be explained by assuming the existence of only one locus of incompatibility and of the following genotypes:

Genotype	♂	S_1S_2	S_1S_3	S_2S_3	S_3S_4	S_2S_5	S_5S_6
♀	No. of plant	L_3	K_{15}	L_7	L_{14}	L_{17}	L_{16}
S_1S_2	L_3	S	S	F	F	F	F
S_1S_3	L_{15}	S	S	S	S	F	F
S_2S_3	L_7	S	S	S	S	S	—
S_3S_4	L_{14}	F	S	S	S	F	—
S_2S_5	L_{17}	F	F	—	F	S	F
S_5S_6	L_{16}	F	F	F	F	S	S

The assumption is made, moreover, that in determining pollen reaction S_3 dominates over S_2 and S_6 over S_5 , while in determining pistil reactions

S_1 dominates over S_2 and S_5 over S_2 . Thus a population composed of six plants would have to include six different alleles of incompatibility.

Obviously the results obtained with initial populations are by no means decisive. The final conclusions can be based only on the results obtained for selfs and for the progeny of controlled crosses.

If it is assumed that incompatibility in the radish varieties covered by this investigation is determined by one locus only, then the highest possible number of genotypes in the first self generation is three and the maximum number of phenotypes is also three or two if one allele was fully dominant.

Nevertheless, the results obtained for the first self generation of plant Sa11 (Table 3) show that this generation comprised four phenotypes, while the first self generation of plant Sa6 (Table 5) comprised five. Among the four investigated individuals in the progeny of plant Sa10 there were three phenotypes and this result can be interpreted according to the hypothesis of one locus of incompatibility when the following genotypes are assumed in the plants:

Genotype	♂	S_1S_2	S_1S_1	S_1S_1	S_2S_2
♀	No. of plant	(1)	(2)	(3)	(5)
S_1S_2	(1)	S	S	S	S
S_1S_1	(2)	F	S	S	F
S_1S_1	(3)	F	S	S	F
S_2S_2	(4)	S	F	F	S

When it is assumed that incompatibility is determined by one locus and that the parent plants differ with regard to one pair of alleles the greatest possible number of phenotypes in F_1 of crosses is four. The phenotypes may be fewer if one allele dominates over the others, but their number can never be more than four. In the cross Sa11 $\times$ Sa16 the flowers of the mother plant, which to some extent manifested pseudo-compatibility, were not castrated, and thus the progeny in this experiment might have consisted partly of actual crosses and partly of selfs of the mother plant. If this was so, the maximum number of genotypes would then be seven (four crosses and three selfs), and though the number of phenotypes might be smaller it never could be greater. Nevertheless, the number of phenotypes actually distinguished in this group of plants was 14 (Table 7).

In the progeny of the reciprocal cross Sa16 $\times$ Sa11 seven phenotypes were discriminated and it may thus seem that in this case there were

four groups of crosses and three groups of selfs. However, when the results are scrutinized carefully such an interpretation must be rejected. Another possibility would be that plants Sa11 and Sa16 had one common allele, since they were both sterile with regard to Sa10. Then the genotype of Sa11 could be e.g. S_1S_2 and of Sa16 e.g. S_1S_3 , and the population derived from the cross $Sa16 \times Sa11$ and from self-pollination of Sa16 would thus consist of the following five genotypes: S_3S_3 , S_1S_1 , S_1S_3 , S_1S_2 , and S_2S_3 . Actually the number of phenotypes was seven and the supposition of one common allele must be rejected. If, on the other hand, plants Sa11 and Sa16 had no common allele, and if the genotypes of Sa11 and Sa16 were e.g. S_1S_2 and S_3S_4 respectively, then the population derived from these two plants would consist of selfs descended from the mother plant Sa16 with genotypes S_3S_3 , S_3S_4 , and S_4S_4 , as well as of crosses with genotypes S_1S_3 , S_1S_4 , S_2S_3 , and S_2S_4 . This population was crossed among others also with plants from the second self generation of plant Sa11. These selfs could have one of the following genotypes: S_1S_1 , S_1S_2 , and S_2S_2 , of which each would be fertile with regard to any of the three genotypes of selfs derived from plant Sa16. Consequently, of the seven phenotypes distinguished in the population $Sa16 \times Sa11$ at least three would have to be fertile towards plant Sa11 (2) — S_2 , which was not the case since only two such phenotypes were identified. If the plants belonging to these two phenotypes were presumable selfs of the mother plant, then the other plants — derived from the $Sa16 \times Sa11$ cross — would have to belong to five different phenotypes. Such a result would be impossible if in this experimental variety of radish incompatibility was regulated by one locus only.

Thus, in two sample populations, in three progenies of selfs (the phenotypically uniform second self generation of plant Sa11 is here disregarded), and in two progenies of crosses — a total of 103 plants — that were examined only the results for one population of six plants and for one self progeny of four plants can be interpreted on the assumption of one incompatibility locus. The behaviour in all the other groups shows that there must be more than one of incompatibility locus.

The above results are not isolated. Tatebe (1957) in experiments with eastern varieties of *R. sativus* found that incompatibility in these plants was determined by two loci*. In the progeny of one of the crosses of *R. raphanistrum* Kroh (1956) distinguished three main intrasterile groups (A, B, C) each of which he further divided into subgroups accord-

* Unfortunately I have had no access to Tatebe's report and I know of his results only from a summary in the Biological Abstracts.

ing to the behaviour of the plants in intergroup crosses. Altogether, in the progeny of one cross consisting of 12 plants K r o h identified eight phenotypes. Similarly, in populations of *B. oleracea* incompatibility seems to be determined by more than one locus. P e a r s o n (1930) reached the conclusion that in cabbages of his experiments there were two or three loci of incompatibility. In broccoli S e a r s (1937) distinguished five phenotypes in the progeny of one of the crosses, whereas M i z u s h i m a and K a t s u o (1954) working with a variety of cabbage reached the conclusion that incompatibility in their experiments was determined by two loci.

The question, therefore, arises what is the cause of the differences between the results obtained by various workers.

Experimental work on incompatibility has its own specific methods and aspects. When the phenotypes of say ten plants are to be defined accurately it is necessary to cross them in all possible combinations, i.e. 90 crosses have to be made. Because of this the number of individuals in experiments must be strictly limited. For instance, T h o m p s o n (1957) experimented with five families of cabbage consisting altogether of 62 plants; S a m p s o n (1957b) worked with 7 families of radish numbering 47 individuals; P a n d e y (1957) established the principles according to which incompatibility is inherited in *Physalis ixocarpa* from experiments on 22 individuals. P a n d e y states that the results of a further series of experiments confirmed this interpretation but she does not say what these results were. It is doubtful whether anybody would risk to explain the mechanism of heredity of e.g. the colour in flowers on so limited data.

Furthermore, there is always the danger of committing a mistake in classifying the particular crosses as compatible or incompatible. It is not only a question of pseudocompatibility which undoubtedly obliterates the experimental results. To obtain the results of crosses as early as possible S a m p s o n (1957b) defined crosses as fertile or sterile by staining the stigmata with acetocarmine 24 hours after pollination. Since the emptied pollen tube, did not, and the full ones did stain in acetocarmine, counts of the empty and full pollen grains could be made. When in one preparation composed of stigmata from four flowers there were 10 or less unstained pollen grains S a m p s o n classified the cross as sterile and when the number of unstained pollen grains was 10 to 50 as partly fertile. Crosses were defined as fertile if the number of unstained pollen grains was more than 50. The three initial plants in S a m p s o n's experiments did not set seeds in self-pollination, but "...were self-compatible by the stigma squash method" (p. 26, op. cit.). In spite of this in further ex-

periments Sampson defined compatibility by the very same stigma squash method*.

In order to estimate correctly another source of possible error in experiments on incompatibility let us consider the results obtained by Sirks (1913, quoted according to Lawrence, 1930) on *Verbascum phoeniceum*. The species is a tetraploid and has, according to Lawrence, two loci determining incompatibility. In Sirks' experiments in the F_1 generation from the first cross all the twenty plants were fertile with regard to all others (whereas the maximum possible number of phenotypes should have been 16). The situation was the same in F_1 of the cross between two plants from the first cross as well as in one more generation. It is not till the fourth generation of sib breeding that the particular phenotypes consisted of a few plants. Thus the conclusion may be drawn that if incompatibility is determined by two (or more?) loci with series of alleles, then the plants having some common alleles will be mutually compatible and sib breeding will favour the development of homozygosis. This means that researches on the genetics of incompatibility produce reliable results only when the initial parent plants were not sib bred.

In the light of what has been said above let us now consider the experimental data concerning incompatibility in *Cruciferae*. In Riley's (1932, 1936) experiments on *Capsella grandiflora* there were in the progeny of each of the particular crosses two or three intrasterile groups. However, Riley stresses that the number of incompatibility alleles cannot be established from the number of phenotypes distinguished by him, since "...many [alleles] may have been eliminated by close breeding". The seeds of *Iberis amara* which were used as the starting material by Bateman (1945b) in his investigations were collected in botanical gardens; the six initial plants in the first series of these experiments "...appeared to belong to two compatibility groups..." (p. 306, loc. cit.) and among the plants from which the material of the second series was derived cross-incompatibility was also common. This means that as a result of sib breeding homozygosis was far advanced in both initial populations. The contradictory results in experiments with cabbages and radish may be connected with the differences in the breeding of the particular varieties: in populations derived from few individuals the number of incompatibility alleles, and thus of intrasterile groups, would be smaller than in populations derived from numerous individuals where the diversity of incompatibility genotypes would be greater.

* Is it possible that in Sampson's report there is a printing error and that the above quotation should run "...were self-incompatible..." and not "self-compatible"?.

It seems that the sporophytic determination of pollen reactions in *Cruciferae* is now fully demonstrated. One of the characteristic manifestations of the sporophytic determination is the domination of some alleles by others. The consequence of this is that phenotypically identical plants may have different genotypes. In F_1 of a cross between plants belonging to two different varieties of radish Gavin Brown (unpublished, quoted according to Bateman 1955) found only two intrasterile groups and Bateman believes that these plants must have had one common allele, which means that the number of incompatibility alleles in *R. sativus* must be small. It seems, however, that the results obtained by Gavin Brown can also have a different interpretation than the one accepted by Bateman. It is conceivable that the S alleles of one variety may dominate fully over the alleles of the other variety. Then plants having two different genotypes would be indistinguishable with regard to their phenotype. E.g. there are only two phenotypes in the cross $S_1S_2 \times S_3S_4 \rightarrow S_1S_3, S_1S_4, S_2S_3, S_2S_4$ if alleles S_1 and S_2 fully dominate over alleles S_3 and S_4 . When two loci of incompatibility, of which one is in homozygous state, are assumed the result is the same: $S_1S_2Z_1Z_1 \times S_3S_4Z_2Z_2 \rightarrow S_1S_3Z_1Z_2, S_1S_4Z_1Z_2, S_2S_3Z_1Z_2, S_2S_4Z_1Z_2$. Here also there are only two phenotypes when S_1 and S_2 dominate over S_3 and S_4 .

The results of domination are two-fold: 1) the differences between the fertility of reciprocal crosses and 2) the different behaviour of intersterile plants with regard to other genotypes. For instance, in Kroh's experiments already mentioned here, the plants of group A were intersterile, but in crosses with plants from group C their behaviour differed. A similar result was obtained by Attia and Munger (1950) in cabbage. Thus, the identification of all phenotypes in a population or a family is possible only when adequate test plants are available. Indeed in the course of my investigations 14 phenotypes were distinguished in the family $Sa11 \times Sa16$ and only seven phenotypes in the family $Sa16 \times Sa11$, although it had seemed probable that actually genotypes and phenotypes would be equally numerous in both families. However, the plants in the former of these families were pollinated with pollen of plants belonging to the family itself as well as of plants having four different phenotypes — three plants from the family $Sa11$, S_1 and plant $Sa16(2)$. On the other hand in the family derived from the latter cross besides the plants from the same family only two "testers" with the same phenotypes, and probably also with the same genotypes, were used. It seems that the lack of adequate testers may have prevented the identification of all phenotypes in these two families.

None of the varieties and families in the experiments covered by this investigation manifested complete self-incompatibility. Nevertheless, most plants in the particular families were either completely self-sterile or produced not more than 0.4 seed per flower from self-pollination, though in each family there were always some plants which gave 2—3 seeds per flower and some which were seemingly completely self-fertile. Let us consider from this point of view the most interesting cases. Plants Sa11, Sa16, and Sa2 manifested some pseudocompatibility, the trait being more marked in the first two of these plants. In the second self generations of plants Sa11 and Sa16 pseudocompatibility was well marked. In F_1 of the cross Sa11 $\times$ Sa16 and of the reciprocal cross pseudocompatibility was less frequent. Similarly the degree of self-sterility was very high in the cross Sa2 $\times$ Sa11, whereas in the first generation of the cross Sa2 $\times$ Sa16 and of the reciprocal cross all the intermediate characters ranging from full self-sterility to seemingly full self-fertility appeared. In S_1 of the fully self-fertile plant C3 (Graph. 2) there were fully self-sterile, intermediate, and self-fertile individuals.

The occurrence of self-fertile individuals in the progeny of self-sterile plants was noted by Kakizaki (1930), Sears (1937) and Sampson (1957b) in *Brassica oleracea*, by Stout (1922) in *Br. Pekinensis* and *Br. chinensis*, and by Bateman (1954b) in *Iberis amara*. Pseudocompatibility in species usually self-sterile was noted by many workers, e.g. Malinowski (1916) in *R. sativus*, Kroh (1956) in *R. raphanistrum*, Odland and Noll (1950), Attia and Munger (1950) and Sampson (1957a) in *Br. oleracea*, and Owen (1942) in *Beta vulgaris*.

My experiments on the speed of pollen germination and pollen growth included 21 plants manifesting the ability for self-pollination in various degrees. Of these 21 plants in one (C3) only pollen from self-pollination germinated and grew — at least in the first stage — as rapidly as foreign pollen. In the progeny of this plant there were completely self-sterile individuals as well as individuals manifesting various degrees of self-fertility. In one of these plants — C3 (6) — pollen germinated relatively rapidly (Graph 2), but when self-pollinated flowers were additionally pollinated with foreign pollen the overwhelming majority of seeds developed from fertilization by foreign pollen (Table 10). Thus, even this plant was not fully self-fertile and it is perhaps most accurate to define it as manifesting cryptic self-incompatibility (Bateman 1956). In so far as all the other plants are concerned self-sterility, manifested in various degrees, was demonstrated beyond doubt.

All the facts assembled here confirm the opinion of Kakizaki

(1930) and Kroh (1957) that self-compatibility — or to be more accurate cryptic self-incompatibility — is determined by various alleles of the same loci that determine full self-incompatibility. It seems that the same can be said of pseudocompatibility. The based explanation of the problem is probably supplied, regardless of the actual number of loci determining self-sterility, by Bateman's hypothesis according to which different degrees of self-sterility are controlled by a definite co-operation of various alleles. The alleles may be completely or partly dominant, then one allele abolishes the effects of another allele, they may also mutually enhance or weaken their effects which results in the stronger or weaker manifestation of self-fertility.

CONCLUSIONS

1. Incompatibility in *Raphanus sativus* is determined by more than one locus with numerous alleles.
2. The determination of the pollen reaction is sporophytic.
3. Pseudocompatibility and cryptic self-incompatibility are determined by the co-operation of the same alleles that determine incompatibility.

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