# SELF-STERILITY IN *ANTIRRHINUM* AND *PETUNIA*

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## INTRODUCTION

SELF-STERILITY is widely distributed in the angiosperms, and there can be no doubt that it has arisen independently in many different families. There are many genera whose species are all self-fertile, but hardly any whose species are uniformly self-sterile. It is of interest that cultivated species are very often completely or partially self-fertile while their wild relatives are self-sterile (Brieger, 1935).

The present study is an analysis of the occurrence and inheritance of self-fertility in two cultivated plants, *Antirrhinum* and *Petunia*, whose wild ancestors are largely self-sterile.

## PART I. *ANTIRRHINUM*

Many wild species of *Antirrhinum* are found in the Mediterranean, notably in Spain, Portugal and southern France. Nearly every individual found wild is self-sterile (Gruber, 1930). All the cultivated varieties, however, are self-fertile. It is impossible to say how long *Antirrhinum* has been in cultivation, but it is supposed to have been widely distributed by mediaeval monasteries.

The plants of *Antirrhinum* studied were largely $F_2$ plants of crosses between cultivated *majus* and several wild species, e.g. *A. hispanicum* and *A. latifolium* (cf. Brieger, 1935). They were diploids, $2n = 16$.

Brieger (1935) has shown that in *Antirrhinum* self-sterility is due to a single dominant factor. The inheritance of self-sterility has recently been studied by Brieger (1930, 1935), Gruber (1930) and Gruber & Kühl (1932). There is a large series of multiple factors (S) controlling pollen-tube growth. Pollen tubes carrying an S allelomorph which is also present in the stigma pollinated are not able to develop normally or fertilize any egg. The fertility factor of *majus* overcomes the inhibiting action of the allelomorphs of *majus*, $S_m$, but not that of allelomorphs of wild species,

$S_w$. Selfing an $F_2$ plant from the cross *majus* × wild type we should expect the following behaviour:

| | | | |
|---|---|---|---|
| $F_1$ plants: | $F\,S_m$ | Gametes $F\,S_m$ functioning after selfing. | |
| | $f\,S_w$ | $F\,S_w$ not functioning after selfing. | |
| | | $f\,S_m$ functioning after selfing. | |
| | | $f\,S_w$ not functioning after selfing. | |
| $F_2$ plants: | 6 plants $F-\,--$ | All self-fertile. | |
| | 1 plant $ff\,S_m S_m$ } | Both self-sterile. | |
| | 1  „   $ff\,S_w S_m$ } | | |

The genetic formula given shows that we should expect three-quarters of the $F_2$ plants to be self-fertile and the remaining quarter to be self-sterile. This proportion had been obtained by all previous workers. It is true, as Brieger (1935) points out, that there is a shortage of recessives, but this is a phenomenon apparently common to all recessive factors segregating in the *majus* wild species crosses and is not necessarily connected with self-sterility.

The self-sterile offspring in $F_2$ should always consist of two classes of genotype, members of each class being cross-sterile with one another while members of the different classes are inter-fertile. This point has not yet been verified, and one of the original objects of this study was to test it.

If the self-steriles in $F_2$ fall into two classes we should confirm Brieger's assumption that self-sterile *majus* carries allelomorphs of **S** which are hypostatic to **F**. There is an alternative possibility, however, that *majus* carries an indifferent allelomorph which has no effect on pollen-tube development, whether the plants carry **F** or **ff**. The presence of one or of two self-sterile classes in $F_2$ would furnish a final proof of one or other genetic constitution. In the latter case the percentage of self-sterile offspring in $F_2$ would be lowered to 12·5 %. However, the exact percentage of recessives obtained in these $F_2$'s is not critical evidence, there being always, as mentioned above, a significant deficiency of recessives.

Another point arises in this connexion. As Brieger pointed out (1930) the abnormal segregation of the factor for peloric flowers (**Rad/rad**) in these crosses can best be explained by a very close or even complete linkage between this gene and the series of **S** allelomorphs. The data compiled by Gruber & Kühl (1932) and Brieger (1935) support this hypothesis. Unfortunately the factors always go into the cross in the repulsion phase, the self-fertile peloric *majus* being crossed with self-sterile normal-flowered plants. Cross-over plants were not available at the beginning of these experiments.

Below are the genetic formulae of $F_1$ and $F_2$ including F/f, Rad/rad and the two allelomorphs $S_m/S_w$:

$$F_1 \quad \frac{F\ S_m\ rad}{f\ \ S_w\ Rad} \qquad \text{Self-fertile with normal flowers}$$

$$F_2 \quad 3\ \text{plants}\ \frac{F\ S_w\ Rad}{-\ S_m rad} \qquad 3\ \text{plants}\ \frac{F\ S_m\ rad}{-\ S_m rad}$$

$$1\ \text{plant}\ \frac{f\ S_w\ Rad}{f\ S_m rad} \qquad 1\ \text{plant}\ \frac{f\ S_m\ rad}{f\ S_m rad}$$

The fact that the peloric flowers are shared in equal proportions between the self-fertile and the self-sterile plants has been ascertained by previous authors. From this we may conclude that there is almost no crossing-over between the **S** allelomorphs and the **Rad/rad** factor in the male. If no crossing-over occurs in the female either, the data would be in complete agreement, and the division of the self-steriles into two classes for sterility and for flower-shape should be identical. On the other hand, crossing-over in the female would produce, among the self-sterile offspring, two additional types:

$$\frac{f\ S_w rad}{f\ S_m rad} \quad \text{and} \quad \frac{f\ S_m\ Rad}{f\ S_m rad}.$$

The analysis of the self-sterile offspring in $F_2$ should therefore answer both these questions: (1) whether *majus* contains indifferent or active allelomorphs in the **S** locus, and (2) whether there is an appreciable amount of crossing-over between the **Rad/rad** genes and the **S** allelomorphs in the female.

The experiment as a whole was handicapped by very bad attacks of *Antirrhinum* rust (*Puccinia antirrhini*) both in 1934 and 1935, and the numbers obtained were very small. The first self-sterility test was easily carried out. Four flowers on every individual were selfed, the results being as a rule quite consistent, i.e. all fertile or all sterile. The test for sterility groups had to be started afterwards and necessitated a large number of test pollinations between brothers and sisters. Before these could be completed and the results scored the plants showed strong signs of the disease and all tended to become sterile. Thus several points could not be followed up. It was, for instance, impossible to determine exactly the crossing-over percentage. It was also impossible to decide whether all the *majus* plants contained the same allelomorph of **S** or several different allelomorphs.

In the statistical analysis the standard error has been determined, using the usual formula. For each family $d/\sigma$ has been determined, and for groups of families the $\chi^2$ sums have been calculated by adding all

the $(d/\sigma)^2$ of every family, since for monofactorial segregations giving two classes only $\chi$ is equal to $d/\sigma$. Values expected with a frequency of less than 1 in 100 were considered statistically significant. This limit corresponds closely to a deviation which is $2\frac{1}{2}$ times its standard error.

### TABLE I

*Segregation for peloric*

| Family | $N$ | No. of rad | % | $d/m$ | $\chi^2$ |
|---|---|---|---|---|---|
| 444 | 115 | 57 | 49·6 | − 0·08 | 0·006 |
| 448 | 118 | 52 | 45·6 | − 0·96 | 0·92 |
| 498 | 74 | 32 | 43·2 | − 1·17 | 1·37 |
| 499 | 107 | 62 | 58·0 | + 1·63 | 2·66 |
| 502 | 115 | 56 | 48·7 | − 0·28 | 0·08 |
| 503 | 118 | 53 | 44·9 | − 1·11 | 1·23 |
| 504 | 112 | 50 | 45·4 | − 0·96 | 0·92 |
| 505 | 115 | 58 | 50·4 | + 0·08 | 0·006 |
| 506 | 65 | 38 | 58·4 | + 1·37 | 1·88 |
| Total | 939 | 458 | $\bar{v} = 49·4$ | − 0·01 | 9·072 |

### TABLE II

*Segregation for self-fertility*

| | Family | $N$ | % of − | $d/m$ | $\chi^2$ | % of rad in self-fertiles | % of rad in self-steriles |
|---|---|---|---|---|---|---|---|
| $F_2$ | 443 | 71 | 9·9 | − 1·2 | 1·44 | — | — |
| | 444 | 117 | 12·3 | − 0·6 | 0·36 | 48·5 | 57·1 |
| | 445 | 55 | 20·0 | + 1·8 | 3·24 | — | — |
| | 448 | 112 | 9·8 | − 1·6 | 2·56 | 45·5 | 45·4 |
| | 502 | 115 | 24·3 | + 4·2 | 17·64 | 44·8 | 60·7 |
| | 504 | 111 | 5·4 | − 3·4 | 11·56 | 46·2 | 66·6 |
| | 505 | 115 | 13·0 | − 0·3 | 0·09 | 48·4 | 60·0 |
| | 506 | 63 | 15·8 | + 0·6 | 0·36 | 57·4 | 66·6 |
| | Total | 759 | $\overline{V} = 13·8$ | | | | |
| Back-cross | 446 | 95 | 50·5 | + 1·0 | 1·00 | | |
| | 447 | 68 | 39·9 | − 0·9 | 0·81 | | |
| | Total | 163 | $\bar{v} = 45·2$ | | | | |

### Results

The percentage of self-steriles obtained in eight families is given in Table II. All values are obviously smaller than the expected 25 %, and the majority are significantly different. With the exception of two values the percentage varies round the common mean of 13·8 % in a normal way, as indicated by the $\chi^2$ total. The two exceptional families with 24·3 and 5·4 % give deviations which are very significant but which are in opposite directions.

In six families the flower shape also segregated, and there were equal numbers of peloric and non-peloric plants as expected.

One of the two back-cross families gave nearly 50 % self-sterile

plants, the other only 39%. Neither differed significantly from the common mean of 45·2%.

In nine $F_2$ families for F/f the segregation of the Rad/rad factor pair has been studied as a back-cross. None of the families differed significantly from the expected value of 50% peloric, and the general mean amounted to 49·4% with $\chi^2 = 9·1$ for 9 degrees of freedom.

Thus the results agree with expectation on a basis of the results previously obtained by others. The deficiency of recessives common to these hybrids has, according to Brieger, been found only in regard to the F/f segregation and not the Rad/rad segregation.

## TABLE III

*The self-sterility groups in family 444*

| ♀ | | ♂ 15 | 25 | 68 | 94 | | |
|---|---|---|---|---|---|---|---|
| | 15 | 4 − | 3 − | 3 − | 2 − 1 + | Rad | |
| | 25 | 1 − | 4 − | 2 − | 1 − | Rad | |
| | 34 | 2 − | 2 − | 2 − | 2 − | Rad | |
| | 61 | 2 − | 1 − | 2 − | 2 − | Rad | 5 Rad − |
| | 68 | 2 − 3 + | 3 − 1 + | 4 − | 4 − | rad | 2 rad − |
| | 94 | 4 − | 3 − | 6 − | 4 − | rad | |
| | 100 | 2 − | 2 − | 3 − | 2 − | Rad | |
| | 7 | 3 + | 2 + | 4 + | 4 + | rad | |
| | 9 | 3 + 1 − | 4 + | 5 + | 4 + | rad | |
| | 47 | 3 + | 2 + | 3 + | 3 + | rad | 4 rad + |
| | 56 | 2 + 1 − | 3 + 1 − | 3 + 1 − | 4 + 1 − | Rad | 1 Rad + |
| | 114 | 3 + | 4 + | 3 + | 3 + 1 − | rad | |

We turn now to the test for group sterility. Each family which gave self-sterile offspring was subjected to such a test, but owing to the rust infection only one, 444, gave definite results. The pollen of four individuals, selected at random as test plants, was used on ten others. Emasculated flowers were used exclusively, to avoid any complication due to pseudo-fertility.

The plants clearly consist of two groups, all four test plants belonging to one group. Which is the $S_m S_m$ and which the $S_w S_m$ group cannot yet be decided (Table III).

The last column of Table III indicates the type of flower of each plant. Both sterility groups contain plants with peloric and with normal flowers, thus indicating that crossing-over has occurred in the females between $S_w/S_m$ and Rad/rad, but the numbers of plants are too small to permit of any definite statement. If however we calculate the crossing-over percentage in the usual way, with three cross-overs to nine non-cross-overs, we obtain a 25% recombination (standard error 12·5%).

## Conclusions

1. Self-fertile lines of *Antirrhinum majus* contain, in addition to the epistatic fertility factor **F**, self-sterility allelomorphs $S_m$ which cause self-sterility and cross-sterility in the usual way in **ff** homozygotes.

2. While the linkage between the factor for peloric flower (**Rad/rad**) and the self-sterility allelomorphs is very close if not complete in the male, crossing-over certainly occurs in the female. The actual recombination value could not be determined with accuracy; $25 \pm 12 \cdot 5 \%$ was found.

## PART II. *PETUNIA HYBRIDA*

In *Petunia hybrida* the present cultivated types are supposedly the offspring of two wild species, *P. violacea* and *P. nyctaginiflora*. The former is completely self-sterile and the latter self-fertile, at least as far as the types at present grown in botanical gardens are concerned (Brieger, unpublished). The first seeds are known to have been imported about a century ago. The plants I have used came from commercial seed obtained from several sources; their genetics have been studied in part by Dr Brieger. They were diploids, $2n = 14$.

Terao (1923) crossed a self-fertile and a self-sterile plant of *Petunia*. He concluded from his results that the self-fertile plant was probably heterozygous for a dominant fertility factor. The self-sterile offspring of the cross segregated into two sterility groups. Later the same author (Terao and U, 1929) met with more complicated behaviour which he was not able fully to resolve. Wergin (1936) found that in one case a dominant fertility factor was present, and believed this to be allelomorphic to the self-sterility genes. In addition he found a factor for pseudo-fertility comparable with the gene **P** described by Brieger (1926, 1930). The nature of this pseudo-fertility depended upon the particular self-sterility genes present.

The inheritance of cross-sterility of self-sterile plants is, according to Terao and U (1929), Harland & Atteck (1933) and Wergin (1936), controlled by a series of oppositional factors $S_1$, $S_2$. These multiple allelomorphs are supposed to control pollen-tube growth as originally postulated by East & Mangelsdorf (1926) for *Nicotiana Sanderae* and by Filzer (1926) for *Veronica syriaca*. However, Brieger (unpublished) has recently found that this factorial scheme is much too simple. While certain *Petunia* plants gave the simple behaviour expected on the **S** factor scheme, others gave complicated results which cannot be explained by it.

*Material*

Dr Brieger in 1934 selected one plant of the variety "Brilliant Rose" and two plants of "Blue Bedder" (from Sutton of Reading) and four plants of "Himmelsröschen" (from Haage and Schmidt, Erfurt). "Brilliant Rose" was found to be fully self-fertile. The other varieties appeared more or less pseudo-fertile or even self-fertile; but this is not certain, as the size of the capsules varied so much that a definite conclusion was impossible. These plants were all selfed in the bud and several crosses made in addition. The experiments were then carried on jointly by Dr Brieger and myself. I shall deal here with the inheritance of self-fertility and self-sterility; Dr Brieger elsewhere reports upon the relations between self- and cross-sterility in the same material.

Two of the original plants proved to be dominant self-fertile ("Brilliant Rose" and "Himmelsröschen", 12 *p* 22/1934) while the others were either self-sterile or recessive self-fertile. These two types of plant will be discussed separately. One family, the offspring of "Himmelsröschen", 4 *p* 22/1934, was found to be true-breeding for self-sterility. Another true-breeding self-sterile plant of the same variety, *p* 22/34, was not used to any extent because even fertile crosses gave only small capsules and the distinction between full fertility and pseudo-fertility was impossible; sometimes even the difference between self-fertility and self-sterility was uncertain.

A very simple technique was employed. Several flowers, at least two but often four, were pollinated after they had been open for at least one day and after the anthers had clearly burst. Pollen was used from the same flower or other flowers of the same plant. The result of the pollination could generally be seen after about a week or at the most ten days. It was found unnecessary to count the number of seeds. By comparing the capsules obtained after selfing with those from successful crosses it was always possible to classify a capsule as "sterile" or "fertile". In scoring, two degrees of fertility were distinguished, but these have not been kept separate in our discussion.

In a few instances male-sterile plants with no good pollen were found. The genetics of this character have not been studied and families containing such plants were used as little as possible.

*Dominant fertility*

One individual of "Brilliant Rose" was selfed in 1934 and gave a family of sixty-five plants the following year, all being fully self-fertile

with large and well-filled capsules. A plant was selfed again and the twelve plants grown in 1935 were all fully fertile.

Fifty plants were obtained from "Himmelsröschen", 12 *p* 22/34. Of these nearly three-quarters (thirty-nine) were self-fertile and one-quarter (eleven plants) were self-sterile. One of the self-fertile plants 1 *p* 141/35 was selfed and its offspring, forty-five plants, were again fully self-fertile.

The plant 1 *p* 141/35 was crossed with a partially fertile plant 1 *p* 135/35. All forty-five plants were fully fertile.

This seems to justify our conclusion that we are here dealing with a simple dominant gene **F** for fertility. Whether its recessive allelomorph for self-sterility is identical with any of the **S** allelomorphs, or whether these occupy another locus cannot be discussed here.

### *Recessive fertility*

I shall first give the results from selfing in the bud as far as concerns plants which gave more or less fertile offspring. Some of the 1935 plants were not scored in full detail, since the relations of self-fertility to pseudo-fertility and self-sterility were not sufficiently clear. This point was studied in more detail in 1936 and it was possible to draw a sharp line between self-fertiles on the one hand and pseudo-fertiles and self-steriles on the other. Special care was taken to use only fully developed flowers for the test pollinations, and never flowers which had just opened.

"*Blue Bedder*", 3 *BB*/34, *selfed* gave 120 plants, of which one was fully self-fertile. The self-sterile plants occasionally showed a slight tendency to pseudo-fertility. The self-fertile plant 1 *p* 133/34 was again selfed in the bud and gave twenty-five self-fertile plants and two self-sterile. Five per cent more plants proved to be completely male-sterile.

"*Blue Bedder*", 11 *BB*/34, *selfed* gave approximately three self-fertiles to one self-sterile in addition to a very large number of male-steriles. A self-fertile plant selfed gave very weak offspring consisting of twenty self-fertiles and two self-steriles.

"*Himmelsröschen*", 10 *p* 22/34, *selfed* gave two self-fertiles and eight self-steriles, in addition to a number of weaklings and male-sterile plants. This family was used only in the initial crosses, and was discarded owing to weakness and male-sterility.

"*Himmelsröschen*", 2 *p* 22/34, *selfed* gave approximately one self-fertile plant to three self-steriles, but it was difficult to distinguish between the different grades of fertility. A self-fertile plant selfed had thirteen self-fertiles and nine self-steriles. The pollen was good in all plants.

"*Himmelsröschen*", 4 *p* 22/34, has been mentioned. It was tested

through three generations and no self-fertile plants were found. The capsules after crossing are quite large.

The most striking results from these selfings are:

(1) Self-fertiles segregate apparently as recessives in small numbers, sometimes about a quarter but in the case of 3 *BB*/34 less than 1%.
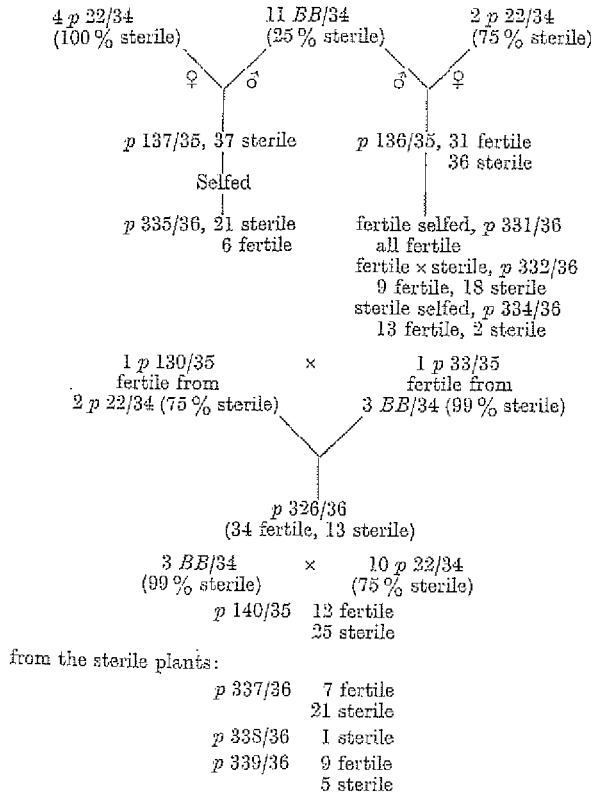


Fig. 1.

The family from 11 *BB*/34 was the only exception, giving more self-fertiles than self-steriles.

(2) The extracted recessive hypostatic self-fertile plants when selfed throw self-steriles in addition to self-fertile individuals.
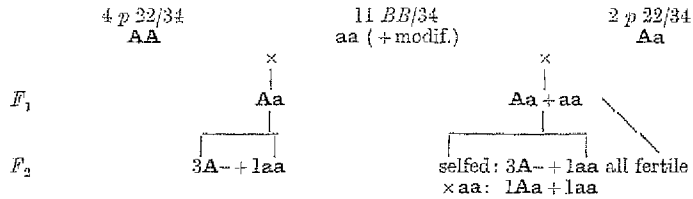
Such behaviour indicates that self-fertility cannot be controlled by one recessive gene only, but must depend on several factors, and that the balance of these sterility modifiers, as we may call them, determines the behaviour of the plants after selfing.

In all cases mentioned above the self-sterile offspring consisted of at least two self-sterile groups which were intra-sterile and inter-fertile.
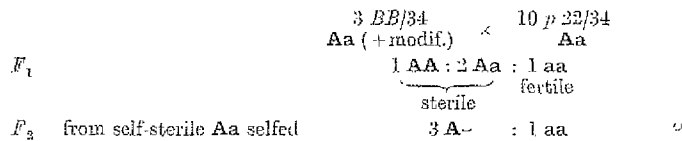
I now proceed to the results obtained from crossing plants of the five families mentioned. The types of cross and their results are summarized in Fig. 1. In the case of each of the original plants the percentage of self-fertile plants obtained after selfing has been added in parentheses.

The plant 11 $BB/34$, which gave 25% self-sterile offspring, when crossed with the true-breeding self-steriles gave only self-steriles in $F_1$ and segregated into self-steriles and self-fertiles in $F_2$. When crossed with a plant which segregated, after selfing, only 25% self-fertiles it gave a monohybrid back-cross ratio. The results of the $F_2$ can best be explained by assuming that all the self-fertiles were homozygous while the self-steriles were heterozygotes. Self-fertiles selfed thus gave only self-fertiles. Self-steriles selfed gave three self-steriles to one self-fertile, while the cross between the two gave a 1 : 1 back-cross ratio.

The following factorial scheme would explain the results quite well:

|  | 4 $p$ 22/34 **AA** | 11 $BB/34$ aa ( + modif.) | 2 $p$ 22/34 **AA** |
|---|---|---|---|
|  |  | × | × |
| $F_1$ | | Aa | Aa + aa |
| $F_2$ | | 3A— + 1aa | selfed: 3A— + 1aa all fertile<br>× aa: 1Aa + 1aa |

The plant 3 $BB/34$, which was almost completely true-breeding for self-sterility, when crossed with a plant which segregated about 25% self-fertiles after selfing, gave a ratio which may represent either a 1 : 1 or a 3 : 1. The self-steriles when selfed or intercrossed segregated into about three self-steriles to one self-fertile. The following formula would explain these results:

|  | 3 $BB/34$ Aa ( + modif.) | × | 10 $p$ 22/34 **Aa** |
|---|---|---|---|
| $F_1$ | | 1 AA : 2 Aa : 1 aa<br>sterile | fertile |
| $F_2$  from self-sterile Aa selfed | | 3 A— : 1 aa | |

We have seen that all data from crosses can be explained by assuming the existence of one recessive fertility factor a. But it must be remembered that the numbers are small, and no attempt has been made to prove the correctness of the hypothesis by statistical means. While it is possible that the data are in fair agreement even from the statistical point of view, it is equally clear that they are not decisive.

We have seen, however, that the results from selfing do not justify such a simple hypothesis. There is one more cross to be discussed which cannot be explained in a simple manner. The self-fertile extracted from 3 BB/34 was crossed to a self-fertile extracted from ♂ p 22/34. Both these plants had been extracted as "recessives" but upon selfing gave again a small percentage of the presumed dominant self-sterile type. The two plants when crossed gave thirty-four self-fertile and thirteen self-sterile plants. Their behaviour both on selfing and crossing may be due to segregation for another recessive gene, which in its turn shifts the "recessive" self-fertility to a "double-recessive" self-sterility.

We may propose as a preliminary working hypothesis the following factorial scheme. There is probably one main recessive fertility factor, provisionally called a. Its action is, however, dependent on other modifiers present. In the crosses these modifiers are randomized and balanced against each other so that the factor pair A/a has a deciding influence. The lines obtained from selfing, however, contain a selected assortment of modifiers which are physiologically unbalanced. Thus the pair A/a has not its full weight and modifier assortments may occur which are stronger in their physiological determination than A or a.

## Conclusions

The experiment on the inheritance of self-fertility and self-sterility carried out in 1934–6 has given the following results.

There are three conditions in *Petunia hybrida*:

(1) *Dominant self-fertility*, probably based upon one factor pair F/f.

(2) *Recessive fertility*, due to at least one other factor pair (called provisionally A/a). The effect of A/a is dependent upon the assortment of modifiers present.

(3) *Self-sterility*. Self-sterile plants must be ff, but may be AA, Aa or even aa, according to the particular combination of modifiers present.

It cannot be decided whether F and a are allelomorphs of the S series for self-sterility present in at least part of the self-sterile families.

All self-sterile plants segregating out in addition to self-fertile plants in the families described above fall into two or more sterility classes.

## Summary

An analysis of the genetics of self-fertility and self-sterility in *Antirrhinum* and *Petunia* has given results similar to those obtained in the analysis of certain *Nicotiana* species. In all three species there is

one dominant self-fertility factor; in *Nicotiana* this is known to be allelomorphic with the sterility factors of the **S** series. In *Antirrhinum* it is definitely not allelomorphic, while in *Petunia* the question cannot be settled on the present evidence.

In addition there are one or more modifiers which may change self-sterility into self-fertility, and this recessive type of self-fertility may be shifted again to a doubly recessive self-sterility. Brieger found a modifier of this kind in *Nicotiana Sanderae*, Gruber in *Antirrhinum*, and data referring to *Petunia* are given above. The action of this modifier depends upon the general physiological action of additional modifiers, which are responsible for the appearance of the so-called double-recessive self-sterility.

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