STUDIES ON SELF-STERILITY VI. THE GENETIC BASIS OF CROSS-STERILITY IN NICOTIANA¹

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INTRODUCTION

The first papers of this series, reporting work done at the Bussey Institution of HARVARD UNIVERSITY between 1910 and 1917, left unsettled a number of questions relating to the genetic behavior of self-sterile plants. It will be remembered that studies of hybrids between *Nicotiana alata* Lk. and Otto var. *grandiflora* Comes² and *Nicotiana Forgetiana* (Hort.) Sand. revealed the presence of cross-sterility of surprisingly regular behavior. Each of the populations studied could be divided, by means of its cross-sterility relationships, into a number of inter-fertile, intra-sterile classes. This may be somewhat clearer if we take a concrete example. The population known as family H was found to consist of three inter-fertile, intra-sterile classes which were arbitrarily named A, B and C. All of the members of each class were sterile with all the other members of that class but were fertile with the members

¹ One of a series of papers submitted to the faculty of the Bussey Institution of HARVARD UNIVERSITY in partial fulfillment of the requirements for the degree of Doctor of Science.

² Hereafter *N. alata grandiflora* will for convenience be referred to as *N. alata*.

of the other two classes. No plant in class A, for example, would set seed when pollinated with pollen from another plant in that same class, though it would set an abundance of seed when pollen from plants in classes B and C was applied. In other words, each class behaved as if it were a single self-sterile individual.

Upon examining the material histologically it was found that pollen germinated normally when applied to the stigmas of the plant on which it was produced and that the pollen-tubes grew down the style at a constant rate of speed. Under normal conditions this growth was not fast enough to allow them to reach the ovule during the "life" of the flower, and therefore no seed was obtained. Precisely the same thing occurred when the pollen was applied to the stigmas of other plants in the same class. When, however, it was applied to the stigmas of plants with which it was cross-fertile, the pollen-tube grew at an increasing rate and reached the ovule in time to cause fertilization and subsequent seed production. These phenomena were interpreted as due to the interaction of various germinal factors. According to this view, plants which were cross-sterile with each other had certain essential factors in common; plants which were cross-fertile with each other differed for some of these factors. If two plants, and hence the pollen-tube and the style, differed for these factors, a stimulus was produced which caused the accelerated growth of cross-fertile matings. When, however, as in a self-pollination or a cross-sterile pollination, the pollen-tube and the style had the same factors, there was no stimulus, no accelerated growth, and fertilization did not occur. A class, according to this view, was made up of a number of plants possessing certain essential factors in common. The present investigation was undertaken to determine the number of distinct classes in the material at hand and to study the manner of their inheritance. While it was not certain that the same system of inter-fertile, intra-sterile classes operated in *N. alata* and *N. Forgetiana* as in their hybrids, there were reasons for believing this to be the case. It was planned to determine this definitely; to find out if there were any classes common to both species; and to investigate the relations between the classes of the two species and those of their hybrids.

MATERIALS AND METHODS

Owing to the exigencies of war work, much of the seed from the earlier cultures on hand was dead when the present writer took up the problem in April 1919. Because of this unfortunate but unavoidable circumstance the work could not be prosecuted as rapidly as had at first been thought possible and it was some time before the project was well under way.

Two species of *Nicotiana* were used, *N. Forgetiana* (Hort.) Sand. and *N. alata* Lk. and Otto var. *grandiflora* Comes. As has already been explained by EAST (1913), the *N. Forgetiana* used throughout the work with self-sterility had its origin in seeds obtained from SANDER AND SONS under the name of *N. Sanderae*. *Nicotiana Sanderae* (*N. alata* $\times$ *N. Forgetiana*) is very variable in color, the flowers ranging from white through pink and magenta to purple and crimson. In size they vary greatly, although they are uniformly larger than those of *N. Forgetiana*. The plants here discussed were constant through five generations for flower size, color and form and showed not the slightest trace of *N. alata* characteristics. They were, moreover, the exact duplicates of SANDER's figure of *N. Forgetiana* published in the Botanical Magazine (No. 8006) and we therefore feel justified in supposing that they originated from seeds of pure *N. Forgetiana* which had been inadvertently mixed with the hybrid *N. Sanderae* seed.

The material was well suited to our needs. It grew splendidly under greenhouse conditions and plants could be brought into flower at practically any season of the year. Single plants could be cut back and made to flower again and again. Ninety-five percent of compatible matings were successful and there was an abundance of seed from each mating. The chief advantage for the present investigation was that the germinal factors affecting self-sterility and self-fertility were much stronger than the environmental ones. It was therefore excellent material in which to attempt to trace the course of germinal factors. Had it been otherwise, cramping the plants in pots and growing them under artificial conditions might have so obscured the effect of the germinal factors that they could not have been studied. Or if, as in many other species, the normal percentage of successes in compatible crosses had been only 50 to 75 instead of 95 it would have been much more difficult to determine whether any two plants were cross-fertile or cross-sterile.

Every precaution was taken to reduce the possibility of experimental error. All seed was planted in sterile soil. All pollinations were made upon emasculated flowers which were inclosed in paper bags. During the last few months' work when large numbers of plants were being classified, these precautions were not observed, but this was during the winter when there were no insects in the greenhouse. At all other times pollen was used only from newly-opened, bagged flowers. Whenever there was any reason to believe that pollen from nearby plants might be a source of contamination all these flowers were destroyed before the paper bag was removed. In emasculating and pollinating, the hands and instruments were washed

in 95 percent alcohol after each operation to destroy any foreign pollen. The efficacy of this method was tested in the following manner; The fingers were dusted with pollen and four pollinations were made. The hands were then rinsed very lightly with alcohol. When the remaining pollen (of which there was a liberal amount) was thoroughly dry, four additional pollinations were made on the same plant. No seeds were produced from these later pollinations, but all those made before the application of alcohol resulted in plump, well-filled capsules.

The work was done under the direction of Professor E. M. EAST to whom the writer is indebted for advice and encouragement. He is also under obligations to Miss DOROTHY MOORE for assistance with the manuscript.

REVIEW OF RECENT LITERATURE

Since the earlier papers of this series were written several interesting articles on the subject have appeared. BAUR (1919) investigated the self-fertility of several species of the *Antirrhinastrum* section of the genus *Antirrhinum* and corroborated many of EAST and PARK's (1917) observations. *Antirrhinum siculum* and a wild Spanish form of *A. majus* were fully self-fertile and set seed as well with their own pollen as when cross-pollinated. *A. tortuosum*, *A. latifolium*, and two wild forms of a Portuguese species were found to be self-sterile during the first year, although they were slightly self-fertile toward the end of the blooming season in the fall, a condition paralleled in *Nicotiana* by the end-season fertility reported by EAST and PARK. Unlike *Nicotiana*, however, these species did not regain their self-sterility with the advent of another blooming period but were very self-fertile the second year. *A. Ibanyezii*, *A. molle*, *A. glutinosum*, *A. hispanicum*, and an undetermined Spanish species were found to be fully self-sterile.

Like COMPTON (1912) and EAST and PARK (1917) BAUR found that crosses between self-sterile species gave self-sterile hybrids and that in crosses between self-fertile and self-sterile species, self-fertility behaved as a dominant. BAUR obtained an F_2 which suggested a 15 : 1 ratio and this conclusion was further borne out by the fact that the self-fertile plants differed among themselves in the expression of their self-fertility, suggesting the presence of a two-factor difference. While EAST and PARK obtained a 3 : 1 ratio, there were certain differences among the self-sterile plants which suggested an additional factor; in other words a 12 : 3 : 1 ratio, a result quite in accord with BAUR's. While BAUR was not able to investigate cross-sterility as extensively as EAST and PARK

(due in part to the nature of his material), his findings are similar. In a cross between two plants of *A. hispanicum* 31 seedlings were obtained. These could be divided by their cross-sterility and cross-fertility relationships into two inter-fertile, intra-sterile groups, approximately equal in size. One group was fertile with both parents, one sterile with one parent but fertile with the other. This is remarkably like the result reported in the present paper, obtained by crossing two plants of *N. Forgetiana*.

LEHMANN (1919) studied the self-sterile species, *Veronica syriaca*. He found inter-fertile, intra-sterile classes, pseudo-fertility, and identical behavior of reciprocal crosses as regards cross-sterility. He had been conducting experiments on this species for several years. During that time he had not found a single self-fertile individual, and had noticed that certain combinations were repeatedly cross-sterile. Accordingly a cross was made between two plants, and a first generation of 198 plants was grown. All were perfectly self-sterile. Of these, 32 were chosen for intensive experiment and 983 of the possible 992 combinations were effected, 233 pollinations being made. The 32 plants could be divided into four intra-sterile, inter-fertile classes, A, B, C and D. Of the many crosses between plants of different classes, 97.5 percent were fertile; of the many between plants of the same class only 1.1 percent set seed and these were small abortive capsules. After these four groups had been determined, crosses were made with the remainder of the first-generation plants in order to classify as many of them as possible. The relationships of 131 plants were determined. They fell into four classes in the following numbers: A, 35; B, 27; C, 37; D, 31.

As *V. syriaca* is neither wild nor cultivated in the region where LEHMANN was working, it was possible to test the cross-sterility of the classes in a very severe manner by growing representatives of each class in isolated plots and allowing insects to make the pollinations. Several plants of each class were isolated, 13 A's, 10 B's, 21 C's, and 12 D's. Of the 8964 flowers recorded on these 56 plants, 8785, or practically 98 percent, set no seed. The other 2 percent for the most part formed small abortive capsules. In fact only 5 seeds were obtained from all the plants. A check plot of plants from all the classes set an abundance of seed.

DEVRIES (1906) seems to have been the first to notice inter-fertile, intra-sterile classes among self-sterile plants. In a short note on *Linaria vulgaris* quoted by CORRENS (1916), he says:

“ . . . dass es zweierlei Arten von Löwenmaul gibt, die man allerdings von aussen nicht unterscheiden kann, die aber doch verschieden sind. Bei jedem Typus sind die einzelnen Pflanzen unter sich unfruchtbar, vereinigt man jedoch zwei Pflanzen, die

verschiedenen Typen angehören, dann gibt es eine normale und reichliche Ernte."

DEVRIES apparently went no further with the matter and there it rested until CORRENS started working with the genus in 1913. He obtained 2 plants of *Linaria vulgaris* from different localities and crossed them. Unfortunately these parent plants died before the next generation came into flower, and it was possible to test the 13 plants of the next generation only among themselves. There were 4 classes, all inter-fertile and intra-sterile, except that class D was fertile with class B when used as a male parent and sterile when used as a female. The number of plants and the number of pollinations are so small that it is difficult to say whether the same sort of thing is in operation here as in *Antirrhinum*, *Veronica* and *Nicotiana*, or whether there are really some minor differences. CORRENS described the phenomenon which EAST (1917) has called pseudo-fertility. He also noted that several cross-sterile matings yielded small abortive capsules.

SIRKS (1917) found quite a different condition in *Verbascum phoenicium*, where conditions are further complicated by the presence of true functional sterility. There was much cross-sterility but no regularity which would permit grouping into classes. Reciprocal crosses very often gave different results. There seemed to be a tendency towards dioecism and the plants could be arranged in a graded series. The extremes at one end of the series usually (about 3 times out of 4) are fertile when used as a female parent, but sterile when used as a male. At the other end are plants which seldom are fertile as females but are nearly always fertile as males.

STOUT (1920) has continued his earlier work (1916) on self-sterility and self-fertility in *Cichorium Intybus* and has made preliminary investigations in several other genera. Before considering his work it will be necessary to define certain terms. If a plant sets abundant seed with its own pollen it is called self-fertile. If it sets no seed at all it is called self-sterile. In describing these two extremes all writers are in agreement. Among self-sterile plants, however, there will be found individuals which are very slightly self-fertile. This fertility may exhibit itself as a swelling of the capsule with few or no seeds produced; in only a few cases will it approach to anything like the fertility of self-fertile plants. EAST (1917), working on *Nicotiana*, showed that it was a variant of self-sterility and named the phenomenon "pseudo-fertility." A similar condition has since been reported from *Veronica syriaca* by LEHMANN (1919), from *Linaria vulgaris* by CORRENS (1916), from *Antirrhinum* by BAUR (1919), and STOUT himself has described its occurrence in several species.

STOUT has used no term to distinguish between perfect self-fertility and this pseudo-fertility and one has to judge from his data which is meant. When he says, for instance, (STOUT 1917, p. 387) that 10 of 101 offspring of two self-sterile plants were self-fertile, one finds by turning to table 8 on pages 381-383 that the percentages of self-fertility of these plants are as follows: 6 percent, 13 percent, 63 percent, 3 percent, 11 percent, 50 percent, 4 percent, 71 percent and 73 percent. Not one of them is perfectly self-fertile, not more than two or three of them even approach to a self-fertility comparable with that of self-fertile plants, and yet they are all described as self-fertile! In the same way he has failed to distinguish between true cross-fertility and pseudo-cross-fertility. His failure to do this undoubtedly lies in the nature of his material. The pseudo-fertility of *Cichorium Intybus* is very variable, much more so than that of *Eschscholtzia californica*, for instance. In some cases it very nearly approaches to true fertility,—just how nearly cannot be calculated, since STOUT gives no complete data for crosses that are unmistakably compatible. The high percentage of failures to set seed (as compared with the percentage in *Nicotiana* for instance) is another factor which has undoubtedly tended to obscure the difference between true fertility and pseudo-fertility.

STOUT finds no end-season fertility (or progressive increase in pseudo-fertility) in *Cichorium Intybus*. While he comes to no definite conclusions as to the inheritance of self-sterility, he seems to recognize the presence of a germinal basis. In speaking of self-fertility and self-sterility he says (STOUT 1920, p. 122),

“Nevertheless, there is a tendency to heritability in these characters. Self-fertile plants³ appear to constitute from 0 to 10 percent of the progeny of self-sterile plants. . . . The offspring of self-fertile plants are more likely to be self-fertile by a proportion of about 5 to 1.”

He also goes on to say that this proportion can be changed slightly by selection.

In *Verbascum phoeniceum*, STOUT, like SIRKS (1917), found a few individuals which were almost completely sterile as males but fertile as females. Upon examination 95 percent of the pollen was found to be shrivelled and empty, showing that there is functional sterility in addition to self-sterility.

Eschscholtzia californica was found to have little pseudo-fertility. Only 1 plant out of nearly 200 grown had a self-fertility comparable with the fertility in compatible crosses. Of these plants, 128 were completely

³ Bear in mind that STOUT includes pseudo-fertile plants under the term self-fertile plants.

self-sterile, 43 bore small seedless pods, 24 had small pods with few seeds. There was no end-seasonal fertility.

Raphanus sativus was even more strongly self-sterile. Only 1 plant out of the nearly 200 grown showed any signs of pseudo-fertility.

In *Brassica pekinensis* a few of the plants showed a mid-seasonal fertility. *Linum grandiflorum* (a heterostyled species) was self-sterile and the same forms were inter-sterile.

SHULL (1923) has recently reported on the self-sterile species *Bursa grandiflora* Bois. He finds that this species is slightly pseudo-fertile and that his cultures are made up of two inter-fertile, intra-sterile classes.

PRESENTATION OF DATA

Nicotiana Forgetiana (Hort.) Sand.

Family AB (open-pollinated *N. Forgetiana*)

Nearly all the seed of *Nicotiana Forgetiana* on hand was dead; the one lot which germinated was an open-pollinated capsule which had been gathered from a field-grown plant at the end of the season. Nineteen plants were raised from this capsule and designated as family AB. One died before coming into flower. Two were strikingly different from the rest and were identical with the hybrids which had previously been made between *N. Forgetiana* and *N. alata*. It may be well to add that hybrids had been raised between *N. Forgetiana* and all the species with which it would cross and that they were all easily recognized. Inasmuch as there was every opportunity for natural crossing between these two species in the field in which the mother plants were grown, there is no reason for believing that these two plants were anything but natural hybrids between *N. Forgetiana* and *N. alata*. They were sterile with each other and fertile with all other plants with which they were crossed. The other 16 plants were all uniform. They possessed the short, deep-red flowers characteristic of *N. Forgetiana* and their corolla length accorded with that previously reported for the species by EAST (1913).

Inasmuch as the procedure followed in studying this family is typical of that followed throughout the whole investigation, it may be well to give it in some detail. In beginning the work, cross-pollinations were made between these different plants. One week after the pollinations were made the plants were re-examined and the crosses recorded as sterile or fertile as the case might be. When any two plants were found to be cross-sterile with each other on repeated trials, they were known to belong to the same intra-sterile class. Cross-pollinations of these plants

with all the other plants were then made to find out if any more plants belonged to this class. In this way the class division of the entire family was worked out. Among about forty families studied in the present investigation, not one has failed to show the division into intra-sterile, inter-fertile classes first reported by EAST and PARK (1917). While there has been an occasional sterile mating between members of different classes, this is logically to be expected and will be discussed below. Among the hundreds of plants studied, however, there has not been a single case in which a plant has been perfectly and repeatedly fertile with certain members of a class and repeatedly sterile with certain other members of the same class.

TABLE 1

Cross-pollinations within family AB. (Explanation in text).

PLANT NUMBER		CLASS l	CLASS f	CLASS g	CLASS i
2	Class l	0-3	4-0	1-0	0-0
7		0-5	2-2	1-0	1-0
15		0-2	8-0	2-0	1-0
4	Class f	3-0	2-4	1-0	1-0
10		1-2	1-10	0-0	1-0
13		3-0	0-8	1-0	1-0
16		1-1	0-5	1-0	1-0
18		3-0	0-8	1-0	1-1
19		2-0	1-7	1-0	0-0
9	Class g	3-0	7-0	0-0	1-0
14	Class i	1-0	6-1	1-1	0-0

The same cross-sterility relationships that had been observed in other self-sterile species of *Nicotiana* were found to obtain in *N. Forgetiana*. The 13 plants which came into flower during the time that family AB was studied, fell into five inter-fertile, intra-sterile classes. One of these classes, as has already been explained, contained 2 *N. Forgetiana* $\times$ *N. alata* hybrids. Table 1 summarizes the results of cross-pollinations with the 4 *N. Forgetiana* classes. The number of sterile and fertile combinations with each class is given for each individual. The first number in each case represents the fertile matings, the second represents the sterile ones.

Plant No. 2, for instance, was in no case fertile with other members of class l and was sterile in 3 crosses with them. It was fertile with members of class f four times, with members of class g once, and was not crossed with class i. It will be seen that only two of the thirty crosses between members of the same class were fertile. In one of these only a very small capsule was produced. It might seem from the table that there were four instead of two fertile crosses. This is because each pollination is entered twice in the table, once from the male side and once from the female. The cross-pollinations made with members of family AB *outside* the family will be discussed later. Suffice it to say that they upset all expectations by showing these four classes to be distinct from any with which they were crossed, either the classes of *N. alata* or those of the [*N. alata* $\times$ *N. Forgetiana* hybrids.

Family AD(7-AB $\times$ 18-AB)

For several reasons *N. Forgetiana* was not as satisfactory to work with as the hybrids between *N. alata* and *N. Forgetiana*. The flowers were smaller and not as easy to emasculate. In a problem involving thousands of controlled pollinations this is a serious hindrance. Furthermore, while plants of this species could be brought into bloom a second and third time, they did not, like the hybrids, regain anything like their former vigor. For these reasons little work was done with *N. Forgetiana*. A second generation was grown, however, from a cross between plant number 7 of class l and plant number 18 of class f. Ninety-four plants were grown, but a number of them died or became diseased before they were classified. The results on the remaining 86, known as family AD, are summarized in table 2. The plants fell into two classes of 41 and 45 plants.

TABLE 2
Summary of cross-pollinations within family AD (7-AB $\times$ 18-AB).

	NUMBER OF TIMES STERILE		NUMBER OF TIMES FERTILE	
	With class l	With class f	With class l	With class f
Class l	150	14	6	134
Class f	14	164	134	4

Results of cross-pollinations between families AD and AB

At the time when cross-pollinations were made between the two families, the parent plants of family AB were well along in their third blooming

period and were not at all vigorous. Whereas, during the first blooming period they had all been well over one meter high, there were now few that approached the half-meter mark and most of them had short, unbranched flower-stalks with only a few flowers. A preliminary test showed a high degree of pseudo-fertility. It might have been expected, therefore, that the back-crosses would give a high degree of pseudo-fertility. The results are shown in table 3.

TABLE 3

Cross-pollinations between family AB and family AD.

Number of sterile matings

	CLASS l-AB	CLASS f-AB	CLASS g-AB
Class l-AD	3	0	0
Class f-AD	0	10	0

Number of fertile matings

	CLASS l-AB	CLASS f-AB	CLASS g-AB
Class l-AD	5	10	6
Class f-AD	6	5	5

There is certainly a high degree of pseudo-fertility but there are no sterile crosses between members of different classes. A few of these plants were kept until the next blooming period. Preliminary tests showed a comparatively low degree of pseudo-fertility. Out of 10 self-pollinations only 1 set seed, and that resulted in a small capsule. Cross-pollinations between these few plants yielded the results shown in table 4.

TABLE 4

Additional cross-pollinations between families AB and AD.

	CLASS l-AB	CLASS f-AB
Number of sterile matings		
Class l-AD	4	0
Class f-AD	0	5
Number of fertile matings		
Class l-AD	0	4
Class f-AD	3	0

By themselves, these results do not give conclusive proof of the identity of classes l and f of family AB with those of family AD. The more numerous data on similar crosses are all in accord with such an interpretation.

Nicotiana alata Lk. and *Otto* var. *grandiflora* Comes

Very little was done with this species, as it was even less satisfactory than *N. Forgetiana*. When grown in pots it has very few flowers and it is not possible to make as large a number of cross-pollinations as is desirable. This condition is aggravated by the fact that because of the extremely long flowers the pistils very often become injured in bagging and unbagging the inflorescence. Furthermore, this species is much more susceptible to leaf mosaic, rendering it difficult to keep parent plants for back-crosses.

Twenty-three plants, designated as family AC, were grown from an open-pollinated capsule of *N. alata*. Not all of them came into flower and it was possible to classify only 18. As shown in table 5, they fall into 3 inter-fertile, intra-sterile classes.

TABLE 5
Cross-pollinations within family AC (open-pollinated N. alata).

	CLASS o	CLASS m	CLASS p
Class o (5 plants)	0-16	19-0	13-0
Class m (6 plants)	19-0	0-14	14-1
Class p (6 plants)	13-1	14-1	2-12

In this table the first figure represents the number of fertile matings, the second the number of sterile matings. The plants of class o, for instance, have sixteen times been sterile with each other and have never been fertile. The 19 matings between classes m and o have all been fertile. The 14 between o and p have been fertile with one exception.

To summarize the results obtained within the two species:

1. The mechanism of cross-sterility in *N. alata* and *N. Forgetiana* is the same as that previously reported for their hybrids.
2. Four inter-fertile, intra-sterile classes were found in 11 plants grown from an open-pollinated seed capsule of *N. Forgetiana*. A cross between two of these classes gave a family the plants of which belonged half to one of these classes and half to the other.
3. Three classes were found in 19 plants grown from an open-pollinated capsule of *N. alata*.

Nicotiana Forgetiana $\times$ *N. alata*

EAST and PARK (1917) studied the progeny of two crosses between *N. alata* and *N. Forgetiana*. Most of the present investigation is concerned with descendants of these two crosses. Diagram 1 shows the relationships

between the various "families."⁴ Each family is inclosed in a bracket. The capital letter above the bracket is the "short-hand" name of the family and agrees with those used in the earlier papers of this series.

CROSS NO. 2.

DIAGRAM 1.—The pedigree of the families of cross No. 2 discussed in this paper. The large letters designate the families, and the small letters are the symbols of the included inter-fertile, intra-sterile classes.

⁴ In the following discussion "family" means a number of plants resulting from a single cross-pollination or self-pollination.

The small letters beneath the bracket are the symbols for the various inter-fertile, intra-sterile classes. Whenever two or more classes are known to be identical in their sterility and fertility relationships they are given the same symbol. To avoid confusion through duplication the class names have been changed and do not agree with those used in the earlier papers.

The results of cross-pollinations within the families will be considered first, deferring the consideration of crosses between the families, in so far as it is possible.

Family L ($H-32 \times F_1-44$)

This family resulted from a cross between a plant in family H and one of its parents. It was found to consist of two classes, a and c, containing 18 and 24 plants, respectively. The results of cross-pollinations with this family are summarized in table 6.

TABLE 6
Summary of cross-pollinations in family L.

	WITHIN FAMILY L		OUTSIDE FAMILY L			
	Class a	Class c	Class a	Class b	Class c	Class d
Sterile with class a....	76	3	14	0	2	0
Fertile with class a....	8	52	0	7	6	1
Sterile with class c....	3	62	2	1	11	0
Fertile with class c....	52	0	5	6	0	0

Family M ($H-317 \times F_1-44$)

This family arose from a cross similar to that which produced family L. It originated from a cross between a plant in the same class of family H back-crossed to the same parent plant. It was found to contain the same two classes as family L. There were 21 individuals belonging to class a and 22 belonging to class c. Table 7 summarizes the results:

TABLE 7
Summary of cross-pollinations with family M.

	WITHIN FAMILY M		OUTSIDE FAMILY M					
	Class a	Class c	Class a	Class b	Class c	Class d	Class x	Class y
Sterile with class a...	60	4	11	0	1	11	0	0
Fertile with class a...	0	63	0	4	11	4	1	0
Sterile with class c...	4	78	3	0	15	0	0	0
Fertile with class c...	63	2	11	3	0	2	1	1

Family N ($H-373 \times F_1-44$)

Families N and O originated from back-crosses with two plants of another class of family H, and the same parent plant used in the two previous back-crosses. Family N was found to consist of two classes, a and b. There were 10 plants in class a and 7 plants in class b. Table 8 summarizes the results.

TABLE 8
Summary of cross-pollinations with family N.

	WITHIN FAMILY N		OUTSIDE FAMILY N				
	Class a	Class b	Class a	Class b	Class c	Class d	Class y
Sterile with class a...	22	2	8	0	1	0	0
Fertile with class a...	2	16	0	3	4	1	3
Sterile with class b...	2	8	0	5	0	0	0
Fertile with class b...	16	0	8	0	5	1	0

Family O ($H-335 \times F_1-44$)

Family O was found to consist of these same two classes. There were 22 plants belonging to class a and 21 plants belonging to class b. Table 9 summarizes the results.

TABLE 9
Summary of cross-pollinations with family O.

	WITHIN FAMILY O		OUTSIDE FAMILY O						
	a	b	a	b	c	d	r	x	y
Sterile with class a.....	68	3	19	0	0	0	0	0	0
Fertile with class a.....	0	68	0	9	15	1	0	3	1
Sterile with class b.....	3	42	4	10	1	0	0	0	0
Fertile with class b.....	68	2	14	0	15	6	4	2	2

Family P ($H-36 \times H-354$)

Families P, Q, R, X, Y, Z and AA were the results of seven different crosses between various members of the same two classes of family H that had been back-crossed to produce families L, M, N and O. Family P was found to consist of 28 plants of class a and 17 plants of class b. The results are summarized in table 10.

TABLE 10

Summary of cross-pollinations with family P.

	WITHIN FAMILY P		OUTSIDE FAMILY P					
	a	b	a	b	c	d	r	x
Sterile with class a.....	110	7	11	1	2	0	0	0
Fertile with class a.....	0	61	0	1	11	0	0	1
Sterile with class b.....	7	14	1	6	0	0	0	0
Fertile with class b.....	61	0	16	1	10	3	1	2

Family Q(H-324 × H-367)

Family Q was found to consist of 13 plants of class a and 21 plants of class c. The results are summarized in table 11.

TABLE 11

Summary of cross-pollinations with family Q.

	WITHIN FAMILY Q		OUTSIDE FAMILY Q				
	a	c	a	b	c	d	x
Sterile with class a...	14	4	9	1	0	0	0
Fertile with class a...	2	29	0	5	4	1	0
Sterile with class c...	4	92	0	0	16	1	0
Fertile with class c...	29	0	16	7	0	1	3

Family R(H-362 × H-381)

Family R contained 17 plants of class a and 20 plants of class c. The results are summarized in table 12.

TABLE 12

Summary of cross-pollinations with family R.

	WITHIN FAMILY R		OUTSIDE FAMILY R					
	a	c	a	b	c	d	x	y
Sterile with class a.....	36	2	9	0	0	0	0	0
Fertile with class a.....	2	42	1	17	11	1	0	0
Sterile with class c.....	2	44	0	0	16	0	0	0
Fertile with class c.....	42	0	17	10	0	1	3	1

Family X(H-381 $\times$ H-321)

Family X consisted of 10 plants of class a and 5 plants of class c. The results are summarized in table 13.

TABLE 13
Summary of cross-pollinations with family X.

	WITHIN FAMILY X		OUTSIDE FAMILY X			
	a	c	a	b	c	y
Sterile with class a.....	22	0	4	0	0	0
Fertile with class a.....	2	3	0	7	5	1
Sterile with class c.....	0	0	0	0	7	0
Fertile with class c.....	3	0	4	4	0	0

Family Y(H-382 $\times$ H-354)

Family Y consisted of 7 plants of class a and 9 plants of class b. The results are summarized in table 14.

TABLE 14
Summary of cross-pollinations with family Y.

	WITHIN FAMILY Y		OUTSIDE FAMILY Y				
	a	b	a	b	c	x	y
Sterile with class a...	8	1	5	0	0	0	0
Fertile with class a...	0	8	0	4	4	1	1
Sterile with class b...	1	20	0	5	0	0	0
Fertile with class b...	8	0	9	2	3	0	0

Family Z(H-354 $\times$ H-373)

Family Z consisted of 5 plants of class a and 9 plants of class b. The results are summarized in table 15.

TABLE 15
Summary of cross-pollinations with family Z.

	WITHIN FAMILY Z		OUTSIDE FAMILY Z			
	a	b	a	b	c	x
Sterile with class a.....	12	0	6	0	0	0
Fertile with class a.....	0	9	0	2	2	0
Sterile with class b.....	0	16	0	3	0	0
Fertile with class b.....	9	0	8	0	2	3

Family AA(H-381 $\times$ H-322)

Family AA consisted of 6 plants of class a and 10 plants of class c. The results are summarized in table 16.

TABLE 16

Summary of cross-pollinations with family AA.

	WITHIN FAMILY AA		OUTSIDE FAMILY AA				
	a	c	a	b	c	d	r
Sterile with class a...	18	0	5	0	0	0	0
Fertile with class a...	0	9	1	6	4	0	1
Sterile with class c...	0	8	0	0	11	0	0
Fertile with class c...	9	0	2	2	0	1	0

Family W(F₆ of cross No. 1)

This family was a sixth-generation descendant of cross No. 1. It was found to consist of two classes, x and y, containing 13 and 18 plants, respectively. Table 17 summarizes the results.

TABLE 17

Summary of cross-pollinations with family W.

	WITHIN FAMILY W		OUTSIDE FAMILY W			
	x	y	a	b	c	d
Sterile with class x.....	22	2	0	0	0	0
Fertile with class x.....	0	7	6	8	10	2
Sterile with class y.....	2	4	0	0	0	0
Fertile with class y.....	7	0	8	2	3	2

Family S(J-473 selfed)

As has already been discussed by EAST and PARK (1917), it is occasionally possible to self-fertilize these self-sterile plants and obtain a small capsule of seed. Two such selfings of plants in family J were grown. One of them, family T, was discarded because the plants were diseased. The other, family S, consisted of only one class, a further corroboration of EAST's earlier work. The results with this family are summarized in table 18.

TABLE 18
Summary of cross-pollinations with family S.

	WITHIN FAMILY S	OUTSIDE FAMILY S				
	d	a	b	c	x	y
Sterile with class d.	116	1	0	2	0	0
Fertile with class d.	2	11	8	14	2	2

Family U(D-175 selfed)

Family U resulted from a selfing of a plant in family D. Six plants were grown. Three of them belonged to class b and three to class r.

Family V(F₁-10 × *N. alata*)

Family V resulted from back-crossing one of the first-generation plants of cross No. 2 to a plant of *N. alata*. It was in a sense similar to families D and E, which had resulted from similar back-crosses. It was found to consist of 13 plants of class a and 18 plants of class c. The results are tabulated in table 19.

TABLE 19
Summary of cross-pollinations with family V.

	WITHIN FAMILY V		OUTSIDE FAMILY V						
	a	c	a	b	c	d	r	x	y
Sterile with class a.	14	3	9	1	0	0	0	0	0
Fertile with class a.	0	33	0	3	5	0	1	0	1
Sterile with class c.	3	70	5	0	13	1	0	0	0
Fertile with class c.	33	0	13	4	0	9	1	3	0

The remainder of the families were grown in very small numbers and no more crosses were made than were necessary to establish the number of classes present and to determine their identity or non-identity with the classes already studied.

Family AH(L-18 × L-20) was found to consist of 8 individuals of class b and 9 individuals of class c.

Family AI(M-30 × M-25) consisted of 9 individuals of class b and 11 individuals of class c.

Family AL(O-32 × O-46) consisted of 8 individuals of class b and 12 of class c.

Family BO($R-2 \times O-2$) consisted of 4 individuals of class a and 6 of class b.

Family BP($N-7 \times R-12$) consisted of 6 individuals of class a and 4 of class c.

Family AO($AA-2 \times AA-13$) consisted of 6 individuals of class b and 4 of class c.

Family AP($R-20 \times R-13$) consisted of 7 individuals of class a and 9 individuals of class b.

Family AT($P-27 \times O-2$) consisted of 11 individuals of class b and 6 individuals of class c.

Family AS($W-1 \times W-5$) had resulted from a cross between the two classes of family W, a descendant of the first cross. No parent plants were available for testing the relationships of the class of family W with those of family AS. The latter was found to consist of two classes, class dd with 8 individuals, and class df with 6.

Families AY($M-21 \times W-11$) and AZ($X-15 \times W-17$) resulted from two crosses between family W and cross No. 2. Family AY consisted of 2 plants of class sa, 3 of class sb, 6 of class sc, and 1 of class sd. Family AZ consisted of 4 plants of class ra and 5 plants of class rb.

The results for all the families are summarized in table 20.

TABLE 20
Summary of all families.

NAME	ORIGIN	CLASSES PRESENT AND NUMBER OF PLANTS IN EACH			
Family L	H-328 $\times$ F ₁ -44	18-a	24-c		
Family M	H-317 $\times$ F ₁ -44	21-l	20-c		
Family N	H-373 $\times$ F ₁ -44	10-a	7-b		
Family O	H-335 $\times$ F ₁ -44	22-a	21-b		
Family P	H-376 $\times$ H-354	28-a	17-b		
Family Q	H-324 $\times$ H-367	13-a	21-c		
Family R	H-362 $\times$ H-381	17-a	20-c		
Family X	H-381 $\times$ H-321	10-a	5-c		
Family Y	H-382 $\times$ H-354	7-a	9-b		
Family Z	H-354 $\times$ H-373	5-a	9-b		
Family AA	H-381 $\times$ H-322	6-a	10-c		
Family S	J-473 selfed	41-d			
Family T	J-489 selfed	?	?		
Family U	D-175 selfed	3-b	3-r		
Family V	F ₁ -10 $\times$ <i>N. alata</i>	13-a	18-c		
Family W	Cross No. 1, F ₅	10-x	8-y		
Family AB	<i>N. Forgetiana</i>	7-f	4-l	2-g	1-i
Family AC	<i>N. alata</i>	6-o	6-p	5-m	
Family AD	AB-7 $\times$ AB-18	40-l	45-f		

TABLE 20 (continued)

Summary of all families.

NAME	ORIGIN	CLASSES PRESENT AND NUMBER OF PLANTS IN EACH			
Family AH	L-18 × L-20	8-b	9-c		
Family AI	M-31 × M-25	9-b	11-c		
Family AL	O-32 × O-46	8-b	12-c		
Family AO	AA-2 × AA-13	6-b	4-c		
Family AP	R-20 × R-13	7-a	9-b		
Family AR	R-38 × L-24	13-b	7-c		
Family AT	P-27 × O-2	11-b	6-c		
Family AS	W-1 × W-5	8-dd	6-df		
Family AY	M-21 × W-11	2-sa	3-sb	6-sc	1-sd
Family AZ	X-15 × W-7	4-ra	5-rb		
Family BO	R-2 × O-2	4-a	6-b		
Family BP	N-7 × R-12	6-a	4-c		

TABLE 21

Summary of cross-pollinations between classes. x=fertile, o=sterile.

a	b	c	d	e	r	l	f	g	i	m	o	p	sa	sb	sc	sd	ra	rb	ga	gb	gc	x	y	dd	df	h
o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	a
	o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	b
		o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	c
			o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	d
				o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	e
					o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	r
						o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	l
							o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	f
								o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	g
									o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	i
										o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	m
											o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	o
												o	x	x	x	x	x	x	x	x	x	x	x	x	x	p
													o	x	x	x	x	x	x	x	x	x	x	x	x	sa
														o	x	x	x	x	x	x	x	x	x	x	x	sb
															o	x	x	x	x	x	x	x	x	x	x	sc
																o	x	x	x	x	x	x	x	x	x	sd
																	o	x	x	x	x	x	x	x	x	ra
																		o	x	x	x	x	x	x	x	rb
																			o	x	x	x	x	x	x	ga
																				o	x	x	x	x	x	gb
																					o	x	x	x	x	gc
																						x	x	x	x	x
																							o	x	x	y
																								o	x	dd
																									o	df
																										h

Cross-pollinations between the families

The same procedure was followed in establishing the relations between the classes of the different families as had been followed in working with the individual families. If crosses between two classes in different families were repeatedly sterile the two classes were known to be identical and were given the same symbol. These data are summarized in table 21. The data for each family have already been presented in tables 6 to 19.

If there had been any need for more proof of the reality of this system of inter-fertile, intra-sterile classes, it was given when all the classes a, all the classes b, and all the classes c, were crossed together. From the results obtained, the a's might all have been from one family, or the b's, or the c's. Each individual was sterile with all the other members of that class—no matter from what family—and fertile with members of all other classes. There were a few exceptions, to be sure, but they formed less than four percent of the cases, and none of them could be duplicated by repeating the same pollination. *There was not a single instance in which a plant was repeatedly sterile with certain members of a class and repeatedly fertile with certain other members of the same class.* Table 22 summarizes the results of these inter-family crosses.

DISCUSSION

Working hypothesis

The following were among the facts established by the earlier work on the subject:

1. Self-sterility is heritable.
2. Under normal conditions, the pollen-tubes produced by pollen from any self-sterile plant will not grow in the styles of that plant with a rapidity sufficient to reach the ovules during the "life" of the flower.
3. Similarly, under normal conditions, the pollen-tubes of this plant will not grow in the styles of any other plant with which it is cross-sterile with a rapidity sufficient to reach the ovules during the "life" of the flower.
4. Pollen-tubes from pollen of cross-fertile plants will grow with a rapidity sufficient to allow fertilization.

This work had suggested certain conclusions and from them the following working hypothesis was assumed in beginning the present investigation:

The phenomena of 2, 3 and 4 are due to the action of certain essential factors. When two plants—and hence the pollen-tube and the style—

differ for these factors, a stimulus is produced which causes the accelerated growth of cross-fertile matings. When, on the other hand, as in 2 and 3, the pollen-tube and the style have the same essential factors in common, there is no stimulus and no accelerated growth. These essential factors are heritable and given suitable material, it should be possible to demonstrate their presence and the manner of their inheritance.

Number of classes

As little had previously been done in identifying the classes of different families with one another, a number of questions immediately presented themselves:

In these crosses between *N. alata* and *N. Forgetiana* are we dealing with a few classes or with a great many? Would we obtain these same classes upon making further crosses between the two species or would we obtain different ones? Is the mechanism of cross-sterility the same in the pure species as in the hybrids? Can we find any of these same classes (and hence the same factors) in *N. alata* and *N. Forgetiana*? How are these classes passed on from generation to generation?

Some of these questions can now be answered definitely: In the first place, there are many more classes than had at first been suspected. In the more or less inbred descendants of cross No. 2 between *N. alata* and *N. Forgetiana* there are at least five and perhaps six different classes, the relationships between two of them never having been determined. In the sixth generation descendants of the first cross (family W) there were two classes which were distinct from the five classes of the second cross with which they were tried. A seventh generation was grown from these plants (family AS) and was found to contain two classes. It was not possible to test them with the parent plants of family W. They were, however, different from any of the classes with which they were crossed. There were at least four classes in the few *N. Forgetiana* plants grown, and three classes in the *N. alata* plants. These seven classes were distinct from each other and from all the other classes with which they were tested. In crosses between family W and cross No. 2, seven classes were obtained. They were all different from each other, from the parent classes, and from all other classes with which tests were made.

All of these data are summarized in table 22 where the inter-fertility relationships of these 27 classes are indicated. We have good reason to believe that the two classes of family AS, dd and df, may be the same as the two parent classes, x and y, of family W. It is also quite possible that class r and class e are identical. All other cases in which nearly related

families might have been expected to contain identical classes have been adequately tested. This leaves 24 classes. In so far as they have been tested, the 24 are all distinct from one another and there is little reason for believing that each one is not distinct from every other one.

In the present investigation we have grown a few more or less inbred descendants of two crosses between *N. alata* and *N. Forgetiana*; two crosses between these two strains; a few plants from an open-pollinated capsule of *N. Forgetiana*; and a few plants from an open-pollinated capsule of *N. alata*. In these few samples 24 classes have been found. It seems probable that in the two species and in the various combinations between them, there must be a great many more possible classes. If this be true it is not at all surprising that the two crosses made by EAST and PARK (1917) differed considerably as regards their class behavior.

Hereditary nature of classes

There was every indication that these classes have a genetic basis. This phase of the work is being continued and for the present the evidence may be summarized as follows:

1. Nearly related families possessed certain classes in common, while the classes of more distantly related families were all distinct from one another.
2. The same classes appeared in successive generations.
3. While the details are yet to be worked out, the classes are apparently inherited in regular Mendelian fashion.

These points are demonstrated in diagram 1. There it will be seen that all of the more or less inbred descendants of family H consisted of only three classes and that there was a certain regularity in the manner of their inheritance. Families U, V and E, less nearly related, contain some of these same classes and certain others which are distinct. The classes in cross No. 2 are distinct from those in cross No. 1, as are also the classes in *N. alata* and *N. Forgetiana*.

SUMMARY

1. The same system of inter-fertile, intra-sterile classes was found to exist in *N. Forgetiana* and in *N. alata* as had previously been found to occur in their hybrids and in other self-sterile species of *Nicotiana*.
2. Among the few strains of *N. Forgetiana*, *N. alata*, and *N. alata* $\times$ *N. Forgetiana* that were studied in the present investigation, there were at least 24 such classes. There must be many more in the two species as a whole. From one open-pollinated capsule of *N. Forgetiana* 4 classes were

TABLE 23
Tabular comparison with other work on self-sterility.

MATERIAL	REPORTED BY	CROSS-STERILITY	INTER-STERILE CLASSES	PSEUDO-FERTILITY	CLASSES INHERITED	STERILITY RECESSIVE IN CROSSES WITH SELF-FERTILE SPECIES
<i>Nicotiana glauca</i>	ANDERSON (this paper)	—	—	—	—	—
<i>N. Forgetiana</i>	ANDERSON (this paper)	—	—	—	—	—
<i>N. glauca</i> × <i>N. Forgetiana</i>	{ EAST and PARK (1917) } ANDERSON (this paper)	—	—	—	—	—
<i>N. commutata</i>	EAST and PARK (1917)	—	—	—	—	—
<i>N. commutata</i> × <i>N. Forgetiana</i>	EAST and PARK (1917)	—	—	—	—	—
<i>N. angustifolia</i>	EAST and PARK (1917)	—	—	—	—	—
<i>N. glutinosa</i>	EAST and PARK (1917)	—	—	—	—	—
<i>Linaria vulgaris</i>	{ DEVRIES (1906) } { CORRENS (1912-1916) }	—	—	—	—	—
<i>Antirrhinum hispanicum</i>	BAUR (1919)	—	—	—	—	—
<i>Veronica syriaca</i>	LEHMANN (1919)	—	—	—	—	—
<i>Cardamine pratensis</i>	CORRENS (1912)	—	—	—	—	—
<i>Reseda odorata</i>	COMPTON (1912)	—	—	—	—	—
<i>Bursa grandiflora</i>	SHULL (1923)	—	—	—	—	—

obtained; from a similar capsule of *N. alata* 3 classes were obtained. These 7 classes were all distinct from each other and from classes in the hybrids.

3. These phenomena are interpreted as due to the action of certain factors. Plants which are cross-sterile with each other (which belong to the same class) have certain essential factors in common. Plants which are cross-fertile with each other (which belong to different classes) differ for these factors.

4. These factors are germinal and are passed down from generation to generation. Two lines of evidence point to this interpretation: a. The common possession of certain classes by nearly related families and the absence of any classes in common by families less closely related. b. The regularity with which these classes appear in subsequent generations.

This, then, is the status of the self-sterility problem in *Nicotiana*. Table 23 shows how certain of these results have been confirmed by the work of other investigators. This close corroboration justifies the suggestion that the conditions reported here may be somewhat general among self-sterile plants.

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