STUDIES ON SELF-STERILITY. III. THE RELATION BETWEEN SELF-FERTILE AND SELF-STERILE PLANTS

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INTRODUCTION

In the first paper of this series (EAST and PARK 1917), where the behavior of self-sterile plants was described in some detail, it was pointed out that the difference between self-fertile and self-sterile plants might prove to be a wholly different problem. This statement has been overlooked by several reviewers who criticized the interpretation of the behavior of self-sterile plants proposed because it failed to take into account the phenomenon of self-fertility. The prediction was not made at random, however. Even at that time various data had been gathered indicating a simple one-factor difference between self-fertile and self-sterile plants in keeping with COMPTON'S previous work (1912) on *Reseda odorata*. It can now be stated unequivocally that the position then taken is correct. In the material investigated self-fertile plants differ from self-sterile plants by a single essential Mendelian factor. Self-fertility is dominant. Adopting a presence-and-absence mode of expression, a plant is self-fertile because of the presence of a determiner for self-fertility; when this determiner is absent, the individual is self-sterile.

COMPTON'S WORK ON RESEDA

The only investigation in which crosses between self-fertile and self-sterile plants have been studied is that of COMPTON (1912, 1913) on the mignonette, *Reseda odorata*. Having had his attention directed to the species by the observations of Darwin, a number of experiments were made with the following results:

(1) Self-sterile plants intercrossed produced only self-sterile offspring. (2) Certain self-fertile plants when self-fertilized threw approximately 3 self-fertile to 1 self-sterile offspring. (3) These same plants when crossed with self-sterile individuals, produced self-fertiles and self-steriles in the ratio one to one. (4) Other self-fertile plants yielded none but self-fertile offspring from selfed seed.

These facts are satisfactorily interpreted by assuming a single factor difference with complete dominance. The recessives produced only recessives. The dominants in part produced only dominants and in part produced both types in the usual ratio of 3 to 1. He was dealing, therefore, in part with homozygous and in part with heterozygous plants, and the behavior of the heterozygous individuals was checked by the back cross with the recessive.

CORROBORATION OF COMPTON'S RESULTS BY EXPERIMENTS ON NICOTIANA

These experiments of COMPTON have been corroborated by crossing two of the self-sterile species used in our previous work, *Nicotiana Forgetiana* and *Nicotiana alata*, with a third species *Nicotiana Langsdorffii*, which is consistently self-fertile.

Nicotiana Forgetiana and *Nicotiana Langsdorffii* were crossed reciprocally. In each case the plants were very vigorous, exceeding both parents somewhat in height. They grew quickly, matured rapidly, and produced a profusion of fertile flowers. The flowers were somewhat intermediate in size but resembled the larger-flowered parent, *Nicotiana Forgetiana*, in form. No difference could be discerned in the reciprocals either in the first or second hybrid generation in appearance or behavior. The two experiments may therefore be considered as one.

About 400 plants were grown and selfed by hand with the usual precautions against cross-pollination. In each case, from 6 to 20 blossoms were operated on. *Every plant was self-fertile.* Seed set in abundance, filling the capsules. Not every flower pollinated produced seed, of course, but the percentage was practically the same as that obtained in check experiments on pure *Nicotiana Langsdorffii*, 85 percent. The work was completed as early in the season as possible in order not to be disturbed by the pseudo self-fertility which is sometimes present in self-sterile plants at the close of the flowering season.

From selfed seed of the cross *N. Forgetiana* $\times$ *N. Langsdorffii*, 89 plants were grown and tested for self-fertility by guarded hand-pollina-

tions such as were made in the first hybrid generation. Of them 70 proved to be self-fertile and 19 self-sterile.

From selfed seed of the reciprocal cross, 92 plants were tested. Of this lot 74 showed self-fertility and 18 self-sterility. There was a sum total, therefore, of 144 self-fertile and 37 self-sterile plants in F_2 , a ratio 3.8 to 1.

If the hypothesis of a one-factor difference is correct the deficiency of recessives is somewhat greater than is to be expected in a population of this size. Nevertheless this failure to measure up to expectation need not disturb us. About one-fourth of the bags used in protecting the flowers were torn by wind, and the plants had to be tested a second time. This unfortunate occurrence prolonged the experiment until well into September when the plants were past their prime. It is not unexpected therefore that some truly self-sterile plants should have been listed as self-fertile because of "end-season" pseudo-fertility. In fact a slight fertility was shown by about 30 percent of the plants classed as self-sterile; i.e., they produced partially filled capsules in about 15 percent of the pollinations.

These plants were tested further by taking them into the greenhouse and bringing them into a second season of flowering. Pollinations were then made at the beginning of the season, and the plants proved to be fully self-sterile.

If this be not sufficient evidence to prove the case, there is the behavior of the third hybrid generation to be relied upon. *All progeny of the recessive (self-sterile) segregates of F_2 were again self-sterile.* About 200 were tested.

The cross between *N. Langsdorffii* and *N. alata* yield results similar to those just described. The plants of the first hybrid generation were all self-fertile; those of the second hybrid generation were partly self-fertile and partly self-sterile. About 200 F_2 plants were tested, of which 38 were self-sterile. Again there was a deficiency of recessives. The progeny of the self-steriles were all self-sterile, but no investigation of the amount of pseudo self-fertility was made. The matter of particular interest in this cross was the cross-fertility of F_2 plants having flowers of very different corolla lengths. Flowers were obtained as short as 2.0 cm and as long as 6.0 cm, yet reciprocal crosses were very easy to make.

It will be remembered that KÖLREUTER was unable to fertilize *Mirabilis longiflora* with pollen from *Mirabilis Jalapa* although the reverse cross could be carried out without difficulty. In interpreting these facts

it has been customary to assume that *M. Jalapa* pollen tubes are short and thus unable to reach the micropyles of the ovaries of *M. longiflora*. From work on pollen-tube growth (EAST and PARK 1918) and observations on the F_2 individuals of the cross between *N. Langsdorffii* and *N. alata*, we believe this assumption to be incorrect. Pollen tubes of all species observed by us have continued to grow as long as the flowers remained unwithered even in many generic crosses. The real cause of the occasional lack of success when a long-flowered plant is pollinated with pollen from a short-flowered plant, therefore, is in the "death" of the flower *before* the pollen tube has had time to reach the micropyle.

Though we may conclude that lack of a particular factor *F* results in self-sterility, there are some other factors to be considered in the behavior of crosses between self-fertile and self-sterile plants. When the self-sterile segregates of the cross between *N. Forgetiana* and *N. Langsdorffii* were examined carefully throughout the second flowering season, the type of self-sterility present did not seem to be the same in all cases. A majority of the plants exhibited a much greater amount of pseudo self-fertility than had ever been found in *N. Forgetiana*. In that species only an occasional plant produced a few selfed seeds and then only at the extreme end of the flowering season. Among the F_2 individuals of the cross, however, pseudo-fertility set in about the middle of the season and from then on it was very easy to get capsules which on casual examination would be said to be full of seed. As a matter of record only about 30 percent of such pollinations were successful and the capsules on the average had only about 70 percent of the normal complement of seed. Nevertheless, some 60 to 75 percent of the F_2 segregates classified as self-sterile showed at least 100 times the pseudo-fertility of the parent species, *N. Forgetiana*. The remaining plants were comparable to the latter in self-sterility.

It was also noticeable that the progeny of the most self-sterile of the F_2 plants were similar to them, while the progeny of the others were in part like their mother plants and in part like *N. Forgetiana*.

The simplest explanation of this state of affairs is that there is really a two-factor difference as regards self-sterility and self-fertility between *N. Forgetiana* and *N. Langsdorffii*. *N. Langsdorffii* is homozygous for a factor *F*; when this factor is absent the plants are self-sterile. It is also homozygous for a dilution factor *D*. The constitution of *N. Forgetiana* is *dd ff*. The F_1 individuals, having the constitution *Ff Dd*, are all self-fertile. In the F_2 generation a ratio of $9 FD : 3 Fd : 3 fD : 1 fd$ is

obtained. There are 3 self-fertile to 1 self-sterile because of the distribution of the allelomorphic pair F and f . But of the self-steriles, those having the constitution fD show a great deal more pseudo self-fertility than those having the constitution fd . Only the fd plants are wholly comparable to *N. Forgetiana*.

In describing the behavior of self-sterile plants this statement was made (EAST and PARK 1917):

"The waning of the reproductive period affects *N. alata* and *N. glutinosa* more markedly than it does *N. Forgetiana* or *N. angustifolia*. This indicates multiple allelomorphism in a fundamental factor the presence [or absence] of which is necessary for the development of self-sterility. This factor should not be confused with any of those assumed in the interpretation of the behavior of self-sterile plants among themselves."

The peculiarities of the cross between *N. Forgetiana* and *N. Langsdorffii* show that subsidiary factors affecting the manifestation of self-sterility, given homozygosity in ff , are as likely to be the interpretation of the differences shown in these four species as is multiple allelomorphism.

SUMMARY

Data are reported showing that in *Nicotiana* self-sterility is due to the presence of the allelomorph of a dominant fertility factor, F . When a population is homozygous for this factor, ff , it is self-sterile.

The factors which control the peculiar and systematic behavior of self-sterile plants when intercrossed among themselves are wholly independent of this factor and the latter does not need to be considered in an interpretation of their expression.

The manifestation of self-sterility as evinced by the degree to which pseudo-fertility shows, is due to a subsidiary inherited factor (or factors), but without the presence of the principal factor ff there is no evidence that it functions.

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