STUDIES ON SELF-STERILITY V. A FAMILY OF SELF-STERILE PLANTS WHOLLY CROSS-STERILE *INTER SE*

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In the first paper of this series (EAST and PARK 1917),¹ the behavior of a number of families of self-sterile plants under various schemes of mating was described. In one cross between the two species *Nicotiana Forgetiana* and *Nicotiana alata*, fifty-three plants of the F₁ generation could be separated into not less than four groups in which each member of every group was cross-sterile with every other member of that group, although showing cross-fertility with every member of every other group. The interpretation given of these and other similar facts was in brief as follows: (1) a self-sterile species exhibits this peculiarity because homozygous for a basic self-sterility factor; (2) a series of partially coupled factors affects the behavior of sterile plants among themselves; (3) these secondary factors act as if sporophytic in nature, so that all gametes produced by a single individual are identical in this regard with the plant on which they originated; (4) the nature of the action of these secondary factors is such that two plants are not fertile together unless they differ by at least one of these factors.

Though the self-sterility and the cross-sterility existent in these plants is fully expressed at the beginning and height of the flowering season, toward the close of the flowering season, particularly in plants exhibiting the effect of adverse environmental conditions, occasionally some fertility is shown. It is possible therefore to obtain seed from truly self-sterile plants and from combinations that are fundamentally incompatible. By taking advantage of this pseudo-fertility it should be possible to obtain families of plants wholly cross-sterile *inter se*. Such a family, apparently, is family E described on pages 565 to 567 of the paper we are discussing. Unfortunately very little work had been done on this family when that paper was written. Since a reserve supply of the seed

¹ EAST, E. M., and PARK, J. B. Studies on self-sterility I. The behavior of self-sterile plants. *Genetics* **2**: 505-609, 1917.

from which the family came had been preserved, however, it has been possible to make a more extended study of the case.

In table 1 are recorded the infertile crosses made upon 54 plants of

TABLE I
Record of infertile crosses made on 54 plants of family E(2). Number of pollinations is shown by subscripts.

Ped. No.	Sterile with Ped. No. ♂	Sterile with Ped. No. ♀
1	3 ₃ , 5 ₃ , 10 ₃ , 50 ₃ , 75	44 ₄ , 57 ₃ , 59 ₃ , 61 ₃ , 72 ₄ , 73 ₃ , 74 ₃
3	5 ₃ , 8 ₃ , 14 ₈ , 23 ₂ , 50 ₃	1 ₃ , 5 ₃ , 69 ₃
5	3 ₃ , 9 ₄ , 10 ₅ , 14 ₃ , 16 ₃ , 23 ₃ , 50 ₃ , 74 ₂	1 ₃ , 3 ₅ , 54 ₃ , 55 ₃ , 56 ₇ , 57 ₃ , 59 ₄ , 60 ₃ , 61 ₇ , 74 ₇
8	9 ₃ , 10 ₃ , 14 ₃ , 16 ₃ , 17 ₃ , 50 ₆	3 ₃
9	10 ₃ , 14 ₃ , 16 ₃ , 17 ₃ , 23 ₃ , 50 ₃	5 ₄ , 8 ₃ , 61 ₃
10	14 ₃ , 17 ₃ , 44 ₃ , 50 ₃	1 ₃ , 5 ₃ , 8 ₃ , 9 ₃ , 45 ₃ , 58 ₃ , 61 ₃ , 67 ₃ , 68 ₈
14	16 ₃ , 17 ₃ , 19 ₃ , 26 ₃ , 43 ₃ , 50 ₉ , 75 ₃	3 ₈ , 5 ₃ , 8 ₃ , 9 ₃ , 10 ₃ , 50 ₂ , 73 ₄
16	17 ₂ , 19 ₃ , 41 ₃ , 42 ₃ , 44 ₃ , 50 ₈	5 ₃ , 8 ₃ , 9 ₃ , 14 ₃
17	22 ₃ , 23 ₃ , 43 ₃ , 44 ₃ , 50 ₃ , 55 ₃	8 ₃ , 9 ₃ , 10 ₃ , 14 ₃ , 16 ₂
19	23 ₄ , 26 ₄ , 29 ₃ , 50 ₃ , 61 ₃ , 62 ₃ , 69 ₄ , 75 ₃	14 ₃ , 16 ₃
22	26 ₃ , 27 ₃ , 31 ₄ , 50 ₃ , 61 ₃ , 62 ₃ , 69 ₃	17 ₃
23	26 ₄ , 41 ₆ , 42 ₆ , 44 ₂ , 50 ₃ , 56 ₃	3 ₂ , 5 ₃ , 9 ₃ , 17 ₃ , 19 ₄ , 53 ₃ , 54 ₄ , 56 ₈ , 63 ₃ , 64 ₃ , 66 ₈ , 72 ₃ , 73 ₃
26	31 ₄ , 35 ₄ , 38 ₃ , 50 ₃ , 61 ₃ , 62 ₃	14 ₃ , 19 ₄ , 22 ₃ , 23 ₄ , 42 ₃ , 44 ₃ , 49 ₃ , 55 ₃
27	29 ₃ , 35 ₃ , 50 ₃ , 61 ₄ , 62 ₃ , 75 ₃	22 ₃
29	31 ₃ , 33 ₃ , 38 ₃ , 50 ₃ , 61 ₄ , 62 ₃ , 68 ₃	19 ₃ , 27 ₃ , 75 ₄
31	33 ₃ , 35 ₄ , 38 ₃ , 50 ₃ , 61 ₄ , 62 ₃ , 73 ₃	22 ₄ , 26 ₄ , 29 ₃ , 42 ₃ , 43 ₃ , 75 ₃
33	35 ₃ , 38 ₆ , 39 ₇ , 40 ₇ , 41 ₇ , 50 ₃	29 ₃ , 31 ₃ , 38 ₄ , 75 ₃
35	38 ₃ , 39 ₃ , 40 ₄ , 42 ₃ , 50 ₃ , 61 ₃ , 69 ₃ , 75 ₃	26 ₄ , 27 ₃ , 31 ₄ , 33 ₃ , 68 ₃ , 70 ₃ , 71 ₃ , 73 ₃
38	33 ₄ , 39 ₃ , 40 ₄ , 42 ₃ , 44 ₃ , 50 ₄ , 61 ₃ , 62 ₄ , 73 ₄	26 ₃ , 29 ₃ , 31 ₃ , 33 ₃ , 33 ₆ , 35 ₃ , 52 ₃ , 75 ₃
39	40 ₄ , 42 ₃ , 43 ₃ , 50 ₇ , 60 ₃ , 61 ₃ , 62 ₃ , 75 ₄	33 ₇ , 35 ₃ , 38 ₃ , 44 ₃ , 49 ₃ , 50 ₃ , 52 ₃ , 63 ₃ , 64 ₃
40	42 ₃ , 44 ₄ , 45 ₃ , 50 ₃ , 52 ₄ , 61 ₄ , 62 ₃ , 63 ₄	33 ₇ , 35 ₄ , 38 ₄ , 39 ₄

TABLE I (continued)

Record of infertile crosses made on 54 plants of family E (2). Number of pollinations is shown by subscripts.

Ped. No	Sterile with Ped. No. ♂	Sterile with Ped No. ♀
41	44 ₃ , 46 ₃ , 52 ₃ , 53 ₃ , 54 ₃ , 74 ₃	16 ₃ , 23 ₆ , 33 ₇ , 43 ₃
42	26 ₃ , 31 ₃ , 44 ₃ , 50 ₃ , 75 ₃	16 ₃ , 23 ₆ , 35 ₃ , 38 ₃ , 39 ₃ , 40 ₃ , 43 ₄
43	31 ₃ , 41 ₃ , 44 ₃ , 50 ₃ , 59 ₃	14 ₃ , 17 ₃ , 39 ₃ , 61 ₄
44	1 ₄ , 26 ₃ , 39 ₃ , 46 ₃ , 49 ₃ , 50 ₆ , 52 ₅ , 53 ₃ , 54 ₄	10 ₃ , 16 ₃ , 17 ₃ , 23 ₂ , 38 ₃ , 40 ₄ , 41 ₃ , 42 ₃ , 43 ₃ , 45 ₃ , 50 ₁₃ , 52 ₃
45	10 ₃ , 44 ₃ , 46 ₃ , 50 ₃ , 61 ₄	40 ₃ , 49 ₃
46		41 ₃ , 44 ₃ , 45 ₃
49	26 ₃ , 39 ₃ , 45 ₃ , 50 ₄ , 51 ₃ , 62 ₃	44 ₃
50	14 ₂ , 39 ₃ , 44 ₁₃ , 52 ₃ , 53 ₄ , 54 ₃ , 56 ₃	1 ₃ , 3 ₃ , 5 ₃ , 8 ₆ , 9 ₃ , 10 ₃ , 14 ₉ , 16 ₃ , 17 ₃ , 19 ₃ , 22 ₃ , 23 ₃ , 26 ₃ , 27 ₃ , 29 ₃ , 31 ₃ , 33 ₃ , 35 ₃ , 38 ₄ , 39 ₇ , 40 ₃ , 42 ₃ , 43 ₃ , 44 ₆ , 45 ₃ , 49 ₄ , 52 ₃ , 53 ₃ , 54 ₆ , 55 ₃ , 56 ₃ , 57 ₄ , 58 ₃ , 59 ₃ , 60 ₃ , 61 ₃ , 63 ₃ , 64 ₃ , 65 ₃ , 66 ₃ , 67 ₃ , 68 ₃ , 69 ₃ , 70 ₃ , 71 ₃ , 72 ₃ , 74 ₃ , 75 ₃
51		49 ₃
52	38 ₃ , 39 ₃ , 44 ₃ , 50 ₃ , 53 ₄ , 54 ₅ , 55 ₄ , 56 ₃ , 57 ₃ , 58 ₃ , 59 ₃ , 68 ₄	40 ₄ , 41 ₃ , 44 ₅ , 50 ₃
53	23 ₃ , 50 ₃ , 54 ₄ , 55 ₃ , 56 ₃ , 57 ₃ , 58 ₄ , 62 ₃ , 64 ₃	41 ₃ , 44 ₃ , 50 ₄ , 52 ₄
54	5 ₃ , 23 ₄ , 50 ₆ , 55 ₃ , 56 ₄ , 57 ₃ , 58 ₃ , 64 ₅	41 ₃ , 44 ₄ , 50 ₃ , 52 ₅ , 53 ₄
55	5 ₃ , 26 ₃ , 50 ₃ , 56 ₃ , 57 ₃ , 58 ₄ , 59 ₃ , 62 ₄	17 ₃ , 52 ₄ , 53 ₃ , 54 ₃
56	5 ₇ , 23 ₃ , 50 ₃ , 57 ₃ , 58 ₃ , 59 ₃ , 60 ₃ , 61 ₃ , 63 ₄ , 64 ₂	23 ₃ , 50 ₃ , 52 ₃ , 53 ₃ , 54 ₄ , 55 ₃
57	1 ₃ , 5 ₃ , 50 ₄ , 58 ₃ , 59 ₄ , 60 ₃ , 61 ₃ , 69 ₄	52 ₃ , 53 ₃ , 54 ₃ , 55 ₃ , 56 ₃
58	10 ₃ , 50 ₃ , 59 ₃ , 60 ₅ , 61 ₃ , 65 ₄ , 73 ₃ , 74 ₄	52 ₃ , 53 ₄ , 54 ₃ , 55 ₄ , 56 ₃ , 57 ₃
59	1 ₃ , 5 ₄ , 50 ₃ , 60 ₃ , 61 ₃ , 71 ₃ , 73 ₃ , 75 ₃	43 ₆ , 52 ₃ , 55 ₃ , 56 ₃ , 57 ₄ , 58 ₃
60	5 ₃ , 50 ₃ , 61 ₃ , 69 ₃ , 71 ₃ , 75 ₄	39 ₃ , 56 ₃ , 57 ₃ , 58 ₅ , 59 ₃
61	1 ₃ , 5 ₃ , 9 ₃ , 10 ₃ , 43 ₄ , 50 ₃ , 69 ₃ , 71 ₄	19 ₃ , 22 ₃ , 26 ₃ , 27 ₄ , 29 ₄ , 31 ₄ , 35 ₃ , 38 ₃ , 39 ₃ , 40 ₄ , 45 ₄ , 56 ₃ , 57 ₃ , 58 ₃ , 59 ₃ , 60 ₃ , 63 ₃ , 64 ₃ , 65 ₃ , 66 ₃ , 74 ₃ , 75 ₄
62		19 ₃ , 22 ₃ , 26 ₃ , 27 ₃ , 29 ₃ , 31 ₃ , 38 ₄ , 39 ₃ , 40 ₃ , 49 ₃ , 53 ₃ , 55 ₄ , 63 ₃ , 64 ₃ , 69 ₃ , 71 ₄ , 72 ₃ , 73 ₃ , 75 ₄

TABLE I (continued)

Record of infertile crosses made on 54 plants of family E (2). Number of pollinations is shown by subscripts.

Ped. No	Sterile with Ped. No. ♂	Sterile with Ped No. ♀
63	23 ₃ , 39 ₃ , 50 ₃ , 61 ₃ , 62 ₃ , 64 ₃ , 65 ₃ , 74 ₃ , 75 ₃	40 ₄ , 56 ₄ , 73 ₃ , 74 ₄
64	23 ₃ , 39 ₃ , 50 ₃ , 61 ₃ , 62 ₃ , 67 ₃ , 68 ₃ , 73 ₄ , 75 ₃	53 ₃ , 54 ₃ , 56 ₂ , 63 ₃ , 65 ₃ , 66 ₃ , 69 ₃ , 70 ₃ , 71 ₄ , 73 ₃
65	1 ₃ , 50 ₃ , 61 ₃ , 64 ₃ , 68 ₃ , 69 ₃ , 70 ₂	58 ₄ , 63 ₃
66	23 ₃ , 50 ₃ , 61 ₃ , 64 ₃ , 71 ₃ , 73 ₃ , 74 ₄	67 ₂ , 68 ₃
67	10 ₃ , 50 ₃ , 67 ₂ , 69 ₃ , 70 ₃ , 71 ₃	64 ₃
68	10 ₃ , 35 ₃ , 50 ₃ , 66 ₃ , 69 ₃ , 70 ₃	29 ₃ , 52 ₄ , 64 ₃ , 65 ₃ , 69 ₃
69	3 ₃ , 50 ₃ , 62 ₃ , 64 ₃ , 68 ₃ , 73 ₃ , 74 ₃ , 75 ₃	19 ₄ , 22 ₃ , 35 ₃ , 57 ₄ , 60 ₃ , 61 ₃ , 65 ₃ , 67 ₃ , 68 ₃ , 70 ₄ , 71 ₆ , 75 ₃
70	35 ₃ , 50 ₃ , 64 ₃ , 69 ₄ , 71 ₃ , 72 ₃ , 73 ₄ , 74 ₃	65 ₂ , 67 ₃ , 68 ₃
71	35 ₃ , 50 ₃ , 62 ₄ , 64 ₄ , 69 ₆ , 72 ₃ , 73 ₃ , 74 ₃	59 ₃ , 60 ₃ , 61 ₄ , 66 ₃ , 67 ₃ , 70 ₃ , 72 ₄
72	1 ₄ , 23 ₃ , 50 ₃ , 62 ₃ , 71 ₄ , 73 ₃ , 74 ₆	70 ₃ , 71 ₃ , 73 ₄
73	1 ₃ , 14 ₄ , 23 ₃ , 35 ₃ , 62 ₃ , 63 ₃ , 64 ₃ , 72 ₄	31 ₃ , 38 ₄ , 58 ₃ , 59 ₃ , 64 ₄ , 66 ₃ , 69 ₃ , 70 ₄ , 71 ₃ , 72 ₃ , 74 ₄
74	1 ₃ , 5 ₇ , 50 ₃ , 61 ₃ , 63 ₄ , 73 ₄ , 75 ₃	52 ₂ , 41 ₃ , 58 ₄ , 63 ₃ , 66 ₄ , 69 ₃ , 70 ₃ , 71 ₃ , 72 ₆
75	29 ₄ , 31 ₃ , 33 ₃ , 38 ₃ , 50 ₃ , 61 ₄ , 62 ₄ , 69 ₃	1 ₁ , 14 ₃ , 19 ₃ , 27 ₃ , 35 ₃ , 39 ₄ , 42 ₃ , 59 ₃ , 60 ₄ , 63 ₃ , 64 ₃ , 69 ₃ , 74 ₃

this family, the subscripts showing the number of attempts made for each combination. The table was constructed by assuming that if a combination had been made one way, the reciprocal had also been made, as explained in our former study (EAST and PARK 1917). Thus it can be seen that while only a fraction of the possible combinations were made, nevertheless the plants were linked together in an unbroken chain. In other words, if it be true that when A is sterile with B and with C, B is sterile with C, then each of these 54 plants is sterile with the other.

It is not true however that no seed at all was obtained in the numerous attempts to combine plants of this family. Table 2 shows that 13 combinations produced capsules. From the number of sterile pollinations made with the same plants and from the fact that nearly all of the fertility appeared at the end of the flowering season, it would seem that

TABLE 2

*Record of fertile crosses made on 54 plants of family E (2),—
presumably pseudo-fertility. First number is female.*

Combination	Number of fertile pollinations	Number of sterile pollinations	Number of sterile reciprocal pollinations
3 × 5	1	5	3
5 × 10	1	5	—
5 × 74	1	2	See 74 × 5
16 × 50	1	8	—
17 × 22	1	3	—
23 × 44	1	2	—
33 × 38	2	6	4
39 × 50	4	7	3
44 × 50	1	6	See 50 × 44
44 × 52	1	5	3
50 × 44	1	13	See 44 × 50
56 × 23	1	8	3
74 × 5	1	7	See 5 × 74

these apparent exceptions are all illustrations of fluctuating pseudo-fertility. There is the whole of our experience with this type of fertility back of such an assertion, but there is also some specific evidence on the case in point.

The number of seeds produced by these plants when crossed with compatible pollen is in general from 300 to 600 per capsule (table 3), while the number of seeds in the presumably pseudo-fertile combinations is usually much less. At the same time 4 of the latter combinations produced what seemed to be full capsules. Combination 16 × 50 produced a full capsule at the seventh attempt, although eight out of nine attempts were failures, and combination 50 × 44 produced a full capsule at the twelfth attempt although thirteen out of fourteen attempts were failures. On the other hand plant 23 gave a full capsule with pollen of plant 44 on the first attempt, plant 33 gave two capsules out of eight attempts with pollen of plant 38, and plant 39 gave four capsules out of eleven attempts with pollen of plant 50. Now combination 33 × 38 was about 50 per cent fertile, and combination 39 × 50 became progressively more fertile as shown by the number of seeds produced. These three plants, 23, 39, and 50 were crossed with a large number of other plants, nevertheless, and showed cross-sterility. Further, at the beginning of another flowering season crosses 23 × 44 and 39 × 50 were impossible. At the same time it is not without the bounds of probability that combination 39 × 50

TABLE 3

Comparison of the number of seeds in capsules of the presumably pseudo-fertile combinations in family E(2) with the number of seeds in the capsules of the same plants when pollinated with pollen from the plant of the F₂ generation of the cross between N. Forgetiana and N. Langsdorffii.

Combination	Number of seeds in capsules	Number of seeds in capsules when pollinated with (314 × 328)
3 × 5	28	
5 × 10	115	365, 382, 421
5 × 74	127	365, 382, 421
16 × 50	418	
17 × 22	27	370
23 × 44	436	
33 × 38	124, 131	
39 × 50	151, 255, 289, 352	
44 × 50	128	
44 × 52	191	
50 × 44	427	
56 × 23	82	
74 × 5	185	

was for some unknown reason more easy to make than other combinations in this family. We have no theory to offer at present as to why this may be true. It may stand as an open question. The general conclusion from all the evidence is that family E (2) may be considered to consist of plants wholly cross-sterile *inter se*.

The question then arises: Is the origin of family E (2) compatible with our previous conclusions as to the behavior of self-sterile plants when crossed *inter se*. First, it must be emphasized that the cross-sterility found has nothing to do with true sterility. A random sample of 25 plants was used in a test with the pollen a single plant coming from the F₂ generation of a cross between *Nicotiana Forgetiana* and *Nicotiana Langsdorffii*. Out of 64 pollinations there were only 2 failures (table 4). Again, out of 51 attempts to use the pollen of these plants in crosses thought to be compatible, there was only 1 failure. The sterility found, therefore, is wholly of the nature termed "self-sterility," or "incompatibility," and must be interpreted as such.

The origin of a family consisting of one class of plants cross-sterile with each other was to have been predicted on the basis of the interpre-

TABLE 4

Record of pollinations made on a random sample of 25 plants of family E(2) with pollen from a single self-sterile plant of the F₂ generation of a cross between Nicotiana Forgetiana and Nicotiana Langsdorffii (814 × 328).

Plant No.	Successful pollinations	Unsuccessful pollinations	Number of seeds in each mature capsule
5	3	0	365, 382, 421
6	3	0	360, 330, 515
9	4	1	390, 500, 400, 370
10	1	0	631
17	1	0	370
22	3	0	358, 405, 230
25	1	0	377
26	2	0	630, 425
31	3	0	481, 404, 470
36	5	0	453, 350, 405, 372, 340
38	2	0	432, 192
40	3	0	271, 195, 317
46	1	1	185
51	4	0	225, 252, 382, 384
53	1	0	157
54	2	0	420, 177
57	4	0	295, 650, 250, 462
58	3	0	700, 618, 902
59	1	0	327
60	1	0	330
61	5	0	635, 588, 580, 468, 678
64	3	0	338, 230, 376
70	2	0	230, 176
71	2	0	480, 240
73	2	0	291, 358
Total	62	2	

tations we have used, by taking advantage of the phenomenon of pseudo self-fertility. Continued self-fertilization is possible by persistent efforts at self-pollination carried to the very end of the flowering season. And continued self-fertilization should bring about homozygosis in the secondary factors affecting the behavior of self-sterile plants among themselves. When such a point is reached, the resulting population should not only be self-sterile but should belong to a single class all members of which are cross-sterile with each other.

Family E (2) was not the result of continued self-pollination and pseudo self-fertility, however. It was produced as follows: The fe-

male parent was No. 58, a plant of *N. alata*, the result of three generations of selfing a self-sterile strain *at the end of the season*. The behavior of No. 58 and of its sister plants when crossed with each other leads one to believe they were all members of one intra-sterile class, but the evidence is hardly sufficient to establish the point. The male parent was a member of the F_1 population (plant 44, *loc. cit.*, p. 559) produced by crossing a self-sterile plant of *N. Forgetiana* with a sister plant of the mother of the *N. alata* plant just described (No. 58).

Now it is obvious that the female parent of this family may have come from a fraternity homozygous for the secondary factors effective on compatibility *inter se*. They may have been, for example, plants with the composition *AABB*. It is possible also that the male parent, though originating from a cross, might have had the formula *AABB*, since its parents might have been *AABB* and *AaBB*. But a whole population having a single formula could not have arisen through a cross except through an illegitimate mating (pseudo-fertility). If then the two parents of the population had the same constitution and produced seed through pseudo-fertility, then family D (*loc. cit.*, p. 563), coming from the same male crossed on a sister of plant 58, ought to be a duplicate of family E (2). This however does not appear to be the case. Family D consisted of at least two intra-sterile classes, unless a good deal of unrecognized pseudo-sterility was present. On the other hand both of the parents, in the few tests made on family E (2), were sterile with their progeny,—a result to be expected on the theory of homozygosis. It seems, then, that the unsettled question, a question which must await further investigation, is, why family D and family E (2) are not similar in composition and behavior.