STUDIES ON SELF-STERILITY. VIII SELF-STERILITY ALLELOMORPHS.*

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INTRODUCTION

In a previous paper of this series (EAST AND MANGELSDORF 1926), the behavior of self-sterile plants of *Nicotiana Sanderæ* Hort. was interpreted by the reactions of 3 allelomorphs S_1 , S_2 , and S_3 . The action of these allelomorphs was such that a plant of constitution $S_1 S_2$, when pollinated by pollen from a plant of constitution $S_2 S_3$, produced two types of progeny, $S_1 S_3$ and $S_2 S_3$, due to the slow growth of the pollen tubes bearing the factor S_2 (which was contained in the mother plant) as compared with the growth of the pollen tubes bearing the factor S_3 . That these 3 factors were allelomorphic forms was shown by their ordinary behavior in crosses, and also (BRIEGER AND MANGELSDORF 1926) by the similar crossover values exhibited when a corolla-color factor C of the same linkage group was involved. Only the three allelomorphic factors were found in the material on hand,—material which had been inbred for several generations; but the results reported in an earlier paper (EAST AND PARK 1917) indicated that additional factors controlling self-sterility are present in *Nicotiana alata grandiflora*, in *Nicotiana Forgetiana*, and in the hybrids known as *Nicotiana Sanderæ*, which involve these two species.

Material was obtained from various seedsmen, therefore, for the purpose of isolating new factors, if such could be found. There were two objectives in view: first, to gather information as to the number of mutations that have taken place in the S locus; second, to find out whether mutations of a second locus are involved in controlling the behavior of self-sterility in these species. The second point has considerable theoretical importance. If mutations in a single locus will account for the genetic behavior of these self-sterile plants, obviously one may assume either that like factors inhibit pollen-tube growth or that unlike factors stimulate it. If two or more loci are involved, one must use the second postulate, since the plants used previously in studying the factors S_1 , S_2 , and S_3 , must have been homozygous for self-sterility factors located in other loci.

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EXPERIMENTAL WORK

The first lot of new material was grown from seed purchased at the firm of R. and J. Farquhar and Company of Boston. One packet of seed was marked *Sanderæ* hybrids, the other was marked *Nicotiana affinis* (= *Nicotiana alata grandiflora*). From among the plants obtained from the seed of the first packet, 4 individuals were investigated. One plant had a previously known genetic formula S_2S_3 , as shown by sterility to pollen of S_2S_2 , S_3S_3 , and S_2S_3 . The other 3 plants each contained the factor S_1 ; and, in addition, 2 of them contained a new factor S_4 , while the third contained another new factor S_5 . That is to say, by critical crossing tests, 1 plant was shown to be S_2S_3 , 2 plants were shown to be S_1S_4 , and 1 plant was shown to be S_1S_5 . From the plants derived from the other packet, 2 were investigated. They proved to have the genetic formulas S_2S_6 and S_2S_7 , respectively.

Thus there were 7 allelomorphs of the S factor which could be used in further tests. To make the proposed tests most effectively, plants were produced having the genetic formulæ S_1S_2 , S_1S_3 , . . . S_1S_7 . Seed was then obtained of *Sanderæ* hybrids and of *Affinis* hybrids from various sources, and 11 plants were selected for investigation. These 11 plants were crossed with the pollen from a plant having the genetic formula S_1S_1 ,—plants therefore which did not contain this particular factor. Each plant of the new material, since it was produced by natural pollination, could be assumed to be heterozygous for sterility factors. Any given population resulting from crossing a plant with S_1 pollen, therefore, should consist of equal numbers of plants S_1S_x and S_1S_y .

The sources of the 11 families thus produced were as follows:-

Family BA	Affinis hybrid	From Dreer
" BB	" "	" Mitchell
" BC	" "	" Dreer
" BD	<i>Sanderæ</i> "	" "
" BE	" "	" Vaughan
" BF	<i>Affinis</i> "	" "
" BG	<i>Sanderæ</i> "	" Dreer
" BH	" "	From Vaughan
" BI	" "	" "
" BK	" "	" Ferry
" BL	<i>Affinis</i> "	" Dreer

When these families began to blossom, a single vigorous plant from each was chosen as a tester (Type I). Each plant of the family was then pollinated with the pollen of that plant. As soon as a fertile union was obtained, the pollen of the second plant (Type II) was used on all of the

plants of the family. For example, all of the plants of Family BB were pollinated with pollen from BB2. The plants sterile with this pollen were assumed to have the genetic formula S_1S_x . But BB1 was fertile to the pollen from BB2. BB1, and all of the plants sterile to its pollen, were assumed, therefore, to have the genetic formula S_1S_y .

The results of the work in classifying the 11 families are shown in the tables 1 to 11. Fertility is designated +; sterility is designated —.

The behavior of Family BA, shown in table 1, is seen to be somewhat exceptional. The mother plant used in the production of the family was

TABLE 1.
Compatibilities of Family BA.

PLANT NUMBER	× BA2	× BA34	SELFED	PLANT NUMBER	× BA2	× BA34	SELFED
1	+	+	+	24	+	—	—
2	+	+	+	25	+	—	—
3	—	—	—	26	+	—	—
4	+	+	+	27	+	+	+
5	+	+	+	28	—	—	—
6	+	—	—	29	+	+	+
7	—	—	—	30	+	—	—
8	+	+	+	31	+	+	+
9	+	—	—	32	+	—	—
10	+	—	—	33	+	—	+
11	+	+	+	34	+	—	—
12	+	—	—	35	+	+	—
13	+	—	—	36	+	+	—
14	+	+	+	37	+	+	+
16	—	—	—	38	+	+	+
18	+	—	—	39	—	+	+
19	+	+	—	40	—	+	+
20	+	+	+	41	+	+	+
21	+	+	+	42	+	+	+
22	+	+	+	43	+	+	+
23	+	+	+				

self-fertile, having the fertility which we have commonly called pseudo-fertility. The term is perhaps disingenuous, but nevertheless it has some merit. The difference between self-fertile plants and self-sterile plants depends upon rapidity of pollen-tube growth, and the speed at which pollen tubes bearing particular factors grow is dependent both upon subsidiary heritable factors and upon environmental conditions. For example, it will be shown in a later paper that *N. Langsdorffii* bears a factor belonging to the *S* series which we have called *S_f*. Now no subsidiary factors tending

to inhibit pollen-tube growth, even in combination with environmental conditions that are disadvantageous, are sufficient to prevent full complements of seed being formed after selfing. Factor S_f , therefore, may be termed a true factor for self-fertility. On the other hand, there are among the S factors several which produce such slow-growing pollen tubes that no combination of stimulating subsidiary heritable factors and optimum environmental conditions is sufficient to cause selfed seed to be produced. But between these two categories are S factors which are on the border line. When inhibiting subsidiary factors and poor environmental conditions (as

TABLE 2.
Compatibilities of Family BB.

PLANT NUMBER	× BB2	× BB1	SELFED	PLANT NUMBER	× BB2	BB1	SELFED
1	+	—	—	27	—	+	
2	—	+	—	28	+	—	—
3	+	—		29	+	—	
4	—	+	—	30	—	+	
5	—	+	—	31	+	—	—
6	+	—		32	+	—	—
7	—	+	—	33	+	—	—
8	—	+	—	34	—	+	
9	—	+		35	—	+	
10	+	—	—	36	—	+	
11	—	+	—	37	—	+	—
12	—	+		38	+	—	
13	—	+		39	+	—	
14	+	—	—	40	+	—	
15	—	+	—	41	+	—	
18	+	—		42	+	—	
19	+	—		43	+	—	
20	—	+		44	+	—	
21	—	+		45	+	—	
22	—	+	—	46	—	+	
23	—	+		47	+	—	
24	—	+		48	—	+	
25	+	—	—	49	—	+	
26	+	—	—	50	—	+	

low temperatures) are combined, no seed results; when accelerating subsidiary factors are combined with optimum environmental factors, seed is produced. This border line fertility we have called pseudo-fertility.

Plant A which served as the mother plant for Family BA was evidently of the latter type. Crossed with S_1S_1 , it gave rise to a population consisting of two groups. There were 18 self-sterile plants and 23 self-fertile

plants. The self-fertile plants were fertile to the pollen of both BA2 and BA34, as would be expected,—with two exceptions. Plants 39 and 40 were sterile to BA2 pollen. Evidently there was just enough difference between plants 39 and 40 and the remaining plants of the group to inhibit the pollen-tube growth of pollen from BA2 sufficiently to prevent fertilization. The behavior of the 18 plants belonging to Type II was also slightly anomalous. It was to have been expected that all of these self-sterile plants would be

TABLE 3
Compatibilities of Family BC.

PLANT NUMBER	× BC1	× BC21	SELFED	PLANT NUMBER	× BC1	× BC21	SELFED
1	—	+		23	+	—	
2	+	—		24	—	+	
3	—	+		25	—	+	—
4	+	+	+ ¹	26	—	+	—
5	—	+		27	—	+	—
6	—	+		28	—	+	—
7	+	—		29	—	+	
8	—	+	+ ¹	30	—	+	
9	+	—		31	—	+	—
10	—	+	—	32	+	—	
11	—	+		33	—	+	—
12	+	—		34	+	—	
13	—	+		35	—	+	
14	+	—		36	—	+	—
15	+	—		37	—	+	
16	—	+	—	38	—	+	
17	—	+		39	+	—	
18	—	+		40	+	—	
19	—	+	—	41	+	—	
20	—	+		42	—	+	
21	+	—		43	—	+	
22	—	+					

¹ Pseudo-fertility small capsules.

fertile to the pollen of BA2 and sterile to the pollen of BA34. Actually, 13 plants behaved in this manner. In addition, plants 3, 7, 18, and 28 were sterile to both testers, while plant 19 was fertile to both testers. Plant 19 may belong to Type I, since it gave a small capsule on one self-pollination. The behavior of the other 4 plants is exceptional. Each was tested more than once with pollen of BA2 and the results were always negative. Possibly we have here a case in which plants of a given constitution are sterile to more than one *S* factor under the proper environmental condi-

tions and with the proper subsidiary factors; if so, it is something not found heretofore.

Family BB, (table 2), also an *Affinis* hybrid, had 48 plants which fell without exception into two groups. There were 23 plants fertile to BB2 and sterile to BB1. There were 25 plants sterile to BB2 and fertile to BB1. A random sample of 18 plants was selfed. Each proved to be self-sterile.

Family BC (table 3), an *Affinis* hybrid from Dreer, contained 43 plants. All of them appeared to be self-sterile, to judge from the small number of capsules that set naturally, with the exception of plants 4 and 8. These 2 plants produced the small capsules usually characteristic of pseudo-

TABLE 4
Compatibilities of Family BD.

PLANT NUMBER	× BD1	× BD44	SELFED	PLANT NUMBER	× BD1	× BD44	SELFED
1	—	+		26	+	—	
2	—	+		28	+	—	
3	—	+		29	—	+	
4	—	+		30	—	+	
5	+	—		31	+	—	
6	+	—		32	—	+	
7	—	+		33	+	—	
8	—	+		34	—	+	
9	+	—		35	—	+	
10	+	—		36	—	+	
12	—	+		37	—	+	
14	+	—		38	—	+	
15	—	+		39	+	—	
16	—	+		40	—	+	
17	—	+		41	—	+	
18	—	+		42	—	+	
19	+	—		43	+	—	
20	—	+		44	+	—	
21	—	+		45	—	+	
22	—	+		46	+	—	
23	+	—		47	—	—	
24	+	—		48	+	—	
25	+	—					

fertility. Plant 8 was sterile to the first tester BC1 and fertile to the second tester BC21. Plant 4, however, produced good capsules with both testers. The remaining 42 plants could be divided definitely into 2 groups. In the first group there are 29 plants, each sterile to BC1 and fertile to BC21. In the second group there are 13 plants, each fertile to BC1 and sterile to BC21.

Family BD (table 4) was produced by a *Sandera* hybrid from Dreer. It consisted of 45 plants. None were selfed, since—from the paucity of capsules set naturally—they all appeared to be self-sterile. One exceptional plant (No. 47) was repeatedly sterile to both testers, though the pollen appeared to be viable. We have no further information as to why it behaved in this manner. The cause may be connected with the self-sterility phenomena in some way not at present understood. But we are not limited

TABLE 5
Compatibilities of Family BE.

PLANT NUMBER	× BE1	× BE28	SELFED	PLANT NUMBER	× BE1	× BE28	SELFED
1	—	+	—	23	—	+	—
2	—	+		24	—	+	
3	—	+		25	—	+	
4	+	—		26	+	—	
5	+	—		27	+	—	
6	—	+		28	+	—	
7	—	+		29	—	+	
8	—	+		30	—	+	
9	+	—		31	—	+	
10	+	—		32	+	—	
11	—	+	—	33	—	+	—
12	—	+		34	—	+	
13	—	+		35	+	—	
14	—	+		36	—	+	
15	—	+		38	+	—	
16	+	—		39	—	+	
17	+	—		40	—	+	
19	+	—		41	+	—	
20	—	+		42	+	—	
21	+	—		43	+	—	
22	—	+					

to such an interpretation. Occasional plants from material such as this show true male sterility. That is to say, they have defective pollen. And there is indication, though no critical proof, that somewhat more rarely female sterility is found. The remaining 44 plants fell into the usual 2 groups. There were 26 plants sterile to BD1 and fertile to BD44; there were 18 plants fertile to BD1 and sterile to BD44.

Family BE (Table 5) came from a *Sandera* hybrid from Vaughan. It consisted of 41 plants. The general appearance of the plants led us to believe that all were self-sterile, except possibly plants 3 and 32. These proved to be self-sterile. All of the plants fell into 2 groups: 24 were ste-

rile to BE1 and fertile to BE28; 17 were fertile to BE1 and sterile to BE28. It should be noted, however, that there was a little difficulty in classifying plants 21, 32, 34, and 38. Plants 21 and 38 produced seed in crosses with BE1, but the capsules were not as full of seed as would normally be expected. They were completely sterile with BE28. Plant 32 produced normal capsules with BE1. With BE28 a failure was recorded with one pollination and a small capsule with a second pollination. Plant 34 produced good capsules with BE28 and a small capsule with a few seeds with BE1.

TABLE 6
Compatibilities of Family BF.

PLANT NUMBER	× BF2	× BF13	SELFED	PLANT NUMBER	× BF2	× BF13	SELFED
1	+	-		23	-	+	
2	-	+		24	+	-	
3	+	-	-	25	+	-	
4	+	-		26	+	-	
5	-	+	-	27	+	-	
6	+	-	-	28	+	-	
7	+	-		29	+	-	
8	+	-	-	30	-	+	
10	+	-	-	31	+	-	
11	+	-		32	+	-	
12	+	-	-	33	+	-	
13	+	-	-	34	-	+	
14	+	-	-	36	+	-	
15	+	-		37	+	-	
16	-	+	-	38	+	-	
17	+	-	-	39	+	-	
18	-	+		40	-	-	
19	-	+	-	41	+	-	
20	-	+		42	-	+	
21	+	-		43	-	+	
22	+	-					

Family BF (table 6) coming from *Affinis* hybrids received from Vaughan, had one exceptional plant. Plant 40 was repeatedly sterile to both testers. The remaining 40 plants fell into two groups. There were 29 plants fertile with BF2 and sterile with BF13; there were 11 plants sterile with BF2 and fertile with BF13. Plants 17, 18, 29, and 37 required repeated tests to be certain of their classification. Plant 17 was fertile once and sterile once with pollen of BF2; it was always sterile with BF13. Plant 18 produced full capsules with BF13 and capsules with a few seeds with BF2. Plants

29 and 37 produced full capsules with BF2, and was sometimes sterile and sometimes partly fertile (few seeds) with BF13.

Family BG (table 7) consisting of 43 plants, was derived from seed of *Sanderæ* hybrids obtained from Dreer. Plant 13 was sterile twice with both testers. Plants 18 and 36, through some oversight were not tested with BG1. If one assumes that the sterility of these plants with pollen of BG32 is sufficient to classify them, then there are 16 plants sterile to BG1 and

TABLE 7
Compatibilities of Family BG.

PLANT NUMBER	× BG1	× BG32	SELFED	PLANT NUMBER	× BG1	× BG32	SELFED
1	—	+		23	+	—	
2	—	+		24	+	—	
3	—	+		25	+	—	=
4	+	—		26	—	+	
5	+	—		27	+	—	
6	—	+		28	+	—	
7	+	—		29	+	—	
8	+	—		30	+	—	
9	—	+		31	—	+	
10	—	+		32	+	—	
11	+	—		33	+	—	
12	+	—		34	—	+	
13	—	—		35	+	—	
14	—	+		36		—	
15	+	—		37	+	—	
16	—	+		38	—	+	
17	+	—		39	+	—	
18		—		40	+	—	
19	+	—		41	—	+	
20	—	+		42	—	+	
21	—	+		43	+	—	
22	+	—					

fertile to BG32, and 26 plants fertile to BG1 and sterile to BG32. Though the plants of this family all appeared to be self-sterile when judged by their ability to set capsules under natural conditions, undoubtedly there were some border line cases. For example, plant 25 gave full capsules with BG1 and proved to be self-sterile under test, but it also gave four partially filled capsules with BG32. Plant 38, which should have been fertile to BG32, having been sterile to BG1, gave one full capsule in one trial and failed to set in one trial. In addition, it should be noted that plants 3, 9, 14, and 34, which were always sterile to BG1, were not fully fertile to BG32. Each

was tested twice with BG32; and while all of the eight pollinations were positive, the capsules were never full of seed.

Family BH (table 8) was derived from the *Sanderæ* hybrids of Vaughan. It consisted of 42 plants, of which 24 were sterile to BH3 and fertile to BH21, and 18 were fertile to BH3 and sterile to BH21. All appeared to be

TABLE 8
Compatibilities of Family BH.

PLANT NUMBER	× BH3	× BH21	SELFED	PLANT NUMBER	× BH3	× BH21	SELFED
1	—	+		22	+	—	
2	—	+		23	—	+	
3	—	+		24	+	—	
4	—	+		25	—	+	
5	+	—		26	—	+	
6	+	—		27	+	—	
7	+	—		28	+	—	
8	+	—		29	+	—	
9	—	+		30	—	+	
10	—	+		31	—	+	
11	—	+		32	—	+	
12	+	—		33	+	—	
13	—	+		34	—	+	
14	+	—		35	—	+	
15	—	+		36	+	—	
16	—	+		37	+	—	
17	—	+		38	+	—	
18	—	+		39	—	+	
19	+	—		40	—	+	
20	—	+		41	—	+	
21	+	—		32	+	—	

self-sterile. In fact, plant 33 was the only plant that showed a slight evidence of pseudo-fertility. The only difficulties encountered in trying to classify the plants of this family were with plants 19, 24, 30, and 33, which had to be tested twice in order to establish their compatibilities in an unmistakable manner.

Family BI (table 9) from Vaughan's stock of *Sanderæ* hybrids, consisted of 50 plants, all of which appeared to be self-sterile. A sample of 9 plants proved to be self-sterile. The plants could be divided into 2 groups without difficulty. There were 30 plants sterile to BI1 and fertile to BI32, and 20 plants fertile to BI1 and sterile to BI32.

Family BK (table 10), from *Sanderæ* hybrid seed of Ferry, consisted of 42 plants. BK1 which was used as one of the testers, exhibited some

pseudo-fertility. It gave a small capsule when selfed. Plants 30, 32, and 33 also showed some pseudo-fertility,—the first and the third yielding small capsules when selfed. These three were the only plants besides BK1 which showed noticeable self-fertility. All three were fertile with both BK3 and BK1; but, judging both from the size of capsules produced after pollination with BK1 as compared with those produced after pollination with BK3, and from the behavior of the four plants (including BK1) when selfed they should be classified as belonging to the type represented by BK1.

TABLE 9
Compatibilities of Family BI.

PLANT NUMBER	× BI1	× BI32	SELFED	PLANT NUMBER	× BI1	× BI32	SELFED
1	—	+	—	26	—	+	
2	+	—	—	27	+	—	
3	—	+	—	28	—	+	
4	—	+	—	29	+	—	
5	—	+		30	+	—	
6	—	+	—	31	—	+	
7	—	+	—	32	+	—	
8	+	—	—	33	+	—	
9	—	+	—	34	—	+	
10	+	—	—	35	+	—	
11	+	—		36	+	—	
12	—	+		37	+	—	
13	+	—		38	—	+	
14	—	+		39	+	—	
15	—	+		40	—	+	
16	—	+		41	—	+	
17	—	+		42	—	+	
18	—	+		43	—	+	
19	+	—		44	—	+	
20	+	—		45	—	+	
21	—	+		47	+	—	
22	—	+		48	—	+	
23	—	+		49	+	—	
24	—	+		50	+	—	
25	+	—		51	—	+	

Omitting these three plants, however, there are two groups, one of 20 plants fertile to BK3 and sterile to BK1, and one of 18 plants sterile to BK3 and fertile to BK1. In addition, it may be noted that plants 39 and 40 showed a slight pseudo-fertility in one pollination with BK1 and complete sterility in a second pollination. Likewise, plants 6, 13, 14 and 20 exhibited a slight degree of pseudo-fertility with BK3.

TABLE 10
Compatibilities of Family BK.

PLANT NUMBER	× BK3	× BK1	SELFED	PLANT NUMBER	× BK3	× BK1	SELFED
1	+	+	—	23	+	—	
2	+	—		24	+	—	
3	—	+		25	—	+	
4	+	—		26	+	—	
5	+	—		27	+	—	
6	—	+		28	—	+	
7	+	—		29	—	+	
8	+	—		30	+	+	+
9	+	—		31	—	+	
10	—	+		32	+	+	—
12	+	—		33	+	+	+
13	—	+		34	+	—	
14	—	+		35	+	—	
15	—	+		36	—	+	
16	—	+		37	—	+	
17	—	+		38	+	—	
18	—	+		39	+	—	
19	+	—		40	+	—	
20	—	+		41	—	+	
21	+	—		42	+	—	
22	—	+		43	+	—	

TABLE 11
Compatibilities of Family BL.

PLANT NUMBER	× BL1	× BL31	SELFED	PLANT NUMBER	× BL1	× BL31	SELFED
1	—	+		23	—	+	
2	—	+		24	—	+	
3	+	—		25	—	+	—
4	+	—		26	+	—	
5	+	—		27	+	—	
7	—	+		28	—	+	
8	—	+		29	—	+	
9	—	+		30	+	—	—
10	+	—		31	+	—	
11	—	+		32	+	—	—
12	—	+		33	—	+	
14	+	—		34	—	+	
15	—	+		35	+	—	
16	—	+		36	—	+	
18	+	—		37	+	—	
19	+	—	—	38	—	+	
20	+	—		39	+	—	
21	+	—		40	+	—	
22	+	—		41	+	—	

Family BL (table 11), was derived from the *Affinis* hybrids of Dreer. From their behavior all of the 38 plants constituting the population were self-sterile although only 4 were tested. No anomalous behavior and no pseudo-fertility was recorded. There were 18 plants sterile to BL1 and fertile to BL31 and 20 plants fertile to BL1 and sterile to BL31.

The data on the B families show that the 11 individuals chosen for crossing with S_1S_1 were heterozygous for definite S factors,—that is that their genetic formulæ as regards self-sterility were S_xS_y , S_wS_z , and so forth. Each family consisted of two groups containing approximately equal numbers of individuals. This is seen to be the case when one compares the family groups with the probable errors expressed in numbers of individuals, as follows:-

Family	Numbers of each type	Deviation from equality	P. E. in Numbers
BA	18-23	2.5	2.2
BB	23-25	1.0	2.3
BC	29-13	8.0	2.2
BD	26-28	4.0	2.2
BE	24-17	3.5	2.2
BF	29-11	9.0	2.1
BG	16-26	5.0	2.2
BH	24-18	3.0	2.2
BI	20-30	5.0	2.4
BK	20-18	1.0	2.1
BL	18-20	1.0	2.1

Of the 11 families, the deviations of the two groups from equality is less than .5 P. E. in 3 families, slightly over 1.0 P. E. in 1 family, less than 2.0 P. E. in 3 families, slightly over 2.0 P. E. in 2 families, over 3.0 P. E. in 1 family, and over 4.0 P. E. in the family showing the greatest discrepancy.

The next point in the investigation was to try to distinguish the different S factors in the various groups. BA Type I, afterwards called BA-I, was tested with BA-II, with the two types of the other 10 families, and with the seven other testers, $S_1S_2 \dots S_1S_7$. It showed fertility in every test. Since the plants of BA-I were self-fertile it may seem queer to call its S factor S_{15} ; but there seems to be no good reason for not so doing. The behavior of S_{15} is merely an extreme case of rapid pollen-tube growth which is uninhibited in styles of plants bearing the same factor. From the different source of the material, we believe that the S_7 factor borne by *N. Langsdorffii* is probably different from S_{15} ; but there is no way of proving the matter.

Table 12 shows the tests made with the plants of Family BA, Type II. It will be noted that there were two cases of incompatibility. Plant BA-II-

12 was sterile to the pollen of plant BE-II-28; and plant BA-II-6 was sterile to the pollen of BG-II-32. Two additional pollinations for each of these combinations confirmed the result. We may take it, then, that

TABLE 12
Tests of Family BA.

TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT
BA-II-34	BA-II-32	—
BA-II-12	BB-I-2	+
BA-II-12	BB-II-1	+
BA-II-12	BC-I-1	+
BA-II-12	BC-II-21	+
BA-II-12	BD-I-1	+
BA-II-12	BD-II-44	+
BA-II-12	BE-I-1	+
BA-II-12	BE-II-28	—
BA-II-12	BF-I-2	+
BA-II-12	BF-II-13	+
BA-II-12	BG-I-1	+
BA-II-6	BG-II-32	—
BA-II-6	BH-I-3	+
BA-II-6	BH-II-21	+
BA-II-6	BI-I-1	+
BA-II-9	BI-II-32	+
BA-II-9	BK-I-3	+
BA-II-9	BK-II-1	+
BA-II-9	BL-I-1	+
BA-II-9	BL-II-31	+
BA-II-34	S1S2	+
BA-II-41	S1S2	+
BA-II-34	S1S3	+
BA-II-41	S1S3	+
BA-II-34	S1S4	+
BA-II-41	S1S4	+
BA-II-34	S1S5	+
BA-II-41	S1S5	+
BA-II-34	S1S6	+
BA-II-41	S1S6	+
BA-II-34	S1S7	+
BA-II-41	S1S7	+

BA-II, BE-II, and BG-II have a common sterility factor which can be designated S_8 . In other words, the plants of these groups are S_1S_8 . Naturally, we look for confirmation of the conclusion by examining other unions where any 2 plants of these 3 groups are involved. In table 16 are found

combinations BE-II-28 BA-II-32 and BE-II-42 BG-II-32 while in table 18 are found combinations BG-II-43 BA-II-32 and BG-II-43 BE-II-28 all show incompatibility as expected.

In table 13 are the tests on Family BB. Among the combinations made with Type I are 2 tests with plants having the genetic formula S_1S_5 . One was fertile, one was sterile. Other tests, however, show that the single failure with S_1S_5 was accidental. For example, combinations made with

TABLE 13
Tests of Family BB.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BB-I-2	BA-I-2	+	BB-II-1	BA-I-2	+
BB-I-4	BA-II-32	+	BB-II-1	BA-II-32	+
BB-I-2	BB-I-2	—	BB-II-1	BB-I-2	+
BB-I-2	BB-II-1	+	BB-II-1	BB-II-1	—
BB-I-2	BC-I-1	+	BB-II-1	BC-I-1	+
BB-I-2	BC-II-21	+	BB-II-1	BC-II-21	+
BB-I-2	BD-I-1	+	BB-II-1	BD-I-1	+
BB-I-2	BD-II-44	+	BB-II-1	BD-II-44	+
BB-I-2	BE-I-1	+	BB-II-1	BE-I-1	+
BB-I-2	BE-II-28	+	BB-II-3	BE-II-28	+
BB-I-2	BF-I-2	+	BB-II-3	BF-I-2	+
BB-I-2	BF-II-13	+	BB-II-3	BF-II-13	+
BB-I-2	BG-I-1	+	BB-II-3	BG-I-1	+
BB-I-4	BG-II-32	+	BB-II-6	BG-II-32	+
BB-I-4	BH-I-3	+	BB-II-6	BH-I-3	+
BB-I-4	BH-II-21	+	BB-II-6	BH-II-21	+
BB-I-4	BI-I-1	+	BB-II-6	BI-I-1	+
BB-I-4	BI-II-32	+	BB-II-6	BI-II-32	—
BB-I-4	BK-I-3	+	BB-II-6	BK-I-3	+
BB-I-4	BK-II-1	+	BB-II-6	BK-II-1	+
BB-I-4	BL-I-1	+	BB-II-6	BL-I-1	+
BB-I-4	BL-II-31	—	BB-II-6	BL-II-31	+
BB-I-4	S1S2	+	BB-II-1	S1S2	+
BB-I-7	S1S2	+	BB-II-10	S1S2	+
BB-I-4	S1S3	+	BB-II-1	S1S3	+
BB-I-7	S1S3	+	BB-II-10	S1S3	+
BB-I-4	S1S4	+	BB-II-1	S1S4	+
BB-I-7	S1S4	+	BB-II-10	S1S4	+
BB-I-4	S1S5	+	BB-II-1	S1S5	—
BB-I-7	S1S5	—	BB-II-10	S1S5	+
BB-I-4	S1S6	—	BB-II-1	S1S6	+
BB-I-7	S1S6	—	BB-II-10	S1S6	+
BB-I-4	S1S7	+	BB-II-1	S1S7	+
BB-I-7	S1S7	+	BB-II-10	S1S7	+

plants from BB-II and from BI-II, which are later shown to be S_1S_5 , are fertile. The only true incompatibility of BB-I is with S_1S_8 and with BL-II-31. And BL-II is also shown to be S_1S_8 by the tests of table 22. BB-II plants have the formula S_1S_5 . Plant BB-II-6 is sterile to pollen of BI-II-32. The reciprocal is also sterile as is seen in table 20. It is true that one test with S_1S_5 showed fertility and one test showed sterility. But additional tests not shown in the table confirmed the fact that BB-II is in truth S_1S_5 and is incompatible with S_1S_5 plants. There were 3 more

TABLE 14
Tests of Family BC.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BC-I-3	BA-II-32	+	BC-II-21	BA-II-32	+
BC-I-1	BB-I-2	+	BC-II-2	BB-I-2	+
BC-I-1	BB-II-1	+	BC-II-2	BB-II-1	+
BC-I-1	BC-I-1	—	BC-II-2	BC-I-1	+
BC-I-1	BC-II-21	+	BC-II-2	BC-II-21	—
BC-I-1	BD-I-1	+	BC-II-2	BD-I-1	—
BC-I-1	BD-II-44	+	BC-II-2	BD-II-44	+
BC-I-1	BE-I-1	+	BC-II-2	BE-I-1	+
BC-I-22	BE-II-28	+	BC-II-23	BE-II-28	+
BC-I-22	BF-I-2	+	BC-II-23	BF-I-2	+
BC-I-22	BF-II-13	+	BC-II-23	BF-II-13	+
BC-I-22	BG-I-1	+	BC-II-23	BG-I-1	+
BC-I-22	BG-II-32	+	BC-II-23	BG-II-32	+
BC-I-22	BH-I-3	+	BC-II-23	BH-I-3	+
BC-I-22	BH-II-21	+	BC-II-23	BH-II-21	+
BC-I-22	BI-I-1	+	BC-II-23	BI-I-1	+
BC-I-22	BI-II-32	+	BC-II-23	BI-II-32	+
BC-I-22	BK-I-3	+	BC-II-23	BK-I-3	+
BC-I-22	BK-II-1	+	BC-II-23	BK-II-1	+
BC-I-22	BL-I-1	+	BC-II-23	BL-I-1	+
BC-I-22	BL-II-31	+	BC-II-23	BL-II-31	+
BC-I-3	S1S2	—	BC-II-21	S1S2	+
BC-I-42	S1S2	—	BC-II-41	S1S2	+
BC-I-3	S1S3	+	BC-II-21	S1S3	+
BC-I-42	S1S3	+	BC-II-41	S1S3	+
BC-I-3	S1S4	+	BC-II-21	S1S4	+
BC-I-42	S1S4	+	BC-II-41	S1S4	+
BC-I-3	S1S5	+	BC-II-21	S1S5	+
BC-I-42	S1S5	+	BC-II-41	S1S5	+
BC-I-3	S1S6	+	BC-II-21	S1S6	+
BC-I-42	S1S6	+	BC-II-41	S1S6	+
BC-I-3	S1S7	+	BC-II-1	S1S7	+
BC-I-42	S1S7	+	BC-II-41	S1S7	+

tests with the pollen of S_1S_5 and 2 reciprocal tests in which S_1S_5 was used as the mother. All failed.

The tests of Family BC are shown in table 14. Incompatibility of Type BC-I was shown only with S_1S_2 . Two additional tests not shown in the table were made with the pollen of S_1S_2 . Two reciprocal tests were also made. In each test failure was recorded. The plants of BC-I, therefore, have the genetic constitution S_1S_2 . The only incompatibility exhibited by plants of BC-II is with BD-I-1. The reciprocal combination also failed

TABLE 15
Tests of Family BD.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BD-I-1	BA-II-32	+	BD-II-26	BA-II-32	+
BD-I-1	BB-I-2	+	BD-II-26	BB-I-2	+
BD-I-1	BB-II-1	+	BD-II-26	BB-II-1	+
BD-I-1	BC-I-1	+	BD-II-26	BC-I-1	+
BD-I-1	BC-II-21	-	BD-II-26	BC-II-21	+
BD-I-1	BD-I-1	-	BD-II-26	BD-I-1	+
BD-I-1	BD-II-44	+	BD-II-26	BD-II-44	-
BD-I-1	BE-I-1	+	BD-II-26	BE-I-1	+
BD-I-1	BE-II-28	+	BD-II-26	BE-II-28	+
BD-I-1	BF-I-2	+	BD-II-26	BF-I-2	+
BD-I-1	BF-II-13	+	BD-II-26	BF-II-13	+
BD-I-1	BG-I-1	+	BD-II-26	BG-I-1	+
BD-I-1	BG-II-32	+	BD-II-26	BG-II-32	+
BD-I-1	BH-I-3	+	BD-II-26	BH-I-3	+
BD-I-1	BH-II-21	+	BD-II-26	BH-II-21	+
BD-I-1	BI-I-1	+	BD-II-26	BI-I-1	+
BD-I-1	BI-II-32	+	BD-II-26	BI-II-32	+
BD-I-1	BK-I-3	+	BD-II-26	BK-I-3	+
BD-I-1	BK-II-1	+	BD-II-26	BK-II-1	-
BD-I-1	BL-I-1	+	BD-II-26	BL-I-1	+
BD-I-1	BL-II-31	+	BD-II-26	BL-II-31	-
BD-I-1	S1S2	+	BD-II-26	S1S2	+
BD-I-45	S1S2	+	BD-II-44	S1S2	+
BD-I-1	S1S3	+	BD-II-26	S1S3	+
BD-I-45	S1S3	+	BD-II-44	S1S3	+
BD-I-1	S1S4	+	BD-II-26	S1S4	+
BD-I-45	S1S4	+	BD-II-44	S1S4	+
BD-I-1	S1S5	+	BD-II-26	S1S5	+
BD-I-45	S1S5	+	BD-II-44	S1S5	+
BD-I-1	S1S6	+	BD-II-26	S1S6	+
BD-I-45	S1S6	+	BD-II-44	S1S6	+
BD-I-1	S1S7	+	BD-II-26	S1S7	+
BD-I-45	S1S7	+	BD-II-44	S1S7	+

(table 15). The plants of this group, then, can be given the formula S_1S_9 .

In table 15 are the tests of Family BD. As is to be expected from the results of table 14, BD-I plants show incompatibility only with BC-II. Since the test plants BD-I-1 and BD-I-45 died before they could be tested with S_1S_6 and S_1S_7 , it is a fair question to ask how we know that they do not belong to either of these groups. The reason is that BD-I plants were tested reciprocally with plants of BB-I and BL-II, two groups having the constitution S_1S_6 ; and were further tested with plants of BG-I and BK-I,

TABLE 16
Tests of Family BE.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BE-I-30	BA-II-32	+	BE-II-28	BA-II-32	—
BE-I-1	BB-I-2	+	BE-II-43	BB-I-2	+
BE-I-1	BB-II-1	+	BE-II-43	BB-II-1	+
BE-I-1	BC-I-1	+	BE-II-43	BC-I-1	+
BE-I-1	BC-II-21	+	BE-II-43	BC-II-21	+
BE-I-1	BD-I-1	+	BE-II-43	BD-I-1	+
BE-I-1	BD-II-44	+	BE-II-43	BD-II-44	+
BE-I-1	BE-I-1	—	BE-II-43	BE-I-1	+
BE-I-1	BE-II-28	+	BE-II-43	BE-II-28	—
BE-I-1	BF-I-2	—	BE-II-43	BF-I-2	+
BE-I-1	BF-II-13	+	BE-II-43	BF-II-13	+
BE-I-1	BG-I-1	+	BE-II-43	BG-I-1	+
BE-I-1	BG-II-32	+	BE-II-42	BG-II-32	—
BE-I-1	BH-I-3	+	BE-II-42	BH-I-3	+
BE-I-1	BH-II-21	+	BE-II-42	BH-II-21	+
BE-I-1	BI-I-1	+	BE-II-42	BI-I-1	+
BE-I-2	BI-II-32	+	BE-II-43	BI-II-32	+
BE-I-2	BK-I-3	+	BE-II-43	BK-I-3	+
BE-I-2	BK-II-1	+	BE-II-43	BK-II-1	+
BE-I-2	BL-I-1	+	BE-II-43	BL-I-1	+
BE-I-1	BL-II-31	+	BE-II-43	BL-II-31	+
BE-I-30	S1S2	+	BE-II-27	S1S2	+
BE-I-31	S1S2	+	BE-II-28	S1S2	+
BE-I-30	S1S3		BE-II-27	S1S3	+
BE-I-31	S1S3	+	BE-II-28	S1S3	+
BE-I-30	S1S4	+	BE-II-27	S1S4	+
BE-I-31	S1S4	+	BE-II-28	S1S4	+
BE-I-30	S1S5	+	BE-II-27	S1S5	+
BE-I-31	S1S5	+	BE-II-28	S1S5	+
BE-I-30	S1S6	+	BE-II-27	S1S6	+
BE-I-31	S1S6	+	BE-II-28	S1S6	+
BE-I-30	S1S7	+	BE-II-27	S1S7	+
BE-I-31	S1S7	+	BE-II-28	S1S7	+

two groups having the constitution S_1S_7 . All of these combinations were fertile. BD-II plants are shown to have the constitution S_1S_{10} . They are persistently sterile only with plants from the group BK-II, other pollinations not shown in the table having been made as a check. It is true that BD-II-26 was sterile to the pollen of BL-II-31 (2 pollinations); but there is reason to believe that this single outstanding exception in the extensive crosses among the plants of the B families was due to particulate true sterility of flowers of a certain branch of plant BL-II-31. In the first place,

TABLE 17
Tests of Family BF.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BF-I-23	BA-II-32	+	BF-II-22	BA-II-32	+
BF-I-2	BB-I-2	+	BF-II-13	BB-I-2	+
BF-I-2	BB-II-1	+	BF-II-13	BB-II-1	+
BF-I-2	BC-I-1	+	BF-II-13	BC-I-1	+
BF-I-2	BC-II-21	+	BF-II-13	BC-II-21	+
BF-I-2	BD-I-1	+	BF-II-13	BD-I-1	+
BF-I-2	BD-II-44	+	BF-II-13	BD-II-44	+
BF-I-2	BE-I-1	-	BF-II-13	BE-I-1	+
BF-I-2	BE-II-28	+	BF-II-13	BE-II-28	+
BF-I-2	BF-I-2	-	BF-II-13	BF-I-2	+
BF-I-2	BF-II-13	+	BF-II-13	BF-II-13	-
BF-I-2	BG-I-1	+	BF-II-13	BG-I-1	+
BF-I-2	BG-II-32	+	BF-II-15	BG-II-32	+
BF-I-2	BH-I-3	+	BF-II-15	BH-I-3	+
BF-I-2	BH-II-21	+	BF-II-15	BH-II-21	+
BF-I-2	BI-I-1	+	BF-II-15	BI-I-1	+
BF-I-2	BI-II-32	+	BF-II-15	BI-II-32	+
BF-I-2	BK-I-3	+	BF-II-15	BK-I-3	+
BF-I-2	BK-II-1	+	BF-II-15	BK-II-1	+
BF-I-2	BL-I-1	+	BF-II-15	BL-I-1	+
BF-I-2	BL-II-31	+	BF-II-15	BL-II-31	+
BF-I-23	S1S2	+	BF-II-22	S1S2	+
BF-I-43	S1S2	+	BF-II-41	S1S2	+
BF-I-23	S1S3	+	BF-II-22	S1S3	+
BF-I-43	S1S3	+	BF-II-41	S1S3	+
BF-I-23	S1S4	+	BF-II-22	S1S4	+
BF-I-43	S1S4	+	BF-II-41	S1S4	+
BF-I-23	S1S5	+	BF-II-22	S1S5	+
BF-I-43	S1S5	+	BF-II-41	S1S5	+
BF-I-23	S1S6	+	BF-II-22	S1S6	+
BF-I-43	S1S6	+	BF-II-41	S1S6	+
BF-I-23	S1S7	+	BF-II-22	S1S7	+
BF-I-43	S1S7	+	BF-II-41	S1S7	+

the reciprocal of this type of mating, BL-II-4 $\times$ BD-II-44, was fertile. Moreover, several critical tests show that BL-II plants have the formula S_1S_6 , as do the plants of BB-I; yet no other plants of the group S_1S_6 , are sterile to plants of BD-II.

Table 16 shows the tests of Family BE. BE-I plants can be given the formula S_1S_{11} . They are sterile only to the pollen of BF-I. The reciprocal is also sterile (table 17). Plant BE-I-30 died before it could be tested against S_1S_3 ; but BE-I-31 was fertile with S_1S_3 and BE-I-1 was fertile

TABLE 18
Tests of Family BG.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BG-I-31	BA-II-32	+	BG-II-43	BA-II-32	—
BG-I-1	BB-I-2	+	BG-II-43	BB-I-2	+
BG-I-1	BB-II-1	+	BG-II-43	BB-II-1	+
BG-I-1	BC-I-1	+	BG-II-43	BC-I-1	+
BG-I-1	BC-II-21	+	BG-II-43	BC-II-21	+
BG-I-1	BD-I-1	+	BG-II-43	BD-I-1	+
BG-I-1	BD-II-44	+	BG-II-43	BD-II-44	+
BG-I-1	BE-I-1	+	BG-II-43	BE-I-1	+
BG-I-2	BE-II-28	+	BG-II-43	BE-II-28	—
BG-I-2	BF-I-2	+	BG-II-43	BF-I-2	+
BG-I-1	BF-II-13	+	BG-II-43	BF-II-13	+
BG-I-1	BG-I-1	—	BG-II-43	BG-I-1	+
BG-I-42	BG-II-32	+	BG-II-4	BG-II-32	—
BG-I-42	BH-I-3	+	BG-II-4	BH-I-3	+
BG-I-42	BH-II-21	+	BG-II-4	BH-II-21	+
BG-I-42	BI-I-1	+	BG-II-4	BI-I-1	+
BG-I-42	BI-II-32	+	BG-II-43	BI-II-32	+
BG-I-42	BK-I-3	—	BG-II-43	BK-I-3	+
BG-I-42	BK-II-1	+	BG-II-43	BK-II-1	+
BG-I-42	BL-I-1	+	BG-II-43	BL-I-1	+
BG-I-41	BL-II-31	+	BG-II-40	BL-II-31	+
BG-I-31	S1S2	+	BG-II-32	S1S2	+
BG-I-42	S1S2	+	BG-II-43	S1S2	+
BG-I-31	S1S3	+	BG-II-32	S1S3	+
BG-I-42	S1S3	+	BG-II-43	S1S3	+
BG-I-31	S1S4	+	BG-II-32	S1S4	+
BG-I-42	S1S4	+	BG-II-43	S1S4	+
BG-I-31	S1S5	+	BG-II-32	S1S5	+
BG-I-42	S1S5	+	BG-II-43	S1S5	+
BG-I-31	S1S6	+	BG-II-32	S1S6	+
BG-I-42	S1S6	+	BG-II-43	S1S6	+
BG-I-31	S1S7	—	BG-II-32	S1S7	+
BG-I-42	S1S7	—	BG-II-43	S1S7	+

with BL-I-1, (also S_1S_3). BE-II plants proved to be S_1S_8 . They were sterile reciprocally with BA-II plants and with BG-II plants,—these last two groups being incompatible with each other, as expected.

In table 17 the results of the tests with Family BF are recorded. BF-I plants, as already noted, have the constitution S_1S_{11} . They belong to the same group as the plants of BE-I. All other combinations are fertile. The plants of BF-II are fertile to the plants of all other groups. They are designated S_1S_{12} .

TABLE 19
Tests of Family BH.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BH-I-2	BA-II-32	+	BH-II-29	BA-II-32	+
BH-I-1	BB-I-2	+	BH-II-42	BB-I-2	+
BH-I-1	BB-II-1	+	BH-II-42	BB-II-1	+
BH-I-1	BC-I-1	+	BH-II-42	BC-I-1	+
BH-I-1	BC-II-21	+	BH-II-42	BC-II-21	+
BH-I-1	BD-I-1	+	BH-II-42	BD-I-1	+
BH-I-1	BD-II-44	+	BH-II-42	BD-II-44	+
BH-I-1	BE-I-1	+	BH-II-42	BE-I-1	+
BH-I-3	BE-II-28	+	BH-II-42	BE-II-28	+
BH-I-3	BF-I-2	+	BH-II-42	BF-I-2	+
BH-I-3	BF-II-13	+	BH-II-42	BF-II-13	+
BH-I-3	BG-I-1	+	BH-II-42	BG-I-1	+
BH-I-41	BG-II-32	+	BH-II-42	BG-I-32	+
BH-I-41	BH-I-3	—	BH-II-42	BH-I-3	+
BH-I-41	BH-II-21	+	BH-II-42	BH-II-21	—
BH-I-41	BI-I-1	+	BH-II-42	BI-181	+
BH-I-40	BI-II-32	+	BH-II-38	BI-II-32	+
BH-I-40	BK-I-3	+	BH-II-38	BK-I-3	+
BH-I-40	BK-II-1	+	BH-II-38	BK-II-11	+
BH-I-40	BL-I-1	+	BH-II-38	BL-I-1	+
BH-I-41	BL-II-31	+	BH-II-38	BL-II-31	+
BH-I-1	S1S2	+	BH-II-28	S1S2	+
BH-I-2	S1S2	+	BH-II-29	S1S2	+
BH-I-1	S1S3	+	BH-II-28	S1S3	+
BH-I-2	S1S3	+	BH-II-29	S1S3	+
BH-I-1	S1S4	+	BH-II-28	S1S4	—
BH-I-2	S1S4	+	BH-II-29	S1S4	—
BH-I-1	S1S5	+	BH-II-28	S1S5	+
BH-I-2	S1S5	+	BH-II-29	S1S5	+
BH-I-1	S1S6	+	BH-II-28	S1S6	+
BH-I-2	S1S6	+	BH-II-29	S1S6	+
BH-I-1	S1S7	+	BH-II-28	S1S7	+
BH-I-2	S1S7	+	BH-II-29	S1S7	+

Table 18 shows the results of the tests with Family BG. BG-I plants are S_1S_7 , as shown by their incompatibility with the pollen of S_1S_7 . S_1S_7 plants were also found to be sterile to the pollen of BG-I plants in 4 tests. BG-I-42 was also sterile to BK-I-3, another S_1S_7 group. This last combination was made with negative results in 3 other cases not recorded in the table. All other combinations were fertile. BG-II plants were fertile in all combinations except those with BA-II and BE-II. This group, therefore, is S_1S_8 .

Table 19 shows the results of the tests with Family BH. The plants of

TABLE 20
Tests of Family BI.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BI-I-1	BA-II-32	+	BI-II-13	BA-II-32	+
BI-I-1	BB-I-2	+	BI-II-2	BB-I-2	+
BI-I-1	BB-II-1	+	BI-II-2	BB-II-1	-
BI-I-1	BC-I-1	+	BI-II-2	BC-I-1	+
BI-I-1	BC-II-21	+	BI-II-2	BC-II-21	+
BI-I-1	BD-I-1	+	BI-II-2	BD-I-1	+
BI-I-1	BD-II-44	+	BI-II-2	BD-II-44	+
BI-I-1	BE-I-1	+	BI-II-2	BE-I-1	+
BI-I-51	BE-II-28	+	BI-II-50	BE-II-28	+
BI-I-51	BF-I-2	+	BI-II-50	BF-I-2	+
BI-I-51	BF-II-13	+	BI-II-50	BF-II-13	+
BI-I-51	BG-I-1	+	BI-II-50	BG-I-1	+
BI-I-51	BG-II-32	+	BI-II-50	BG-II-32	+
BI-I-51	BH-I-3	+	BI-II-50	BH-I-3	+
BI-I-51	BH-II-21	+	BI-II-50	BH-II-21	+
BI-I-51	BI-I-1	-	BI-II-50	BI-I-1	+
BI-I-51	BI-II-32	+	BI-II-50	BI-II-32	-
BI-I-51	BK-I-3	+	BI-II-50	BK-I-3	+
BI-I-51	BK-II-1	+	BI-II-50	BK-II-1	+
BI-I-51	BL-I-1	+	BI-II-50	BL-I-1	+
BI-I-51	BL-II-31	+	BI-II-50	BL-II-31	+
BI-I-1	S1S2	+	BI-II-13	S1S2	+
BI-I-12	S1S2	+	BI-II-25	S1S2	+
BI-I-1	S1S3	+	BI-II-13	S1S3	+
BI-I-12	S1S3	+	BI-II-25	S1S3	+
BI-I-1	S1S4	+	BI-II-13	S1S4	+
BI-I-12	S1S4	+	BI-II-25	S1S4	+
BI-I-1	S1S5	+	BI-II-13	S1S5	-
BI-I-12	S1S5	+	BI-II-25	S1S5	-
BI-I-1	S1S6	+	BI-II-13	S1S6	+
BI-I-12	S1S6	+	BI-II-25	S1S6	+
BI-I-1	S1S7	+	BI-II-13	S1S7	+
BI-I-12	S1S7	+	BI-II-25	S1S7	+

BH-I are S_1S_{13} . They are fertile in all combinations with the other groups. The plants of BH-II are S_1S_4 . They show sterility with the pollen of S_1S_4 as recorded. An S_1S_4 plant was also used as the mother against pollen from BH-II plants in 3 tests not shown in the table, with negative results.

In table 20 are the results of the tests with Family BI. The plants of BI-I are fertile in all combinations, and can be given the formula S_1S_{14} . The plants of BI-II belong to the group S_1S_5 . Besides the tests shown in the table, 3 other tests were made with pollen of S_1S_5 , while 2 tests were

TABLE 21₁
Tests of Family BK.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BK-I-10	BA-II-32	+	BK-II-1	BA-II-32	+
BK-I-3	BB-I-2	+	BK-II-2	BB-I-2	+
BK-I-3	BB-II-1	+	BK-II-2	BB-II-1	+
BK-I-3	BC-I-1	+	BK-II-2	BC-I-1	+
BK-I-3	BC-II-21	+	BK-II-2	BC-II-21	+
BK-I-3	BD-I-1	+	BK-II-2	BD-I-1	+
BK-I-3	BD-II-44	+	BK-II-2	BD-II-44	—
BK-I-3	BE-I-1	+	BK-II-2	BE-I-1	+
BK-I-3	BE-II-28	+	BK-II-42	BE-II-28	+
BK-I-3	BF-I-2	+	BK-II-42	BF-I-2	+
BK-I-3	BF-II-13	+	BK-II-42	BF-II-13	+
BK-I-3	BG-I-1	—	BK-II-42	BG-I-1	+
BK-I-3	BG-II-32	+	BK-II-42	BG-II-32	+
BK-I-3	BH-I-3	+	BK-II-42	BH-I-3	+
BK-I-3	BH-II-21	+	BK-II-42	BH-II-21	+
BK-I-3	BI-I-1	+	BK-II-42	BI-I-1	+
BK-I-3	BI-II-32	+	BK-II-42	BI-II-32	+
BK-I-3	BK-I-3	—	BK-II-42	BK-I-3	+
BK-I-3	BK-II-1	+	BK-II-42	BK-II-1	—
BK-I-3	BL-I-1	+	BK-II-42	BL-I-1	+
BK-I-3	BL-II-31	+	BK-II-42	BL-II-31	+
BK-I-10	S1S2	+	BK-II-1	S1S2	+
BK-I-41	S1S2	+	BK-II-43	S1S2	+
BK-I-10	S1S3	+	BK-II-1	S1S3	+
BK-I-41	S1S3	+	BK-II-43	S1S3	+
BK-I-10	S1S4	+	BK-II-1	S1S4	+
BK-I-41	S1S4	+	BK-II-43	S1S4	+
BK-I-10	S1S5	+	BK-II-1	S1S5	+
BK-I-41	S1S5	+	BK-II-43	S1S5	+
BK-I-10	S1S6	+	BK-II-1	S1S6	+
BK-I-41	S1S6	+	BK-II-43	S1S6	+
BK-I-10	S1S7	—	BK-II-1	S1S7	+
BK-I-41	S1S7	—	BK-II-43	S1S7	+

made of the reciprocal combination. All of these tests showed the matings to be incompatible. Plants of BI-II were also sterile in reciprocal combinations with the other S_1S_5 group BB-II. The other combinations were fertile.

Table 21 shows the tests made with Family BK. The plants of BK-I have the formula S_1S_7 . Besides the tests shown, 3 other matings with S_1S_7 plants failed and 2 matings $S_1S_7 \times$ BK-I failed. BK-I plants were also sterile to the plants of BG-I, as was to be expected. The other combina-

TABLE 22
Tests of Family BL.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BL-I-2	BA-II-32	+	BL-II-27	BA-II-32	+
BL-I-2	BB-I-2	+	BL-II-4	BB-I-2	-
BL-I-2	BB-II-1	+	BL-II-4	BB-II-1	+
BL-I-2	BC-I-1	+	BL-II-4	BC-I-1	+
BL-I-2	BC-II-21	+	BL-II-4	BC-II-21	+
BL-I-2	BD-I-1	+	BL-II-4	BD-I-1	+
BL-I-2	BD-II-44	+	BL-II-4	BD-II-44	+
BL-I-2	BE-I-1	+	BL-II-4	BE-I-1	+
BL-I-2	BE-II-28	+	BL-II-4	BE-II-28	+
BL-I-2	BF-I-2	+	BL-II-4	BF-I-2	+
BL-I-2	BF-II-13	+	BL-II-4	BF-II-13	+
BL-I-2	BG-I-1	+	BL-II-4	BG-I-1	+
BL-I-2	BG-II-32	+	BL-II-4	BG-II-32	+
BL-I-2	BH-I-3	+	BL-II-4	BH-I-3	+
BL-I-2	BH-II-21	+	BL-II-4	BH-II-21	+
BL-I-2	BI-I-1	+	BL-II-4	BI-I-1	+
BL-I-1	BI-II-32	+	BL-II-4	BI-II-32	+
BL-I-1	BK-I-3	+	BL-II-4	BK-I-3	+
BL-I-1	BK-II-1	+	BL-II-4	BK-II-1	+
BL-I-1	BL-I-1	-	BL-II-4	BL-I-1	+
BL-I-1	BL-II-31	+	BL-II-4	BL-II-31	-
BL-I-2	S1S2	+	BL-II-26	S1S2	+
BL-I-25	S1S2	+	BL-II-27	S1S2	+
BL-I-2	S1S3	-	BL-II-26	S1S3	+
BL-I-25	S1S3	-	BL-II-27	S1S3	+
BL-I-2	S1S4	+	BL-II-26	S1S4	+
BL-I-25	S1S4	+	BL-II-27	S1S4	+
BL-I-2	S1S5	+	BL-II-26	S1S5	+
BL-I-25	S1S5	+	BL-II-27	S1S5	+
BL-I-2	S1S6	+	BL-II-26	S1S6	-
BL-I-25	S1S6	+	BL-II-27	S1S6	-
BL-I-2	S1S7	+	BL-II-26	S1S7	+
BL-I-25	S1S7	+	BL-II-27	S1S7	+

tions were fertile. BK-II plants were found to be fertile in all combinations except those involving BD-II. Thus, they belong to the S_1S_{10} group.

The tests of Family BL are shown in table 22. The BL-I plants were fertile in all combinations except with S_1S_3 . The reciprocal combination, $S_1S_3 \times$ BL-I also failed twice. The plants are therefore S_1S_3 . The plants of the BL-II group have the formula S_1S_6 , as shown by their incompatibility to S_1S_6 pollen. Reciprocals were also sterile. They were also sterile in reciprocal combinations to plants of BB-I (S_1S_6). All other combinations were fertile.

DISCUSSION

The original material with which the senior author began his studies on self-sterile plants some 18 years ago consisted of *Nicotiana alata grandiflora* from 4 sources (3 from seedsmen in the United States and 1 from Italy, through the UNITED STATES DEPARTMENT OF AGRICULTURE) and seed from a plant which was determined as *Nicotiana Forgetiana*. The plants of the second type grew from seed obtained from a Gray Herbarium sheet erroneously labeled *Nicotiana Clevelandii*. This plant had been sent in by a Californian botanist. It had been grown from seed obtained from Sander and Sons and had been called *Nicotiana Sanderæ*. Now, *Nicotiana Sanderæ* had been produced by crossing *N. Forgetiana* with *Nicotiana alata grandiflora*, which had produced the well-known large-flowered, many-colored hybrids. And Sander and Sons have repeatedly claimed that they did not distribute seed from the pure species *Nicotiana Forgetiana*,—a South American species which has apparently been collected but once. But since the seeds from the Gray Herbarium sheet produced a *uniform* population of plants having *small, red flowers*, corresponding perfectly with the plate (8006) for the species published in the BOTANICAL MAGAZINE, it is possible that they did indeed belong to *N. Forgetiana*. It is also possible that they were segregates from *Sanderæ* hybrids. Be that as it may, the studies on self-sterility made in this laboratory up to 1924 were made upon this so-called *Nicotiana Forgetiana*, upon *Nicotiana alata grandiflora*, and upon hybrids between the two types. Nearly all of the work was done upon the hybrids. The indications are that the original material contained several *S* factors. This conclusion may be deduced from the fact that in the earlier years cross-fertility was very high. The later experiments were upon inbred lines of this material; and therefore presumably not over 2 of the 3 *S* factors found could have come from the so-called *Nicotiana Forgetiana*.

The new material described earlier in this paper came from *Sanderæ* hybrids and from *Nicotiana alata grandiflora*. It was obtained from 5 different seedsmen. But although *Nicotiana alata grandiflora* was grown in this country long before the *Sanderæ* hybrids were produced, there is no guarantee that the material that we obtained contains a random sample of the *S* factors carried by either *Nicotiana Forgetiana* or by *Nicotiana alata grandiflora*. All that can be claimed is that the 16 plants (besides a second S_1S_4 plant) of new material investigated from a random sample of the *Sanderæ* hybrids and the *alata* hybrids now being grown in this country,—in so far as 16 plants can be a random sample of anything. These 16 plants proved to have the following genetic formulæ:- Farquhar's *alata*, S_2S_6 , S_2S_7 ; Farquhar's *Sanderæ*, S_2S_3 , S_1S_4 , S_1S_5 ; Dreer's *alata*, S_8S_{15} , S_2S_9 , S_3S_6 ; Dreer's *Sanderæ* S_9S_{10} , S_7S_8 ; Mitchell's *alata*, S_5S_6 ; Vaughan's *alata*, $S_{11}S_{12}$; Vaughan's *Sanderæ*, S_8S_{11} , S_4S_{13} , S_5S_{14} ; and Ferry's *Sanderæ*, S_7S_{10} .

It may be seen, then, that factors S_1 , S_2 , and S_3 , which had been isolated from our original material, were again recovered. S_1 was found only in Farquhar's *Sanderæ*; but S_2 and S_3 were found both in *Sanderæ* and in *alata*, and in plants obtained both from Farquhar and from Dreer. Of the other factors found more than once, S_4 and S_{10} were found only in *Sanderæ*, from Farquhar and Vaughan, and from Dreer and Ferry, respectively; S_6 was found only in *alata*, but from the 3 sources Farquhar, Dreer, and Mitchell. The remaining 4 factors that were found more than once were common to both *alata* and *Sanderæ*. Farquhar's *Sanderæ*, Mitchell's *alata*, and Vaughan's *Sanderæ* contained S_5 ; Farquhar's *alata*, Dreer's *Sanderæ*, and Ferry's *Sanderæ* contained S_7 ; Dreer's *alata* and *Sanderæ* and Vaughan's *Sanderæ* contained S_8 ; Dreer's *alata* and *Sanderæ* contained S_9 ; while Vaughan's *alata* and *Sanderæ* contained S_{11} . Thus it is evident that the *alata* hybrids and the *Sanderæ* hybrids are as similar to each other as are different samples of each type. One suspects that the *alata* plants now being grown by horticulturists are merely white-flowered segregates of the *Sanderæ* hybrids, and that all of the stocks sold by the various seedsmen are closely related; but this matter cannot be settled unless a study is made of material *known* to be unrelated to that in current circulation here in this country.

One is tempted, on the assumption that the 16 plants investigated form a random sample, to estimate the probable total number of *S* allelomorphs in the material used; but it is doubtful whether such a 'pastime' can yield results of real value. 32 factors were determined thus:

Factors	S_1	S_2	S_3	S_4	S_5	S_6	S_7	S_8	S_9	S_{10}	S_{11}	S_{12}	S_{13}	S_{14}	S_{15}
Frequency	2	4	2	2	3	3	3	3	2	2	2	1	1	1	1

It is possible to treat this distribution as a normal frequency distribution centering on S_2 , which was met 4 times. The standard deviation of this distribution is $3.5 \pm .3$; and the probable number of classes into which the variates should fall is expressed by the formula $4\sigma^2 + 1$, or 50. But unfortunately, there is no common-sense justification for such a calculation. Another set-up of the problem shows how far the above assumption may lead us astray. Let us assume that the number of factors in our material is exactly 15, or exactly 16, or 20, and that each factor is to be found with the same frequency. If there are exactly 15 factors, the most probable appearance of any particular factor is 2, the next most probable appearance of particular factor is 1 or 3. Actually, 2 appeared 6 times; 1 and 3 appeared 4 times each. Calculation is unnecessary. It is obvious that, with the assumption of equal frequency for all factors, it is quite probable that there are only 15 factors and highly improbable that there are more than 20 factors. But there is no good reason for making the above assumption. Indeed it is the common experience in genetics that factors are not found with equal frequency. Some are plentiful, some are rare. There is even evidence in this case that plants containing certain S factors are less viable than plants containing other S factors. And the more unequal the distribution is assumed to be, the greater the probable number of factors. The reasonable conclusion for us to draw, therefore, should run somewhat like this: other S factors may exist; but the number must be decidedly limited and the frequency so low that a further investigation of a scope humanly possible¹ could hardly be expected to add more than 4 or 5 factors to the present number.

The division of the progeny of all crosses of the type $S_x S_y \times S_1 S_1$ into two approximately equal groups of plants $S_1 S_x \times S_1 S_y$ shows that we are dealing with mutations of a single locus. There is no evidence that factors at a second locus have a direct effect on the behavior of these self-sterile plants. It is probable, however, that, given the presence of a particular S factor, such as $S_1 S_1$, subsidiary factors accelerate or retard pollen-tube growth in a limited fashion. That is to say, our experience leads us to believe that in a plant $S_1 S_2 WW$ the pollen tube may grow faster after an

¹ One would now have to test unknown factors against 15 testers, and this work would increase with every additional factor discovered.

incompatible mating than it will in a plant S_1S_2ww . Moreover, BRIEGER² (1927) has reported the isolation of one such factor " P ", apparently belonging to the same linkage group as the " S " factors, which accelerates the rate of pollen-tube growth where S_3 is involved.

Environmental conditions also have an effect upon pollen-tube growth. Direct evidence that such is the case has been obtained by making pollinations of a given type on certain plants kept under different conditions and studying the stained pollen tubes at various times after pollination. When plants are kept at a temperature around 10°C, the pollen tubes grow somewhat more slowly than they do at 18°C. Similarly, plants in a healthy condition or at the height of their flowering period exhibit slower pollen-tube growth after a given pollination than if they are in a poor physiological condition or are at the end of their flowering period. We believe that this conclusion holds for all types of matings, but it is easier to demonstrate when dealing with incompatible unions where pollen-tube growth is slow. Slight acceleration or retardation of the pollen tubes after a compatible mating has but little effect on time of fertilization. Fertilization occurs after a compatible mating in from 80 to 130 hours, and during the last 5 hours the tube may grow 10 mm. Since 130 hours is long before the flower would fall off if unpollinated, the slowest tubes reach the micropyle and effect fertilization; hence, indirect evidence of differential pollen-tube growth is impossible, and direct evidence is difficult to gain.

Direct evidence of differential pollen-tube growth is also difficult to obtain when two types of pollen tubes are competing and both are compatible unions,—for example, when an S_1S_1 plant is pollinated with S_2S_3 pollen. But the existing indirect genetic evidence—equality of the two classes of progeny—indicates that in all types of compatible mating, the pollen tubes grow at about the same rate. Furthermore, in a union such as $S_1S_1 \times S_1S_2$, where "incompatible" pollen tubes are competing with "compatible" pollen tubes, there is no evidence that the growth of "incompatible" pollen tubes is accelerated beyond their normal rate by the presence of the "compatible" pollen tubes.

Yet the above remarks are not the whole story, as the following argument shows. There seems to be a compensation for different style lengths of such a nature that in families segregating for style length it is not easier to obtain a given union in plants with styles 20 mm. long than it is in plants with styles 60 mm. long. In fact, the families which have shown the highest degree of self-sterility have been—although this is possibly accidental—

² It may be noted that BRIEGER'S " P " factor can also be interpreted as a mutation of S^3 .

families with short styled flowers. Again, unpollinated flowers usually fall off after 3 or 4 days. Flowers pollinated with incompatible pollen often remain on the plant for 10 or 12 days, although no fertilization occurs; which indicates that in incompatible matings the final stage of pollen-tube growth is not linear, as the studies of EAST and PARK (1917) indicated, but shows some retardation. And finally, by bud-pollinations, we have been able to self plants with genetic formulæ S_1S_2 , S_1S_3 , S_2S_4 , S_2S_5 , and S_2S_7 , and have obtained populations of progeny indicating that the two types of pollen tubes grew at about the same rate. But bud-pollinations of S_1S_4 and S_1S_5 have never yielded seed. Thus it seems to follow that S_1 in combination with S_2 and S_3 produces pollen tubes which grow faster than when in combination with S_4 and S_5 .

Thus, although in compatible unions all pollen tubes appear to grow at practically the same rate, there may be slight differences that would be detectable if accurate determinations could be made. And in incompatible unions, the pollen tubes do grow at different rates. For example, plants bearing certain S factors never produce seeds even after bud-pollinations or under other conditions that favor self-fertility. Plants bearing other S factors produce full capsules of seed after selfing in the bud. Plants bearing still other S factors show different degrees of pseudo-fertility under conditions favorable to fertility. If, therefore, the environmental factors affecting rate of pollen-tube growth affect all S factors in approximately the same degree, then plants bearing certain factors produce tubes which normally grow faster than those bearing other factors. For example, the pollen tubes bearing the factor S_4 only with the greatest difficulty can be made to grow fast enough to enable seed to be produced after a self-pollination; but pollen tubes bearing the factor S_7 , which grow normally at a faster rate than those of S_4 , can be shifted over into apparent fertility (our pseudo-fertility) both by favorable external conditions and by the presence of the proper heritable subsidiary factors. It is not improbable, moreover, that various other factors exist which, though they are all S allelomorphs, are characterized by *different* pollen-tube growth-rates that are too rapid to be shifted to a similitude with the self-sterility factors by unfavorable conditions; yet, because seed is always produced, growth-rate differences can be determined only by direct study of the pollen tube velocities. This conclusion seems probable because our factor S_{15} is a factor having a border-line pollen tube velocity. Ordinarily, full capsules of seed are produced after self-fertilization; but under conditions inhibiting pollen tube growth, the plants exhibit some self-sterility. Factor S_f , an S allelomorph coming from *Nicotiana Langsdorffii*, on the other hand, produces

pollen tubes which grow so rapidly that no combination of inhibiting factors will cause self-sterility.

It is natural to speculate as to the bearing of these facts, if any, on the nature of the gene, and in particular on GOLDSCHMIDT's quantitative theory of heredity. We have isolated 16 allelomorphs of the *S* factor (including *S_f*). They are all point mutations, since they all behave as allelomorphs to each other and since the crossover values of 3 of them with the corolla-color factor *C* are approximately the same. It has been demonstrated that certain of these allelomorphs are characterized by pollen-tube growth-rates (after selfing) of different velocities. For instance, *S_f*, *S₁₅*, *S₉*, *S₈*, *S₇*, and *S₄* have different normal growth rates, from high to low in that order. Now, it may be that each of these 16 allelomorphs is characterized by a pollen-tube growth-rate of velocity different from all others. It might even be possible, if these growth-rates could be determined with a high degree of accuracy and classified in descending order, to find that each differed from the other by a definite mutation-quantum expressed in velocity, as a strict interpretation of GOLDSCHMIDT's theory would demand. Unfortunately, we cannot say that no two of these allelomorphs have identical pollen-tube growth-rates. Still more unfortunately, our experience leads us to believe that disturbing variables, both environmental and heritable, definitely prevent growth-rate determinations being made with the accuracy necessary to give us this knowledge.

On the other hand, one may assume that each *S* allelomorph differs from the next in order by a definite quantum expressed in reaction velocity and may speculate as to what conclusions follow, if any, in connection with our conception of the gene. To put the matter most simply: Does a postulate of the above type lead to the conclusion that the different velocities of the reactions directed by the various allelomorphs of a single gene are due to the presence of different quantities of the gene? Arguments in favor of such a conclusion have been presented with much vigor and clarity in the various writings of GOLDSCHMIDT. The writers have only admiration for the brilliant work of the Berlin geneticist and certainly do not wish to be numbered among those who say that his position is "neither sound genetics nor sound physiology," (GOLDSCHMIDT 1928); yet they are of the opinion that a sympathetic and receptive agnosticism in regard to his quantitative theory of gene action is at present the wisest course to take. The reasons for adopting this attitude cannot be set forth adequately in this paper; but the argument, skeletonized, runs somewhat as follows.

The gene is the unit of heredity by definition. Indirectly, we infer the genes to be rather stable physical entities arranged in an orderly manner

within the chromosomes. From calculated crossover values, we diagram their positions in the chromosomes; and we assume, from minimum known crossover values and because multiple allelomorphs show similar crossover values with specific genes in the same linkage group, that the gene physically is small. Calculations based upon minimum crossover values and chromosome size in *Drosophila melanogaster* put the bulk of the gene in the same order as that of a relatively small number of protein molecules. But it should not be forgotten that the last few points in this complex hypothesis rest upon a slender basis. Let us assume, for example, that minimal crossover values do, in fact, determine gene size, and that the minimum unit physically determinable in the fruit fly is one-fifth of one percent, or one five hundredth of the size of the chromosome. Let us assume further that there are portions of the chromosome in which five percent is the lowest crossover value. The following questions then arise: Are there no genes in this second chromosome block, which is twenty-five times the size of the other piece? Is the trouble merely that the genes in this larger piece have not been discovered? Or, more important theoretically, is the actual unit of heredity twenty-five times as large in the second case as it is in the first? We have no information on these points, but they are important to bear in mind when considering the more general aspects of the gene theory.

GOLDSCHMIDT was led to speculate on the nature of the gene from the results of his brilliant experiments on intersexes in the Gypsy moth. And he believes that in these investigations definite quantities of a gene were studied. He admits that no experimental proof has been offered to show that the sex determiners F and M are single genes; but he says that they behave like single genes, or a group of inseparable genes, and therefore the quantitative effects shown by the experiments should be interpreted as the effects of the behavior of different quantities of genes. "A quantitative relation or balance," he says, "has no meaning except in connection with the absolute quantities back of the proportion." But is this conclusion unavoidable? Our physical conception of the gene has been built up on crossover values. And on the question of sex there is no information of this precise kind. It seems valuable, therefore, to preserve the distinction; and, so long as no definite gene loci are found, to interpret sex by "gene balance."

Moreover, there is a second consideration. The gene is a biological unit, presumably different from the chemical unit, the molecule. In last analysis, however, its behavior is chemical, even though more like the working of a chemical laboratory than the reaction of a pure compound;

and it is to be hoped that chemical interpretations or descriptions may at some time become possible. Is it not advisable, then, to utilize chemical analogies where one can? It is a very simple philosophy to hold that back of quantitative behavior of hereditary units there must be a quantitative proportion of those units; but this philosophy may be more naïve than profound, for we know that in chemistry neither the type nor the velocity of a reaction can be predicted by a knowledge of the size of the molecule. It is true that the rate of a chemical reaction is proportional to the molecular concentration of the reacting substances present at a given time, and this chemical law may describe a great many of the processes of ontogeny; but it seems too simple a picture to imagine that the complex chemical laboratory of the gene is conducted solely in this manner. The facts known at present about the gene seem to require a less simple hypothesis, and we have a less simple analogy in the currently accepted hypotheses of stereo-chemistry. Even these hypotheses may be too simple, for stereo-chemistry is confined to the permutations possible in the chemical unit, the molecule. The geneticist is not so closely hedged about. Spatial relations in the larger unit, the gene, open up a wider realm of possibilities.

Both of these arguments should also be weighed, we believe, when considering the evidence from multiple allelomorphs, from triplo-, diplo-, and haplo-chromosome complexes, and from the effect of external conditions upon development. In all of these cases, it is difficult to evaluate the variables present in such a way that it is relatively certain that we are dealing with the behavior of single genes; and when this is done to the best of our ability, it is not hard to imagine a chemical mechanism at work which is quite different from that assumed by GOLDSCHMIDT.

Finally, a third argument of real value in connection with the facts of multiple allelomorphism has been suggested to us by CASTLE. When any two allelomorphs of a series are brought together in an organism, only forms containing these allelomorphs are recovered. If the quantitative theory of heredity is correct, one should expect to recover other forms. For example, let us assume that the action of the three allelomorphs S_1 , S_2 , S_3 is due to the presence of 1, 2, and 3 quanta of S respectively. Then the mating $S_1S_2 \times S_3S_3$ might be expected, in the second generation, to yield plants bearing factors S_1 or possibly S_4 . But such is not the case.

It must be admitted that some of the evidence obtained by STURTEVANT on the bar-eye phenomena in *Drosophila* and some of the evidence presented by various workers on variegation appears to be interpretable most simply by hypotheses of the GOLDSCHMIDT type. Yet they may yield to other explanations. Until critical experiments are made which drive geneticists

to a definite hypothesis, therefore, it seems the part of wisdom to remain dispassionately unattached to a particular mode of explanation of these phenomena.

SUMMARY

1. Fifteen allelomorphs of the *S* factor for self-sterility have been isolated from material of the forms known as *Nicotiana alata graneiflora* and *Nicotiana Sanderae*.

2. From the frequency distribution of the *S* allelomorphs studied, one may conclude that presumably other allelomorphs exist in this material; but they are probably few in number and presumably rare.

3. The two supposedly distinct types studied form homogeneous material, in so far as the distribution of *S* factors is concerned.

4. It is unlikely that there is a second primary locus affecting self-sterility in these forms; but subsidiary hereditary factors and certain environmental factors have noticeable effects upon the rapidity of pollen-tube growth in plants characterized by particular *S* factors.

5. The effects of subsidiary factors and of changed external conditions are not sufficient to prevent the classification of identical *S* factors by means of cross-sterility tests.

6. A number of these allelomorphs are characterized by different rates of pollen-tube growth after selfing.

7. The fact that numerous mutations have occurred in a single factor giving allelomorphs having characteristically distinct velocities of reaction, as shown by pollen-tube growth-rates, does not lead us to believe that different quantities of the *S* factor are involved.

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