the torsional problem of curved beams is reached also for those sections, with no further limitations than those existing in the solutions of the corresponding torsional problem in straight members, and the postulation of the principal of superposition.

If the forces applied are not pure couples, they can in each section be reduced to a couple and a force. This force will in general cause in the further sections an additional bending around the y and z axes, which will be added to the expressions of M_y and M_z in equations (2).

This method can also be used for non-prismatic beams provided the variations of profile are sufficiently slow as to make the disturbance caused thereby on the stress distribution negligible.

[1] The moment vectors M_x, M_y, M_z could also be obtained by graphical addition of the vectors $\overline{AA'}$, $\overline{BB'}$, etc., and subsequent decomposition of the resultant vector into the s, y and z components.

[2] For complete treatment of curved members with circular, elliptical and rectangular cross-sections, see Paul Heymans and W. J. Heymans, *J. Math. and Physic, M. I. T.*, **4**, 1, 1924.

[3] The notations used are those of A. E. H. Love, "Treatise on the Mathematical Theory of Elasticity."

[4] Heymans, *loc. cit.*

[5] *Loc. cit.*

A NEW INTERPRETATION OF THE HEREDITARY BEHAVIOR OF SELF-STERILE PLANTS

By E. M. EAST AND A. J. MANGELSDORF

BUSSEY INSTITUTION, HARVARD UNIVERSITY

Communicated December 30, 1924

Among the results appearing from the studies of self-sterility in the genus Nicotiana carried on in this laboratory are the following:

1. Self-sterility is a Mendelian recessive in crosses between self-fertile and self-sterile species. Self-sterile plants, therefore, breed true to self-sterility.

2. Self-sterility in such self-sterile species as *Nicotiana alata* Lk. and Otto and *Nicotiana forgetiana* Hort. (Sand.), or their hybrids, is controlled by numerous inherited factors. Like combinations of these factors give like groups of individuals as far as their compatibility with each other is concerned, just as like factorial combinations which lie at the basis of morphological differences give groups which are alike in those characters.

3. All members of a given self-sterility group are cross-sterile with each other in reciprocal crosses, and all are cross-fertile with members of every other group, with certain limitations as shown in the new data presented in this paper.

4. Not less than fifteen and possibly as high as twenty-five such intra-sterile, inter-fertile groups are found in the material used in these studies.

5. The basis upon which these variations in compatibility rest are hereditarily controlled reactions whereby some pollen tubes (compatible matings) show a rapidly accelerated rate of growth, while other pollen tubes (incompatible matings) show a slow and steady rate of growth which ordinarily does not permit fertilization to occur within the life of the flower.

6. Conditions can be so controlled that (*a*) the length of "life" of the flower is prolonged, (*b*) the rapidity of the growth of the pollen tube is stimulated, and (*c*) the opportunity for pollen-tube action is lengthened.

By taking advantage of various methods mentioned under heading No. 6, chief of which is simply the pollination of the young bud, selfed strains of our self-sterile hybrids between *N. alata and N. forgetiana* have been carried through twelve generations. This lengthy manipulation was carried out with a purpose. If the factors controlling the behavior of these self-sterile plants are distributed according to the regular Mendelian procedure,[1] successive selfings should tend to eliminate heterozygotes. If, furthermore, compatibility between self-sterile plants is brought about by the existence of constitutional differences in certain factors, then one ought to be able to produce near homozygous populations by selfing which would consist of very few intra-sterile, inter-fertile classes.

This expectation has been realized. Numerous families have been raised which consist of two intra-sterile, inter-fertile groups. A smaller number of families have been found to consist of a single group of this type, each individual being cross-sterile with every other individual, though fertile with individuals in other families.

Some twenty-five thousand pollinations have now been made in testing the reactions of this type of family. Data on a few of these families have been published in the sixth paper of these "Studies on Self-sterility"[2] by Dr. Edgar Anderson. We shall call attention first to a peculiarity in these results as follows:

NAME	ORIGIN	CLASSES CROSSED ♀ × ♂	CLASSES RESULTING AND NUMBER OF PLANTS OF EACH	
Family A O	AA–2 × AA–13	a × b	6–b	4–c
Family A L	O–32 × O–46	a × b	8–b	12–c
Family A T	P–27 × O–2	a × b	11–b	6–c
Family A H	L–18 × L–20	a × c	8–b	9–c
Family A I	M–31 × M–25	a × c	9–b	11–c
Family A R	R–38 × L–24	a × c	13–b	7–c
Family A P	R–20 × R–13	c × a	7–a	9–b
Family B P	N–7 × R–12	b × c	6–a	4–c
Family B O	R–2 × O–2	c × b	4–a	6–b

In all of these cases it will be noticed that the class to which the female parent belongs is absent in the progeny. We are dealing with three classes, a, b and c. Each individual of any one of these classes is sterile reciprocally with any other individual of the class to which it belongs and is fertile reciprocally with every individual belonging to either of the other two classes. But the progeny resulting from reciprocal crosses is different. Class "a" × Class "c" gives "b" individuals and "c" individuals only, while Class "c" × Class "a" gives "a" individuals and "b" individuals only. Two classes always appear in what seems to be an approximation to equal numbers, *but the class of the mother is never represented.*

These results have been corroborated numerous times by data obtained since Dr. Anderson's figures were reported, as the following table shows. The classes are here called X, Y and Z, though they prove to be the same classes with which Anderson dealt, when tested by the proper crosses.

NAME	ORIGIN	CLASSES CROSSED ♀ × ♂	CLASSES RESULTING AND NUMBER OF PLANTS OF EACH	
			Class Y	Class Z
Family Q_1 N_1	Q_1 x N_1	Class X × Class Y	21	19
Family R_3 E_2	R_3 x E_2	Class X × Class Y	13	15
Family R_3 R_1	R_3 x R_1	Class X × Class Y	21	13
		Total	55	47
			Class X	Class Z
Family E_2 R_3	E_2 x R_3	Class Y × Class X	21	9
Family O_1 O_2	O_1 x O_2	Class Y × Class X	23	17
Family Q_2 Q_1	Q_2 x Q_1	Class Y × Class X	18	20
		Total	62	46
			Class Y	Class Z
Family O_2 L_1	O_2 x L_1	Class X × Class Z	8	16
Family Q_1 L_1	Q_1 x L_1	Class X × Class Z	21	18
Family R_3 C_{13}	R_3 x C_{13}	Class X × Class Z	20	16
		Total	49	50
			Class X	Class Y
Family L_1 O_2	L_1 x O_2	Class Z × Class X	22	16
Family L_1 Q_1	L_1 x Q_1	Class Z × Class X	8	12
		Total	30	28
			Class X	Class Z
Family N_1 L_1	N_1 x L_1	Class Y × Class Z	11	8
Family Q_2 L_1	Q_2 x L_1	Class Y × Class Z	29	9
Family R_1 C_{13}	R_1 x C_{13}	Class Y × Class Z	12	20
Family R_1 L_1	R_1 x L_1	Class Y × Class Z	16	24
		Total	68	61
			Class X	Class Y
Family R	C_{13} x E_2	Class Z × Class Y	10	10
Family L_1 O_1	L_1 x O_1	Class Z × Class Y	23	13
Family L_1 Q_2	L_1 x Q_2	Class Z × Class Y	23	17
		Total	56	40

It is clear that the same phenomenon is exhibited. When individuals of any two classes are crossed, *two* classes appear in approximately equal numbers, but the class to which the female parent belongs is never represented.

X ♀ × Y ♂	gives	Y and Z	Z ♀ × X ♂	gives	X and Y
Y ♀ × X ♂	gives	X and Z	Y ♀ × Z ♂	gives	X and Z
X ♀ × Z ♂	gives	Y and Z	Z ♀ × Y ♂	gives	X and Y

At first sight one might suppose that these results, differing as they do from any hitherto obtained in genetic work, are due to a novel type of gamete distribution; yet such a supposition is rendered unlikely by two facts. Morphological characters in these varieties appear to be transmitted in the normal Mendelian manner; furthermore the ratios in which the classes appear here are strikingly like those expected when F_1 monohybrids are backcrossed with pure recessives.

To be brief, we believe that the inheritance in these cases is of the ordinary type, but that there are physiological limitations to the opportunity for fertilization.

Assume that in these populations there are three allelomorphs, S_1, S_2 and S_3; and that

Class X = S_1 S_3, Class Y = S_1 S_2, Class Z = S_2 S_3.

Assume further that a plant affords stimulus only to pollen which bears sterility factors other than its own. Thus a Class Z plant (S_2 S_3) affords proper stimulus only to gametes carrying factors other than S_2 or S_3. In other words, of the three factors present in these various populations, the Z plants afford stimulus only to S_1 gametes.

Now what happens when one crosses a Z female by an X male? Only the S_1 pollen is stimulated and functions. The Z female being S_2 S_3 in composition stimulates neither S_2 nor S_3 pollen grains. The resulting progeny consists therefore of two classes, S_1 S_2 (Class Y) and S_1 S_3 (Class X) in equal numbers. In the reciprocal cross, X female (S_1 S_3) by Z male (S_2 S_3), the X female again affords stimulus only to gametes-bearing factors other than its own—this time, the S_2 pollen. The resulting progeny is therefore solely of the two classes Y (S_1 S_2) and Z (S_2 S_3).

The results to be expected according to this hypothesis are in accordance with the data in hand in that (*a*) the class of the female parent is always absent in the progeny, (*b*) the progeny of reciprocal crosses is not the same two classes, and (*c*) the progeny consists of two classes other than the female parent in approximately equal numbers regardless of which of the other two classes serves as the male parent.

This hypothesis can be tested further by selfing individuals or by crossing individuals belonging to the same class. This is done, as explained above, by taking advantage of the "pseudo-fertility" which occurs when non-compatible pollen is given the *opportunity* to effect fertilization. In practice this is usually done by pollinating young buds.

Family R_1 (Class Y = S_1 S_2) selfed produced 32 plants. Of these individuals, 19 were Class Y (S_1 S_2), and showed typical Class Y behavior. Two new classes also appeared. Of the first class, Class Z Y, there were 7 individuals. These plants were fertile as females with all classes except their own, and sterile as males with their own class and also with classes Z and Y. The second class, Class XY of which there were 6 individuals, was fertile as a female with all classes except its own, and was sterile as a male with its own class and also with Classes X and Y.

Similarly Family Q_2 (Class Y = S_1 S_2) selfed gave 24 individuals of Class Y, 14 individuals of Class Z Y and 1 individual of Class X Y.

According to the selective pollen stimulation hypothesis, what happens is this:

Class Y (S_1 S_2), when selfed in the very young bud, gives

1 S_1 S_1 (Class XY) + 2 S_1 S_2 (Class Y) + 1 S_2 S_2 (Class Z Y).

The S_1 S_1 plants (Class X Y) are fertile as females with

1. Class Z (S_2 S_3) because they accept both S_2 and S_3 pollen,
2. Class X (S_1 S_3) because they accept S_3 pollen, and
3. Class Y (S_1 S_2) because they accept S_2 pollen.

They are fertile as males with Class Z (S_2 S_3) because Z accepts S_1 pollen; but, they are sterile as males with both Class X (S_1 S_3) and Class Y (S_1 S_2), because neither of these classes accept S_1 pollen.

For analogous reasons, individuals of Class Z Y (S_2 S_2) are fertile as females with Classes Z, X and Y, but are sterile as males with Classes Z and Y.

In two other families Y plants were crossed with each other. This should give the same results as when Y's are selfed. The first cross (No. E_2 × No. R_1) gave 17 Class Y + 5 Class Z Y + 1 Class X Y. The second cross (No. R_1 × No. E_2), a reciprocal, gave 21 Class Y + 12 Class Z Y + 6 Class X Y. The total results from Class Y × Class Y(S_1 S_2 × S_1 S_2), therefore are 81 Class Y (S_1 S_2) + 38 Class Z Y (S_1 S_1) + 14 X Y (S_2 S_2). There is a marked deficiency in Class X Y which we are not able yet to ascribe definitely either to differential pollen stimulation or to a lethal effect when S_2 fertilizes S_2. It seems more likely in this particular case to be due to the first cause cited.

There is one bit of evidence on this point. According to the hypothesis, when a Y female (S_1 S_2) is pollinated by an X male (S_1 S_3) only the S_3 pollen should function, resulting in progeny of two classes, viz., Class X (S_1 S_3) and Class Z (S_2 S_3). Such results are normally obtained. But if pollinations are made in the *very young* bud, some of the S_1 pollen might be expected to have the opportunity to function. One family has been obtained from such a pollination, Family R_1 R_3, coming from a pollination of R_1 female of Class Y by R_3 male of Class X. The population obtained consisted of 34 individuals belonging to the following classes, 13 Class X

$(S_1\ S_3)$ + 13 Class Z $(S_2\ S_3)$ + 4 Class Y $(S_1\ S_2)$ + 4 Class X Y $(S_1\ S_1)$. According to hypothesis, the cross of $S_1\ S_2$ by $S_1\ S_3$ gave large numbers of Class X $(S_1\ S_3)$ and of Class Z $(S_2\ S_3)$ because the Class Y female $(S_1\ S_2)$ afforded a decided stimulus to S_3 pollen, and gave small numbers of Class Y $(S_2\ S_1)$ and Class X Y $(S_1\ S_1)$ because very little stimulus was afforded to S_1 pollen. But fertilization with S_1 pollen *was* possible, when the opportunity was forthcoming.

On the other hand, Class Z $(S_2\ S_3)$ selfed, which might be expected to give 1 Class Z Y $(S_2\ S_2)$ + 2 Class Z $(S_2\ S_3)$ + 1 Class Z X $(S_2\ S_3)$, excepting as the ratio were disturbed by selective pollen stimulation, did in fact give no plants of Class Z X $(S_3\ S_3)$. There were obtained 17 individuals of Class Z $(S_2\ S_3)$ and 12 individuals of Class Z Y $(S_2\ S_2)$. Likewise, Class X $(S_1\ S_3)$, selfed, in two different cases gave 57 individuals of Class X $(S_1\ S_3)$ and 20 individuals of Class X Y $(S_1\ S_1)$, but not a single individual of Class Z X $(S_3\ S_3)$. Since the number of plants in Classes Z Y $(S_2\ S_2)$ and X Y $(S_1\ S_1)$, respectively, in these two cases showed no particular excess when compared with the heterozygous classes, one must conclude that the heterozygous classes were not composed wholly of S_3 ovules fertilized by S_2 pollen and of S_3 ovules fertilized by S_1 pollen. In each example S_3 pollen must have reached the ovaries and have functioned in the production of heterozygotes. For this reason, it seems as if one were forced to conclude that S_3 is lethal when in the homozygous condition.

[1] Conceivably methods of inheritance which are non-Mendelian might bring about similar results.

[2] The genetic basis of cross-sterility in *Nicotiana*. *Genetics*, **9**, 13–40, 1924.