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FERTILITY IN CICHORIUM INTYBUS: THE SPORADIC OCCURRENCE OF SELF-FERTILE PLANTS AMONG THE PROGENY OF SELF-STERILE PLANTS

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The writer (1916) has already presented the evidence that the very prevalent self-sterility (and cross-sterility as well) in chicory can be ascribed to a *physiological incompatibility* operating between sex organs or sex cells that are fully formed, anatomically perfect, potentially functional and of simultaneous development. It was noted that this type of sexual sterility is sharply to be distinguished from sterility due to *anatomical incompatibility* (more or less purely structural differences and adaptations such as herkogamy), *impotence* (failure to produce gametes) or *embryo abortion* (death of egg after fertilization or death of young embryo). I also at that time discussed and summarized the literature bearing on such phenomena.

From my studies made in 1912 and 1913, it appears (Stout 1916, p. 365-366) that self-sterility is the rule in chicory. Three plants (designated *A*, *B*, and *C*) of wild stock were found to be self-sterile, as were 52 plants grown from the open fertilized seed of these plants, and all plants tested of ten cultivated varieties were self-sterile. In one variety (Barbe de Capucin), 29 plants of one planting and 5 of another were tested, and of other varieties about five plants of each were tested. The total of about 135 plants from these various sources were self-sterile.

However, in the pedigreed cultures grown in 1913, a few plants exhibiting varying degrees of self-fertility appeared quite sporadically among the F_1 progeny of various crosses between self-sterile plants. Of the 75 plants derived by crossing plant *A* with plant *E22* (of the variety Barbe de Capucin), only eight were self-fertile. Of 21 plants,

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the offspring of A and E_3 , four were self-fertile. Seventeen plants, the offspring of C and E_3 , were self-sterile, as were 30 plants from seed of a cross between a white-flowered plant, ($A \times C$) *no. 1*, of wild stock and a plant of the variety "improved striped-leaf." The number of self-fertile plants, therefore, varied greatly in the different series, but in no series was the proportion very large.

The self-fertile plants mentioned above appeared after only one generation of ancestry known to be self-sterile. Furthermore, the parents in each cross were not closely related and were somewhat different in vegetative habit and flower color. As previously recognized (1916, p. 415), these results raised some question regarding the influence of wide-crossing as compared with that of inbreeding on the development of self-compatibilities, especially as continued inbreeding in the variety "red-leaved Treviso" had in two generations given only one feebly self-fertile plant out of a total of 49 plants (complete data given in 1916, Table 7).

In order to obtain further data on this question, it was planned to continue inbreeding within this variety, increasing the number of plants grown in 1916, and at the same time to grow for comparison an F_1 generation from crosses between plants of this variety and a self-sterile plant of a wild stock. The present paper will deal especially with the data obtained from these cultures.

DESCRIPTION OF THE CULTURES

The variety "red-leaved Treviso" is a cultivated salad chicory that has been developed in continental Europe. As grown for commercial seed production the variety is biennial, seed being sown one summer for a crop that matures in the following summer. As grown in my culture the plants are more nearly annual. Seed is sown in January in flats, and the seedlings are potted and kept in continuous growth in the greenhouse until spring, when they are planted in the field. Under such treatment the plants, as a rule, reach full development in the following August. The general habit of growth of the mature plants is well shown in text-figure 1. The height has ranged from $4\frac{1}{2}$ to $6\frac{1}{2}$ feet with the greater number of plants about 5 feet tall. The plants are rather sparsely branched near the base but rather abundantly branched above. In the early stages of growth the rosette leaves are numerous, of large size, and erect. One of the marked characteristics of the family I have grown is the development of a type of fasciation



FIG. 1. Typical plants of the variety red-leaved Treviso. The marker stands by self-fertile plant (R. Ser. 10, No. 8); all other plants in the view were self-sterile. From photograph taken in the afternoon when all flower heads are closed.

involving duplication and cohesion of the main axis. Two main stems develop with a single root system. Occasionally these are separated

from the root upward, but most usually the two are more or less fused for a distance, the fusion finally becoming complete near the top of the plant. None of the plants of this variety have shown any tendency to live over winter. The maturity and death of the stems and branches is accompanied by death of the roots. Several attempts to obtain new plants from root cuttings taken at the time of the maturity of plants have failed.

The wild white-flowered plant used in crosses with plants of the red-leaved Treviso is perennial as are wild plants of chicory in general. In the five years it has been under observation its mature height has ranged from $2\frac{1}{4}$ to $2\frac{1}{2}$ feet. Its rosette leaves are few, much smaller in size than those of the red-leaved Treviso, and are flat in habit of growth. The branches are few and strongly horizontal, giving the plant a sparsely branched and scraggly appearance.

The F_1 generation plants of the crosses between plants of the red-leaved Treviso variety and the wild plant just mentioned were more like the red-leaved Treviso in habit of growth. They were all blue-flowered. Their height ranged from 4 to 6 feet, and they were abundantly and profusely branched from the base. The degree of the duplication of the main stem was much less than in the family of the red-leaved Treviso. As shown in text figure 2, the plants of this hybrid generation were large and well developed and of marked vegetative vigor. They were far more robust and vigorous in growth than the wild parent, and in respect to the degree of branching they were more developed than plants of the red-leaved Treviso strain.

The sex vigor of these plants and of plants of the Treviso variety in respect to *production* of flowers was commensurate with the vegetative vigor. From statistical data obtained in studies of flower number, it was found that the total number of flower heads produced by individual plants ranged roughly from 2,000 to 3,500 with the average number of flowers per head at about 17. At the climax of development as many as 100 to 150 flower heads opened in a single day. These statements together with the descriptions given and the illustrations in the accompanying text-figures give some conception of the full and complete sex vigor seen in the profuse production of flowers that set seed when pollinated with pollen that was compatible.

It will also readily be observed that the inbreeding within the family of red-leaved Treviso involved crosses between plants of close blood relationship and of decided similarity, and that the fertilization in



FIG. 2. Typical plants of the F_1 generation of the crosses between plants of the Treviso variety and the wild plant A.

these plants with pollen from the wild plant A constitutes a comparatively wide cross both in respect to blood relationship and to the vegetative characteristics of the respective parents.

RESULTS OF THE SELF-POLLINATIONS OF THE 1916 CROP OF
"IMPROVED RED-LEAVED TREVISO"

A total of 103 plants were grown in this crop. All were descended from two plants of the 1913 crop, and all but two had three generations of parentage known to be self-sterile. The data for the self-pollinations made on these plants are given in Table 1. Here the plants are grouped, as they were grown, in series according to the immediate parentage. The table gives the total number of heads upon which controlled self-pollinations were made, the number of heads producing no seed, the number of heads with seed, the number of seeds per head, and the percentage of fertility. Frequently birds ate seeds, indicated in the tables by "B," and thus interfered somewhat with the determination of the percentage of fertility.

The 10 sister plants of Ser. 7 were all self-sterile; of the 19 sister plants of Ser. 8, one was feebly self-fertile; of the 25 plants of Ser. 9, three were self-fertile; of Ser. 10, one of 10 plants was self-fertile; of Ser. 11, five out of 19 were self-fertile; and one of the 18 plants of Ser. 12 was self-fertile. Of the total 101 plants descended from self-sterile parentage, 11 were self-fertile in some degree. With the exception of Ser. 7, one or more self-fertile plants appeared in each series. It may be noted that three self-fertile plants, two of which were rather highly self-fertile, appeared in Ser. 9, which was derived by crossing two sister plants of the previous generation. This series was from a more closely inbred parentage than were the other series.

The total number of flower heads pollinated in these series is 1205. As a rule, not less than 10 heads were pollinated on a plant, and in nearly all cases this total includes pollinations made on several different days. When it became evident that some plants were self-fertile, special efforts were made to continue self-pollination on them in order to secure an abundance of seed for future progeny. However, as shown in the table, the number of heads pollinated on plants completely self-sterile is also often high.

The degree of self-fertility, judged by the percentage of flowers setting seed, varied considerably. Most of the self-fertile plants were feebly self-fertile, producing as a rule only a few seed per head in only a few of the heads manipulated. Others, as no. 34 of Ser. 9 and no. 8 of Ser. 10, set seed in every head pollinated, and in numerous heads the numbers were nearly equal or even equal to all that were

TABLE I

Record in 1916 for Self-pollinations of the Cultures of "Improved Red-leaved Treviso"

		Record for Heads Pollinated			Fertility (%)
		Total No. Heads.	With No Seed	With Seed	
Series 6 ...					
No. 3 ...	10	10	0	Parentage, Series 4, no. 21. A self-fertile plant	
" 4 ...	15	15	0		
Series 7....				Parentage, Ser. 1, no. 8×Ser. 5, no. 5.	
No. 1....	14	14	0		
" 2....	15	15	0		
" 3....	20	20	0		
" 8....	10	10	0		
" 10....	13	13	0		
" 12....	11	11	0		
" 17....	7	7	0		
" 19....	10	10	0		
" 20....	10	10	0		
" 21....	10	10	0		
Series 8....				Parentage, Ser. 4, no. 12×Ser. 5, no. 8.	
No. 1....	15	15	0		
" 2....	10	10	0		
" 3....	13	13	0		
" 4....	14	14	0		
" 5....	14	14	0		
" 7....	13	10	3	1, 2, 10.	0.06
" 8....	12	12	0		
" 10....	12	12	0		
" 11....	11	11	0		
" 12....	14	14	0		
" 13....	10	10	0		
" 14....	10	10	0		
" 15....	11	11	0		
" 16....	12	12	0		
" 17....	12	12	0		
" 18....	12	12	0		
" 19....	21	21	0		
" 20....	10	10	0		
" 22....	10	10	0		
Series 9....				Parentage, Ser. 5, no. 1×Ser. 5, no. 6.	
No. 1....	10	10	0		
" 2....	12	12	0		
" 3....	15	15	0		
" 6....	27	1	26	1, 4, 6, 6, 6, 7, 7, 7, 8, 8, 9, 9, 9, 9, 10, 10, 10, 11, 11, 11, 11, 12, 13, 13, 13, B	0.50
" 7....	10	10	0		
" 10....	14	14	0		
" 12....	14	14	0		
" 13....	10	10	0		
" 19....	12	12	0		
" 20....	10	10	0		
" 21....	5	5	0		
" 25....	24	24	0		
" 26....	12	12	0		

TABLE I—*Continued*

	Record for Heads Pollinated				Fertility (%)
	Total No. Heads	With No Seed	With Seed	Seeds per Head. Remarks	
No. 28....	9	9	0		
" 29....	10	10	0		
" 30....	15	15	0		
" 31....	10	1	9	B, B, B, 1, 2, 2, 2, 3, 4	0.13
" 32....	12	12	0		
" 34....	23	0	23	3, 6, 7, 9, 9, 10, 10, 10, 10, 10, 11, 12, 12, 12, 13, 13, 14, 14, 14, 14, 14, 15, 18	0.71
" 37....	9	9	0		
" 38....	5	5	0		
" 40....	10	10	0		
" 42....	15	15	0		
" 43....	10	10	0		
" 47....	13	13	0		
Series 10....				Parentage, Ser. 4, no. 12 × Ser. 5, no. 9	
No. 1....	12	12	0		
" 2....	17	17	0		
" 3....	10	10	0		
" 4....	10	10	0		
" 5....	9	9	0		
" 6....	9	9	0		
" 7....	20	20	0		
" 8....	24	0	24	4, 6, 8, 8, 8, 9, 9, 9, 10, 10, 11, 11, 11, 12, 12, 12, 12, 13, 13, 14, 14, 15, 16, 17	0.63
" 10....	11	11	0		
" 11....	8	8	0		
Series 11....				Parentage, Ser. 5, no. 1 × Ser. 1, no. 8	
No. 1....	13	13	0		
" 4....	14	14	0		
" 8....	11	11	0		
" 11....	10	10	0		
" 12....	12	10	2	1, 5	0.03
" 16....	9	9	0		
" 24....	8	3	5	1, 1, 3, 4, 5	0.11
" 25....	14	14	0		
" 27....	11	11	0		
" 28....	10	10	0		
" 29....	10	8	2	2, 4	0.04
" 31....	10	10	0		
" 32....	12	9	3	1, 1, 3	0.03
" 35....	8	8	0		
" 37....	18	17	1	12	0.04
" 40....	10	10	0		
" 43....	11	11	0		
" 44....	11	11	0		
" 49....	8	8	0		
Series 12....				Parentage, Ser. 5, no. 9 × Ser. 4, no. 18	
No. 1....	10	10	0		
" 2....	10	10	0		
" 3....	12	12	0		
" 4....	12	12	0		
" 5....	11	11	0		

TABLE I—*Continued*

		Record for Heads Pollinated				Fertility (%)
		Total No. Heads	With No Seed	With Seed	Seeds per Head. Remarks	
No	6....	9	9	0		0.73?
"	7....	10	10	0		
"	8....	13	13	0		
"	9....	12	12	0		
"	10....	10	10	0		
"	11....	13	0	13	B, B, 3+B, 3+B, 3+B, 5+B, 7, 8, 10, 10, 11, 18, 22	
"	12....	10	10	0		
"	13....	12	12	0		
"	16....	10	10	0		
"	17....	11	11	0		
"	18....	10	10	0		
"	19....	13	13	0		
"	20....	5	5	0		

possible. It is not to be considered that the degree of fertility is absolutely determined, and especially in those cases when birds (Ser. 12, no. 11) ate all or a part of the seed produced in certain heads. The detailed data, however, make it quite clear that various degrees of self-compatibility may exist. The evidence in this particular is quite identical with that already reported in 1916. In Ser. 11 a comparatively large proportion of plants, 5 out of 19, were self-sterile, but the fertility was low in each case.

The two plants of Ser. 6 were derived from self-fertilized seed of a plant that was feebly self-fertile and which was the only self-fertile plant that appeared in my crops of this variety previous to 1916. The two plants were self-sterile.

SELF-COMPATIBILITIES AND INCOMPATIBILITIES AMONG PLANTS OF
THE 1916 CROP OF F_1 GENERATION OBTAINED BY CROSSING
A PLANT (A) OF WILD STOCK WITH PLANTS OF THE
VARIETY "RED-LEAVED TREVISO"

The data for the self-pollinations of this generation are presented in Table 2. The wild white-flowered plant A was the pollen parent for Series 1-4 and the seed parent of Series 5. Five different plants of the 1915 generation of "red-leaved Treviso" were concerned in the parentage, as indicated in the table. The uncertainties of securing compatible cross-pollinations among self-sterile plants (Stout, 1916,

TABLE 2

Data for Self-pollinations of F_1 generation Derived by Crossing a Wild White-flowered Self-sterile Plant (A) With Self-sterile plants of the Variety "Red-leaved Treviso"

Plant.	Data for the Heads Pollinated				Fertility (%)
	Total No. Heads	Heads With No Seed	Heads With Seed	Seeds per Head. Remarks	
RA. Ser. 1.				Parentage, R. Ser. 1, no. 7×A	
No. 1.	10	10	0		
" 2.	10	6	4	1, 1, 1, 5	0.05
" 3.	11	11	0		
" 4.	10	10	0		
" 5.	11	11	0		
" 6.	12	12	0		
" 7.	14	14	0		
" 8.	10	10	0		
" 9.	10	10	0		
" 10.	12	12	0		
" 11.	10	10	0		
" 12.	11	11	0		
" 13.	12	12	0		
RA. Ser. 2.				Parentage, R. Ser. 1, no. 2×A	
No. 1.	12	12	0		
" 2.	15	15	0		
" 3.	15	15	0		
" 6.	13	13	0		
" 7.	14	14	0		
RA. Ser. 3.				Parentage, R. Ser. 1, no. 6×A	
No. 1.	10	10	0		
" 2.	11	11	0		
" 3.	11	11	0		
" 4.	11	11	0		
" 5.	12	12	0		
" 7.	12	12	0		
" 8.	15	15	0		
" 9.	11	11	0		
" 10.	17	17	0		
" 13.	10	10	0		
" 14.	10	10	0		
" 15.	12	12	0		
" 16.	12	12	0		
" 17.	11	11	0		
" 18.	16	16	0		
" 19.	11	11	0		
" 20.	11	11	0		
" 21.	16	16	0		
" 22.	10	10	0		
" 23.	11	4	7	1, 3, 4, 5, 6, 7, 11	0.19
" 24.	12	12	0		
RA. Ser. 4.				Parentage, R. Ser. 5, no. 16×A	
No. 1.	10	10	0		
" 2.	10	10	0		
" 3.	10	10	0		
" 4.	19	19	0		

TABLE 2—*Continued*

Plant	Data for the Heads Pollinated				Fertility (%)
	Total No. Heads	Heads With No Seed	Heads With Seed	Seeds per Head. Remarks	
No. 5.	12	12	0	Parentage, A × R. Ser. I, no. I	
" 6.	15	15	0		
" 8.	10	10	0		
" 9.	14	14	0		
" 10.	10	10	0		
" 11.	13	13	0		
" 12.	10	10	0		
" 13.	10	10	0		
" 14.	12	12	0		
" 15.	11	11	0		
" 16.	10	10	0		
AR. Ser. 5.					
No. 1.	10	10	0		
" 2.	11	11	0		
" 3.	10	10	0		
" 4.	10	10	0		
" 5.	10	10	0		
" 6.	10	10	0		
" 7.	10	10	0		
" 8.	12	12	0		
" 9.	12	12	0		
" 10.	10	10	0		
" 11.	10	10	0		
" 12.	13	13	0		
" 13.	12	12	0		
" 14.	12	12	0		
" 15.	13	13	0		
" 16.	9	9	0		
" 17.	12	12	0		
" 18.	8	8	0		
" 19.	12	12	0		

Table 14) made it somewhat difficult to limit the parentage of the various series to the same parents, which would, of course, be highly desirable. Thus it happens that the immediate parents of these series are not the same as those of the series reported in Table 1; the plants involved are, however, closely related sister plants.

In making the cross-pollinations between the self-sterile parents here involved, no attempts were made to emasculate or to depollinate the seed parent. In brushing a flower head of a prospective seed parent with a flower head from a plant selected for a pollen parent, there was necessarily a full and rather thorough mixture of the two lots of pollen with apparently an equal chance that both should be distributed on stigmatic surfaces. A total of 54 plants were derived

from four different seed parents of the red-leaved Treviso (Ser. 1-4, Table 2) and 19 were derived from the wild white-flowered plant as a seed parent. All these plants were unmistakably hybrids. In no case did a plant's own pollen function in fertilization.

It may be noted here that East (1915) has made the suggestion that the physiological conditions operating in self-incompatibility involve a failure on the part of the plant's own pollen to stimulate the proper secretions in its pistil necessary for growth of the pollen tubes. If this were the case, it would seem that self-sterility might be removed, in part at least, by mixing pollen as I have done in the crosses referred to above. Such, however, was not the result. It is possible that such results might more readily be obtained in species in which the fertilization processes are much less rapid than in chicory.

Of the 73 plants of this F_1 generation, only two plants were self-fertile with percentages of 5 and 19. In only two cases were the number of heads pollinated less than 10. The results are therefore very decided. All of these plants were blue-flowered and were quite similar in general vegetative habit and appearance. All flowered profusely throughout the season, and, as is the case with plants having only this type of sterility (physiological incompatibility), all set abundant seed in many heads open-pollinated.

CROSS-INCOMPATIBILITIES AMONG THE PLANTS GROWN IN 1916

A brief summary may here be given regarding the results of cross-pollinations made during 1916. Of the cultures of red-leaved Treviso (R), 37 different plants were tested in a total of 34 different combinations; of these 16 were sterile and 18 fertile in some degree. Among the plants of the F_1 generation (RA), 24 combinations of cross-pollinations were made involving 37 different plants. Of these 9 were sterile and 15 were fertile in some degree. As indicated by the figures, the combinations among the R plants involved fewer plants proportionally and more reciprocals than did those among the RA plants. No particular emphasis can be given to the number here obtained in its bearing on the influence of inbreeding or cross-breeding. The data obtained from these plants selected at random, however, indicate that cross-incompatibilities exist in marked degree. The results in this respect are quite in agreement with those already reported (1916, Tables 9-14), not only for the red-leaved Treviso but for other cultures of chicory.

DISCUSSION AND CONCLUSION

The sporadic development of self-compatibility giving self-fertility among the progeny of self-sterile lines of descent is in decided evidence in the cultures reported above. No doubt if a larger number of the "red-leaved Treviso" variety had been grown and tested, more than one self-fertile plant would have been found previous to the crop of 1916. However, they were not found and the variety was kept in pedigreed cultures by crossing self-sterile plants.

Self-compatibility is therefore a characteristic that was new in expression, at least to the particular and immediate line of descent involved. A total of 101 plants of the 1916 crop had three generations of ancestry known to be self-sterile; of these 11 plants were self-fertile.

There is, therefore, much in the occurrence of these plants that suggests discontinuous variation or mutation. However, the fertilities of these self-fertile plants vary. They grade over to complete self-sterility. The variation in the self-fertility of plants grown from self-fertile parents (Stout, 1916, Table 6) is much more continuous and is indicative that the irregular and somewhat discontinuous variation seen in the intensity of fertilities is only an apparent one due to the few cases observed.

It is to be noted that there have been scarcely any attempts made to study the progeny of self-sterile plants in species and varieties known to be strongly self-sterile by continued inbreeding in pedigreed lines of descent. Compton (1912, 1913) has reported that in *Reseda odorata* "self-sterile plants when bred *inter se* throw self-sterile offspring only," but he has not published data regarding the number of such families, the number of plants, or the number of generations tested. East (1915) has reported that the inter-specific hybrids between *Nicotiana forgetiana* and *N. alata grandiflora* have been completely self-sterile for four generations, and that a total of over 500 plants were tested. Data on the behavior of the parent plants, or even of the two parent species, were evidently not obtained. Correns (1912, 1913) was especially interested in the study of cross-incompatibilities and evidently tested the self-fertility of only 13 of the total of 60 sister plants obtained by crossing two self-sterile plants of *Cardamine pratense*. Of these, however, three plants appear to have been self-fertile.

In view of the prevalence of self-incompatibilities in many plants of economic importance, such as cabbage, rye, apple, plum, prune,

cherry, blueberry, etc., it is somewhat surprising that more searching studies have not been made on the sporadic occurrence of self-fertile plants. It is somewhat in doubt, therefore, whether there exists a species, a variety, or even a strain of plants in which self-sterility due to physiological incompatibility is absolute. However, such may exist especially among certain hybrid strains as is suggested by East's data. Many further data are needed to allow of any adequate statement of the various degrees and intensities of such self-sterility in species or in different strains as a whole. The general evidence, however, suggests that in many such cases the sporadic occurrence of self-fertile plants may be quite as it is in chicory.

The almost complete self-incompatibility of the F_1 progeny of the crosses between plants of the "red-leaved Treviso" variety and the wild white-flowered plant *A* is noticeable. The occurrence of only two self-fertile plants of feeble fertility out of 73 such plants emphasizes the sporadic nature of the development of self-compatibility. This may also be considered as evidence that wide crossing inside the species does not especially favor the development of self-compatibility. In fact, a comparison of the behavior of these plants with that of the 1916 crop of the inbred plants of the "red-leaved Treviso" variety leads to the conclusion that inbreeding is more favorable to the development of self-compatibility than is wide crossing. In East's results (1915) all plants tested, some 500 in number, of the F_1 , F_2 , F_3 , and F_4 generations were found to be self-sterile. As these were the offspring of an interspecific cross, it does not seem that wide crossing has here favored the development of self-compatibility. It should be noted that East suggests that there may be some increase in the development of cross-incompatibilities among the later generations, which he considers may be due to an increased homozygosity, but the evidence is not conclusive on this point.

I have not sufficient data to judge adequately of the frequency of cross-incompatibilities among the various series and generations of chicory grown. Cross-incompatibility has occurred in each generation of the red-leaved Treviso variety (for data obtained in 1914 and 1915 see Stout, 1916, Table 14) as it has in all other families thus far tested (Stout, 1916, Tables 9-13). Everywhere that I have tested for cross-incompatibility in chicory it has been found to be very general and to exist in various grades of intensity.

The numbers of self-fertile plants which appeared among the F_1

generation of crosses between the wild plant *A* and plants of the cultivated common chicory (*E* Series) are somewhat higher than those of the F_1 generation (RA plants) derived by crossing this same wild plant with plants of the red-leaved Treviso here reported. The strain (*E*) has not, however, been inbred in pedigreed cultures as has the red-leaved Treviso strain, so there are less adequate data on the comparative value of inbreeding and crossing with this variety.

The character of physiological self-compatibility giving fertility appears in a very irregular and sporadic manner, and it exists in different degrees of intensity in different plants. It has appeared in chicory in a family of the variety known as red-leaved Treviso after three generations of self-sterile ancestry and no doubt would occur with equal irregularity and intensity after many generations of such ancestry. It seems very conclusive therefore that the causes of self-incompatibilities are not to be ascribed to a similarity of nuclear constitution involving definite hereditary units of germ plasm which either directly determine incompatibilities (especially Correns's view of line-stuffs) or which indirectly determine them (East's view). Furthermore, the variability of the offspring grown from self-fertile plants in chicory shows a very irregular inheritance of the characteristic of self-compatibility and makes it quite clear that the expression of self-compatibility is quite of the nature of a fluctuating variability, and that self-compatibility and self-incompatibility, in chicory at least, are not to be described in terms of dominant and recessive characters which behave in any sort of Mendelian manner.

The evidence seems conclusive that the actual conditions giving the various grades of self-compatibility, and of self-incompatibility (undoubtedly there are various grades of incompatibility giving complete sterility) as well, are decidedly individual. Various aspects of this question in relation to conceptions of fertilization and to the phenomena of serum incompatibilities have already been discussed (Stout, 1916). It must be remembered that a plant whose two sets of sex-organs are completely incompatible is itself derived from the fusion of two cells that were compatible. The interactions between pistil and pollen-tubes were compatible. The germ plasms of the two sex cells were compatible in fusion, in the somatic life of the diploid cell structure of the resulting individual, and in the more intricate interactions involved in sporogenesis occurring in that individual. Yet in cases of complete self-incompatibility none of the pollen grains are functional on the pistil of the plant.

Such conditions emphasize the marked individuality of the development of conditions giving incompatibility. The conditions are fundamentally physiological and arise apparently in connection with the differentiation of the two sets of so-called sex organs. Important to an understanding of the facts of differentiation here involved are the phenomena of cross-incompatibilities. Three sister sporophytes which are quite identical in all vegetative characters may possess sex organs that are incompatible to the extent that complete self-sterility is in evidence; no. 1 may be incompatible with the male sex organs (microgametophytes and gametes) of no. 2, but compatible with those of no. 3. This difference in relation is certainly indicative of differences in the physiological qualities of the two lots of male gametophytes. Conversely the microgametophytes and gametes produced by a single sporophyte may act quite differently on the female sex organs borne on two other sporophytes, being compatible in one case and incompatible in the other. This indicates, likewise, a difference in the condition of the two sets of female organs (including pistils). Furthermore, the data as to the occurrence of cross-incompatibilities in chicory even indicate that reciprocal crosses between two plants may give quite the opposite results, showing that the relations of the two sets of sex organs may not be interchangeable.

In such phenomena we may recognize a loss of sex-vigor which is concerned with the function of gametophytes and gametes. The decrease in fertility is entirely independent of a decrease in the production of spores. Furthermore, there appears to be full and complete development of the macrogametophyte and its egg; its development is certainly not inhibited by the condition of the pistil in which it develops. There is no evidence that the microgametophyte is not fully developed with reference to its differentiation. Although often involving a decreased vegetative growth of the pollen-tube, the inhibition appears fundamentally to involve function.

The reactions involved in self- and cross-incompatibilities do seem to involve, to some extent at least, as Jost (1907) and East (1915) have especially emphasized, an interaction between the haploid pollen-tube and the diploid tissues of the pistil. There may be some question as to what extent these relations are involved.

Incompatibilities are evidently indicated not only by an inability to produce embryos, but also sometimes by a feeble viability of those that are produced. This death of embryos among seed produced by

the self-pollination of different sister plants is quite as fluctuating in degree as is the production of seed itself. In its effect it is often quite like the conditions observed in the "zygotic sterility" which Davis (1915*a*, 1915*b*, 1916) has observed in the *Oenotheras*, especially those of hybrid origin. In chicory, however, the noticeable failure in seed production suggests that much of the embryo abortion observed may also involve a sort of sexual incompatibility. Embryo abortion, however, may be due purely to conditions of nutrition, especially in those species which exhibit no physiological incompatibility.

The incompatibilities in chicory are obviously not purely a question of haploid against diploid, but of a particular kind of haploid and diploid relationship. In discussing these various points, the writer (1916, p. 436-440) has pointed out that our knowledge of the physiology of pollen-tubes is scarcely sufficient to decide whether the critical point in the growth of the pollen-tube is determined by purely nutritive reactions with the pistil as such or whether it is really determined by the diffusion of secretions (hormones) from the macrogametophyte. The writer hopes to be able to state later somewhat definitely from cytological investigation what the relative developments and nuclear phenomena in chicory are.

In discussing the various aspects of the relation of cell organization to the development of compatibilities and incompatibilities, the writer (1916, p. 416) has pointed out that the role of any particular combination of germ plasm elements, as far as can be judged by their expression as characters in parents, in sister plants and in offspring, must be quite secondary as far as incompatibilities are concerned to a more general quality of the tissue and cell organization that develops in connection with ontogenetic growth and development. The conceptions of Jost (1907), Morgan (1904, 1910), and East (1915) are fundamentally based on this same generalization as I there pointed out.

Much the same idea, if I understand their position aright, has since been expressed by Goodspeed and Clausen in stating that such cases of physiological incompatibility seem to involve "non-specific" disturbances in the "reaction systems" (germ plasm) (1917*a*, p. 46). These authors have embodied in the conception of "reaction systems" (1916, 1917*a*) a view which in some measure is a revolt against the extreme formalism of the Mendelian factorial hypothesis, and in this sense the conception is useful in the interpretation of the phenomena of sterility especially of the type I have called impotence. In their

application of this conception to the almost complete impotence of the F_1 hybrids of *Nicotiana Tabacum* $\times$ *N. sylvestris*, they are dealing with the well-known cases of degeneration so often observed during sporogenesis in interspecific hybrids. They believe that the very few perfect spores formed represent the *Tabacum* and *sylvestris* extremes of a combination series. In other words, these few spores represent the cases where the parental germ plasms segregated without mutual influence. The greater number of recombinations, however, were incompatible combinations of various elements derived from the two germ plasms. There are very few of the two original combinations that survive reduction and sporogenesis. In somatogeneses the incompatibility is seen, they believe, in a complete dominance of the *Tabacum* characters (1917a, 1917b). Whether involving chemical or mechanical reactions or involving differences in developmental tendencies in the sense used by Tischler (1907), (Stout, 1916, p. 423-427) such intra-cellular incompatibilities arise especially in the reorganization of cells during or immediately following reduction as has long been known.

In the case of physiological incompatibility, as in chicory, there appears to be no impotence except of a purely accidental sort. Any recombination system may survive, and in chicory sporogenesis in the offspring of crosses between the red-leaved Treviso variety and a wild white-flowered plant must, it would seem, give many new recombinations. The range of these recombinations must be quite the same in the various sister plants both of the F_1 generation hybrids and of the various series of red-leaved Treviso. Yet for the self-sterile plants, and these are here in greater number, all the pollen grains fail to function irrespective of the character of the particular germ plasm organization from which they came and of which they may be variously composed. On the other hand in the self-fertile plants that are sister plants of such self-sterile plants, germ cells of much the same hereditary constitutions (as judged by the characters of the plants that bear them) are compatible.

Furthermore, in the cases of self-fertility of any degree (or cross-fertility as well), the evidence thus far obtained from hybrid generations does not indicate that the fertilizations involved selective or preferential mating which favored fusion between particular recombinations of germ plasm with respect to hereditary characters.

The determination of whether physiological self- and cross-incom-

patibilities giving sterility involve similarity or dissimilarity of constitutional organization is, of course, very fundamental to the understanding of the nature of fertilization. Although rather widely differing in particular applications, the conceptions advanced as to the causes of physiological sexual self-incompatibility in such hermaphrodite plants as *Eschscholtzia* (Darwin, 1877), *Cardamine* (Correns, 1912, 1913), *Reseda* (Compton, 1912, 1913), *Nicotiana* (East, 1915), and in such hermaphrodite animals as *Ciona* (Morgan, 1904, 1910) have in general agreed in considering that a similarity or lack of differentiation is responsible for the sterility. The writer has already (1916) discussed these conceptions and has presented for consideration the view that the evidence is more readily to be interpreted on the basis of the principle that in general a marked degree of similarity in constitution is necessary for sexual fertility. In this relation it is to be noted that inbreeding in the variety "red-leaved Treviso" has led to a somewhat greater similarity in general characteristics than existed in the original stock grown from commercial seed. In this sense the continued inbreeding of sister plants has led to a greater homozygosity. It is in the 1916 cultures of the offspring of inbred plants that self-fertile plants appeared as noted above. As far as the results in chicory extend, and it may be said that there are no more comprehensive data to be had for any other species, the general results are not in disagreement with the view expressed above.

The sporadic variability of the sex relations and their fluctuating inheritance is very obvious in chicory. Self-fertile plants appear irregularly among the offspring of wide crosses and among plants of inbred strains which are prevailing self-sterile. In both types of offspring the number of self-fertile plants that appear varies considerably. The manner of their appearance is not to be correlated closely with similarities or dissimilarities as these are ordinarily judged by the expression of characters. The condition of complete functional sex vigor is in many hermaphrodites so complete that it appears to be very definitely fixed in heredity. In chicory, however, we see that highly individual and epigenetic developments may arise, evidently in differentiation and in the transition to the gametophytic stage, which lead to wide and sporadic variations in the functional sex vigor.

The various phenomena of self- and cross-compatibility and incompatibility raise many questions that are fundamental to an under-

standing of morphogenetic differentiation involved in sexuality, but of which we have at the present time only a superficial knowledge.

When does physiological incompatibility begin to develop? Is it a steady and progressive development through the whole diploid association of the two parental cell elements involved, or is it achieved suddenly at some particular point in ontogeny? Also, when does the sexual condition as distinct from the asexual condition actually arise?

Does incompatibility arise because of sex? Are the two the same? It would seem most definitely that they are not and that incompatibilities are not merely due to sexuality. But even if independent, where incompatibilities do arise, where, how, and to what extent are they correlated with sex and is the development of the two ever parallel? To what extent are the physiological interrelations of sexuality and incompatibility dependent on such mechanical or chemical interactions as are involved in reduction and sporogenesis?

Are the differences of intra-varietal physiological compatibility and incompatibility (both self and cross) indicative of differences in sexuality as such? Are some of the organs of either sex (microgametophytes and macrogametophytes with their respective gametes) sometimes more sexual or of greater sex vigor than are others?

To what degree are the incompatibilities, and compatibilities as well, determined by nutritive relations that are to be considered as vegetative functions? Is sexuality in its origin and in its phenomena of cell fusions, as some have held, to be considered in reality as a phase of vegetative function? To what extent are the sexual incompatibilities related to phenomena of serum incompatibilities and to immunity and what are the fundamental reactions involved in the development and operation of these?

These are among the fundamental questions that naturally arise in connection with such sporadic behavior of functional sex vigor as is seen in chicory in which self-fertile plants of varying degrees of fertility arise among a progeny even after three generations of parentage known to be self-sterile.

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