

## A Model for the Generation of Self-Sterility Alleles

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### 1. Introduction

One of the commonest genetic situations interpretable as a self-sterility mechanism, is that in which a number of alleles exist, presumably at the same locus, with antigenic properties such that the style tissue shall arrest the progress of pollen tubes containing either of the genes of the seed parent. The seed parent is supposed to accept pollen of all other save these two kinds.

As more species showing these peculiarities have come to be studied, two curious facts have emerged.

(a) The number of alleles which must exist in most species is remarkably large. Although a population could be maintained with three alleles only, without allowing any illegitimate fertilization, yet it is probable that the number in most natural populations runs to hundreds, and even in the species *Oenothera organensis* which, when discovered, was exceedingly sparse in individuals, yet these contained something like forty alleles (Emerson, 1939 ; Fisher, 1961).

(b) The hypothetical mutational process by which a new allele might be produced, has never been observed. Lewis's (1949) extensive studies in self-pollination show no such case, and it would require a mutation-rate less than  $10^{-9}$  in each generation to explain this absence, if new alleles really were being created by mutation.

It appeared to the author more probable that new alleles were synthesized by recombination, and that a new allele formed in this way would not be acceptable in a style secreting antibodies to both parent alleles. In this way the supply of new alleles might be comparatively abundant, without their revealing themselves in the technique of self-pollination.

As the situation proposed is not familiar to geneticists, I shall exemplify its working by a simple hypothetical case, in which, in a population containing only three alleles, a fourth allele is formed by recombination of two of these.

## 2. The Model Population

Let us imagine a population with three genes A, B and C, and consequently three genotypes BC, AC, AB each of which will accept only one kind of pollen. Each, therefore, produces seed of the two genotypes other than itself. Equilibrium in which each genotype is equally frequent will be approached rapidly, for, as is easily seen, if  $u$ ,  $v$  and  $w$  are the three frequencies, the compounds

$$2u - v - w$$

$$2v - u - w$$

$$2w - u - v$$

will each be diminished in the next generation with change of sign, so that in fact it is multiplied by  $(-\frac{1}{2})$ . Disturbances due to random sampling, often called "drift", are not only trifling in magnitude in a population of no more than 100, but reverse the sign of their effect in each succeeding generation, as they rapidly die away.

Suppose now that the heterozygous genotype AB produces by recombination a gamete carrying a new allele X. The new allele is at no disadvantage in an ovule, and is capable of being fertilized by A, B or C pollen. In a pollen grain, however, it will be effectual on stigmas of genotypes AC, BC. In the male gamete, therefore, it has a 2 : 1 advantage, so that as it appears equally in pollen and in ovule, the ratio of its increase is  $3/2$  in every generation. In a large population the logarithm (to the base 10) of frequency increases by

$$0.17609$$

in each generation ; Table 1 illustrates the effect of such an event occurring in a large inter-breeding population.

TABLE 1

Generation from crossover	Expected number of loci occupied by new alleles
5	7.594
10	57.66
15	437.9
20	3,325
25	25,250

It should be remarked that these expectations are not influenced by the fact that a single occurrence may die out in the first few generations. The probability of this can be easily calculated from the relation

$$\frac{\log_e p^{-1}}{1 - p} = 1.5,$$

showing that the probability of extinction is in fact

$$p = 0.41718835,$$

or not far from 3/7. If the crossover survives, therefore, the expected number of descendants in the table above should be multiplied by about 7/4. The figures in the table are the expectations when it is not known whether the new allele will survive or not.

### 3. Equilibrium in a Finite Population

The loci containing the new allele will be distributed among the new genotypes AX, BX, CX. As long as these constitute a negligible proportion of the population of each generation, so long will the geometric increase continue.

In principle, the constitution of the population in statistical equilibrium may be ascertained by equating the proportion of the six genotypes to those of their products by random fertilization. In more complicated cases the degree of the equations to be solved may be very high. In the case immediately under discussion, they are of the fourth degree, but the relevant root is rational, and the solution rather simple.

Table 2 enables the correctness of the solution to be checked and exhibits the details of a system of a kind not hitherto discussed.

TABLE 2

*Table of reproduction in each generation*

Genotype of seed-parent	AB	AC	BC	CX	AX	BX	Total
Relative frequencies	42	52	52	36	26	26	234
Acceptable pollen	C only	B,X	A,X	A,B	B,C	A,C	
Pollen ratio		15 : 11	15 : 11	1 : 1	6 : 7	6 : 7	
Seed genotypes							
AB	—	15	15	—	6	6	42
AC	21	—	15	9	7	—	52
BC	21	15	—	9	—	7	52
CX	—	11	11	—	7	7	36
AX	—	11	—	9	—	6	26
BX	—	—	11	9	6	—	26

The proportions of the four genes in the population are:

A	B	C	X	Total
30	30	35	22	117

and the four types of pollen should occur in the same ratios. However, on any particular seed parent, the relevant proportions are those of eligible pollen only. Even if C pollen were not the most abundant, it would have to account for all seeds born on AB plants.

An observable feature in such a population, if uncomplicated by later recombinations, is that one of the six genotypes, AB, gives seed progenies of only two classes, whereas all others are expected to give four. The source of the new allele is, therefore, recognizable in future generations. In a large outcrossing population with only 3 alleles, grown from seed year after year, at first every plant yields seed of only two genotypes. The first sign of a new allele will probably be the appearance in some seed progenies of a rare third class, fertile to the pollen of both sister types, but with pollen acceptable to only one of them.

In a population of only three genes, grown year after year by open pollination, the initial condition is that progenies from any seed-parent consist of only two genotypes, mutually cross-fertile. The first sign of the appearance of a new allele would probably be that a few seed progenies would contain a new rare genotype, accepting pollen from both classes of its sibs, but with pollen acceptable to perhaps only one of them. From such an exceptional plant the hypothetical system, if realized, could be verified in detail.

A short strip of chromosome with ten or twenty antigenically active points, not unlike some of the blood-group loci in man, could provide a thousand or more distinguishable combinations capable of acting as self-sterility alleles. The feature that antibodies effective against two alleles should also be effective against recombinations of them would perhaps show most clearly in such a three allele population as has been described.

#### REFERENCES

- EMERSON, S. (1939). A preliminary survey of the *Oenothera organensis* population. *Genetics*, **24**, 524.  
 FISHER, R. A. (1930). "The Genetical Theory of Natural Selection". Oxford University Press; reprinted in Dover Publications.  
 FISHER, R. A. (1961). Possible differentiation in the wild population of *Oenothera organensis*. *Aust. J. biol. Sci.* **14**, 76.  
 LEWIS, D. (1949). Structure of the incompatibility gene. *Heredity*, **3**, 339.

\* Delete these two sentences - R.A.F.