POSSIBLE DIFFERENTIATION IN THE WILD POPULATION OF *OENOTHERA ORGANENSIS*

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Summary

Two explanations, by Wright and the author respectively, have been suggested for the high number of self-sterility alleles observed in a very small wild population of *Oenothera organensis*. Wright's explanation depends on the possible differentiation due to isolation of a number of small subpopulations. Emerson's original data, however, provide a means of putting this proposal to a test, and it appears that the different subpopulations are not in fact genetically differentiated.

I. Self-sterility Alleles

In 1939 Emerson recorded his observations on the habitat and distribution of the rare species *Oenothera organensis*. The case was remarkable in that from rather few plants about 40 different self-sterility alleles were collected.

In the second edition (1958) of the "Genetical Theory of Natural Selection" I have given the solution of the problem of the distribution of the number of representations of different self-sterility allelomorphs, from which the chance of extinction may be calculated. The number of alleles observed is clearly not in equilibrium with replacement by mutation unless very high mutation rates may be postulated. It would be, however, by no means extraordinary if the species population had diminished since the last glacial period from something like 10,000 to its present small number. During this diminution many of the rarer genes would doubtless have been lost, but the rate of loss among the surviving commoner genes would be exceedingly small. Consequently, we have no right to apply the conditions of equilibrium.

Wright (1939) had earlier proposed a different solution of the problem, namely that the existing population sampled by Emerson consisted of a number of isolated populations, each maintaining its own alleles, in equilibrium with its small number, so that the aggregate of the alleles obtainable from all subdivisions could exceed the equilibrium made for an equivalent panmictic species.

Until we have clearer notions as to the nature of the process by which new alleles come into existence it would perhaps be premature to discuss this point.

Experiments on self-fertilization by Lewis (1949) have been interpreted as indicating a mutation rate for new alleles of less than 10^{-9}. However, such calculations ignore the possibility that the antibodies of the style are effective not only against the parent alleles, but against any new allele derived from them only. In any case, the proposal that there is genetic differentiation between the subpopulations sampled by Emerson can be examined from his own data.

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II. Emerson's Topographical Data

From the identifications given by Emerson (1939, p. 537) it is possible to classify 31 alleles appearing as either ovule or pollen in (*a*) McAllister Canyon, (*b*) in East Fork, and (*c*) in North Fork, these being the principal collecting grounds. I have avoided basing conclusions on the frequencies of occurrence, since a single insect carrying pollen might have introduced the paternal gamete of a number of plants, the occurrence of which could not, therefore, be regarded as independent. If, however, there were effective isolation of the kind postulated by Wright, the occurrence of an allele in one locality would be a reason for not expecting it to occur at all in some other locality. The question is whether any tendency exists for the different localities to harbour different alleles.

Table 1

CLASSIFICATION OF 31 ALLELES ACCORDING TO THEIR DISTRIBUTION

Locality	Number	Algebraic Expectation
McAllister's Canyon (A) only	9	$p_1q_2q_3$
East Fork (B) only	6	$q_1p_2q_3$
North Fork (C) only	3	$q_1q_2p_3$
B and C	2	$q_1p_2p_3$
C and A	5	$p_1q_2p_3$
A and B	4	$p_1p_2q_3$
A, B, and C	2	$p_1p_2p_3$
Total	31	

III. The Test of Independence

The classification available for discussion is that of Table 1. We wish to compare these numbers observed, with numbers expected, appropriate to the view that the occurrence of one allele in a locality does not affect the probability of its occurrence in another. If p_1, p_2, and p_3 are the probabilities of an allele chosen at random occurring in the three localities, and if in each case $p+q = 1$, then the expansion of the product

$$(p_1+q_1)(p_2+q_2)(p_3+q_3)$$

will give the relative frequencies of the seven classes observed, together with an eighth unobservable class, in which the allele happens to be absent from all three localities.

To find the appropriate values of p_1, p_2, and p_3 we may use the device of the so-called "missing plot", and suppose that an unknown number x had been observed to be absent from all three localities. Thus in terms of x, we may set

$$\begin{aligned} p_1 &= 20/(x+31) & q_1 &= (x+11)/(x+31)\\ p_2 &= 14/(x+31) & q_2 &= (x+17)/(x+31)\\ p_3 &= 12/(x+31) & q_3 &= (x+19)/(x+31) \end{aligned}$$

so that we may obtain an equation for x by setting

$$q_1q_2q_3(x+31) = x,$$

or

$$(x+11)(x+17)(x+19) = x(x+31)^2.$$

This leads to the quadratic equation $15x^2+242x-3553 = 0$, of which the positive root is $[\sqrt{(67936)}-121]/15$ or $139\cdot645/15 = 9\cdot3097$, giving

$$\begin{array}{lll} p_1 = 0\cdot49616 & p_2 = 0\cdot34731 & p_3 = 0\cdot29770 \\ q_1 = 0\cdot50384 & q_2 = 0\cdot65269 & q_3 = 0\cdot70230 \end{array}$$

The comparison of expected and observed frequencies is shown in Table 2.

TABLE 2

COMPARISON OF OBSERVED AND EXPECTED FREQUENCIES

Locality*	Observed ($m+x$)	Expected (m)	(x^2/m)
No locality	—	9·3096	—
A only	9	9·1677	0·0031
B only	6	4·9539	0·2209
C only	3	3·9463	0·2269
B and C	2	2·0999	0·0048
C and A	5	3·8861	0·3193
A and B	4	4·8783	0·1581
A, B, and C	2	2·0679	0·0022
Totals	31	40·3097	0·9354 = χ^2

* See Table 1.

After fitting the three probabilities there are only three degrees of freedom for deviations from expectation. With χ^2 less than unity, there is no sign of any deviation beyond pure chance. With partial isolation of the alleles the expectation would be that the first three cells should appear in excess of expectation and that the last cell should be greatly deficient. Evidently, on the contrary, the frequencies observed by Emerson are indistinguishable from what would have appeared if instead of distinguishing the localities, the plants had been divided arbitrarily and by chance into three sections.

It seems likely that organisms affecting cross-pollination travelled freely over all the three localities sampled. However, if there really is isolation it has clearly led to no differentiation between the subpopulations.

IV. References

EMERSON, S. (1939).—A preliminary survey of the *Oenothera organensis* population. *Genetics* **24**: 524–37.

FISHER, R. A. (1958).—"The Genetical Theory of Natural Selection." (Dover Publications Inc.: New York.)

LEWIS, D. (1949).—Structure of the incompatibility gene. *Heredity* **3**: 339–55.

WRIGHT, S. (1939).—The distribution of self-sterility alleles in populations. *Genetics* **24**: 538–52.