18

EVOLUTION BY SELECTION

THE IMPLICATIONS OF WINTER'S SELECTION EXPERIMENT*

[*Eugenics Review*, XXIV (1933), p. 293]

FOR some time after the publication of the *Origin of Species* it was generally held by those who accepted Darwin's reasoning that species originated by the accumulation of small variations in the same direction under the influence of natural selection; and the occurrence of large "mutations", such as the Ancon sheep, was perhaps rather overlooked. The rediscovery of Mendelism, however, has tended to emphasize the latter portion of Darwin's work, rather to the exclusion of the former, until it is actually held in certain quarters that the selection of small differences can only lead to small, or at all events strictly limited, changes of type.

Yet it cannot be denied that, apart from colours and other "fancy" points, the actual improvement of domestic animals has usually proceeded by just this accumulation of small differences.

If I am not mistaken, the view that selection is limited can be traced back to Johannsen's work, where he showed that from an ordinary stock of beans there could be isolated a number of "pure lines", which differed from each other in the mean weight of their seed, but within each of which no appreciable genetic variation in seed weight could be detected.

His work has led to a considerable advance in the selection of cereal seed, since it is quite certain that for practical purposes "pure line" seed will behave in much the same way as if the plants were propagated vegetatively; they will start growing together and will ripen together, and their seed will be uniform and behave uniformly in its turn. Yet Johannsen, working of course with self-fertilizing material, found pure *lines*, not *a* pure line. Obviously, therefore, mutations had occurred with sufficient frequency to produce them; and, given time, it may be supposed that even in self-fertilized organisms progress could be made merely by selecting the extreme pure line, waiting for a mutation, selecting again, and so on. Tedious work—but for the Origin of Species there is now plenty of time.

From a practical point of view, however, the plant breeder cannot afford to wait for favourable mutations; he cross-fertilizes—and so in most cases does

* Winter, Floyd L., "Continuous selection for composition in corn", *J. Agric. Res.* July-December 1929, pp. 451–75.

nature. Now until experience has been accumulated, the results of cross-fertilization are unpredictable; but very soon certain facts begin to emerge—"Tall is dominant to dwarf", "Two rowed is dominant to six rowed", and so forth, and such things attract attention and rather obscure other equally important facts. Cross a "dense" and a "lax" variety, and among the ultimate progeny may be found plants "denser" than the "dense" parent and "laxer" than the "lax" and almost anything between. Cross high and low protein, and the same overlapping will be found when the first mix-up has sorted itself out.

Try to explain this on Mendelian lines and it will soon become obvious that even in self-fertilized plants there must be a tremendous variety of genetical make-up; one or two relevant genes will be quite inadequate to explain the facts, ten or twenty will complicate the calculation, but will be none too many. Perhaps it would be better to postulate 200–300 and reduce the problem to mathematics.

Since characters which do not affect the survival of the organism are not encountering selection, an ordinary cross-fertilizing population must be expected to accumulate among all its members very large numbers of genes corresponding to such unessential characters. In ordinary times these would roughly *neutralize one another*, each individual carrying a mixture of genes which would produce variation in opposite directions, so that only a limited genetic variation would result; but with a change of environment this reservoir of genes would serve a very useful purpose as raw material for selection: some characters, formerly neutral, would then affect survival and all those genes which produce favourable somatic variation would tend to be preserved while their opposite numbers would be eliminated. Thus the accumulation of small variations in the same direction could proceed far beyond the original range.*

* Perhaps this argument may be clarified by an illustration. Suppose during a period when height is of no particular importance to an organism two hundred small mutations have succeeded in establishing themselves in equilibrium, each of which affects height to an equal extent, say, 1 mm. We may represent the first gene as either a_1, present, or b_1, absent, the second as a_2 or b_2, and so on. Then any individual will contain either a_1a_1, a_1b_1, or b_1b_1 and the proportions in which these possibilities occur will be assumed for the sake of illustration to be 1.2.1; similarly with the other subscripts, so that the distribution of individuals according to the numbers of "a" genes which they contain will be in proportion to the coefficients of the binomial $(a^2+2ab+b^2)^{200}$ or of $(a+b)^{400}$.

The standard deviation of this binomial distribution is 10, so that although it would be possible for an individual to contain the "a" genes in any number from 0 to 400, yet in practice even a population of 100,000,000 would be very unlikely to outrange 140–260 corresponding to 120 mm. of height between the highest and the lowest individual, less than one-third the possible range.

If now we imagine only the highest half of the population to mate (at random) we should get a rise in "a" content of 8 in the mean value, to 208, while the standard deviation and range would hardly be altered, so that the process could be repeated, a further rise of 8 mm. obtained, and so on until the mean would rise well beyond the value of the original extreme individual: and all this without fresh mutations. Of course this illustration has been simplified to the point of absurdity, but it may serve to exhibit the possibility of such potential variation.

That such a state of things does indeed exist seems to be indicated by Winter's paper, to which I am now drawing attention. This describes a very determined experiment carried out on "corn", i.e. maize. Now maize is commonly cross-fertilized; unless cross-fertilization takes place, the stock is apt to die out—which makes pure line selection very difficult. Nevertheless much may be done by mass selection, and it is with mass selection that Winter was concerned.

Premising that he selected continuously for twenty-eight years, from 1896 to 1924, it is perhaps best to quote his description of the procedure verbatim:

> One hundred and sixty-three ears of a variety known as "Burr's White" were used as foundation stock from which selections were made in four different directions, namely for high oil, low oil, high protein and low protein.
>
> These four strains were carried on in the same way. In the high protein, for example, twenty-four ears highest in protein were selected for seed and planted in an isolated plot, each ear in a separate row. These ears were harvested separately and the seed for the next crop selected from the ears which were found to be highest in protein. Nine years later the system was modified somewhat in an attempt to prevent loss of vigour by inbreeding. Alternate rows were detasselled and seed was selected only from the highest yielding detasselled rows. In 1921 this system was again modified to reduce the amount of inbreeding. Two seed ears were taken from each of the detasselled rows regardless of yield.
>
> The high oil, low oil and low protein tests were similarly conducted, selection being made each year of ears highest in oil, lowest in oil and lowest in protein, respectively.

For a proper appreciation of the work the original paper should be consulted, but only a few figures will be necessary to display the interest of the results:

I will deal with the figures giving the percentage of oil, which are the more striking, but the facts are similar in the case of the protein.

(1) Two strains have been selected, one which has a mean percentage of oil about *twelve* times the standard deviation of the original population above the original mean, and the other about *seven* times below. As illustrating this, the minimum value in the high race during the last five years is considerably higher than the maximum value found during the first four years and, on the other hand, the maximum value in the low race is even more markedly below the lowest in the first four years.

(2) Although the standard deviation of the high race has risen and that of the low has fallen during the experiment, it would be hard to say whether on the whole there has been a decrease or an increase in variability owing to the selection.*

We may assume the variance to be composed of two parts, one inherent and therefore subject to selection, and the other environmental, or "fluctuating", and therefore a hindrance to selection. Just what proportion we should allot to

* Dr Rasmussen, of Svalof, has pointed out to me that this might perhaps be explained by an exaggeration in the environmental effect when acting on plants enfeebled by inbreeding. But the steady rise in oil percentage right up to the end of experiment seems to require an almost undiminished genetic variability.

PROTEIN

Year	Mean value %		Standard deviation		Lowest variate		Highest variate	
1896	10·93		1·04		8·3		13·9	
	High	Low	High	Low	High	Low	High	Low
1897	10·99	10·63	1·16	0·90	8·3	8·2	13·6	14·0
1898	10·98	10·49	1·22	1·32	7·7	7·5	14·9	13·4
1899	11·62	9·59	1·28	1·01	8·4	6·7	14·8	13·1
1920	14·01	7·54	1·79	0·89	9·5	6·0	17·4	10·5
1921	16·66	9·14	1·84	1·35	9·4	6·6	18·8	13·4
1922	17·34	7·42	1·24	0·70	12·6	6·1	20·6	9·6
1923	16·53	6·48	1·41	0·73	13·1	5·0	19·7	9·4
1924	16·60	8·38	1·19	1·17	14·6	6·1	19·2	11·8

OIL

Year	Mean value % of oil		Standard deviation		Lowest variate		Highest variate	
1896	4·68		0·41		3·9		6·0	
	High	Low	High	Low	High	Low	High	Low
1897	4·79	4·10	0·38	0·29	3·6	3·4	5·7	4·7
1898	5·10	3·59	0·48	0·32	4·1	3·2	6·7	4·8
1899	5·65	3·85	0·42	0·32	4·3	2·8	6·5	4·6
1920	9·28	1·80	0·52	0·21	7·8	1·0	10·6	2·4
1921	9·94	1·71	0·66	0·15	8·4	1·0	11·7	2·3
1922	9·86	1·68	0·54	0·19	8·7	0·9	11·3	2·2
1923	10·08	1·58	0·65	0·24	8·3	1·1	11·8	2·1
1924	9·86	1·51	0·61	0·22	8·4	0·9	11·7	2·2

each of these we have no sure means of judging, but in both cases the latter is, I believe, likely to be very large. Incidentally it may perhaps account in both cases for the obvious correlation* between the mean and the standard deviation.

In any case the inherent part of the variation had of course a *smaller* standard deviation than that observed for the whole, perhaps much smaller, so that the movements of the means were, respectively, *more* than twelve and seven times this "inherent" standard deviation. Hence either the possibilities of variation latent in the original material were enormous or a steady stream of favourable mutations was maintained to carry the means along.

In any case, these results cannot be explained on the basis of a few easily detected genes. But by reducing the problem to the simplest possible basis—starting from the intensity of selection, the rate of movement of the means at first, and the difference between the initial and final values of the mean—it is possible to make some sort of calculation of the minimum number of genes which might allow of so large a change by repeated selection. And I find that the order of these numbers is 100–300. There is little indication, however, that selection

* It is reasonable to suppose that a given variation in environment would produce greater variation in a high genetic stock than in a low one.

had yet reached its limit after twenty-eight years, and we should probably be within the mark if we assumed that the number of genes affecting oil (or protein) content in Burr's White Maize may run up to thousands.

But if we have thousands of genes, continuous selection in one direction may, in fact must, result in progress almost without limit (at all events until the progress itself induces counter-selection as perhaps it does in the case of low oil content) for although the selection will reduce the number of genes there will be time for fresh mutations to occur to keep up the possibility of further selection.

Summary and Conclusion

To sum up: Winter has in this experiment succeeded, by continuous mass selection, in producing two races of maize, one of which has more than twice, and the other less than one-third, the normal oil content.

In a character so influenced by environment the progress has, of course, not been uniform in its manifestation; but it appears to have been comparatively so genetically, and shows little or no indication that it has reached its limit in either direction.

It does not appear that such steady progress could be obtained with less than hundreds of genes affecting oil content and it seems not unlikely that there are thousands. In any case it is clear that the possibilities of continuous selection of small variations for the formation of new species are likely to be very much greater than would appear merely from a consideration of Johannsen's work on pure lines, which was carried out on a self-fertilizing organism.

And so we reach the conception of species patiently accumulating a store of genes, of no value under existing conditions and for the most part neutralized by other genes of opposite sign. When, however, conditions change, unless too suddenly or drastically, the species finds in this store genes which give rise to just the variation which will enable it to adapt itself to the change.

It follows that the change appears to have produced the variation which it has merely selected from among those potentially present. Thus we can reconcile the view held, amongst other people, by the late Walter Heape, that the environment produces the required variation, with the older Darwinian selection of random variations, to which it appears at first sight to be diametrically opposed.