THE BALANCE OF POLYGENIC COMBINATIONS

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1. LINKAGE AND VARIATION

It is axiomatic that selection can produce an effect on the genetical composition of a population only if there exists a certain amount of genetical heterogeneity. This heterogeneity will commonly depend on the segregation and recombination of genes controlling the character on which selection is being exercised. Indeed, unless segregation and recombination are both occurring the reaction to selection will cease after a very few generations. Segregation itself, without recombination, can produce only a short-lived advance with selection. The reaction to a selective force must be largely dependent on the recombination of genes where a number of these affect the character in question, as is the case with polygenic characters.

The number of genotypes possible with \( n \) segregating genes, each of two allelomorphs, is \( 3^n \) in a diploid organism, and it is clear that if \( n \) is at all large, say 10 or more, it would be necessary to raise a great number of individuals in order that each genotype should be represented in a progeny or population. Even, however, if the possible genotypes are not all represented in any one generation some of those present will enjoy a selective advantage over the others and advances with selection will occur. The selected individuals will in turn give rise to fresh progenies containing segregant types and further selection will thus be possible in the next generation. This process will be repeated for a number of generations depending on the population size, the rigour of selection and the organization of the polygenes affecting the character. In general, all the valuable genotypes can be produced with a relatively small number of individuals in each generation provided that a sufficient number
of generations are raised, during each of which selection is exercised. The advance in each generation is small, but when continued over many generations will be in total a large one.

The speed of this reaction is conditioned by the freedom of recombination of the genes involved, as Goodale (1938) has pointed out. If all genes recombined freely the rate of advance would depend on the number of genes segregating, the size and breeding system of the population, the rigour of selection and the magnitude of the damping effect exerted by environmental influences on the manifestation of the character. Where, on the other hand, many of the genes are linked into a number of groups, depending on the number of chromosomes of the organism, the rate of advance with selection must also be influenced by the organization of the combinations of these polygenes within the chromosomes. If genes acting in opposite directions, conveniently described as plus and minus, are intermingled along the chromosomes many cross-overs will be necessary before the combination most favoured by selection is produced. Selection will be slow in action. If, however, the plus genes tend to occur in one or more chromosomes and the minus genes in others, the number of effective recombinations necessary for the full advance with selection will be small—smaller indeed than where all the genes are unlinked. Selection will then be very rapid. In this way the rate of advance in a given stock may be either decreased or increased by linkage. So in order to understand the action of selection on populations it is necessary first to know something of the organization of the polygenic combinations in the chromosomes.

Now the effect of linkage on the rate of advance will vanish when a large number of experimental crosses or a heterogeneous and previously unselected population is considered; for in such a case all types of combination in a chromosome will be involved, and for every combination which slows down advance there will be another which has an accelerating action. This can be seen from a simple example. Consider the effect of selfing doubly heterozygous individuals AaBb. When the loci of A, a and B, b recombine freely the various types of progeny are expected with the relative frequencies

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<thead>
<tr>
<th></th>
<th>AA</th>
<th>Aa</th>
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<tbody>
<tr>
<td>BB</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Bb</td>
<td>2</td>
<td>4</td>
<td>2</td>
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<tr>
<td>bb</td>
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If we then suppose that the degree of expression of some polygenic character affected by both genes is equal to the number of capital letters in the genotype, the phenotypes will be