represent the heterogametic sex, giving after selfing a number of hermaphrodites and some females. After a pollination of a female with pollen from a hermaphrodite plant about 50 per cent hermaphrodites and 50 per cent females are obtained.

The tetraploid plants show a very great power of vegetative propagation, which is not met in my material of other species of Rumex, as cuttings may be taken from different parts of the plant.

Although it is not very likely that this tetraploid form has arisen from a diœcious or almost diœcious form with the same type of sex determination as met in *R. Acetosa*, it is not a fully excluded possibility. All tetraploid intersexual types of *R. Acetosa* are, however, almost completely sterile, while the hermaphroditic plants of *R. Lunaria* show an almost complete fertility. If experimentally produced tetraploids of, for example, the diploid gynodiœcious species *R. hastatus* will be found to be gynodiœcious, it must be regarded as a good support for the suggestion that the tetraploid *R. Lunaria* originates from a gynodiœcious diploid, and it would also give strength to the above-mentioned hypothesis on the two different lines of evolution of sex mechanisms in the two groups of the genus Rumex.

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Polygenes in Development

IN criticizing my conclusions[1] regarding the relations between polygenic buffering systems and oligogenic switching, or key, systems, and in considering the advisability of dispensing with the term polygene, Dr. Waddington[2] rests his case on three main points, namely :

(1) That switching systems may depend on the joint action of a number of genes each of relatively small effect and so cannot be considered to be distinct from other systems of genes each of small effect.

(2) That many genes are known to have large main effects combined with smaller secondary effects, so leading to the conclusion that a gene may simultaneously determine oligogenic and polygenic variation.

(3) That genes producing "very minor changes in a character must be acting as rather ineffectual buffering agents on the last phases of its development".

Let us consider these points further.

The first begins with a statement which is true—so far as it goes. But such jointly acting genes cannot constitute a switching system which is efficient, and hence able to survive the test of natural selection, unless they are completely linked and segregate as a unit. They will thus jointly act, and will appear in genetic analysis, as one gene of large effect, that is, as a major gene, not as polygenes. This is in fact one of the ways in which I envisaged the evolution of switching genes from polygenes in the discussion which is being criticized.

The second point is also true so far as it concerns the manifold action of some genes. But can the secondary effects of such genes be regarded as determining polygenic variation ? The polygene notion was developed (see ref. 3) in relation to the action of selection, both in experiment and in Nature. Natural selection must act on the total phenotypic effect of a gene, and hence genes of the kind Waddington considers will be selected almost entirely on their drastic main effects. Their secondary effects cannot thus give rise to polygenic variation of the kind which I have discussed. Nor can it be supposed that natural polygenic variation is of this secondary kind. It is rarely if ever associated with any detectable major effects, and such association would surely have been detected in a proportion of cases in intensively investigated organisms, like Drosophila, maize or man, were it a regular feature of the system.

Thirdly, we have the statement that genes causing "very minor changes" are "rather ineffectual buffering agents". This, however, misses the essential point that small gene changes can accumulate by selection without mechanical limit. Though the effect of one gene change may be minor, a number of them acting in aggregate can be far from ineffectual ; and, in accumulating, such changes will provide just that fine adjustment which is requisite in a buffering system, and which cannot be provided by the mutation and recombination of major genes.

In conclusion, I must mention Waddington's equation of polygenes to Nilsson-Ehle's polymeric genes. The latter are defined only by similarity of action to one another, whereas the former are defined also by the magnitude of their individual effects, which are small when compared with the total non-heritable fluctuation[1,3,4,5]. Nilsson-Ehle's original polymeric genes in wheat and oats had effects much larger than non-heritable fluctuation (or he could not have scored them individually by the Mendelian technique) and so cannot be regarded as polygenes. They were polymeric only by virtue of the allopolyploidy of these cereals, and it was this accidental circumstance which provided the basis for interpreting quantitative inheritance. It is indeed most important to recognize that major genes, as well as polygenes, can show polymeric action, and that in doing so they do not become polygenes.

Polygenes, as I have derived the notion from my experiments, are distinct from major genes and must play a different part in the selective adjustment of development.

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