ON THE PROBABILITY THEORY OF LINKAGE IN MENDELIAN HEREDITY

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1. Introduction. If for a certain generation the distribution of genotypes is known and a certain law of heredity is assumed, the distribution of genotypes in the next generation can be computed. Suppose there are N different genotypes in the nth generation in the proportions $x_1^{(n)}, \cdots, x_N^{(n)}$ where $\sum_{i=1}^{N} x_i^{(n)} = 1$ and denote by $p_{\kappa\lambda}^{i}$ the probability that an offspring of two parents of types κ and λ be of type i where $\sum_{i=1}^{N} p_{\kappa\lambda}^{i} = 1$ for all κ and λ, and $p_{\kappa\lambda}^{i} = p_{\lambda\kappa}^{i}$. Assuming panmixia, identical distributions $x_i^{(n)}$ for males and females, etc., we can derive $x_i^{(n+1)}$ from $x_i^{(n)}$ by means of the formula

$$x_i^{(n+1)} = \sum_{\kappa,\lambda=1}^{N} p_{\kappa\lambda}^{i} x_\kappa^{(n)} x_\lambda^{(n)} \qquad (i = 1, 2, \cdots N). \tag{1}$$

Thus if the distribution $x_i^{(0)}$ is given for an initial generation we can deduce successively the $x_i^{(1)}, x_i^{(2)}, \cdots$ for subsequent generations. Besides, one may wish to express the $x_i^{(n)}$, for any n, explicitly in terms of the initial distribution $x_i^{(0)}$, i.e. to "solve" the system (1). A further problem consists in determining the limit-distribution of the genotypes $\lim_{n\to\infty} x_i^{(n)}$ $(i = 1, \cdots, N)$.

Mendel's heredity theory is based on some ingenious assumptions which are known as Mendel's first and second law. They enable us to define the possible genotypes and to establish the recurrence formula (1); they will be explained and formulated in sections 2 and 3. It is well known that in Mendel's theory it makes an essential difference whether one or more "Mendelian characters" are considered. In the first case Mendel's first law only is used; there are with respect to this character but $N = 3$ different types and the recurrence formula (1) can be derived without difficulty. As early as 1908 G. H. Hardy [5] established the simple but most remarkable result that under random breeding a state of equilibrium is reached in the first filial generation, i.e. $x_i^{(1)} \neq x_i^{(0)}$ (in general) but $x_i^{(n)} = x_i^{(1)}$ $(n = 2, 3, \cdots,)$.[1]

In the case of $m \geqq 2$ Mendelian characters Mendel assumed *independent assortment* of these characters (Mendel's second law). However, within four years after the dramatic rediscovery of Mendel's fundamental paper [10], observations were reported that did not show the results expected for two independent characters. T. H. Morgan [11] and collaborators in basic contributions, con-

[1] See also [12] where the stability of the particular ratio 1:2:1 is recognized.