MATH. SCAND. 10 (1962), 25–44

GENETIC ALGEBRAS STUDIED RECURSIVELY AND BY MEANS OF DIFFERENTIAL OPERATORS

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1. Introduction.

An algebra may be defined as a vector space together with a multiplication rule for the vectors such that

(1.1) The vector space is closed with respect to multiplication.
(1.2) Multiplication is distributive with respect to vector addition.
(1.3) A scalar factor may be moved freely within a product of vectors.

We shall consider a particular kind of non-associative algebras which have been called genetic algebras because of their application in population genetics. The study of these algebras and their genetical interpretations was initiated by I. M. H. Etherington [2]-[7]. Papers on genetic algebras have also been published by Gonshor [12], Raffin [17] and Schafer [18].

In this paper I shall present a new method of studying genetic algebras. One aspect of the method is that the multiplication rules are expressed by means of differential operators and that these operators are used in the study of the algebras. This makes it possible to avoid an explicit consideration of the components of the elements. Another aspect of the method is that the algebras are studied recursively. In the study of a genetic algebra corresponding to k linked loci we make use of certain homomorphisms of this algebra onto algebras corresponding to smaller numbers of loci. In this way we may use results already found for the latter algebras in the derivation of results for the algebra corresponding to k linked loci.

In the present paper we shall consider genetic algebras in the case of haploid gametes only, and further restrict the study to the case when the linkage distribution is the same for both sexes. It is evident, however, that the method is applicable to other genetic algebras.

2. Preliminaries on differential operators.

Let f and g be functions of a set of variables $x_1,\ldots,x_m$ such that the

Received June 18, 1960.

derivatives considered in the following exist. In the present paper the differential operators will be applied to polynomials only, so that all derivatives exist. We note that derivatives of polynomials may be defined algebraically, and in this paper all operators may be regarded as purely algebraic operators.

Let D_{x_i} be defined by

$$D_{x_i}f = \frac{\partial f}{\partial x_i} \tag{2.1}$$

and let a linear form in the D_{x_i} be defined by

$$\left(\sum_{i=1}^{m} c_i D_{x_i}\right) f = \sum_{i=1}^{m} c_i (D_{x_i} f) , \tag{2.2}$$

where $c_1, \ldots, c_m$ are constants. The operator

$$D = \sum_{i=1}^{m} c_i D_{x_i} \tag{2.3}$$

has the same properties as a differential operator with respect to a single variable,

$$D(f+g) = Df+Dg , \tag{2.4}$$

$$D(cf) = c(Df) , \tag{2.5}$$

$$D(fg) = f(Dg)+g(Df) . \tag{2.6}$$

We may similarly define polynomials in the operators D_{x_i}. If D is such a polynomial, (2.4) and (2.5) are still valid. If D_1 and D_2 are two polynomials in the D_{x_i} with constant coefficients we have in addition

$$(D_1+D_2)f = D_1 f+D_2 f , \tag{2.7}$$

$$(D_1 D_2)f = D_1(D_2 f) , \tag{2.8}$$

$$(cD)f = c(Df) . \tag{2.9}$$

Let us next consider k differential operators $D_1, \ldots, D_k$ each of which is a linear form in the operators D_{x_i} with constant coefficients. If each D_i operates on a product fg we may instead of D_i consider two operators D_{i1} and D_{i2} defined by

$$D_{i1}(fg) = g(D_i f) , \tag{2.10}$$

$$D_{i2}(fg) = f(D_i g) . \tag{2.11}$$

(Compare Stephens [19, p. 33].) Then

$$D_i = D_{i1}+D_{i2} . \tag{2.12}$$

If we have an expression of the form

$$D_1^{\alpha_1}\dots D_k^{\alpha_k}(D_1^{\beta_1}\dots D_k^{\beta_k}f)(D_1^{\gamma_1}\dots D_k^{\gamma_k}g)\,, \tag{2.13}$$

where each D_i within a parenthesis operates only within the parenthesis, while the $D_i^{\alpha_i}$ operate on the product of the two parentheses, then we may replace each D_i which operates on both factors by $D_{i1}+D_{i2}$, each D_i which operates on f only by D_{i1}, and each D_i which operates on g only by D_{i2}. Formula (2.13) may thus be rewritten in the form

$$\prod_{i=1}^{k}(D_{i1}+D_{i2})^{\alpha_i}D_{i1}^{\beta_i}D_{i2}^{\gamma_i}fg\,. \tag{2.14}$$

If we have a sum of terms of the form (2.13), each multiplied by a constant, then we may write each term in the form (2.14) and get an expression of the form

$$P(D_{11}, D_{12}, \dots, D_{k1}, D_{k2})fg\,, \tag{2.15}$$

where P denotes a polynomial with constant coefficients.

If $\Omega, \Omega_1, \Omega_2$ are polynomials in $D_{11}, D_{12}, \dots, D_{k1}, D_{k2}$ we have

$$\Omega(f_1g_1+f_2g_2) = \Omega(f_1g_1)+\Omega(f_2g_2)\,, \tag{2.16}$$

$$\Omega(cfg) = c\Omega(fg)\,, \tag{2.17}$$

$$(\Omega_1+\Omega_2)fg = \Omega_1fg+\Omega_2fg\,, \tag{2.18}$$

$$(\Omega_1\Omega_2)fg = \Omega_1(\Omega_2fg)\,, \tag{2.19}$$

$$(\Omega_1\Omega_2)fg = (\Omega_2\Omega_1)fg\,. \tag{2.20}$$

3. Preliminaries on linear difference equations with constant coefficients.

We shall give a summary of those results which are needed for the purpose of the present paper. For a more detailed treatment the reader is referred to textbooks on finite differences or difference equations, for instance the textbook by Jordan [13].

We consider a linear difference equation

$$\sum_{i=0}^{k} b_i f(n+i) = g(n)\,, \tag{3.1}$$

where $g(n)$ is a known function and $b_0, b_1, \dots, b_k$ are constants. The variable n will be supposed to take integer values only. Using the operator E, defined by $Ef(n)=f(n+1)$, we may write (3.1) in the form

$$\psi(E)f(n) = g(n)\,, \tag{3.2}$$

where

$$\psi(E) = \sum_{i=0}^{k} b_i E^i\,. \tag{3.3}$$

Let us first consider the homogeneous equation

$$\psi(E)f(n) = 0 . \tag{3.4}$$

If the equation $\psi(x)=0$ has roots $r_1, r_2, \ldots, r_k$ which are all distinct, the general solution of (3.4) is

$$f(n) = \sum_{i=1}^{k} c_i r_i^n , \tag{3.5}$$

where the c_i are arbitrary constants (real or complex).

If $r_1 = r_2 = \ldots = r_m$ the m first terms on the right-hand side of (3.5) will be replaced by

$$(c_1 + c_2 n + \ldots + c_m n^{m-1}) r_1^n . \tag{3.6}$$

A similar rule holds for any multiple root.

Let us next consider equation (3.2) when $g(n)$ has the form

$$g(n) = \sum_{i=1}^{h} q_i a_i^n . \tag{3.7}$$

If $\psi(a_i) \neq 0$ for every i, then (3.2) has the solution

$$f(n) = \sum_{i=1}^{h} \frac{q_i}{\psi(a_i)} a_i^n , \tag{3.8}$$

and the general solution of (3.2) is the sum of (3.8) and the general solution of (3.4). The case when $g(n)$ contains a constant term is a special case of (3.7) which we obtain by setting one of the a_i equal to 1.

If $g(n)$ is of the form

$$g(n) = P(n) a^n , \tag{3.9}$$

where $P(n)$ is a polynomial in n and a is a root of $\psi(x)$ of multiplicity m, then (3.2) has a solution of the form

$$f(n) = Q(n) a^n , \tag{3.10}$$

where $Q(n)$ is a polynomial whose degree is greater than the degree of $P(n)$ by m. The m coefficients of the terms of degree lower than m in $Q(n)$ will be arbitrary. The other coefficients of $Q(n)$ may be determined by insertion of (3.10) with undetermined coefficients in the difference equation and comparing coefficients on both sides.

If we have a solution $f_i(n)$ of the equation

$$\psi(E) f(n) = g_i(n)$$

for $i = 1, 2, \ldots, q$, then the equation

$$\psi(E)\,f(n) = \textstyle\sum_{i=1}^{q} g_i(n)$$

has the solution $f(n) = \sum_{i=1}^{q} f_i(n)$.

4. Recombination operators.

Let us consider a set S of integers and the partitions of this set into two disjoint subsets. When we include the empty set and the set S itself as subsets of S, the number of such partitions is 2^{k-1}, where k is the number of elements of S. Let U' and U'' be two complementary disjoint subsets of S and let

$$U = (U', U'') = (U'', U')$$

denote the partition of S defined by the subsets U' and U''. Let $A = a_1 a_2 \ldots a_k$ and $B = b_1 b_2 \ldots b_k$. Let U be a partition of the set $S = (1, 2, \ldots, k)$. The *recombination operator* $R(U)$ will be defined by

$$R(U)(A,B) = \tfrac{1}{2}\left(\left(\textstyle\prod_{i\in U'} a_i\right)\left(\prod_{i\in U''} b_i\right) + \left(\prod_{i\in U''} a_i\right)\left(\prod_{i\in U'} b_i\right)\right). \tag{4.1}$$

Let D_{a_i} and D_{b_i} denote the differential operators $\partial/\partial a_i$ and $\partial/\partial b_i$. Since

$$\textstyle\prod_{i\in U'} a_i = \left(\prod_{i\in U''} D_{a_i}\right) A \tag{4.2}$$

and

$$\textstyle\prod_{i\in U''} a_i = \left(\prod_{i\in U'} D_{a_i}\right) A\,, \tag{4.3}$$

we get from (4.1)

$$R(U)(A,B) = \tfrac{1}{2}\left(\left(\textstyle\prod_{i\in U'} D_{a_i}\right)\left(\prod_{i\in U''} D_{b_i}\right) + \left(\prod_{i\in U''} D_{a_i}\right)\left(\prod_{i\in U'} D_{b_i}\right)\right) AB$$

or

$$R(U)\,(A,B) = R(U)\left(\textstyle\prod_{i\in S} D_{a_i}, \prod_{i\in S} D_{b_i}\right) AB\,, \tag{4.4}$$

where $R(U)$ on the right hand side operates on the differential operators only, not on AB.

5. Presentation of the algebras.

We shall consider an algebra $\mathscr{A}_k$ whose elements G are multilinear forms

$$G = \sum_{i_1=1}^{m_1} \cdots \sum_{i_k=1}^{m_k} g_{i_1\ldots i_k}\, a_{1i_1} \ldots a_{ki_k}\,, \tag{5.1}$$

where the $g_{i_1\ldots i_k}$ are real numbers and the a_{ji_j} are variables. Each element of the form (5.1) with real coefficients will be supposed to belong to the algebra.

Addition of two elements of the algebra is taken to mean addition of polynomials in the usual sense, i.e.

$$(5.2)\quad \begin{cases} \sum_{i_1=1}^{m_1}\cdots\sum_{i_n=1}^{m_k} g_{i_1\ldots i_k} a_{1i_1}\cdots a_{ki_k} + \sum_{i_1=1}^{m_1}\cdots\sum_{i_k=1}^{m_k} g'_{i_1\ldots i_k} a_{1i_1}\cdots a_{ki_k} \\ = \sum_{i_1=1}^{m_1}\cdots\sum_{i_k=1}^{m_k} (g_{i_1\ldots i_k}+g'_{i_1\ldots i_k}) a_{1i_1}\cdots a_{ki_k} . \end{cases}$$

Multiplication of G by a constant (a real number) is taken to mean multiplication of the polynomial by the real number in the usual sense, i.e.

$$(5.3)\qquad cG = \sum_{i_1=1}^{m_1}\cdots\sum_{i_k=1}^{m_k} c g_{i_1\ldots i_k} a_{1i_1}\cdots a_{ki_k} .$$

We shall next define a multiplication rule for the algebra. We shall use $\times$ as a symbol for this multiplication and we shall call it cross multiplication. We shall let G_1G_2 denote the product of the two polynomials G_1 and G_2 in the usual sense. If G_1 and G_2 belong to $\mathscr{A}_k$, then G_1G_2 does not belong to $\mathscr{A}_k$ because $\mathscr{A}_k$ contains polynomials of a fixed degree k, while the degree of G_1G_2 is $2k$.

The multiplication $G_1 \times G_2$ will be defined in such a way that:

(5.4) If G_1 and G_2 belong to $\mathscr{A}_k$, then $G_1 \times G_2$ belongs to $\mathscr{A}_k$.

(5.5) $G_1 \times G_2 = G_2 \times G_1$.

(5.6) $(cG_1) \times G_2 = c(G_1 \times G_2)$.

(5.7) $G_1 \times (G_2+G_3) = (G_1 \times G_2) + (G_1 \times G_3)$.

The $m_1m_2\ldots m_k$ elements of the form $A = a_{1i_1}a_{2i_2}\ldots a_{ki_k}$ form a basis of the algebra $\mathscr{A}_k$. Because of (5.6) and (5.7) the multiplication rule of the algebra will be determined if it is given for any pair of basis elements. The product of two basis elements A_1 and A_2 is defined by

$$(5.8)\qquad A_1 \times A_2 = \sum_{U \in W(S)} \lambda(U)\, R(U)\, A_1 A_2 ,$$

where $W(S)$ is the set of all partitions of the set $S = (1,2,\ldots,k)$ into two disjoint subsets, where $\lambda(U)$ is a real number which is a function of U, and where $\sum_{U \in W(S)} \lambda(U) = 1$.

Let

$$(5.9)\qquad D_j = \sum_{i=1}^{m_j} D_{a_{ji}}$$

and let us use the notation

$$D_{j1}(A_1A_2) = A_2(D_jA_1) , \qquad D_{j2}(A_1A_2) = A_1(D_jA_2) ,$$

which we used previously in Section 2. The multiplication rule may be rewritten in the form

$$(5.10)\qquad A_1 \times A_2 = \sum_{U \in W(S)} \lambda(U) \left(R(U) \left(\prod_{j \in S} D_{j1}, \prod_{j \in S} D_{j2} \right) \right) A_1 A_2 \,,$$

where $R(U)$ operates on the differential operators, not on A_1A_2. The proof is as follows: Since D_{j1} operates on A_1 only, and since A_1 contains only one a_{ji}, say a_{ji_j}, for each j, the operator D_{j1} is in this case equivalent to the operator $D_{a_{ji_j}}$ and the equivalence between (5.8) and (5.10) follows from (4.4).

Since the operator $R(U)(\prod_{j \in S} D_{j1}, \prod_{j \in S} D_{j2})$ is independent of A_1A_2, we get by means of (2.16)–(2.18)

$$(5.11)\qquad G_1 \times G_2 = \sum_{U \in W(S)} \lambda(U)\, R(U) \left(\prod_{j \in S} D_{j1}, \prod_{j \in S} D_{j2} \right) G_1 G_2 \,,$$

where G_1 and G_2 are any two elements of the algebra $\mathscr{A}_k$. It is easy to see that the multiplication defined by (5.11) actually satisfies (5.4)–(5.7). We may thus state

THEOREM 1. *The set of all multilinear forms of the form* (5.1) *with real coefficients together with an addition defined by* (5.2), *a multiplication by a scalar defined by* (5.3) *and a cross multiplication defined by* (5.11) *forms a commutative algebra. The multiplication rule of the basis elements is given by* (5.8).

We have considered a set S consisting of the integers $1, 2, \ldots, k$. It is a formal generalization only to consider a set S consisting of any given set of k positive integers. With obvious modifications of (5.1)–(5.3), the results of this section are still valid.

We have considered an algebra with parameters which are real numbers. If we vary the parameters we get a family of algebras. Let us denote a particular algebra by $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$, where $\boldsymbol{m}_S$ denotes the set of m_j for which j belongs to S, and where $\boldsymbol{\lambda}_S$ denotes the set of all $\lambda(U)$ for which U belongs to $W(S)$. Let us denote by $(\mathscr{A}_k)$ the class of all algebras where the set S consists of k integers.

We shall write down more explicitly the multiplication rule for the first values of k. Instead of $\lambda(U) = \lambda((U', U''))$ we shall write $\lambda(U', U'')$, and we shall write $\lambda(S)$ when U is the partition consisting of S and the empty set.

In the algebra $\mathscr{A}_1(m_1)$

$$(5.12)\qquad G_1 \times G_2 = \tfrac{1}{2}\left(G_1(D_1G_2) + G_2(D_1G_1)\right).$$

In an algebra of the class $(\mathscr{A}_2)$

$$(5.13)\qquad \begin{aligned} G_1 \times G_2 = {} & \tfrac{1}{2}\lambda(12)\left(G_1(D_1D_2G_2) + G_2(D_1D_2G_1)\right) + \\ & + \tfrac{1}{2}\lambda(1,2)\left((D_1G_1)(D_2G_2) + (D_2G_1)(D_1G_2)\right). \end{aligned}$$

In an algebra of the class $(\mathscr{A}_3)$

$$(5.14)\qquad G_1\times G_2 = \tfrac{1}{2}\lambda(123)\left(G_1(D_1D_2D_3G_2)+G_2(D_1D_2D_3G_1)\right) + \\ + \tfrac{1}{2}\sum_{i=1}^{3}\lambda(i,jk)\left((D_iG_1)(D_jD_kG_2)+(D_iG_2)(D_jD_kG_1)\right),$$

where (ijk) is a permutation of (123).

In an algebra of the class $(\mathscr{A}_4)$

$$(5.15)\quad G_1\times G_2 = \tfrac{1}{2}\lambda(1234)\left(G_1(D_1D_2D_3D_4G_2)+G_2(D_1D_2D_3D_4G_1)\right) + \\ + \tfrac{1}{2}\sum_{i=1}^{4}\lambda(i,jkh)\left((D_iG_1)(D_jD_kD_hG_2)+(D_iG_2)(D_jD_kD_hG_1)\right) + \\ + \tfrac{1}{2}\sum_{i<j}\lambda(ij,kh)\left((D_iD_jG_1)(D_kD_hG_2)+(D_iD_jG_2)(D_kD_hG_1)\right),$$

where $(ijkh)$ is a permutation of (1234).

In the formulae (5.13)–(5.15) each D_i operates only within the parenthesis in which it is situated.

We note finally that the effect of the operator D_j on an element G of the form (5.1) is to remove the factor a_{ji_j} from each term. We have for instance

$$(5.16)\qquad D_kG = \sum_{i_1=1}^{m_1}\cdots\sum_{i_{k-1}=1}^{m_{k-1}} g'_{i_1\ldots i_{k-1}}a_{1i_1}\cdots a_{k-1,i_{k-1}},$$

where

$$(5.17)\qquad g'_{i_1\ldots i_{k-1}} = \sum_{i_k=1}^{m_k} g_{i_1\ldots i_k}.$$

The operator D_j is therefore essentially a summation operator. From the point of view of probability distributions the operator D_j may be said to perform a marginalization of a distribution.

6. Genetic interpretations of Section 5.

A basis element $a_{1i_1}a_{2i_2}\ldots a_{ki_k}$ is interpreted as representing a gamete having the allele a_{1i_1} at locus 1, the allele a_{2i_2} at locus 2, and so on. An element (5.1) of the algebra whose coefficients are non-negative with sum one is interpreted as a probability distribution of the gametic types. The product (5.8) represents the probability distribution of gametes resulting from an individual of genotype A_1A_2. The set of numbers $\lambda(U)$ represents what H. Geiringer [8] has called the *linkage distribution*. In the case $k=2$, $\lambda(1,2)$ represents the recombination probability. In the genetic interpretation the $\lambda(U)$ must be non-negative. Moreover they are restricted by other inequalities.

The recombination operator $R(U)$ applied to two given gametes A_1 and A_2 represents the effect of crossing over during meiosis.

The product $G_1 \times G_2$ represents the probability distribution of gametes of the offspring when one population with gametic probability distribution G_1 mates at random with a population with gametic probability distribution G_2.

The linear combination $cG_1 + (1-c)G_2$, where $0 \leqq c \leqq 1$, represents the gametic probability distribution of a mixture of two populations with gametic probability distributions G_1 and G_2.

If two or more loci are completely linked, they may be treated as one locus. In the case $k=2$ complete linkage means that $\lambda(1,2)=0$, and we get the multiplication rule

$$(6.1) \qquad G_1 \times G_2 = \tfrac{1}{2}\big(G_1(D_1D_2G_2) + G_2(D_1D_2G_1)\big) ,$$

and if $a_{1i_1}a_{2i_2}$ is replaced by a single symbol b_{1v} then the multiplication rule will be the same as in the case of one locus.

If in the case $k=3$ we have complete linkage between loci 2 and 3, then $\lambda(2,13)=\lambda(3,12)=0$, and we get the multiplication rule

$$(6.2) \qquad \begin{aligned} G_1 \times G_2 = {} & \tfrac{1}{2}\lambda(123)\big(G_1(D_1D_2D_3G_2) + G_2(D_1D_2D_3G_1)\big) + \\ & + \tfrac{1}{2}\lambda(1,23)\big((D_1G_1)(D_2D_3G_2) + (D_1G_2)(D_2D_3G_1)\big) . \end{aligned}$$

Replacing $a_{2i_2}a_{3i_3}$ by a single variable b_{2v} we get a multiplication rule of the form (5.13).

7. Sequences of powers and products connected with the different generations under panmixia.

Since multiplication is non-associative in the algebras defined in Section 5, there are different powers of the same degree having different *shapes* (Etherington [2]). We shall consider powers and products of two particular shapes. We shall consider the sequence of *plenary powers* defined by

$$(7.1) \qquad G(n+1) = G(n) \times G(n), \qquad n = 0, 1, 2, \ldots .$$

Secondly, we shall consider the sequence of products defined by

$$(7.2) \qquad H(n+2) = H(n) \times H(n+1), \qquad n = 0, 1, 2, \ldots .$$

If $H(0)=H(1)$ the sequence $\{H(n)\}$ will also be a sequence of powers. These powers are, however, different from the plenary powers.

The plenary power $G(n)$ represents the probability distribution of the gametic types in the n'th generation when the following conditions hold:

(7.3) The population is infinite.
(7.4) There is panmixia in each generation.
(7.5) All loci considered are in autosomes (i.e. chromosomes which are not sex chromosomes).
(7.6) The gametic probability distribution of generation 0 is $G(0)$.

The sequence $\{H(n)\}$ gives the probability distributions of the X chromosomes if (7.3) and (7.4) hold. The X chromosome of a male in the n'th generation comes from a female of the $(n-1)$'th generation. Of the two X chromosomes of a female in the n'th generation one comes from a male and the other from a female of the $(n-1)$'th generation. When (7.3) and (7.4) hold, the female X chromosome in the n'th generation coming from a female in the preceding generation must have the same probability distribution as the X chromosome of a male in the n'th generation. Assuming that generation 0 has also been generated by panmixia, we may set

(7.7) $H(0)=$ the probability distribution of the female X chromosome in generation 0 which comes from a male in the preceding generation.
(7.8) $H(1)=$ the probability distribution of the other female X chromosome and the male X chromosome in generation 0.

Then in the n'th generation the male X chromosome will have the probability distribution $H(n+1)$ and the female X chromosomes will have the probability distributions $H(n)$ and $H(n+1)$.

Other sequences of powers and products which have a genetic interpretation are the sequence of *principal powers* and the sequence of *primary products* (Etherington [3]). These sequences will not be considered in the present paper.

8. Homomorphisms between the algebras.

A mapping $G \to \eta(G)$ of an algebra $\mathscr{A}$ into an algebra $\mathscr{B}$ is called a *homomorphism* if

$$\eta(G_1+G_2) = \eta(G_1)+\eta(G_2)\,,$$
$$\eta(cG) = c\eta(G)\,,$$
$$\eta(G_1\times G_2) = \eta(G_1)\times\eta(G_2)\,,$$

for any elements G_1, G_2, G which belong to $\mathscr{A}$ and any real number c.

We shall show that each of the differential operators D_j defined by (5.9) generates a homomorphism of an algebra of the class $(\mathscr{A}_k)$ onto an algebra of the class $(\mathscr{A}_{k-1})$.

We have noted at the end of Section 5 that the effect of D_j on G is to remove the factor a_{ji_j} from each term such that we get a multilinear form of a degree which is one less than the degree of G. If G_1 and G_2 are two elements of the algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$ and if j is an integer belonging to the set S, then the elements $D_j G_1$ and $D_j G_2$ will belong to an algebra $\mathscr{A}(\boldsymbol{m}_{S-j}, \boldsymbol{\lambda}_{S-j})$ where $S-j$ denotes the set of integers which we obtain when j is removed from S. From (2.4) and (2.5) follows that

$$D_j(G_1+G_2) = D_j G_1 + D_j G_2 , \tag{8.1}$$

$$D_j(cG) = cD_j G , \tag{8.2}$$

when c is a constant. We shall next consider

$$D_j(G_1 \times G_2) = \sum_U \lambda(U)\, D_j \big(R(U)(\textstyle\prod_{h\in S} D_{h1}, \prod_{h\in S} D_{h2})\big)\, G_1 G_2 . \tag{8.3}$$

Using (2.20) and (4.1) we get

$$\begin{aligned} D_j R(U) & (\textstyle\prod_{h\in S} D_{h1}, \prod_{h\in S} D_{h2}) \\ &= \tfrac{1}{2}(\textstyle\prod_{h\in U'} D_{h1} \prod_{h\in U''} D_{h2} + \prod_{h\in U''} D_{h1} \prod_{h\in U'} D_{h2}) D_j . \end{aligned} \tag{8.4}$$

Each of the two terms in the parenthesis on the right-hand side of (8.4) contains one and only one of the factors D_{j1} and D_{j2}. Furthermore

$$D_{j1} D_j G_1 G_2 = D_{j2} D_j G_1 G_2 = D_{j1} D_{j2} G_1 G_2 .$$

Hence (8.4) multiplied by $G_1\, G_2$ is equal to

$$\big(R(U'-j,\, U''-j)(\textstyle\prod_{h\in S-j} D_{h1}, \prod_{h\in S-j} D_{h2})\big) D_{j1} D_{j2} G_1 G_2 , \tag{8.5}$$

where, of course, only one of the sets U' and U'' contains j, such that if j belongs to U' then $U''-j=U''$. From (8.3)–(8.5) we get

$$D_j(G_1 \times G_2) = \sum_{U\in W(S-j)} \lambda(U) R(U) (\textstyle\prod_{h\in S-j} D_{h1}, \prod_{h\in S-j} D_{h2}) D_{j1} D_{j2} G_1 G_2 , \tag{8.6}$$

where

$$\lambda(U', U'') = \lambda(U_j', U'') + \lambda(U', U_j'') \tag{8.7}$$

if we write U'_j for the union of U' and the set which contains the element j only. Evidently (8.6) means that

$$D_j(G_1 \times G_2) = (D_j G_1) \times (D_j G_2) , \tag{8.8}$$

where $\boldsymbol{\lambda}_{S-j}$ is expressed in terms of $\boldsymbol{\lambda}_S$ by (8.7). We have thus shown that D_j generates a homomorphism. Evidently any basis element of $\mathscr{A}(\boldsymbol{m}_{S-j}, \boldsymbol{\lambda}_{S-j})$ is the image of a basis element of $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$. Hence any element of the former algebra is the image of an element of the latter algebra. This means that the mapping generated by D_j is a mapping *onto* the algebra $\mathscr{A}(\boldsymbol{m}_{S-j}, \boldsymbol{\lambda}_{S-j})$. We shall formulate our results in the following theorem:

THEOREM 2. *If G belongs to the algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$, where S contains the integer j and at least one other integer, then the mapping $G \to D_j G$ is a homomorphism of the algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$ onto the algebra $\mathscr{A}(\boldsymbol{m}_{S-j}, \boldsymbol{\lambda}_{S-j})$, where $\boldsymbol{\lambda}_{S-j}$ is expressed in terms of $\boldsymbol{\lambda}_S$ by* (8.7).

Let T be a proper subset of S and let D_T denote the product

$$D_T = \prod_{j \in T} D_j \,. \tag{8.9}$$

Since the product of two homomorphisms is a homomorphism, we get

THEOREM 3. *If G belongs to the algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$, then the mapping $G \to D_T G$ is a homomorphism of $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$ onto $\mathscr{A}(\boldsymbol{m}_{S-T}, \boldsymbol{\lambda}_{S-T})$, where $\boldsymbol{\lambda}_{S-T}$ may be expressed in terms of $\boldsymbol{\lambda}_S$ by repeated application of* (8.7).

If G belongs to $\mathscr{A}(m_1)$ the mapping $G \to D_1 G$ evidently is a homomorphism of $\mathscr{A}(m_1)$ onto the set of real numbers. Combining this with Theorem 3 we see that if G belongs to the algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$, then the mapping $G \to D_S G$ is a homomorphism of $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$ onto the set of real numbers. An algebra for which there exists a non-trivial homomorphism into the set of real numbers is called a *baric algebra* (Etherington [3]), and the real number which is the image of the element G is called the *weight* of G. Using this terminology we may state

THEOREM 4. *The algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$ is a baric algebra with weight function $\xi(G) = D_S G$.*

The weight $\xi(G)$ is the sum of the coefficients in the expression (5.1). The weight of an element G which represents a probability distribution is thus equal to 1.

Since $D_{S-T} D_T G = D_S G$, we have

$$\xi(D_T G) = \xi(G) \,. \tag{8.10}$$

The homomorphism $G \to D_T G$ thus preserves the weights of the elements.

It is evident that a sequence of products or powers is mapped onto a sequence of products or powers of the same shape. For instance a sequence of plenary powers is mapped onto a sequence of plenary powers, and a sequence $\{H(n)\}$ defined by (7.2) is mapped onto a sequence of the same type.

9. Explicit expressions and recurrence formulae for $G(n)$.

9.1. The sequence $\{G(n)\}$ of plenary powers was defined by (7.1). We noted that a sequence of plenary powers gives the gametic probability distribution in successive generations when there is panmixia, when the population is infinite, and when the loci are located in autosomes.

In the rest of this paper we shall consider algebras which have a genetic interpretation. This means that we consider the case when $\boldsymbol{\lambda}_S$ is a probability distribution, in other words the case when all $\lambda(U)$ are non-negative. Furthermore we shall suppose that $G(0)=G$ is a probability distribution. Then $G(n)$ is a probability distribution for every n and $\xi(G(n))=1$ for every n.

In the case of one single locus we get from (5.12)

$$G \times G = G . \tag{9.1}$$

In this case any power of G of any degree and of any shape will be equal to G. In particular

$$G(n) = G \tag{9.2}$$

for every n.

9.2. The case of two loci. In the following we shall always assume that no two loci are completely linked, for if they were completely linked we could regard them as one single locus. (See Section 6).

Setting $G_1=G_2=G(n)$ in (5.13) we get

$$G(n+1) = \lambda(12)G(n) + \lambda(1,2)\big(D_1G(n)\big)\big(D_2G(n)\big) . \tag{9.3}$$

According to Theorem 2, $D_1G(n)$ and $D_2G(n)$ are plenary powers in the algebras $\mathscr{A}(m_2)$ and $\mathscr{A}(m_1)$, respectively. According to (9.2) we thus have $D_1G(n)=D_1G$ and $D_2G(n)=D_2G$ for every n. The difference equation (9.3) may thus be rewritten in the form

$$\big(E-\lambda(12)\big)G(n) = \lambda(1,2)(D_1G)(D_2G) . \tag{9.4}$$

In this difference equation the values of the function $G(n)$ are not numbers but elements of an algebra. It is, however, easy to see that the results summarized in Section 3 apply to this case with a change of interpretation of the symbols. In (3.5) for instance the c_i will now mean elements of the algebra, while the r_i are still real or complex numbers. If some of the r_i are complex numbers we shall also have to consider elements of the algebra where the coefficients of (5.1) are complex numbers, i.e. we must consider an algebra having as elements all multilinear forms (5.1) with complex coefficients. The properties of the algebras which we have found in the real case will hold also in the complex case. In the examples given in the present paper no complex roots occur.

The general solution of (9.4) is

$$G(n) = (D_1G)(D_2G) + C(\lambda(12))^n, \tag{9.5}$$

where C is an element of the algebra which does not depend on n. Setting $n=0$ in (9.5) we get $C=G-(D_1G)(D_2G)$ which we insert in (9.5) to get

$$G(n) = (D_1G)(D_2G) + (\lambda(12))^n(G-(D_1G)(D_2G)). \tag{9.6}$$

If a particular G is given and if we wish to calculate $G(n)$ for some separate values of n, we should use (9.6). If we wish to calculate all $G(n)$ for a sequence of successive generations it is easier to use the difference equation (9.4) for recurrent computation of successive $G(n)$. Alternately we may use the homogeneous difference equation of the second order

$$(E-1)(E-\lambda(12))G(n) = 0$$

which for the purpose of recurrent computation of $G(n)$ may be written in the form

$$G(n) = G(n-1) + \lambda(12)(G(n-1)-G(n-2)).$$

9.3. Three loci. Setting $G_1=G_2=G(n)$ in (5.14) we get

$$G(n+1) = \lambda(123)G(n)+\sum_{i=1}^{3}\lambda(i,jk)(D_iG(n))(D_jD_kG(n)). \tag{9.7}$$

According to Theorems 2 and 3, $D_jD_kG(n)$ is a plenary power in the algebra $\mathscr{A}(m_i)$, and $D_iG(n)$ is a plenary power in the algebra

$$\mathscr{A}(m_j, m_k, \lambda(jk), \lambda(j, k)).$$

Using (9.2) and (9.6) we thus get

$$D_jD_kG(n) = D_jD_kG, \tag{9.8}$$

$$D_iG(n) = (D_iD_jG)(D_iD_kG) + (\lambda(jk))^n((D_iG)-(D_iD_jG)(D_iD_kG)). \tag{9.9}$$

Inserting (9.8) and (9.9) in (9.7) we get the difference equation

$$\begin{aligned}(E-\lambda(123))G(n) = {} & (1-\lambda(123))(D_2D_3G)(D_1D_3G)(D_1D_2G)+ \\ & +\sum_{i=1}^{3}\lambda(i,jk)(D_jD_kG)(D_iG-(D_iD_jG)(D_iD_kG))(\lambda(jk))^n.\end{aligned} \tag{9.10}$$

If $\lambda(123)\neq\lambda(jk)$ for every pair of values j,k, then the general solution of (9.10) is

$$\begin{aligned}G(n) = {} & (D_2D_3G)(D_1D_3G)(D_1D_2G) + C(\lambda(123))^n + \\ & +\sum_{i=1}^{3}(D_jD_kG)(D_iG-(D_iD_jG)(D_iD_kG))(\lambda(jk))^n,\end{aligned} \tag{9.11}$$

where C is an arbitrary element of the algebra. Setting $n=0$ we find

$$(9.12)\quad C = G + 2(D_2D_3G)(D_1D_3G)(D_1D_2G) - \sum_{i=1}^{3} (D_iG)(D_jD_kG)\,.$$

If for instance $\lambda(123)=\lambda(23)$, then $\lambda(1,23)=0$. The coefficient of $(\lambda(23))^n$ in (9.10) thus is equal to zero. The solution will then be (9.11) after deletion of the term containing $(\lambda(23))^n$.

As in the case $k=2$ it is clear that we should use the explicit expression for computation if we wish to compute $G(n)$ for some separate values of n. If we wish to compute all $G(n)$ for a sequence of successive generations we may compute the $D_iG(n)$ recurrently by means of (9.4) and use (9.7) for recurrent computation of $G(n)$. An alternative method of recurrent computation is to use the difference equation

$$(9.13)\quad \big(E-\lambda(123)\big)\big(E-\lambda(23)\big)\big(E-\lambda(13)\big)\big(E-\lambda(12)\big)\,G(n)$$
$$= \big(1-\lambda(123)\big)\big(1-\lambda(23)\big)\big(1-\lambda(13)\big)\big(1-\lambda(12)\big)(D_2D_3G)(D_1D_3G)(D_1D_2G)\ .$$

That $G(n)$ satisfies this difference equation is seen by application of the operator $\big(E-\lambda(23)\big)\big(E-\lambda(13)\big)\big(E-\lambda(12)\big)$ to both sides of (9.10).

Since (9.13) is a difference equation of order four, it cannot be used for computation of $G(1)$, $G(2)$ and $G(3)$. These values may, however, be computed in the manner previously described, and after that we may use (9.13) for recurrent computation of $G(4)$, $G(5)$, and so on.

There is no great difference between the amount of numerical work required by the two methods. If we compute each $G(n)$ by both methods we get a good checking of each individual value.

If we apply the operator $E-1$ to (9.13) we see that $G(n)$ satisfies the homogeneous difference equation

$$(9.14)\quad (E-1)\big(E-\lambda(123)\big)\big(E-\lambda(23)\big)\big(E-\lambda(13)\big)\big(E-\lambda(12)\big)G(n) = 0$$

which is called the *train equation* of the plenary powers.

9.4. Remarks on the general case. The method we have used may in principle be used for calculation of explicit expressions and linear difference equations for $G(n)$ for any number of loci. The explicit expression for $G(n)$ in the algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$ will be of the form $\sum_i C_i r_i^n$, where the C_i are independent of n or polynomials in n. In accordance with the terminology of Etherington the r_i will be called the *train roots* of $G(n)$ in the algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$. They are roots of the characteristic equation of the homogeneous linear difference equation (*train equation*) of $G(n)$ in the algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$.

In the general case we get

$$G(n+1) = \sum_{U \in W(S)} \lambda(U) \left(\prod_{j \in U'} D_j G(n)\right)\left(\prod_{j \in U''} D_j G(n)\right). \tag{9.15}$$

One of the terms on the right-hand side of (9.15) is $\lambda(S)G(n)$. The other terms are products of plenary powers corresponding to smaller numbers of loci. If we have already found explicit formulae for these powers, (9.15) gives an explicit formula for $G(n)$ in the algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$, except for a single coefficient which is independent of n and which may be determined by setting $n=0$.

THEOREM 5. *The train roots of $G(n)$ in the algebra $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$ are $\lambda(S)$, the train roots of the $G(n)$ in the algebras $\mathscr{A}(\boldsymbol{m}_{S-j}, \boldsymbol{\lambda}_{S-j})$ for every $j \in S$ and the products of the train roots of $G(n)$ in $\mathscr{A}(\boldsymbol{m}_T, \boldsymbol{\lambda}_T)$ with the train roots of $G(n)$ in $\mathscr{A}(\boldsymbol{m}_{S-T}, \boldsymbol{\lambda}_{S-T})$ for every subset T of S which contains at least two elements and for which the number of elements of T does not exceed the number of elements of $S-T$. The train roots are all real and are situated in the interval* $]0,1]$.

The proof of the first part of this theorem is obvious from a consideration of (9.15). The last part of the theorem is a consequence of the fact that $0 < \lambda(S) \leqq 1$ for every algebra which has a genetical interpretation.

10. Explicit expressions and recurrence formulae for $H(n)$.

10.1. The sequence of products $\{H(n)\}$ defined by (7.2) gives the probability distributions of an X chromosome in successive generations when there is panmixia and the population is infinite.

Let us set $H(0)=G_0$ and $H(1)=G_1$ and let us suppose that G_0 and G_1 are probability distributions. Then $\xi(H(n))=1$ for every n.

In the case of a single locus we get

$$H(n+2) = H(n+1) \times H(n) = \tfrac{1}{2}H(n+1) + \tfrac{1}{2}H(n).$$

We thus already have a difference equation for $H(n)$ which may be rewritten in the form

$$(E-1)(E+\tfrac{1}{2})H(n) = 0. \tag{10.1}$$

The general solution of this equation is

$$H(n) = C_1 + C_2(-\tfrac{1}{2})^n. \tag{10.2}$$

Setting $n=0$ and $n=1$ in (10.2) we get

$$C_1 = \tfrac{1}{3}(G_0 + 2G_1), \tag{10.3}$$

$$C_2 = \tfrac{2}{3}(G_0 - G_1). \tag{10.4}$$

10.2. Two loci. For the sake of brevity we shall write θ instead of $\lambda(1, 2)$. Then

$$(10.5)\quad H(n+2) = \tfrac{1}{2}(1-\theta)\big(H(n)+H(n+1)\big) + \\ + \tfrac{1}{2}\theta\Big(\big(D_1H(n)\big(D_2H(n+1)\big)+\big(D_2H(n)\big)\big(D_1H(n+1)\big)\Big),$$

Applying (10.2) to $D_1H(n)$ and $D_2H(n)$ we get

$$(10.6)\quad \big(E^2-\tfrac{1}{2}(1-\theta)E-\tfrac{1}{2}(1-\theta)\big)H(n) = \theta\big(C_3+C_4(-\tfrac{1}{2})^n+C_5(\tfrac{1}{4})^n\big),$$

where

$$(10.7)\quad C_3 = (D_1C_1)(D_2C_1),$$

$$(10.8)\quad C_4 = \tfrac{1}{4}\big((D_1C_1)(D_2C_2)+(D_2C_1)(D_1C_2)\big),$$

$$(10.9)\quad C_5 = -\tfrac{1}{2}(D_1C_2)(D_2C_2).$$

Let r_1 and r_2 be the two roots of the equation

$$(10.10)\quad x^2-\tfrac{1}{2}(1-\theta)x-\tfrac{1}{2}(1-\theta) = 0.$$

In the genetic interpretation θ is situated in the interval $[0, 1]$ and cannot be much greater than $\frac{1}{2}$. Then r_1 and r_2 must be real and have opposite signs since their product is $-\frac{1}{2}(1-\theta)$. Equation (10.10) has the roots 1 and $-\frac{1}{2}$ if and only if $\theta=0$. This means that the two loci are completely linked and can be analyzed as one single locus. Equation (10.10) has the root $\frac{1}{4}$ if and only if $\theta=0{,}9$. This is an impossible value in the genetic interpretation. In all cases of genetic interest we can therefore assume that the numbers r_1, r_2, $-\frac{1}{2}$, $\frac{1}{4}$ and 1 are all different. Then the solution of the difference equation (10.6) is given by

$$(10.11)\quad H(n) = C_3+C_4(-\tfrac{1}{2})^{n-2}+\frac{\theta C_5}{10\theta-9}\left(\frac{1}{4}\right)^{n-2}+C_6r_1^{\,n}+C_7r_2^{\,n},$$

where C_6 and C_7 are determined by setting $n=0$ and $n=1$.

Applying the operator $(E+\frac{1}{2})(E-\frac{1}{4})$ to (10.6) we get

$$(10.12)\quad (E+\tfrac{1}{2})(E-\tfrac{1}{4})\big(E^2-\tfrac{1}{2}(1-\theta)E-\tfrac{1}{2}(1-\theta)\big)H(n) = \tfrac{9}{8}\theta C_3.$$

Applying the operator $E-1$ to this equation we get the homogeneous difference equation

$$(10.13)\quad (E-1)(E+\tfrac{1}{2})(E-\tfrac{1}{4})\big(E^2-\tfrac{1}{2}(1-\theta)E-\tfrac{1}{2}(1-\theta)\big)H(n) = 0.$$

10.3. Train roots and asymptotic distribution in the general case. It is clear from the method we have used that the probability distribution $H(n)$ in the general case will be a sum of exponential terms $r_i^{\,n}$ with coefficients which are independent of n or polynomials in n. We shall call the r_i the train roots of $H(n)$ in the algebra considered. Two of the train roots of $H(n)$ in $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$ will be the roots of

$$x^2 - \tfrac{1}{2}\lambda(S)x - \tfrac{1}{2}\lambda(S) = 0\,. \tag{10.14}$$

These roots are real and have opposite signs since their product is $-\frac{1}{2}\lambda(S)$ where $\lambda(S) > 0$. Let r_1 be the positive root and r_2 the negative root. We see that $r_1 \leqq 1$ and that $r_1 + r_2 = \frac{1}{2}\lambda(S)$ is positive. Hence $r_2 > -1$. We get

THEOREM 6. *The train roots of $H(n)$ in $\mathscr{A}(\boldsymbol{m}_S, \boldsymbol{\lambda}_S)$ are the roots of* (10.14), *the train roots of $H(n)$ in $\mathscr{A}(\boldsymbol{m}_{S-j}, \boldsymbol{\lambda}_{S-j})$ for every $j \in S$, and the products of the train roots of $H(n)$ in the algebra $\mathscr{A}(\boldsymbol{m}_T, \boldsymbol{\lambda}_T)$ with the train roots of $H(n)$ in $\mathscr{A}(\boldsymbol{m}_{S-T}, \boldsymbol{\lambda}_{S-T})$ for every subset T of S which has at least two elements and for which the number of elements of T does not exceed the number of elements of $S-T$. The train roots are all real and are situated in the interval* $]-1, 1]$.

The positive root of (10.14) is equal to 1 if and only if $\lambda(S) = 1$. Then $\lambda(U) = 0$ for any other element U of $W(S)$. Using (5.11) we again get (10.1) corresponding to the fact that all loci are completely linked and can be analyzed as one single locus. The term in the expansion of $H(n)$ corresponding to a train root 1 will thus always be a constant, not a polynomial in n.

We conclude from these results that $H(n)$ converges to a limit when n tends to infinity. This limit $H(\infty)$ is found by letting $n \to \infty$ in (7.2). We then get $H(\infty) = H(\infty) \times H(\infty)$. Thus $H(\infty)$ is an idempotent element of the algebra. An idempotent element must, however, have the form $\prod_{j \in S} \Gamma_j$, where Γ_j is a linear form in the variables a_{ji_j}. This is easily proved by induction using (9.15).

11. Concluding remarks.

In the introduction I noted that one new aspect of the present paper is the use of recursion in the study of genetic algebras. Geiringer [8]–[11] has, however, applied a recursive approach to the individual probabilities without considering algebras. She obtained the scalar version of formula (9.15) [8, formula (31)]. She notes that this formula gives a system of difference equations. She does not, however, seem to be aware of the possibility of solving this system recursively. She indicates a method of solution which is unnecessarily complicated.

Bennet [1] indicated another method of solving the system. His method is also more complicated than the method given in the present paper.

Geiringer [9] carried through the solution in the case of three loci and got an explicit expression which is the scalar version of (9.11) and (9.12) of the present paper. It may be noted, however, that this explicit formula follows easily from the train equation (9.14) which had previously been published by Etherington [5].

The results given for one locus and two loci in the case of autosomes and one locus in the case of X-chromosomes have been known for a long time and can be found in textbooks (Li [15, Chapters 4, 5, 8], Kempthorne [14, Chapter 2]).

The sequence $H(n)$ defined by (7.2) and its genetic interpretation do not seem to have been considered before, and the results of Sections 10.2 and 10.3 seem to be new.

The use of the sequence $H(n)$ in the study of sex-linked traits presupposes that the traits are represented by loci in the X chromosomes only, not in the Y chromosomes. This seems to be the usual case. (See for instance [16, p. 64]).

REFERENCES

1. J. H. Bennet, *On the theory of random mating*, Ann. Eugenics 18 (1954), 311–317.
2. I. M. H. Etherington, *On non-associative combinations*, Proc. Roy. Soc. Edinburgh 59 (1939), 153–162.
3. I. M. H. Etherington, *Genetic algebras*, Proc. Roy. Soc. Edinburgh 59 (1939), 242–258.
4. I. M. H. Etherington, *Commutative train algebras of ranks 2 and 3*, J. London Math. Soc. 15 (1940), 136–148.
5. I. M. H. Etherington, *Special train algebras*, Quart. J. Math. Oxford Ser. (2) 12 (1941), 1–8.
6. I. M. H. Etherington, *Duplication of linear algebras*, Proc. Edinburgh Math. Soc. (2) 6 (1941), 222–230.
7. I. M. H. Etherington, *Non-associative algebra and the symbolism of genetics*, Proc. Roy. Soc. Edinburgh Sect. B 61 (1941), 24–42.
8. H. Geiringer, *On the probability theory of linkage in Mendelian heredity*, Ann. Math. Statist. 15 (1944), 25–57.
9. H. Geiringer, *Further remarks on linkage theory in Mendelian heredity*, Ann. Math. Statist. 16 (1945), 390–393.
10. H. Geiringer, *On the mathematics of random mating in case of different recombination values for males and females*, Genetics 33 (1948), 548–564.
11. H. Geiringer, *On some mathematical problems arising in the development of Mendelian genetics*, J. Amer. Statist. Assoc. 44 (1949), 526–547.
12. H. Gonshor, *Special train algebras arising in genetics*, Proc. Edinburgh Math. Soc. (2) 12 (1960), 41–53.
13. C. Jordan, *Calculus of finite differences*, Budapest, 1939.
14. O. Kempthorne, *An introduction to genetic statistics*, New York, 1957.
15. C. C. Li, *Population genetics*, Chicago, 1955.

16. N. E. Morton, *Further scoring types in sequential linkage tests, with a critical review of autosomal and partial sex linkage in man*, Amer. J. Human Genetics 9 (1957), 55–75.
17. R. Raffin, *Axiomatisation des algèbres génétiques*, Acad. Roy. Belg. Bull. Cl. Sci. (5) 37 (1951), 359–366.
18. R. D. Schafer, *Structure of genetic algebras*, Amer. J. Math. 71 (1949), 121–135.
19. E. Stephens, *The elementary theory of operational mathematics*, New York, 1937.

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