

The Linear Algebra for Linked Loci with Mutation

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ABSTRACT

A linear algebra is defined describing this situation: Any number of loci are linked with arbitrary linkage distribution, and each allele may mutate into the other alleles with given frequencies. Mutations at different loci are assumed independent. It is shown that this gives a genetic algebra (in the sense of Gonsior or Schafer) which is also a special train algebra, and the train roots are found.

1. INTRODUCTION

Linear commutative nonassociative algebras over the complex numbers were introduced in mathematical genetics by Etherington [4, 6]. The fundamental idea is to define a basis G_1, G_2, \dots, G_n with one-to-one correspondence to the genotypes g_1, g_2, \dots, g_n considered, and then give a multiplication table so that the product $G_i G_j$ of two basis elements will be equal to a linear combination $\sum_k p_{ijk} G_k$, where p_{ijk} is the probability of getting genotype g_k in a cross between g_i and g_j individuals. The genotype distribution after random mating between two infinite populations may be found by calculating the product of two suitable linear combinations of the basis elements. Products with more than two factors will give the offspring distribution in more complicated pedigrees.

One of the reasons for considering such algebras is the possibility of proving general theorems for different kinds of sequences of algebra elements, representing successive generations in various mating systems, as for instance Theorems 2.1 and 2.2 in Ref. 8, Theorem 3 in Ref. 12 and Theorem 5.1 in Ref. 11. Most such theorems apply to what is defined by Gonsior [9] to be *genetic algebras*: An algebra is genetic if it is possible to find a basis C_0, C_1, \dots, C_n giving a multiplication table

$$C_i C_j = \sum_{k=0}^n \gamma_{ijk} C_k,$$

where $\gamma_{000} = 1$, $\gamma_{0jk} = 0$ for $k < j$ and $\gamma_{ijk} = 0$ for $k \leq \max(i, j)$; $i, j = 1, 2, \dots, n$. This basis is said to be *canonical*. The *train roots* 1,

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$\gamma_{011}, \dots, \gamma_{0nn}$ are important when we want to construct expressions for the general member of various sequences. The definition of a genetic algebra given by Schafer [15] is equivalent to the one above (Theorem 2.1 in Ref. [9]), but Gonshor's is more suitable for practical applications. An algebra is *baric* if there exists a nontrivial homomorphism w to the scalar field [4]. Then w is called the *weight function*. Genetic algebras are baric with $w(C_0) = 1, w(C_j) = 0$ for $j > 0$. A *special train algebra* [4, 5] is a baric algebra where the nilideal N of elements with weight 0 is nilpotent, and where all powers of N are ideals in the total algebra. Every special train algebra is genetic [5]; an example of a genetic algebra which is not a special train algebra is furnished by the copular algebra for simple Mendelian inheritance treated in Ref. 15.

The deterministic model for any number of arbitrarily linked loci was first studied by Geiringer [7], and later by Bennett [1]. Limit theorems for a more general situation are given by Ellison [2]. A treatment by means of linear algebras is found in [13]. Algebras for linked loci are also used in [14] and [10], though the methods applied are quite different from ours. Algebras for mutation have been considered in connection with one autosomal locus and sex-linkage [8], and polyploidy [8, 9].

2. ELEMENTARY ALGEBRAS

Assume that E is an algebra with basis A_0, A_1, \dots, A_r and multiplication table

$$A_i A_j = (A_i + A_j)/2; \quad i, j = 0, 1, \dots, r.$$

Then E is called *elementary* ([13], Sec. 2), and we will refer to the basis used here as the *natural basis*. E is baric with weight given by $w(A_i) = 1$ for all i . Using any basis C_0, C_1, \dots, C_r with $w(C_0) = 1, w(C_i) = 0$ for $i > 0$, we find a multiplication table

$$C_0^2 = C_0; \quad C_0 C_i = C_i/2, \quad i = 1, 2, \dots, r; \quad C_i C_j = 0 \text{ otherwise.}$$

(Introduce for instance $C_0 = A_0, C_i = A_0 - A_i$.) Hence the elementary algebra E is a special train algebra with train roots 1 and $\frac{1}{2}$, the latter with multiplicity r , see Ref. 13.

Let E_1, E_2, \dots, E_k be k elementary algebras such that E_m has natural basis $A_{m0}, A_{m1}, \dots, A_{mr_m}$. We now introduce a vector space V_k with basis elements $A_{1i_1} A_{2i_2} \dots A_{ki_k}$ constructed by juxtaposition of basis elements from the k algebras. Following Holgate ([13], Sec. 3) we will write

$$\prod_{m=1}^k \left(\sum_{j=0}^{r_m} a_{mj} A_{mj} \right),$$

for the element

$$\sum_{j_1} \dots \sum_{j_k} a_{1j_1} a_{2j_2} \dots a_{kj_k} A_{1j_1} A_{2j_2} \dots A_{kj_k},$$

in V_k . Suppose that for $m = 1, 2, \dots, k$, $B_{m0}, B_{m1}, \dots, B_{mr_m}$ is an arbitrary basis in E_m . Then it is seen that any sequence of all elements of the form $B_{1j_1} B_{2j_2} \dots B_{kj_k}$ will give a basis in V_k .

The *linked product* E^* of the elementary algebras E_1, E_2, \dots, E_k was introduced by Holgate in Ref. 13. This is an algebra over V_k with multiplication given by

$$(A_{1i_1} A_{2i_2} \dots A_{ki_k})(A_{1j_1} A_{2j_2} \dots A_{kj_k}) = (A_{1i_1} A_{2i_2} \dots A_{ki_k} + A_{1j_1} A_{2j_2} \dots A_{kj_k})/2.$$

E^* will itself be elementary with the sequence of all $A_{1i_1} A_{2i_2} \dots A_{ki_k}$ as the natural basis. When $C_{m0}, C_{m1}, \dots, C_{mr_m}$ for $m = 1, 2, \dots, k$ are arbitrary canonical bases for the original algebras, then we find that $C_{10} C_{20} \dots C_{k0}$ will have weight 1 in E^* , and all other $C_{1i_1} C_{2i_2} \dots C_{ki_k}$ have weight 0. Thus any sequence of all $C_{1i_1} C_{2i_2} \dots C_{ki_k}$ with $C_{10} C_{20} \dots C_{k0}$ as the first member will constitute a canonical basis in E^* .

3. RECOMBINATION ALGEBRAS

We set $S = \{1, 2, \dots, k\}$. Suppose that U' and U'' are complementary subsets of S . Then we let

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

stand for the (non-ordered) partition of S given by U' and U'' . The collection of all such partitions will be designated as $W(S)$. This notation is identical with that introduced in Ref. 14. For given elementary algebras E_1, \dots, E_k we will now define the *recombination algebra* $X(U)$ with respect to U formed from E_1, \dots, E_k . This is to be an algebra over V_k with multiplication given by

$$\left(\prod_{m \in U'} A_{mi_m}\right) \left(\prod_{m \in U''} A_{mj_m}\right) = \left[\left(\prod_{m \in U'} A_{mi_m}\right) \left(\prod_{m \in U''} A_{mj_m}\right) + \left(\prod_{m \in U''} A_{mi_m}\right) \left(\prod_{m \in U'} A_{mj_m}\right)\right]/2, \tag{1}$$

where the A_{mi} are elements in the natural bases as before. We adopt the convention that products without specifications should be taken over all $m \in S$. If $U' = S$ and $U'' = \phi$, then $X(U) = E^*$.

Consider in particular $X(U)$ for $k = 2$ and $U = (1, 2)$. Let B and B' be elements in E_1 with weight 1, and C and C' elements in E_2 also having weight 1. Expressing these elements in terms of the natural bases in E_1 and E_2 , we find that

$$(BC)(B'C') = (BC' + B'C)/2. \tag{2}$$

Now let $D_{10}, D_{11}, \dots, D_{1r_1}$ and $D_{20}, D_{21}, \dots, D_{2r_2}$ be any canonical bases for E_1 and E_2 , respectively. Then all $D_{10} - D_{1i_1}$ and $D_{20} - D_{2i_2}$ have weight 1 in E_1 and E_2 , and applying Eq. (2) we construct the following multiplication table in $X(U)$:

$$\begin{aligned}
 (D_{10}D_{20})^2 &= D_{10}D_{20}, & (D_{10}D_{20})(D_{10}D_{2j}) &= D_{10}D_{2j}/2, \\
 (D_{10}D_{20})(D_{1i}D_{20}) &= (D_{1i}D_{20})/2, & (D_{1i}D_{20})(D_{10}D_{2j}) &= D_{1i}D_{2j}/2, \quad (3) \\
 i &= 1, 2, \dots, r_1, & j &= 1, 2, \dots, r_2,
 \end{aligned}$$

all other products $(D_{1i}D_{2j})(D_{1h}D_{2s})$ being equal to 0.

We return to the case with arbitrary k and U . If we denote the linked product of all E_m with $m \in U'$ by L_1 , and similarly the linked product of E_m with $m \in U''$ by L_2 , then L_1 and L_2 will be elementary. Furthermore, the recombination algebra $X(U)$ defined by Eq. (1) will be identical with the recombination algebra formed from L_1 and L_2 with respect to the partition $U = (1, 2)$. Assume as before that $C_{m0}, C_{m1}, \dots, C_{mr_m}$ is any canonical basis for E_m . Then L_1 has a canonical basis consisting of the elements $\prod_{m \in U'} C_{mi_m}$ obtained when all i_m vary between 0 and r_m . The first element in this basis must be $\prod_{m \in U'} C_{m0}$, but apart from this the ordering is arbitrary. We now want to construct the general multiplication table in $X(U)$ using the table (3). For this purpose we set $\prod_{m \in U'} C_{m0} = D_{10}$, and then each of the elements $\prod_{m \in U'} C_{mi_m}$ with at least one $i_m \neq 0$ is identified with one of D_{11}, D_{12}, \dots used in Eq. (3). (r_1 in the basis in Eq. (3) will correspond to $\prod_{m \in U'} (r_m + 1) - 1$.) L_2 may be treated in the same way, and so we find in $X(U)$

$$(\prod C_{m0})^2 = (D_{10}D_{20})^2 = \prod C_{m0}. \tag{4}$$

If there exists a $m \in U'$ with $i_m \neq 0$ we have (with a suitable $t \neq 0$)

$$\begin{aligned}
 (\prod C_{m0}) (\prod_{m \in U'} C_{mi_m} \prod_{m \in U''} C_{m0}) \\
 = (D_{10}D_{20})(D_{1t}D_{20}) = 1/2 (\prod_{m \in U'} C_{mi_m} \prod_{m \in U''} C_{m0}). \tag{5}
 \end{aligned}$$

This result is symmetric in U' and U'' . Moreover,

$$(\prod C_{m0}) (\prod_{m \in U'} C_{mi_m} \prod_{m \in U''} C_{mj_m}) = (D_{10}D_{20})(D_{1t}D_{2u}) = 0 \tag{6}$$

if $i_m \neq 0$ for at least one $m \in U'$ and $j_n \neq 0$ for one $n \in U''$. Multiplying two elements $\prod C_{mi_m}$ and $\prod C_{mj_m}$ with $i_m \neq 0$ for some m and $j_n \neq 0$ for some n , we see that the product is 0 if any of U' or U'' contains an m with $i_m \neq 0$ and at the same time an n with $j_n \neq 0$. Otherwise we have, with suitable t and u ,

$$(\prod C_{mi_m}) (\prod C_{mj_m}) = (D_{1t}D_{20})(D_{10}D_{2u}) = 1/2 (D_{1t}D_{2u}). \tag{7}$$

Here $D_{1t}D_{2u}$ will correspond to a $\prod C_{mv_m}$, where $v_m = i_m$ if $i_m \neq 0$, $v_m = j_m$ if $j_m \neq 0$, and $v_m = 0$ if $i_m = j_m = 0$.

4. THE BIOLOGICAL SITUATION

We consider haploid individuals with k linked autosomal loci without selection. The possible alleles in locus number m are $A_{m0}, A_{m1}, \dots, A_{mr_m}$. What happens regarding recombination during meiosis in a particular

zygote may be described by specifying a partition $U = (U', U'')$ of the set S . Genes in loci with indices in the same set U' or U'' will behave as an entity, while the blocks represented by U' and U'' are recombined. The degree of linkage between the k loci is given by a *linkage distribution* $\{\lambda(U)\}$ over $W(S)$. For this distribution we use the same notation as Reiersøl in Ref. 14.

The allele A_{mi} is assumed to mutate to A_{mj} with a frequency of v_{mij} per generation, and it will remain unchanged with a frequency v_{mii} ($i, j = 0, 1, \dots, r_m; i \neq j$). For each locus m we thus obtain a $(r_m + 1) \times (r_m + 1)$ mutation matrix $v_m = (v_{mij})_{i,j}$, which may also be regarded as the transition matrix for a discrete time Markov chain. We assume that it is possible to find a complete set linearly independent eigenvectors for every transition matrix. It is also assumed that genes in different loci mutate independently.

Consider the Markov chain for locus number m . Let the ordering of the states $0, 1, \dots, r_m$ in the chain be such that all states in the same recurrent class follow each other, and all recurrent states precede the transient ones. The recurrent classes may then be given as

$$\{0, 1, \dots, y_0\}, \{y_0 + 1, \dots, y_1\}, \dots, \{y_{s_m-1} + 1, \dots, y_{s_m}\}.$$

Thus the eigenvalue $\mu = 1$ has multiplicity $s_m + 1$. Let the stationary distribution for recurrent class number t be given by the quantities $p_j; j = y_{t-1} + 1, \dots, y_t$ (with an obvious modification for $t = 0$). We may then take as a left eigenvector for $\mu = 1$ a row vector consisting of zeros except for elements $j = y_{t-1} + 1, \dots, y_t$, where the values p_j are inserted. The remaining $r_m - s_m$ left eigenvectors, corresponding to eigenvalues different from 1, will be written as $(x_{t0}, x_{t1}, \dots, x_{tr_m}); t = s_m + 1, s_m + 2, \dots, r_m$.

5. THE COMPLETE ALGEBRA

Without mutations the inheritance for each separate locus would be described by an elementary algebra E_m with natural basis $A_{m0}, A_{m1}, \dots, A_{mr_m}$ (we identify the basis elements with the genotypes). The effect of mutation during one generation is obtained by applying the linear operator M defined by

$$M(A_{mi}) = \sum_{j=0}^{r_m} v_{mij} A_{mj}.$$

We now construct a particular canonical basis for each E_m . As the first element we take

$$C_{m0} = \sum_{j=0}^{y_0} p_j A_{mj}, \quad (8)$$

which has weight 1. For $i = 1, 2, \dots, s_m$ we set

$$C_{mi} = C_{m0} - \sum_{j=y_{i-1}+1}^{y_i} p_j A_{mj}, \tag{9}$$

with weight 0, and for $i = s_m + 1, s_m + 2, \dots, r_m$ we define

$$C_{mi} = \sum_{j=0}^{r_m} x_{ij} A_{mj}. \tag{10}$$

Since the right eigenvector $(1, 1, \dots, 1)'$ for $\mu = 1$ and each $(x_{i0}, x_{i1}, \dots, x_{ir_m})$ are orthogonal, these C_{mi} will also have weight 0 in E_m . Because of the existence of a complete set of eigenvectors, $C_{m0}, C_{m1}, \dots, C_{mr_m}$ will actually constitute a basis, and it must be canonical since E_m is elementary. Furthermore,

$$M(C_{m0}) = C_{m0}; \quad M(C_{mi}) = C_{mi}, \quad i = 1, 2, \dots, s_m,$$

and, if μ_{mi} is the eigenvalue corresponding to $(x_{i0}, \dots, x_{ir_m})$, then

$$M(C_{mi}) = \mu_{mi} C_{mi}, \quad i = s_m + 1, \dots, r_m. \tag{11}$$

The eigenvalues $\mu_{m0}, \mu_{m1}, \dots, \mu_{ms_m}$ are equal to 1, hence Eq. (11) may be used for all $i = 0, 1, \dots, r_m$.

The simultaneous inheritance for all k loci without mutation may be described by an algebra X over V_k given by

$$\begin{aligned} & (\prod A_{mi_m})(\prod A_{mj_m}) \\ &= 1/2 \sum_{U \in W(S)} \lambda(U) (\prod_{m \in U'} A_{mi_m} \prod_{m \in U''} A_{mj_m} + \prod_{m \in U''} A_{mi_m} \prod_{m \in U'} A_{mj_m}). \end{aligned}$$

It is seen that X may be expressed as a *mixture* (see Ref. 13) of the recombination algebras $X(U)$

$$X = \sum_{U \in W(S)} \lambda(U) X(U). \tag{12}$$

Introducing the canonical bases constructed above for E_1, E_2, \dots, E_k and using Eqs. (4)–(7), we can now find the multiplication table for X in terms of the basis of all $C_{1i_1} C_{2i_2} \dots C_{ki_k}$. We then obtain the multiplication rules in the complete algebra X_M for the case with mutations by operating with M on the right hand side of the equations in this table and using

$$M(C_{1i_1} C_{2i_2} \dots C_{ki_k}) = M(C_{1i_1}) M(C_{2i_2}) \dots M(C_{ki_k}),$$

which is valid because of the independence for mutations in different loci.

For any k -tuple $i = (i_1, i_2, \dots, i_k)$ of non-negative integers we will define a subset $Q(i) = Q(i_1, \dots, i_k)$ in $W(S)$. This subset is to consist of those partitions $U = (U', U'')$ of S where all m with nonzero i_m are elements in the same set U' or U'' . We now find in X_M

$$(\prod C_{m0})^2 = \prod C_{m0}.$$

With at least one $i_m \neq 0$ we have

$$(\prod C_{m0})(\prod C_{mi_m}) = (1/2 \sum_{U \in Q(i)} \lambda(U) \cdot \prod \mu_{mi_m}) \prod C_{mi_m}. \tag{13}$$

Assume that $i = (i_1, \dots, i_k)$ and $j = (j_1, \dots, j_k)$ satisfy the condition that if $i_m \neq 0$ and $j_n \neq 0$ then $m \neq n$, and that $i_m \neq 0$ and $j_n \neq 0$ for at least one m and n . Then

$$(\prod C_{mi_m})(\prod C_{mj_m}) = (1/2 \sum_{U \in R(i,j)} \lambda(U) \cdot \prod \mu_{mt_m}) \prod C_{mt_m}. \tag{14}$$

Here t_1, \dots, t_k are given by $t_m = i_m$ if $i_m \neq 0$, $t_m = j_m$ if $j_m \neq 0$, $t_m = 0$ otherwise, and $R(i, j)$ is the collection of the partitions U where m with $i_m \neq 0$ are contained in one of the sets U' and U'' and n with $j_n \neq 0$ are contained in the other. If there exists an m with both $i_m \neq 0$ and $j_m \neq 0$, then

$$(\prod C_{mi_m})(\prod C_{mj_m}) = 0. \tag{15}$$

Thus we have established:

THEOREM 1

X_M is a genetic algebra. The train roots are 1 and all values

$$1/2 \sum_{U \in Q(i)} \lambda(U) \cdot \prod \mu_{mi_m} \tag{16}$$

obtained when $i = (i_1, \dots, i_k)$ varies under the condition that at least one i_m is nonzero. A canonical basis can consist of all $C_{1i_1} C_{2i_2} \dots C_{ki_k}$ (where the C_{mi} are defined by Eqs. (8)–(10)); the ordering in this basis may for instance be lexicographic, that is $C_{1i_1} \dots C_{ki_k}$ precedes $C_{1j_1} \dots C_{kj_k}$ if $i_1 = j_1, \dots, i_{u-1} = j_{u-1}, i_u < j_u$ for some u .

We also have

THEOREM 2

X_M is a special train algebra.

Proof. The subspace N of all elements in X_M of weight 0 is spanned by the elements

$$C_{1i_1} C_{2i_2} \dots C_{ki_k} \tag{17}$$

with at least one $i_m \neq 0$. Let T_d be the collection of all elements (17) equal to a product of d other elements (17) where the shape of the product is primary (that is, where the factors are absorbed one at a time, see Ref. 3, Sec. 2). Suppose that P is an arbitrary primary product with d factors in N . Expressing these factors as linear combinations of elements (17), we see that the total product P must be a linear combination of elements in T_d , since it follows from Eqs. (14) and (15) that every product

$$(C_{1i_1} \dots C_{ki_k})(C_{1j_1} \dots C_{kj_k})$$

in N will either be 0 or may be expressed by one single element (17). The power N^d of N is the set of all linear combinations of such products P , hence N^d will be the space spanned by T_d . Then, according to Eq. (13), every product $(C_{10} C_{20} \dots C_{k0})F$ with $F \in N^d$ will lie in N^d , and N^d will

be an ideal in X_M . This is sufficient for concluding that X_M is a special train algebra, since it is already established that X_M is genetic. ■

The actual extent of T_d and N^d may vary with the choice of values v_{mij} and $\lambda(U)$. If $\lambda(U) > 0$ for all $U \in \mathcal{W}(S)$, and no eigenvalues μ_{mi} are 0, then T_d will consist of those $C_{1i_1}C_{2i_2} \cdots C_{ki_k}$ with at least d nonzero i_m . This may be shown by induction with respect to d . On the other hand, consider as an example the case with $k = 4$ without mutation where $\lambda(ij, tu) > 0$, all $\lambda(ijt, u) = 0$ and $\lambda(1234) > 0$. Then T_2 will consist of all $C_{1i_1}C_{2i_2}C_{3i_3}C_{4i_4}$ with at least two nonzero i_m , T_3 of all such elements with three or four nonzero i_m , while T_4 is empty and $N^4 = \{0\}$.

6. CONNECTIONS WITH PREVIOUS RESULTS

The case without mutations corresponds to $v_{mii} = 1$, $v_{mij} = 0$ for $i \neq j$. Then the definitions (8)–(10) reduce to $C_{m0} = A_{m0}$, $C_{mi} = A_{m0} - A_{mi}$, and our theorems may be compared with the results in Ref. 13, Sec. 5. It is there stated that a proof has been given for the proposition that X is a special train algebra. But the definition quoted of this concept in Ref. 13, Sec. 1 is identical with Gonshor's later definition [9] of a genetic algebra rather than Etherington's definition of a special train algebra. Thus the conclusion in Ref. 13 gives the same as our Theorem 1, but Theorem 2 is new even for the particular case with no mutations. (However, the situation with only 3 loci was treated in Ref. 4.) When all $\mu_{mi} = 1$ the train roots (16) are seen to coincide with the values given in Eq. (24) in Ref. 13.

The treatment in Ref. 13 is based on a different mixture than Eq. (12), and the algebraic manipulations seem more complicated. One of the reasons for this may be that the scalars $\alpha(I)$ appearing in the mixture in Ref. 13 do not correspond to any obvious parameters connected with the linkage distribution characterizing the biological situation, although this situation is defined in Ref. 13 in a manner similar to ours, with a quantity $p(I)$ corresponding to our $\lambda(U)$. Furthermore, the algebras $A(I)$ in Ref. 13 are introduced by consideration of blocks of loci with successive indices, even though linearity of chromosomes is not used in the deductions, and the model could be applied even in theoretical situations where the linkage distribution would contradict such a hypothesis.

The consequences of Theorems 1 and 2 for various sequences and for the diploid case will be treated elsewhere.

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