

SEQUENCES OF PRODUCTS ARISING IN SOME MENDELIAN SEMIALGEBRAS

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Abstract

With the aid of matrix algebra, the author has examined the analytical behavior of several sequences of products arising in some special Mendelian semialgebras. These sequences can be directly applied to the study of change in the distribution of genetic types produced in the successive nonoverlapping generations of such genetic systems as are subject to linkage of loci, selfing, self-sterility, sex-linkage, or mixed selfing and random mating.

Introduction

By a *linear algebra* \mathcal{A} over a field \mathcal{F} we shall mean a finite-dimensional vector space over \mathcal{F} on which a multiplication is defined such that with respect to this multiplication \mathcal{A} is a commutative ring (not necessarily associative) and such that the vector space structure is interlocked with the ring structure by means of the equation: $\alpha(xy) = (\alpha x)y = x(\alpha y)$ for all $x, y \in \mathcal{A}$ and all $\alpha \in \mathcal{F}$. Such concept was first introduced in the study of Mendelian genetics by Etherington [1939, 1940, 1941a, b, c]. His main idea is to construct a linear algebra \mathcal{A} over the field \mathcal{R} of real numbers by identifying a basis, called the *natural basis*, of \mathcal{A} with a set $\{g_1, \dots, g_n\}$ of distinct genetic types which exist in a certain genetic system so that the multiplication table of \mathcal{A} is given by

$$(1) \quad g_i g_j (= g_j g_i) = \sum_{k=1}^n r_{ijk} g_k \quad (i, j=1, \dots, n),$$

where r_{ijk} is the probability of obtaining genetic type g_k in a cross between genetic types g_i and g_j . In some special cases, it is more natural to require that, for given i and j , the r_{ijk} 's be determined only up to a proportionality constant. Further, it may also happen that $g_i g_j = g_j g_i = 0$ for some i and j because a crossing between genetic types g_i and g_j is impossible or otherwise gives no offspring. For the sake of convenience, the class of linear algebras described above will be generically referred to as *Mendelian algebras*. Strictly speaking, these algebras should be called *Mendelian algebras over \mathcal{R}* , for in

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some algebraic situations it may call for the extension of \mathcal{R} to \mathbb{C} , the field of complex numbers. On the other hand, if the coefficient field is restricted to the set \mathcal{R}° of nonnegative real numbers, they will then be called *Mendelian semialgebras* over \mathcal{R}° , in the sense that \mathcal{R}° is in fact a *semifield* (cf. Rédei [1967], p. 36). Similarly, a vector space with its coefficient field restricted to \mathcal{R}° will be called a *semivector space* over \mathcal{R}° .

One major concern of Mendelian genetics is to study the distribution of genetic types in the successive generations of a given genetic system. In this connection, a distribution of genetic types in the initial generation may be represented by a *convex combination* (coefficients being in \mathcal{R}° and summing up to unity) of those elements belonging to the natural basis of the underlying Mendelian algebra or semialgebra. Such a convex combination will be referred to as a *population element*. The successive generations (assumed to be discrete and nonoverlapping in the sequel) are then representable by an appropriate sequence of products (inclusive of powers) involving the initial population element. By examining the analytical behavior of such a sequence, we may thus be able to perceive the picture of the underlying genetic dynamics. In this aspect, the following sequences are especially important: Let x and y be two arbitrary elements of a Mendelian algebra or semialgebra. The t -th *primary product* of x by y , denoted by $x_t^{(y)}$, is defined recursively as

$$(2) \quad x_1^{(y)} = x; \quad x_t^{(y)} = x_{t-1}^{(y)} y \quad (t=2, 3, \dots).$$

If in particular $y=x$, then we may write $x^t = x_t^{(x)}$ and call it the t -th *principal power* of x . Further, the t -th *plenary power* of x , denoted by $x^{[t]}$, is defined recursively as

$$(3) \quad x^{[1]} = x; \quad x^{[t]} = x^{[t-1]} x^{[t-1]} \quad (t=2, 3, \dots).$$

In the sequel, we shall be concerned with sequences of the above nomenclature, together with a so-called sequence of *M-products* to be introduced later (see §6), all arising from the various Mendelian semialgebras which represent such genetic systems as are subject to linkage of loci, selfing, self-sterility, sex-linkage, or mixed selfing and random mating.

Ever since the publication of Etherington's pioneer works, many authors have paid attention to a particular class of Mendelian algebras called *genetic algebras*. A brief review of the theory of genetic algebras is therefore in order. Let \mathcal{A} be a Mendelian algebra with its coefficient field \mathcal{R} having been extended to the field \mathbb{C} of complex numbers. We say that \mathcal{A} is a *baric* Mendelian algebra if it admits a nontrivial homomorphism $x \rightarrow \omega(x)$ onto \mathbb{C} . Here ω is called a *weight function* of \mathcal{A} and $\omega(x)$, the *weight* of x (cf. Etherington [1939]). Let \mathcal{N} be the kernel of the weight function ω so that \mathcal{N} is necessarily an *ideal*

of \mathcal{A} . Schafer [1949] has pointed out that the Mendelian algebra \mathcal{A} is baric iff it contains an ideal \mathcal{N} such that the *difference algebra* $\mathcal{A}-\mathcal{N}$ is isomorphic with \mathbb{C} . For a fixed element $a \in \mathcal{A}$, let E_a denote the linear transformation defined on \mathcal{A} by $x \rightarrow xa$. Further, let $\mathcal{J}(\mathcal{A})$ denote the *transformation algebra* of \mathcal{A} so that an arbitrary element $T \in \mathcal{J}(\mathcal{A})$ takes on the form

$$T = \alpha I + f(E_{a_1}, E_{a_2}, \dots),$$

where $\alpha \in \mathbb{C}$, I is the identity element of $\mathcal{J}(\mathcal{A})$, and $f(\cdot)$ is a polynomial in E_{a_1}, E_{a_2}, \dots with coefficients in \mathbb{C} . Schafer [1949] has defined a *genetic algebra* to be a baric Mendelian algebra for which the coefficients of the characteristic polynomial $|\lambda I - T|$ depends on the elements a_1, a_2, \dots only through their weights $\omega(a_1), \omega(a_2), \dots$. While Schafer's definition is given in a basis-free manner, another definition has been supplied by Gonshor [1971] in a basis form. According to Gonshor, (1971) a Mendelian algebra \mathcal{A} with extended coefficient field \mathbb{C} is called a *genetic algebra* if \mathcal{A} has a basis $\{c_0, c_1, \dots, c_{n-1}\}$ such that the multiplication table of \mathcal{A} is given by

$$c_i c_j = \sum_{k=0}^{n-1} \lambda_{ijk} c_k \quad (i, j = 0, 1, \dots, n-1),$$

where $\lambda_{000} = 1$, $\lambda_{0jk} = 0$ for $k < j$ and $\lambda_{ijk} = 0$ for $i, j > 0$ and $k \leq \max(i, j)$. The basis $\{c_0, c_1, \dots, c_{n-1}\}$ is said to be *canonical* and the values λ_{0jj} ($j = 0, 1, \dots, n-1$) are called the *train roots* of the genetic algebra. The genetic algebra as characterized by Gonshor is baric with $\omega(c_0) = 1$, $\omega(c_k) = 0$ ($k = 1, 2, \dots, n-1$), and has been proven to be equivalent to that as characterized by Schafer (cf. Gonshor [1971], Theorem 2.1). Gonshor [1960] has also proven that a genetic algebra has exactly one non-zero idempotent if no train root thereof equals $\frac{1}{2}$, and that the sequence of plenary powers of an element of weight 1 in a genetic algebra whose train roots other than $\lambda_{000} = 1$ all have absolute value less than $\frac{1}{2}$ converges (coordinatewise) to an idempotent. We note that such an idempotent is important in genetical applications since it represents a population in equilibrium under random mating.

While the theory of genetic algebras has delivered elegant proofs of some classical stability theorems in Mendelian genetics (see, e.g., Etherinton [1939, 1940, 1941a], Gonshor [1960, 1965, 1971], and Holgate [1967]), it still leaves much to be done in the area where the conditions for baricity, geneticity and/or idempotency are not satisfied or difficult to check up. In this paper we shall give proofs of several stability theorems for the various sequences of products we mentioned earlier. Since the method of approach will be essentially that of matrix algebra, it requires no more than the setup of a Mendelian semialgebra, and no checkup on the above-mentioned conditions will be necessary except for making supplementary remarks.

For the discussion to be presented below, it is necessary to introduce a few more conventions in notation: We shall use $\mathcal{R}^\circ\{g_1, \dots, g_n\}$ to denote a Mendelian semialgebra spanned by the basis $\{g_1, \dots, g_n\}$ over \mathcal{R}° . The similar notation will also be used for Mendelian algebras (including genetic algebras). For any fixed element $a \in \mathcal{R}^\circ\{g_1, \dots, g_n\}$, the linear transformation $E_a: x \rightarrow xa$ will be referred to as the *multiplication operator* associated with a , and the matrix representing this operator with respect to the given basis $\{g_1, \dots, g_n\}$ will also be denoted by E_a . Thus, insofar as the basis remains fixed, we shall make no essential distinction between the product xa and xE_a , the image of x under the operator E_a .

A Sequence of Plenary Powers From a Linkage Semialgebra

Consider two linked biallelic loci in a diploid population with recombination fraction $\rho (0 \leq \rho \leq \frac{1}{2})$. Suppose that one of the loci has alleles $a_1^{(1)}, a_2^{(1)}$ and the other has $a_1^{(2)}, a_2^{(2)}$. Then there are four possible gametic types, namely,

$$a_{11} = a_1^{(1)}a_1^{(2)}, \quad a_{12} = a_1^{(1)}a_2^{(2)}, \quad a_{21} = a_2^{(1)}a_1^{(2)}, \quad a_{22} = a_2^{(1)}a_2^{(2)}.$$

If the individuals mate one another normally, the system may be represented by the Mendelian semialgebra $\mathcal{R}^\circ\{a_{11}, a_{12}, a_{21}, a_{22}\}$ with multiplication table

	a_{11}	a_{12}	a_{21}	a_{22}
a_{11}	a_{11}	$\frac{1}{2}(a_{11} + a_{12})$	$\frac{1}{2}(a_{11} + a_{21})$	$\frac{1}{2}(1 - \rho)(a_{11} + a_{22}) + \frac{1}{2}\rho(a_{12} + a_{21})$
a_{12}		a_{12}	$\frac{1}{2}(1 - \rho)(a_{12} + a_{21}) + \frac{1}{2}\rho(a_{11} + a_{22})$	$\frac{1}{2}(a_{12} + a_{22})$
a_{21}			a_{21}	$\frac{1}{2}(a_{21} + a_{22})$
a_{22}		Symmetric		a_{22}

We shall refer to $\mathcal{R}^\circ\{a_{11}, a_{12}, a_{21}, a_{22}\}$ as a *linkage semialgebra*. In passing, it may be noted that $\mathcal{G}\{a_{11}, a_{12}, a_{21}, a_{22}\}$ is in fact a genetic algebra.

THEOREM 1. If $x = \xi_{11}a_{11} + \xi_{21}a_{12} + \xi_{31}a_{21} + \xi_{41}a_{22}$ is a population element of the linkage semialgebra $\mathcal{R}^\circ\{a_{11}, a_{12}, a_{21}, a_{22}\}$ with recombination fraction $\rho (0 \leq \rho \leq \frac{1}{2})$, then the $(t+1)st$ plenary power of x is given by

$$(4) \quad x^{t+1} = \{\xi_{11} - (1 - (1 - \rho)^t)\delta_1\}a_{11} + \{\xi_{21} + (1 - (1 - \rho)^t)\delta_1\}a_{12} \\ + \{\xi_{31} + (1 - (1 - \rho)^t)\delta_1\}a_{21} + \{\xi_{41} - (1 - (1 - \rho)^t)\delta_1\}a_{22},$$

where $\delta_1 = \xi_{11}\xi_{41} - \xi_{21}\xi_{31}$, and

$$(5) \quad x^{t \infty} = \lim_{t \rightarrow \infty} x^{t+1} = (\xi_{11} - \delta_1)a_{11} + (\xi_{21} + \delta_1)a_{12} + (\xi_{31} + \delta_1)a_{21} + (\xi_{41} - \delta_1)a_{22}.$$

Proof. Let

$$(6) \quad x^{t+1} = \xi_{1, t+1}a_{11} + \xi_{2, t+1}a_{12} + \xi_{3, t+1}a_{21} + \xi_{4, t+1}a_{22},$$

and let $E_t = E_{x^t}$, the multiplication operator associated with the t -th plenary power x^t . Then E_t can be represented by the matrix

$$E_t = \begin{bmatrix} \xi_{1t} + \frac{1}{2}\xi_{2t} + \frac{1}{2}\xi_{3t} + \frac{1}{2}(1-\rho)\xi_{4t} & \frac{1}{2}\xi_{2t} + \frac{1}{2}\rho\xi_{4t} \\ \frac{1}{2}\xi_{1t} + \frac{1}{2}\rho\xi_{3t} & \frac{1}{2}\xi_{1t} + \xi_{2t} + \frac{1}{2}(1-\rho)\xi_{3t} + \frac{1}{2}\xi_{4t} \\ \frac{1}{2}\xi_{1t} + \frac{1}{2}\rho\xi_{2t} & \frac{1}{2}(1-\rho)\xi_{2t} \\ \frac{1}{2}(1-\rho)\xi_{1t} & \frac{1}{2}\rho\xi_{1t} + \frac{1}{2}\xi_{2t} \\ \frac{1}{2}\xi_{3t} + \frac{1}{2}\rho\xi_{4t} & \frac{1}{2}(1-\rho)\xi_{4t} \\ \frac{1}{2}(1-\rho)\xi_{3t} & \frac{1}{2}\rho\xi_{3t} + \frac{1}{2}\xi_{4t} \\ \frac{1}{2}\xi_{1t} + \frac{1}{2}(1-\rho)\xi_{2t} + \xi_{3t} + \frac{1}{2}\xi_{4t} & \frac{1}{2}\rho\xi_{2t} + \frac{1}{2}\xi_{4t} \\ \frac{1}{2}\rho\xi_{1t} + \frac{1}{2}\xi_{3t} & \frac{1}{2}(1-\rho)\xi_{1t} + \frac{1}{2}\xi_{2t} + \frac{1}{2}\xi_{3t} + \xi_{4t} \end{bmatrix}$$

Since then $x^{t+1} = x^t E_t$, direct calculation of $x^{t+1} E_t$ yields

$$(7) \quad x^{t+1} = (\xi_{1t} - \rho\delta_t)a_{11} + (\xi_{2t} + \rho\delta_t)a_{12} + (\xi_{3t} + \rho\delta_t)a_{21} + (\xi_{4t} - \rho\delta_t)a_{22},$$

where $\delta_t = \xi_{1t}\xi_{4t} - \xi_{2t}\xi_{3t}$ ($t=1, 2, \dots$). Comparing (7) with (6) and iterating, we obtain

$$(8) \quad \xi_{i, t+1} = \begin{cases} \xi_{i1} - (1 - (1-\rho)^t)\delta_1 & \text{for } i=1, 4, \\ \xi_{i1} + (1 - (1-\rho)^t)\delta_1 & \text{for } i=2, 3, \end{cases}$$

thus establishing equation (4).

The proof of equation (5) is trivial. Q. E. D.

We note that the limiting element x^{∞} in equation (5) is in fact an idempotent population element in $\mathcal{R}^o\{a_{11}, a_{12}, a_{21}, a_{22}\}$. From the genetical point of view, this implies that, in the absence of selection and other disturbing factors, the distribution of gametic types identifiable in terms of two loci in a random-mating population will eventually reach a state of equilibrium.

The following is an immediate consequence of Theorem 1.

COROLLARY. If in Theorem 1 $\rho = \frac{1}{2}$, then

$$(4') \quad x^{t+1} = \{\xi_{11} - (1 - (\frac{1}{2})^t)\delta_1\}a_{11} + \{\xi_{21} + (1 - (\frac{1}{2})^t)\delta_1\}a_{12} \\ + \{\xi_{31} + (1 - (\frac{1}{2})^t)\delta_1\}a_{21} + \{\xi_{41} - (1 - (\frac{1}{2})^t)\delta_1\}a_{22}, \quad \text{and}$$

$$(5') \quad x^{\infty} = (\xi_{11} - \delta_1)a_{11} + (\xi_{21} + \delta_1)a_{12} + (\xi_{31} + \delta_1)a_{21} + (\xi_{41} - \delta_1)a_{22}.$$

According to this corollary, the system will tend to a state of equilibrium the most rapidly when $\rho = \frac{1}{2}$, i. e., when the two loci are unlinked or genetically independent.

A Sequence of Primary Products From a Selfing Semialgebra

Consider a biallelic locus of a diploid population which breeds by means of selfing (as is often the case in flowering plants and in some lower animals). Let a_1, a_2 denote the alleles occurring at this locus so that there are three possible genotypes, namely

$$(9) \quad b_1 = a_1a_1, \quad b_2 = a_1a_2 (= a_2a_1), \quad b_3 = a_2a_2.$$

This system can be represented by the Mendelian semialgebra $\mathcal{A} = \mathcal{R}^\circ\{b_1, b_2, b_3\}$ with multiplication table

$$(10) \quad \begin{aligned} b_1b_1 &= b_1, & b_2b_2 &= \frac{1}{4}b_1 + \frac{1}{2}b_2 + \frac{1}{4}b_3, & b_3b_3 &= b_3 \\ b_ib_j &= b_jb_i = 0 & (i, j &= 1, 2, 3; i \neq j). \end{aligned}$$

This semialgebra will be referred to as a *selfing semialgebra*. We note that \mathcal{A} is baric, in the sense that it admits a weight function ω onto \mathcal{R}° defined by

$$\omega(x) = \frac{1}{2}\xi_2 \text{ for all } x = \xi_1b_1 + \xi_2b_2 + \xi_3b_3 \text{ in } \mathcal{A}.$$

The following theorem reflects the genetic dynamics of the selfing population under consideration.

THEOREM 2. Let $x = \xi_1b_1 + \xi_2b_2 + \xi_3b_3$ be a population element of the selfing semialgebra $\mathcal{A} = \mathcal{R}^\circ\{b_1, b_2, b_3\}$ and let $y = b_1 + b_2 + b_3$. Then the $(t+1)$ st primary product of x by y is given by

$$(11) \quad x_i^{(y)} = \{\xi_1 + \frac{1}{2}(1 - (\frac{1}{2})^t)\xi_2\}b_1 + (\frac{1}{2})^t\xi_2b_2 + \{\xi_3 + \frac{1}{2}(1 - (\frac{1}{2})^t)\xi_2\}b_3, \text{ and}$$

$$(12) \quad x_i^{(y)} = \lim_{t \rightarrow \infty} x_i^{(y)} = (\xi_1 + \frac{1}{2}\xi_2)b_1 + (\xi_3 + \frac{1}{2}\xi_2)b_3.$$

To prove this theorem, we need the following lemma:

LEMMA 1. Let $x_t (t=1, 2, \dots)$ be an n -dimensional row vector with real entries, and consider the recursive equation

$$x_{t+1} = x_t(A/\alpha),$$

where A is an $n \times n$ real matrix of full rank and α is an eigenvalue of A with multiplicity r . If α is real, positive, and strictly larger in absolute value than all the remaining eigenvalues of A , then

$$(13) \quad x_{t+1} = x_1S\{J(A)/\alpha\}^tS^{-1}, \text{ and}$$

$$(14) \quad \lim_{t \rightarrow \infty} x_t = x_1S \begin{bmatrix} I_r & 0 \\ 0 & 0 \end{bmatrix} S^{-1},$$

where $J(A)$ is the Jordan canonical form of A , S is an $n \times n$ nonsingular matrix such that $S^{-1}AS = J(A)$, and I_r is the identity matrix of order r .

The proof of this lemma is routine and can be derived, *e.g.*, from Exercise 7, p. 16 of Verga [1962].

Proof of Theorem 2. Since $x_{i+1}^{(y)} = x_i^{(y)}E_y$, where E_y is the multiplication operator associated with the element y , we may obtain by iteration

$$x_{i+1}^{(y)} = xE_y^t.$$

On the other hand, the operator E_y can be represented by the matrix

$$(15) \quad E_y = \begin{bmatrix} 1 & 0 & 0 \\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ 0 & 0 & 1 \end{bmatrix},$$

which has eigenvalues 1, $\frac{1}{2}$, 1. By means of the nonsingular matrix

$$S = \begin{bmatrix} 1 & 0 & 0 \\ \frac{1}{2} & 1 & \frac{1}{2} \\ 0 & 0 & 1 \end{bmatrix},$$

we can then express E_y in the form

$$E_y = SJ(E_y)S^{-1},$$

where $J(E_y) = \text{diag} (1, \frac{1}{2}, 1)$. Thus equations (11) and (12) follow immediately from Lemma 1. Q.E.D.

We note that the limiting element $x^{(g)}$ in equation (12) turns out to be a population element with zero weight. It is not an idempotent, however.

A Sequence of Normalized Plenary Powers From a Self-sterile Semialgebra

Self-sterility also occurs very often in flowering plants. Genetic analyses have revealed that this phenomenon may be regulated by different hereditary mechanisms. The most frequent and most refined method is based on multiple alleles that are expressed in the pollen grains as well as pistil tissues (East and Mangelsdorf [1925]). A pollen grain functions only on a pistil neither of whose two alleles at the self-sterile locus is the same as that of the pollen grain, thus preventing selfing. Consider the case where there are m alleles s_1, \dots, s_m at the self-sterile locus. The system can then be represented by the Mendelian semialgebra $\mathcal{R}^\circ\{s_1, \dots, s_m\}$ with multiplication table

$$(16) \quad \begin{aligned} s_i s_j (= s_j s_i) &= \frac{1}{2} (s_i + s_j) \quad (i, j=1, \dots, m; i \neq j) \\ s_i s_i &= 0 \quad (i=1, \dots, m). \end{aligned}$$

We shall refer to $\mathcal{R}^\circ\{s_1, \dots, s_m\}$ as a *self-sterile semialgebra*. It may be noted that the Mendelian algebra $\mathcal{G}\{s_1, \dots, s_m\}$ can not be genetic. For, as can be seen from the multiplication table (16), all elements in the natural basis of $\mathcal{G}\{s_1, \dots, s_m\}$ are *nilpotent* (an element x of a Mendelian algebra is said to be *nilpotent* if there exists an interger $r > 1$ such that $x^r = 0$ and $x^{r-1} \neq 0$, where x^r is the r -th principal power of x), which makes it impossible for $\mathcal{G}\{s_1, \dots, s_m\}$ to admit a weight function.

We observed that a plenary power of a population element in the self-sterile semialgebra $\mathcal{R}^\circ\{s_1, \dots, s_m\}$ is not necessarily a population element. To rectify this, we shall introduce the following definition: Let x be a population element in a Mendelian semialgebra $\mathcal{R}^\circ\{g_1, \dots, g_n\}$. The t -th *normalized plenary power* of x , denoted by X^{t1} , is then defined recursively as

$$(17) \quad X^{11} = x; \quad X^{t1} = X^{t-11} X^{t-11} / \nu_{t-1} \quad (t=2, 3, \dots),$$

where ν_{t-1} is a normalizing factor obtained by adding up all the coefficients appearing in a linear combination of g_1, \dots, g_n which uniquely represents the product $X^{t-1} X^{t-1}$. Such a normalized plenary power exists as long as the corresponding normalizing factor does not vanish. We are now in a position to present the next theorem which will help shed some light on the genetic dynamics of a random mating population subject to self-sterility.

THEOREM 3. If $x = \sum_{i=1}^m \xi_i s_i$, where $m \geq 2$ and $\xi_i > 0$ for at least two i 's, is population element of the self-sterile semialgebra $\mathcal{R}^0\{s_1, \dots, s_m\}$, then the sequency (X^{t+1}) of normalized plenary powers of x converges (coordinatewise) to

$$(18) \quad x^{t \rightarrow \infty} = \sum_{i=1}^m \sigma_i(x) s_i / \#(x),$$

where $\sigma_i(x) = 1$ or 0 according as ξ_i is > 0 or $= 0$, and $\#(x)$ is the number of nonzero ξ_i 's in x .

Proof. Let $\#(x) = r$ ($2 \leq r \leq m$) and, without loss of generality, let $\xi_i > 0$ for $i = 1, \dots, r$. Further, let $X^{t+1} = \sum_{i=1}^r \xi_i s_i$ so that the associated multiplication operator can be represented by the $r \times r$ matrix

$$E_t = \frac{1}{\nu_t} \begin{bmatrix} 1 - \xi_{1t} & \xi_{2t} & \dots & \xi_{rt} \\ \xi_{1t} & 1 - \xi_{2t} & \dots & \xi_{rt} \\ \cdot & \cdot & \ddots & \cdot \\ \xi_{1t} & \xi_{2t} & \dots & 1 - \xi_{rt} \end{bmatrix}.$$

It then follows that

$$(19) \quad X^{t+1} = X^{t+1} E_t / \nu_t = \sum_{i=1}^r \xi_{it} (1 - \xi_{it}) / \nu_t,$$

where $\nu_t = 1 - \sum_{i=1}^r \xi_{it}^2$ is the normalizing factor. Now, let us write X^{t+1} in its vector form, namely

$$X^{t+1} = (\xi_{1t}, \dots, \xi_{rt}),$$

and let

$$D(X^{t+1}) = \text{diag}(\xi_{1t}, \dots, \xi_{rt}),$$

$$A = \begin{bmatrix} 0 & 1 & \dots & 1 \\ 1 & 0 & \dots & 1 \\ \cdot & \cdot & \ddots & \cdot \\ 1 & 1 & \dots & 0 \end{bmatrix}.$$

We may then write equation (19) in the matrix form

$$(20) \quad X^{t+1} = X^{t+1} A D(X^{t+1}) / X^{t+1} A X^{t+1},$$

where X^{t+1} denotes the transpose of X^{t+1} . By definition (see, e. g., Kingman [1961], p. 574), $X^{t \rightarrow \infty}$ is an equilibrium point of the system (20) if

$$(21) \quad X^{t \rightarrow \infty} = \{X^{t \rightarrow \infty} A D(X^{t \rightarrow \infty})\} / X^{t \rightarrow \infty} A X^{t \rightarrow \infty}.$$

Since the diagonal matrix $D(X^{t\infty})$ is obviously nonsingular, equation (21) reduces to

$$(22) \quad l = (X^{t\infty}A)/X^{t\infty}AX^{t\infty}l,$$

where $l = (1, 1, 1)$. Solving equation (22) for $X^{t\infty}$, we obtain

$$X^{t\infty} = (lA^{-1})/lA^{-1}l = (1/r)l,$$

where

$$A^{-1} = \frac{1}{r-1} \begin{bmatrix} -(r-2) & 1 & \cdots & 1 \\ 1 & -(r-2) & \cdots & 1 \\ \cdot & \cdot & \ddots & \cdot \\ 1 & 1 & \cdots & -(r-2) \end{bmatrix}.$$

Thus the proof is complete. Q. E. D.

A Sequence of Normalized Plenary Powers From a Sex-Linked Semialgebra

Consider a sex-linked locus in an amphimictic diploid population with the males being heterogametic. There are three distinct genotypes for the females, namely a_1a_1 , a_1a_2 , a_2a_2 , and two for the males, namely a_1 , a_2 . Let

$$b_1 = a_1a_1, \quad b_2 = a_1a_2, \quad b_3 = a_2a_2, \quad b_4 = a_1, \quad b_5 = a_2.$$

Then the system may be represented by the Mendelian semialgebra $\mathcal{R}^\circ\{b_1, \dots, b_5\}$ with multiplication table

$$(23) \quad \begin{aligned} b_1b_4 (=b_4b_1) &= \frac{1}{2}(b_1+b_4), & b_1b_5 (=b_5b_1) &= \frac{1}{2}(b_2+b_4) \\ b_2b_4 (=b_4b_2) &= \frac{1}{4}(b_1+b_2+b_4+b_5), & b_2b_5 (=b_5b_2) &= \frac{1}{4}(b_2+b_3+b_4+b_5) \\ b_3b_4 (=b_4b_3) &= \frac{1}{2}(b_2+b_5), & b_3b_5 (=b_5b_3) &= \frac{1}{2}(b_3+b_5) \\ b_i b_i &= 0 & (i=1, \dots, 5). \end{aligned}$$

We shall refer to $\mathcal{R}^\circ\{b_1, \dots, b_5\}$ as a *sex-linked semialgebra*. As in the case of a self-sterile semialgebra, this semialgebra is no genetic either. The genetic dynamics of the successive generations in this system can also be described by a sequence of normalized plenary powers of a population element, as is shown in the following theorem:

THEOREM 4. If $x = \alpha_1 b_1 + \beta_1 b_2 + \gamma_1 b_3 + \xi_1 b_4 + \eta_1 b_5$ is a population element of the sex-linked semialgebra $\mathcal{R}^\circ\{b_1, \dots, b_5\}$ such that $0 < \xi_1 + \eta_1 < 1$, then the $(t+1)st$ normalized plenary power of x is given by

$$(24) \quad \begin{aligned} X^{t+1} &= (2/9) \{ \xi_1 + 2\xi_2 + (-\frac{1}{2})^{t-1}(\xi_2 - \xi_1) \} \{ \xi_1 + 2\xi_2 + (-\frac{1}{2})^{t-2}(\xi_2 - \xi_1) \} b_1 \\ &+ (2/9) [\{ \xi_1 + 2\xi_2 + (-\frac{1}{2})^{t-1}(\xi_2 - \xi_1) \} \{ \eta_1 + 2\eta_2 + (-\frac{1}{2})^{t-2}(\eta_2 - \eta_1) \} \\ &\quad + \{ \eta_1 + 2\eta_2 + (-\frac{1}{2})^{t-1}(\eta_2 - \eta_1) \} \{ \xi_1 + 2\xi_2 + (-\frac{1}{2})^{t-2}(\xi_2 - \xi_1) \}] b_2 \\ &+ (2/9) \{ \eta_1 + 2\eta_2 + (-\frac{1}{2})^{t-1}(\eta_2 - \eta_1) \} \{ \eta_1 + 2\eta_2 + (-\frac{1}{2})^{t-2}(\eta_2 - \eta_1) \} b_3 \\ &+ (1/3) \{ \xi_1 + 2\xi_2 + (-\frac{1}{2})^{t-1}(\xi_2 - \xi_1) \} b_4 \\ &+ (1/3) \{ \eta_1 + 2\eta_2 + (-\frac{1}{2})^{t-1}(\eta_2 - \eta_1) \} b_5 \quad (t=2, 3, \dots), \text{ and} \end{aligned}$$

$$(25) \quad X^{t\infty 1} = (2/9)\{(\xi_1 + 2\xi_2)^2 b_1 + 2(\xi_1 + 2\xi_2)(\eta_1 + 2\eta_2)b_2 + (\eta_1 + 2\eta_2)^2 b_3\} \\ + (1/3)\{(\xi_1 + 2\xi_2)b_4 + (\eta_1 + 2\eta_2)b_5\},$$

where

$$(26) \quad \xi_2 = \frac{1}{2}(\alpha_1 + \frac{1}{2}\beta_1)/(\alpha_1 + \beta_1 + \gamma_1) \quad \text{and} \quad \eta_2 = \frac{1}{2}(\gamma_1 + \frac{1}{2}\beta_1)/(\alpha_1 + \beta_1 + \gamma_1).$$

Proof. Let

$$(27) \quad X^{t+1} = \alpha_{t+1}b_1 + \beta_{t+1}b_2 + \gamma_{t+1}b_3 + \xi_{t+1}b_4 + \eta_{t+1}b_5$$

and note that the multiplication operator associated with X^{t+1} has the matrix representation

$$E_t = \frac{1}{2} \begin{bmatrix} \xi_t & \eta_t & 0 & \xi_t + \eta_t & 0 \\ \frac{1}{2}\xi_t & \frac{1}{2}(\xi_t + \eta_t) & \frac{1}{2}\eta_t & \frac{1}{2}(\xi_t + \eta_t) & \frac{1}{2}(\xi_t + \eta_t) \\ 0 & \xi_t & \eta_t & 0 & \xi_t + \eta_t \\ \alpha_t + \frac{1}{2}\beta_t & \gamma_t + \frac{1}{2}\beta_t & 0 & \alpha_t + \frac{1}{2}\beta_t & \gamma_t + \frac{1}{2}\beta_t \\ 0 & \alpha_t + \frac{1}{2}\beta_t & \gamma_t + \frac{1}{2}\beta_t & \alpha_t + \frac{1}{2}\beta_t & \gamma_t + \frac{1}{2}\beta_t \end{bmatrix}.$$

By direct calculation, we obtain

$$(28) \quad X^{t+1} = X^{t+1}E_t/\nu_t \\ = (1/\nu_t)[(\alpha_t + \frac{1}{2}\beta_t)\xi_t b_1 + \{(\alpha_t + \frac{1}{2}\beta_t)\eta_t + (\gamma_t + \frac{1}{2}\beta_t)\xi_t\}b_2 + (\gamma_t + \frac{1}{2}\beta_t)\eta_t b_3 \\ + (\alpha_t + \frac{1}{2}\beta_t)(\xi_t + \eta_t)b_4 + (\gamma_t + \frac{1}{2}\beta_t)(\xi_t + \eta_t)b_5],$$

where $\nu_t = 2(\alpha_t + \beta_t + \gamma_t)(\xi_t + \eta_t)$. Comparing (28) with (27) and noting that

$$(29) \quad \alpha_t + \beta_t + \gamma_t = \xi_t + \eta_t = \nu_t = \frac{1}{2} \quad (t=2, 3, \dots),$$

we obtain

$$(30) \quad \alpha_{t+1} = 2\xi_{t+1}\xi_t \\ \beta_{t+1} = 2(\xi_{t+1}\eta_t + \eta_{t+1}\xi_t) \\ \gamma_{t+1} = 2\eta_{t+1}\eta_t \\ \xi_{t+1} = \frac{1}{2}(\xi_t + \xi_{t-1}) \\ \eta_{t+1} = \frac{1}{2}(\eta_t + \eta_{t-1}).$$

Since the first three equations depends on the last two, the system (30) can be solved by merely solving the last two equations simultaneously. Applying the usual method for solving second-order difference equations, we find that

$$(31) \quad \xi_{t+1} = (1/3)\{\xi_1 + 2\xi_2 + (-\frac{1}{2})^{t-1}(\xi_2 - \xi_1)\} \\ \eta_{t+1} = (1/3)\{\eta_1 + 2\eta_2 + (-\frac{1}{2})^{t-1}(\eta_2 - \eta_1)\}.$$

Substituting (31) into the first three equations of (30), we immediately see that the result (24) indeed holds; that ξ_2 and η_2 are given by (26) can also be checked up by setting $t=1$ in (28) and calculating the coefficients of b_4 and b_5 .

The result (25) is obvious. Q. E. D.

The matrix E_t in this case is singular since the sum of the first three

columns is equal to that of the last two. That the first three equations in (30) depend on the last two is just a reflection of this particular property of E_t .

The result (29) is indicative that, under the conditions set out for Theorem 4, males and females will occur with equal frequency in at most two generations of random matings.

It may also be noted that the limiting element $X^{(\infty)}$ in (25) is not a population element unless $\xi_1 + \eta_1 = \frac{1}{2}$, i. e., unless males and females occur with equal frequency in the initial generation. It will certainly become a population element when divided through by the normalizing factor

$$(\xi_1 + \eta_1 + 1)(2\xi_1 + 2\eta_1 + 5)/9.$$

A Sequence of M-Products Arising in a Mixture of a Selfing Semialgebra and a Zygotic Semialgebra

In the plant kingdom, purely selfing populations seldom exist—they are to be found probably only in a plant breeder's garden where the mating process can be artificially controlled. So we shall proceed to look into the genetic dynamics of a population which breeds by mixed selfing and random mating. First of all, let us define a mixture of two Mendelian semialgebras: Let $\mathcal{A}_1 = \mathcal{R}^\circ\{g_1, \dots, g_n\}$ and $\mathcal{A}_2 = \mathcal{R}^\circ\{g_1, \dots, g_n\}$ be two Mendelian semialgebras with the respective multiplication tables

$$(32) \quad g_i g_j (= g_j g_i) = \sum_{k=1}^n r_{ij}^{(1)} g_k \quad (i, j=1, \dots, n),$$

$$(33) \quad g_i g_j (= g_j g_i) = \sum_{k=1}^n r_{ij}^{(2)} g_k \quad (i, j=1, \dots, n).$$

Then, the Mendelian semialgebra $\mathcal{A}_{1,2} = \mathcal{R}^\circ\{g_1, \dots, g_n\}$ with multiplication table

$$(34) \quad g_i g_j (= g_j g_i) = \sum_{k=1}^n \{(1-\theta)r_{ij}^{(1)} + \theta r_{ij}^{(2)}\} g_k \quad (i, j=1, \dots, n; 0 \leq \theta \leq 1)$$

is called a *mixture* of \mathcal{A}_1 and \mathcal{A}_2 , and we shall symbolize this by writing

$$(35) \quad \mathcal{A}_{1,2} = (1-\theta)\mathcal{A}_1 + \theta\mathcal{A}_2 \quad (0 \leq \theta \leq 1).$$

Symbolically $\mathcal{A}_{1,2}$ may be regarded as a convex combination of \mathcal{A}_1 and \mathcal{A}_2 .

A notational difficulty has arisen when we write $\mathcal{A}_1 = \mathcal{R}^\circ\{g_1, \dots, g_n\}$, $\mathcal{A}_2 = \mathcal{R}^\circ\{g_1, \dots, g_n\}$ and $\mathcal{A}_{1,2} = \mathcal{R}^\circ\{g_1, \dots, g_n\}$, together with their respective multiplication tables given in (32), (33) and (34). Algebraically \mathcal{A}_1 , \mathcal{A}_2 and $\mathcal{A}_{1,2}$ must not be regarded as identical since their multiplication tables do not necessarily coincide. The merit of these notations, however, has been to signify that \mathcal{A}_1 , \mathcal{A}_2 and $\mathcal{A}_{1,2}$ as semivector spaces over \mathcal{R}° are all spanned by a common basis $\{g_1, \dots, g_n\}$, although they as Mendelian semialgebras may differ from one another in the manner of multiplication. Further, these notations also reflect the genetical fact that genetic systems having the same set of genetic types may breed by different means of mating.

For the discussion to follow, it is necessary to define a so-called *M-product*: Let $\mathcal{A}_{1,2}$, \mathcal{A}_1 and \mathcal{A}_2 be defined as before and let $x = \sum_{i=1}^n \xi_i g_i$ and $y = \sum_{i=1}^n \eta_i g_i$ be two elements in the semivector space common to $\mathcal{A}_{1,2}$, \mathcal{A}_1 and \mathcal{A}_2 . The product of x and y will then be denoted by xy , $x * y$ or $x \cdot y$ according as it belongs to $\mathcal{A}_{1,2}$, \mathcal{A}_1 or \mathcal{A}_2 . These three forms of products are in fact related to one another as follows:

$$xy = (1-\theta)x * y + x \cdot y \quad (0 \leq \theta \leq 1).$$

In particular, the t -th *M-product* of x by y , denoted by $x_t^{(y)}$, is defined recursively as

$$(36) \quad x_1^{(y)} = x; \quad x_t^{(y)} = (1-\theta)x_{t-1}^{(y)} * y + \theta x^{t-1} \cdot x^{t-1} \quad (t=2, 3, \dots),$$

where $x_{t-1}^{(y)}$ and x^{t-1} denote, respectively, the $(t-1)$ st primary product of x by y and the $(t-1)$ st plenary power of x .

Consider now a biallelic locus of a diploid population with two distinct alleles a_1, a_2 . If the population undergoes random mating, there are also three distinct genotypes as are listed in (9) for a selfing population. However, the system should be represented by the Mendelian semialgebra $\mathcal{Z} = \mathcal{R}^\circ\{b_1, b_2, b_3\}$ with multiplication table

$$(37) \quad \begin{aligned} b_i b_i &= b_i \quad (i=1, 3), \quad b_2 b_2 = \frac{1}{4} b_1 + \frac{1}{2} b_2 + \frac{1}{4} b_3, \quad b_1 b_3 (= b_3 b_1) = b_2 \\ b_1 b_2 (= b_2 b_1) &= \frac{1}{2} (b_1 + b_2), \quad b_2 b_3 (= b_3 b_2) = \frac{1}{2} (b_2 + b_3). \end{aligned}$$

Following Etherington's ([1939], §7) nomenclature, we shall refer to this semialgebra as a *zygotic semialgebra*. Suppose then that the population breeds by mixed selfing and random mating and thus the system can be represented by a mixture $\mathcal{M} = \mathcal{R}^\circ\{b_1, b_2, b_3\}$ such that

$$(38) \quad \mathcal{M} = (1-\theta)\varphi + \theta\mathcal{Z} \quad (0 \leq \theta \leq 1),$$

where $\varphi = \mathcal{R}^\circ\{b_1, b_2, b_3\}$ is the selfing semialgebra introduced in §3 and $\mathcal{Z} = \mathcal{R}^\circ\{b_1, b_2, b_3\}$, the zygotic semialgebra just described above. The multiplication table of \mathcal{M} is given by

$$(39) \quad \begin{aligned} b_i b_i &= b_i \quad (i=1, 3), \quad b_2 b_2 = \frac{1}{4} b_1 + \frac{1}{2} b_2 + \frac{1}{4} b_3, \quad b_1 b_3 (= b_3 b_1) = \theta b_2 \\ b_1 b_2 (= b_2 b_1) &= \frac{1}{2} \theta (b_1 + b_2), \quad b_2 b_3 (= b_3 b_2) = \frac{1}{2} \theta (b_2 + b_3). \end{aligned}$$

It may be noted that the mixture \mathcal{M} is baric, in the sense that it admits a weight function ω onto \mathcal{R}° defined by

$$(40) \quad \omega(x) = \theta \xi_1 + \frac{1}{2} (1+\theta) \xi_2 + \theta \xi_3 \quad \text{for all } x = \xi_1 b_1 + \xi_2 b_2 + \xi_3 b_3 \text{ in } \mathcal{M}.$$

The genetic dynamics of a mixed-selfing-and-random-mating population can now be described by the following theorem:

THEOREM 5. Let $\mathcal{M} = (1-\theta)\varphi + \theta\mathcal{Z}$ ($0 < \theta < 1$) be a mixture of the selfing

semialgebra $\varphi = \mathcal{R}^{\circ}\{b_1, b_2, b_3\}$ and the zygotical semialgebra $\mathcal{Z} = \mathcal{R}^{\circ}\{b_1, b_2, b_3\}$, let $x = \xi_1 b_1 + \xi_2 b_2 + \xi_3 b_3$ be a population element of \mathcal{M} , and let $y = b_1 + b_2 + b_3$. Then the $(t+1)st$ M-product of x by y is given by

$$(41) \quad x_i^{(y)} = [(1 - (1 - \theta)^t) \varphi^2 + ((1 - \theta)/(1 + \theta)) \{(1 + \theta)(1 - (1 - \theta)^{t-1}) - \theta(1 - (\frac{1}{2}(1 - \theta))^{t-1})\} \varphi \psi + (1 - \theta)^t (\xi_1 + \frac{1}{2}(1 - (\frac{1}{2})^t) \xi_2)] b_1 \\ + [(4\theta/(1 + \theta))(1 - (\frac{1}{2}(1 - \theta))^t) \varphi \psi + (\frac{1}{2}(1 - \theta))^t \xi_2] b_2 \\ + [(1 - (1 - \theta)^t) \psi^2 + ((1 - \theta)/(1 + \theta)) \{(1 + \theta)(1 - (1 - \theta)^{t-1}) - \theta(1 - (\frac{1}{2}(1 - \theta))^{t-1})\} \varphi \psi + (1 - \theta)^t (\xi_3 + \frac{1}{2}(1 - (\frac{1}{2})^t) \xi_2)] b_3, \text{ and}$$

$$(42) \quad x_i^{(y)} = \{\varphi^2 + ((1 - \theta)/(1 + \theta)) \varphi \psi\} b_1 + \{(4\theta/(1 + \theta)) \varphi \psi\} b_2 \\ + \{\psi^2 + ((1 - \theta)/(1 + \theta)) \varphi \psi\} b_3,$$

where $\varphi = \xi_1 + \frac{1}{2} \xi_2$ and $\psi = \xi_3 + \frac{1}{2} \xi_2$.

We shall prove this theorem *via* the following lemma:

LEMMA 2. Let $x_t (t=1, 2, \dots)$ and $y_t (t=2, 3, \dots)$ be n -dimensional row vectors with real entries. Let t_0 be a positive integer such that $t > t_0 \Rightarrow y_t = c$, a constant vector, and consider the recursive equation

$$(43) \quad x_{t+1} = x_t(A/\alpha) + \beta y_{t+1},$$

where A is an $n \times n$ nonnegative real matrix of full rank and α, β are real numbers with $\alpha > \mu(A)$, the spectral radius of A . Then, the following holds:

$$(44) \quad x_{t+1} = \begin{cases} x_1 S \{J(A)/\alpha\}^t S^{-1} + \beta \sum_{s=0}^{t-1} y_{t-s+1} S \{J(A)/\alpha\}^s S^{-1} & \text{for } t < t_0, \\ x_1 S \{J(A)/\alpha\}^t S^{-1} + \beta c \sum_{s=0}^{t-t_0} S \{J(A)/\alpha\}^s S^{-1} \\ \quad + \beta \sum_{s=t-t_0+1}^{t-1} y_{t-s+1} S \{J(A)/\alpha\}^s S^{-1} & \text{for } t \geq t_0, \end{cases}$$

$$(45) \quad \lim_{t \rightarrow \infty} x_t = \alpha \beta c (\alpha I_n - A)^{-1},$$

where $S, J(A)$ and I_n are defined similarly as in Lemma 1. Further, if the absolute values of entries in y_t are ≤ 1 for all t and the condition $t > t_0 \Rightarrow y_t = c$ is replaced by the condition $\lim_{t \rightarrow \infty} y_t = c$, then equation (44) reduces to

$$(46) \quad x_{t+1} = x_1 S \{J(A)/\alpha\}^t S^{-1} + \beta \sum_{s=0}^{t-1} y_{t-s+1} S \{J(A)/\alpha\}^s S^{-1} \quad (t=1, 2, \dots)$$

and equation (45) holds unaltered.

While equations (44) and (46) can be obtained by direct iteration, the rest of the lemma follows from Theorems 1.4 and 3.8 of Varga ([1962]; p. 13 and 83, respectively) and from the *Dominated Convergence Theorem of Power Series* (see, e.g., Eggleston [1962], p. 63).

Proof of Theorem 5. By definition,

$$x_1^{(y)} = x; \quad x_t^{(y)} = (1 - \theta) x_{t-1}^{(y)} * y + \theta x^{t-1} * x^{t-1} \quad (t=2, 3, \dots).$$

Here x as a population element in \mathcal{Z} has the property that

$$x^{t-1} * x^{t-1} = x^{t-1} = x^{2t-1} \quad (t=2, 3, \dots),$$

which has been proven by Etherington ([1939], p. 253 *ff*). On the other hand, we have (see proof of Theorem 2 in §3)

$$x_{t+1}^{(y)} * y = x_t^{(y)} E_y,$$

where E_y is the same as given in (15). Thus,

$$x_{t+1}^{(y)} = (1-\theta)x^{(y)}E_y + \theta x^{t^2} \quad (t=1, 2, \dots),$$

and the theorem follows immediately from Lemma 2. Q. E. D.

We note that the limiting element in equation (42) is indeed a population element. It is hardly an idempotent, however.

As immediate consequences of the above theorem, we obtain the following corollaries:

COROLLARY 1. If in Theorem 5 $\theta=0$, then Theorem 5 reduces to Theorem 2.

COROLLARY 2. If in Theorem 5 $\theta=1$, then we have

$$(47) \quad x_{t+1}^{(y)} = x^{t^2} = (\xi_1 + \frac{1}{2}\xi_2)^2 b_1 + 2(\xi_1 + \frac{1}{2}\xi_2)(\xi_3 + \frac{1}{2}\xi_2)b_2 + (\xi_3 + \frac{1}{2}\xi_2)^2 b_3 \quad (t=1, 2, \dots).$$

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源自各種孟德爾擬代數的積元數列

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本文的目標在於檢討源自各種孟德爾擬代數的積元數列之解析性質。這些數列可直接應用於世代不重疊的遺傳體系之研究，尤其用以分析「連鎖」，「自交」，「自交不孕」，「性連鎖」，以及「自交與雜交混合」等機構對於遺傳性狀在世代交替過程中的機率分配之效應，最為合適。