IMA Journal of Mathematics Applied in Medicine & Biology (1990) **7**, 33–40

On *k*th-Order Bernstein Algebras and Stability at the *k*+1 Generation in Polyploids

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[Received 27 September 1989]

Some properties of kth-order Bernstein algebras are obtained, a class of examples constructed, and polyploid populations with multiple alleles subject to mutation characterized, whatever the initial distribution, where the frequency distribution of the gametic types is in equilibrium after $k+1$ generations.

Keywords: nonassociative algebra; genetic algebra; polyploidy; mutation; stable state.

1. Introduction

LET A be a commutative nonassociative algebra over a field K. We define the plenary powers of an element x of A by $x^{[1]}=x$, $x^{[2]}=x^2,\dots,x^{[n+1]}=x^{[n]}x^{[n]}, \dots$. A is called a kth-order Bernstein algebra ($k \geqslant 1$) if A has a nontrivial algebra homomorphism $\omega: A \to K$ and the plenary powers of any element $x \in A$ satisfy the identity

$$x^{[k+2]} = \omega(x)^{2^k} x^{[k+1]}. \tag{1.1}$$

If A is a stochastic algebra describing a population (Wörz-Busekros, 1980; p. 12) and the element y of A represents a frequency distribution of genotypes in the initial generation (in this case, $\omega(y)=1$), then $y^{[k]}$ represents the frequency distribution in the kth generation. Now, if A satisfies the identity (1.1), we have $y^{[k+2]}=y^{[k+1]}$, and this indicates the fact that the population is in equilibrium after $k+1$ generations. This means that, whatever the initial distribution of frequencies, the population achieves a stable state in the $(k+1)$th generation.

In the case where $k=1$, we have the so-called Bernstein algebras. These algebras have been studied extensively (see e.g. Holgate, 1975; Lyubich, 1978, 1987; Hentzel & Peresi 1989). The definition of kth-order Bernstein algebras and some examples for $k=2$ were given by Abraham (1980: p. 361).

The object of this paper is to obtain some properties of kth-order Bernstein algebras, construct examples, and characterize polyploid multiple allelic gametic algebras which are kth-order Bernstein.

2. Basic properties and examples

Throughout this section, A will be a kth-order Bernstein algebra, with nontrivial algebra homomorphism ω, over a field K of characteristic $\neq 2$ with at least 2^{k+1} elements.

Let $x_0 \in A$ such that $\omega(x_0) \neq 0$. From the identity (1.1), it follows that $e = \omega(x_0)^{-2^k} x_0^{[k+1]}$ is an idempotent of A. Let N denote the kernel of ω. Then, A/N is isomorphic to k and so $A = Ke \oplus N$ (additive direct sum).

We note that ω is uniquely determined. Assume that $\psi : A \to K$ is a nontrivial algebra homomorphism. If $x \in N$, then $x^{[k+2]} = 0$ by identity (1.1); it follows that $[\psi(x)]^{[k+2]} = 0$, i.e. $\psi(x) = 0$. Thus $\psi(N) = 0$. Now, since $e^2 = e$, we have $\omega(e) = 0$ or $\omega(e) = 1$. If $\omega(e) = 0$, we would have $\omega = 0$, a contradiction. Then $\omega(e) = 1$. Analogously, $\psi(e) = 1$. Therefore $\psi = \omega$.

PROPOSITION *Let $L : N \to N$ denote left multiplication by the idempotent e. Denote by U the image of L^k and by Z the kernel of L^k. Then*

(i) $L^{k+1} = \frac{1}{2}L^k$;

(ii) $A = Ke \oplus U \oplus Z$ *(additive direct sum)*;

(iii) $U = \{N \in N : en = \frac{1}{2}n\}, \quad U^2 \subseteq Z.$

Proof. Let $x = \alpha e + n$ $(\alpha \in K,\ n \in N)$. For any $l > 1$,

$$x^{[l]} = x^{2^{l-1}}e + \alpha^{(2^{l-1}-1)}2^{l-1}L^{l-1}(n) + y_l,$$

where y_l is the sum of terms of lesser degree in α. Thus, from (1.1), it follows that

$$x^{2^{k+1}}e + \alpha^{(2^{k+1}-1)}2^{k+1}L^{k+1}(n) + y_{k+2} = \alpha^{2^k}\left(\alpha^{2^k}e + \alpha^{(2^k-1)}2^kL^k(n) + y_{k+1}\right).$$

Since K has enough elements, these two expressions can be equal if and only if they agree term by term. Thus, comparing the terms in $\alpha^{(2^{k+1}-1)}$, we obtain $L^{k+1}(n) = \frac{1}{2}L^k(n)$. This proves (i).

If $n \in N$, then $n = L^k(2^kn) + (n - L^k(2^kn))$, where $L^k(2^kn)$ is in U by definition and $n - L^k(2^kn)$ is in Z since $L^{2k}(n) = 2^{-k}L^k(n)$ by (i) and so $L^k(n - L^k(2^kn)) = 0$. It follows that $N = U + Z$. Now, if $x \in U \cap Z$, then $x = L^k(n)$ for some $n \in N$. Thus, $2^{-k}x = L^k(x) = 0$, and so $x = 0$. Therefore $N = U \oplus Z$ and (ii) is proved.

Finally, we prove (iii). Let $u \in U$. From the definition of U and (i), it is clear that $eu = \frac{1}{2}u$. On the other hand, if $n \in N$ and $en = \frac{1}{2}n$, then $n = L^k(2^kn) \in U$. Thus $U = \{n \in N : en = \frac{1}{2}n\}$. Now, let $x = \alpha e + u$ $(\alpha \in K,\ u \in U)$. For any $l > 1$, we have

$$x^{[l]} = \alpha^{2^{l-1}}e + \alpha^{(2^{l-1}-1)}u + \alpha^{(2^{l-1}-2)}P_l(L)(u^2) + (\text{terms of lesser degree in } \alpha),$$

where P_l is the polynomial $2^{l-2}t^{l-2} + 2^{l-3}t^{l-3} + \cdots + 2t + 1$. From identity (1.1), it then follows by comparing terms in $\alpha^{2^{k+1}-2}$ that $(P_{k+2}(L) - P_{k+1}(L))(u^2) = 0.$

Now, write $u^2 = u' + z'$, where $u' \in U$ and $z' \in Z$. Since

$$P_{k+2}(L)(u') = (k+1)u', \qquad P_{k+1}(L)(u') = ku',$$
$$P_{k+2}(L)(z') \in Z, \qquad P_{k+1}(L)(z') \in Z,$$

it then follows that $u' + z'' = 0$ for some $z'' \in Z$ and so $u' = 0$. Therefore $u^2 = z' \in Z$, and the fact that $U^2 \subseteq Z$ follows. □

The conditions established in the preceding proposition suggest the following class of examples. Let P and Q be vector spaces over K, and $T: Q \to Q$ be a linear map. In the Cartesian product $K \times P \times Q$, we define addition and multiplication by elements of K componentwise, and multiplication by

$$(\alpha, x, y)(\alpha', x', y') = \big(\alpha\alpha', \tfrac{1}{2}(\alpha x' + \alpha' x), \tfrac{1}{2}T(\alpha y' + \alpha' y)\big). \tag{2.1}$$

Define $\omega\big((\alpha, x, y)\big) = \alpha$. Since, for any $l > 1$,

$$(\alpha, x, y)^{[l]} = \big(\alpha^{2^{l-1}}, \alpha^{(2^{l-1}-1)}x, \alpha^{(2^{l-1}-1)}T^{l-1}(y)\big),$$

the condition (1.1) is satisfied if and only if $T^{k+1}(y) = T^k(y)$ for any $y \in Q$. Thus the algebra $K \times P \times Q$ is kth-order Bernstein if and only if $T^{k+1} = T^k$. Note that, if this is the case and $e = (1, 0, 0)$, then $U = \{0\} \times P \times \{y \in Q : T(y) = y\} = \{0\} \times P \times \operatorname{Im} T^k$ and $Z = \{0\} \times \{0\} \times$ kernel of T^k. Note also that $N^2 = 0$. For a specific example, let $P = K^p$ and $Q = K^q$ $(0 \leqslant p \leqslant \infty,\ 1 \leqslant q \leqslant \infty)$ and, for $1 \leqslant k \leqslant q$ $(k \neq \infty)$, set

$$T[(y_1, \dots, y_k, y_{k+1}, \dots, y_q)] = 2(0, y_1, \dots, y_{k-1}, 0, \dots, 0).$$

(We are setting $K^0 = 0$.) We have $T^k = 0$ and, of course, $T^{k+1} = T^k$. We denote this algebra by $A_k(p, q)$.

Assume now that the algebra A satisfies the condition $N^2 = 0$. We know from the preceding proposition that $N = U \oplus Z$, where $U = \{n \in N : en = \frac{1}{2}n\}$ and $L^k(Z) = 0$. For any $\alpha, \alpha' \in K$, $u, u' \in U$, and $z, z' \in Z$, we have

$$(\alpha e + u + z)(\alpha' e + u' + z') = \alpha\alpha' e + \tfrac{1}{2}(\alpha u' + \alpha' u) + e(\alpha z' + \alpha' z).$$

Thus, if we identify A with $K \times U \times Z$, the multiplication in A is given by (2.1), where $T = 2L$. Assume that $L(Z) \neq 0$ and let s be the greatest integer such that $1 < s \leqslant k$ and $L^{s-1}(Z) \neq 0$. Let $z_1 \in Z$ be such that $L^{s-1}(z_1) \neq 0$ and let $z_{i+1} = L^i(z_1)$ $(1 \leqslant i < s)$. It is clear that $\{z_1, \dots, z_s\}$ is a linearly independent subset of Z. Denote by I_1 the subspace of A spanned by $z_1, \dots, z_s$. Let I be the maximal subspace of A that is invariant under L and satisfies the condition $I_1 \cap I = 0$. As in the proof of lemma 6.5.4 in Herstein (1975), we may conclude that $Z = I_1 \oplus I$ (additive direct sum). It follows then that $eI \subset I$. On the other hand, $(U \oplus Z)I = 0$ since $N^2 = 0$. Thus, I is an ideal of A, and $A = Ke \oplus U \oplus I_1 \oplus I$ (additive direct sum). Also, $A/I \simeq Ke + U + I_1$ as algebras. Let p be the dimension of U. If we identify A/I with $K \times K^p \times K^s$, we see that the multiplication in A/I is given by (2.1), where T is defined by $T(y_1, \dots, y_s) = 2(0, y_1, \dots, y_{s-1})$. Therefore A/I is isomorphic to $A_s(p, s)$.

In all the examples considered so far, we have the condition $N^2 = 0$. We now give an example where this does not happen. Let S be a commutative plenary nil algebra of index $k+1$, i.e. an algebra such that $k+1$ is the smallest positive integer satisfying $y^{[k+1]}=0$ for all $y \in S$. In the vector space $K \times S \times S$, define the following multiplication:

$$(\alpha, x, y)(\alpha', x', y') = \left(\alpha\alpha', \tfrac{1}{2}(\alpha x' + \alpha' x), yy'\right).$$

Since $(\alpha, x, y)^{[k+1]} = (\alpha^{2^k}, \alpha^{(2^k-1)}x, y^{[k+1]}) = (\alpha^{2^k}, \alpha^{(2^k-1)}x, 0)$, it follows that condition (1.1) is fulfilled. Thus, the algebra obtained is kth-order Bernstein. Let y be an element of S such that $y^2 \neq 0$. We have $(0,0,y)(0,0,y) = (0,0,y^2) \neq 0$. Thus $N^2 \neq 0$. For a specific example, we take S to be the algebra with basis $c_1,\ldots, c_{2^k-1}$ and multiplication table given by $c_ic_j = c_jc_i = c_{i+j}$ if $i+j \leqslant 2^k - 1$ and the other products zero.

3. Polyploidy with multiple alleles

Consider a $2m$-ploid population with $n+1$ alleles $A_0, A_1,\ldots, A_n$. Each monomial in the variables $A_0,\ldots, A_n$ of degree m represents one of the gametic types of the population. The output of a zygote formed by the union of gametes $A_0^{i_0} \cdots A_n^{i_n}$ and $A_0^{j_0} \cdots A_n^{j_n}$ is described by the identity

$$(A_0^{i_0} \cdots A_n^{i_n})(A_0^{j_0} \cdots A_n^{j_n}) = \binom{2m}{m}^{-1} \sum_{k_0+\cdots+k_n=m} \binom{i_0+j_0}{k_0} \cdots \binom{i_n+j_n}{k_n} A_0^{k_0} \cdots A_n^{k_n}. \quad (3.1)$$

If the probability that allele A_i changes to allele A_j is m_{ij} and the probability that it stays the same is m_{ii} in each generation (note that $m_{ij} \geqslant 0$ and $\sum_{j=0}^n m_{ij} = 1$), the analogue of (3.1) is given by

$$A_0^{i_0} \cdots A_n^{i_n} * A_0^{j_0} \cdots A_n^{j_n} = [(A_0M)^{i_0} \cdots (A_nM)^{i_n}][(a_0M)^{j_0} \cdots (A_nM)^{j_n}], \quad (3.2)$$

where $M = (m_{ij})$ and $A_iM = \sum_{j=0}^n m_{ij}A_j$. If we consider the real vector space generated by all monomials $a_0^{i_0} \cdots a_n^{i_n}$ of degree m and define multiplication as in (3.2), we obtain a nonassociative algebra which we shall denote by $G(n+1, 2m, M)$. Define the linear map $\omega : G(n+1, 2m, M) \to \mathbb{R}$ by $\omega(A_0^{i_0} \cdots A_n^{i_n}) = 1$. As is readily seen, ω is a nontrivial algebra homomorphism. $G(n+1, 2m, M)$ is a genetic algebra in the sense defined by Gonshor (1971), as shown in his theorem 4.1, and a genetic algebra has only one nontrivial algebra homomorphism (Wörz-Busekros, 1980: corollary 3.11, p. 40). Thus, ω is uniquely determined.

In what follows, we establish conditions under which $G(n+1, 2m, M)$ is a kth-order Bernstein algebra, or, equivalently, when the gametic distribution of the population is in equilibrium after $k+1$ generations whatever the initial distribution.

We start by noticing that $G(n+1, 2m, I)$ is not a Bernstein algebra of any order for $m > 1$. This follows because the necessary condition established in part (i) of the Proposition is not fulfilled. Since A_0^m is an idempotent, $c = A_0^{m-2}(A_0 - A_1)^2$ is in $\ker \omega$ and, if L denotes left multiplication by A_0^m, we have $L^k(c) = \binom{2m}{2}^{-k}\binom{m}{2}^k c$ and then $L^{k+1}(c) \neq \frac{1}{2}L^k(c)$ for any $k \geqslant 1$.

Let us call the space $L(n+1)$ of linear forms in the symbols $A_0, A_1,\ldots, A_n$ the *allelic space* of $G(n+1, 2m, M)$. The vector space underlying $G(n+1, 2m, M)$ is the nth symmetric tensor power of $L(n+1)$. The choice of a canonical basis

$C_0, C_1, \ldots, C_n$ in $L(n+1)$ defined by $C_0 = A_0$, $C_i = A_0 - A_i$ $(i \geq 1)$, induces a canonical basis in $G(n+1, 2m, M)$. Its multiplication table, in the case $M = I$, is (see e.g. Campos & Holgate, 1987; eqn (2.4))

$$(C_0^{p_0} C_1^{p_1} \cdots C_n^{p_n})(C_0^{q_0} C_1^{q_1} \cdots C_n^{q_n}) = \binom{2m}{m}^{-1} \binom{p_0 + q_0}{m} C_0^{p_0+q_0} C_1^{p_1+q_1} \cdots C_n^{p_n+q_n}.$$

We note the following.

(i) Ker ω is spanned by the set of monomials of degree m in $C_0, C_1, \ldots, C_n$ with the exception of C_0^m.

(ii) $G(n+1, 2m, M)$ is a graded algebra, the component of degree k being spanned by the monomials $C_0^{p_0} C_1^{p_1} \cdots C_n^{p_n}$ for which $p_1 + p_2 + \cdots + p_n = k$. This is evident from the multiplication table in the case $M = I$. In general, the linear mapping M leaves invariant the subspace of $L(n+1)$ spanned by $C_1, \ldots, C_n$, which will be denoted by $\ker_L \omega$, and hence leaves each component of the grading just described invariant. Thus it is also a grading for $G(n+1, 2m, M)$.

(iii) The automorphisms of $G(n+1, 2m, M)$ are exactly those induced by the symmetric tensor product construction from the affine group of linear transforms of $L(n+1)$ that leave invariant $\ker_L \omega$ (Micali & Revoy, 1986; §4).

We define a vector space homomorphism H to $L(n+1)$ from the space carrying $G(n+1, 2m, M)$ by $H(\prod A_i^{p_i}) = m^{-1} \sum p_i A_i$. In biological terms, if $a \in G(n+1, 2m, M)$ is the distribution of gametic types, $H(a) \in L(n+1)$ is the distribution of allelic proportions that it implies. From the definition of products, we have the following.

(i) $H(aM) = H(a)M$.

(ii) $H(ab) = \frac{1}{2}[H(a) + H(b)]$, and in particular $H(a^2) = H(a)$.

(iii) $H(a * b) = H(aM \cdot bM) = \frac{1}{2}[H(aM) + H(bM)] = \frac{1}{2}H(a+b)M = H(ab)M$.

In particular,

$$H(a * a) = H(a)M. \tag{3.3}$$

THEOREM

(i) The algebra $G(n+1, 2, M)$ is a kth-order Bernstein algebra if and only if $M^k = M^{k+1}$, $M^j \neq M^{j+1}$ $(j = 1, \ldots, k-1)$.

(ii) The algebra $G(n+1, 2m, M)$ $(m > 1)$ is a k-th order Bernstein algebra for some $k \leq n$ if and only if 0 is a characteristic root of M with multiplicity n.

Proof. In $G(n+1, 2, I)$, every element d of weight 1 (i.e. every element that is mapped into 1 by ω) is idempotent. Hence its jth plenary power in $G(n+1, 2, M)$ is $d^{*[j]} = dM^{j-1}$. The assertion (i) follows immediately.

Now consider part (ii). Assume that 0 is a characteristic root of M with multiplicity n. A mutation matrix is just a transition matrix of a finite discrete Markov chain. This type of matrix has 1 as one of its eigenvalues. The characteristic polynomial of M is then $x^n(x-1)$. By analogy with Markov chain theory, an allele A_i will be called transient if there is another allele A_j such that A_i can mutate to A_j in a finite number of steps, but the reverse mutation is not possible. Otherwise A_i will be called persistent. Suppose that there are s transient alleles. Then

$$M = \begin{bmatrix} M_{11} & 0 \\ M_{21} & M_{22} \end{bmatrix},$$

where M_{22} is the submatrix corresponding to the transient allelic subset. The characteristic roots of M are those of M_{11} together with those of M_{22}, and clearly the single nonzero (unit) root must belong to M_{11}. Hence we have $M_{22}^s = 0$. Thus, after s generations, the allelic distribution is concentrated entirely on the persistent alleles. The evolution after that is described by the subalgebra obtained by deleting the transient alleles, for which M_{11} is the mutation matrix. Therefore it is sufficient to study the case where there are no transient alleles, i.e. the irreducible case. Under our conditions, M must be aperiodic. This follows because the number of characteristic roots of unit modulus of a periodic Markov matrix is at least equal to its period. Hence, by the results of Brosh & Gerchak (1978: theorem 3, (1)$\leftrightarrow$(2)), our conditions are equivalent to the existence of an allelic distribution element π such that for any allelic distribution vector c we have $cM^k = \pi$. For every i $(1 \leqslant i \leqslant n)$, we have $C_i M^k = A_0 M^k - A_i M^k = \pi - \pi = 0$. Hence $dM^k = 0$ for $d \in \ker_L \omega$ since $\ker_L \omega$ is spanned by $C_1, \dots, C_n$.

Let us define $K_0 = \ker_L \omega$, $K_1 = K_0 M$, $K_2 = K_1 M = K_0 M^2, \dots, K_{k-1} = K_0 M^{k-1}$, $K_k = K_0 M^k = 0$. We now choose a basis for $L(n+1)$,

$$d_{00}, d_{11}, \dots, d_{1j_1}, d_{21}, \dots, d_{2j_2}, \dots, d_{k-1,1}, \dots, d_{k-1,j_{k-1}},$$

such that $d_{ij} \in K_i / K_{i+1}$ (as a quotient vector space) for $i = 1, \dots, k-1$. The contractive effect of M on $L(n+1)$ is expressed by

$$d_{ij} M = \sum_{u=i+1}^{k-1} \sum_{v} x_{uv} d_{uv}.$$

An element that represents a gametic distribution can be written in terms of the canonical basis,

$$d = \sum x_p d_{00}^{p_{00}} d_{11}^{p_{11}} \cdots d_{k-1,t}^{p_{k-1,t}},$$

where $t = j_{k-1}$ and $p = (p_{00}, p_{11} \cdots p_{k-1,t})$. Note that d starts with the term d_{00}^m. Suppose that d only involves powers of those d_{ij} with $i \geqslant u$. Then dM will only involve powers of d_{ij} with $i \geqslant u+1$. We now make use of the facts that the change to the basis in the d_{ij} does not alter the multiplication table and that $d * d = (dM)^2$. Consider the evaluation of $d^{*[k+1]}$. It will begin with the term $(d_{00}^m)^{*[k+1]}$, and potentially contain other terms arising as products in the $*$ multiplication involving the terms from $d - d_{00}^m$. But each of these is a $(k+1)$-fold product, and hence through the k-fold action of M, it vanishes. Thus after $k+1$ generations we have $d^{*[k+1]} = (d_{00}^m)^{*[k+1]}$. Moreover, $d^{*[k+2]} = (d^{*2})^{*[k+1]} = (d_{00}^m)^{*[k+1]}$. This proves that $G(n+1, 2m, M)$ is a kth-order Bernstein algebra, if there are no transient alleles.

We now prove the converse. On iterating identity (3.3), we find that $H(d^{*[j]}) = H(d)M^{j-1}$. Since we are assuming that $G(n+1, 2m, M)$ is a kth-order Bernstein algebra $d^{*[k+2]} = d^{*[k+1]}$. Thus $H(d)M^{k+1} = H(d)M^k$ and, since d is an arbitrary gametic distribution, we have $M^{k+1} = M^k$. In biological terms, the stationarity of the distribution of gametes implies the stationarity of the distribution of allelic proportions. This implies that all characteristic roots of M are 1 or 0. If the conditions of the theorem are not satisfied, the multiplicity of 1 as a characteristic root must be at least 2. Appealing to the ergodic theory of finite Markov chains, and noting that the powers of M are not periodic, we deduce that the set of alleles must be separable into a number of subsets $S_1, S_2, \ldots$ such that any allele in S_i will only produce alleles in S_i, no matter how many times the transformation M is applied (i.e. how many generations occur). These correspond to the 'recurrent' or 'persistent' sets of Markov chain theory, and there may in addition be a set of transient alleles such that it is impossible to obtain them by mutation from any member of a persistent class, but which can mutate into members of persistent classes. Suppose that there are s persistent sets of alleles, but that the transient set is empty. Then the linear transform defined by mapping every allele A_j into the symbol S_i of the persistent set to which it belongs, defines a homomorphism from $G(n+1, 2m, M)$ to $G(s, 2m, I)$. And this latter is not a Bernstein algebra of any order for $m > 1$ as already noticed. Finally, suppose that there are transient alleles. The subalgebra obtained by deleting them is not Bernstein of any order by the previous case, and hence the algebra of the full system cannot be Bernstein of any order.

It is readily seen from the theorem that $G(2, 2m, M)$ is a Bernstein algebra of some order if and only if

$$m = 1 \quad \text{and} \quad M = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} \quad \text{or} \quad m \geqslant 1 \quad \text{and} \quad M = \begin{bmatrix} 1-r & r \\ 1-r & r \end{bmatrix} \quad (0 \leqslant r \leqslant 1).$$

In any case, the equilibrium state is achieved in the second generation. This last fact has been noticed by Gonshor (1960: p. 52). This particular result can also be proved directly as follows. Let

$$M = \begin{bmatrix} 1-r & r \\ s & 1-s \end{bmatrix}$$

and assume that $G(2, 2m, M)$ is a kth-order Bernstein algebra. Let $c_0, c_1, \ldots, c_m$ denote the canonical basis constructed by Gonshor (1960: theorem 7.1). The algebra $G(2, 2m, M)$ has an idempotent e (Gonshor, 1960: p. 52), $G(2, 2m, M) = \mathbb{R}e \oplus \operatorname{Ker} \omega$, and $\operatorname{Ker} \omega$ is generated by $c_1, \ldots, c_m$. Since $e = c_0 + f$ for some $f \in \operatorname{Ker} \omega$, it follows from the multiplication table that $L^t(c_1) = 2^{-t}(1 - r - s)^t c_1 + x_t$ for $t \geqslant 1$, where L denotes left multiplication by e and x_t is a linear combination of $c_2, \ldots, c_m$. Hence, since $L^{k+1} = \frac{1}{2}L^k$, we have $r + s = 1$ or $r = s = 0$ and the result follows.

4. Discussion

Bernstein (1923) posed the problem of determining all the equations of inheritance at the population level that would be in equilibrium in the second generation. With restriction imposed by the framework of genetics, the problem has been solved by Lyubich (1973).

This paper is concerned with equilibrium after a finite number of generations in polyploid populations with mutation. In Section 3, we have given a characterization of these populations in terms of the mutation rates matrix. The two parts of the Theorem illustrate the two features of a polyploid system that can lead to its achieving exact equilibrium after a finite number of generations. In a diploid system, the effect of random breeding described by the Hardy–Weinberg law is so strong that it is sufficient for mutation to produce any stationary distribution whatsoever of allelic types. In a system of higher ploidy, the stronger requirement of a unique exactly stationary distribution is necessary in order that the superconverging effect of the mutation should overwhelm the merely geometric rate of convergence produced by the breeding system.

Acknowledgements

Part of this paper was written while the second named author was visiting Iowa State University on a grant from the CNPq of Brazil.

REFERENCES

Abraham, V. M. 1980 Linearizing quadratic transformations in genetic algebras. *Proc. Lond. Math. Soc.* (3) **40,** 346–63.

Bernstein, S. 1923 Principe de stationarité et généralisation de la loi de Mendel. *C.R. Acad. Sci. Paris* **177,** 581–4.

Brosh, I., & Gerchak, Y. 1978 Markov chains with finite convergence time. *Stochastic Processes Applic.* **7,** 247–53.

Campos, T. M. M., & Holgate, P. 1987 Algebraic isotopy in genetics. *IMA J. Math. Appl. Med. Biol.* **4,** 215–22.

Gonshor, H. 1960 Special train algebras arising in genetics. *Proc. Edinb. Math. Soc.* (2) **12,** 41–53.

Gonshor, H. 1971 Contributions to genetic algebras. *Proc. Edinb. Math. Soc.* (2) **17,** 289–98.

Hentzel, I. R., & Peresi, L. A. 1989 Semiprime Bernstein algebras. *Arch. Math.* **52,** 539–43.

Herstein, I. N. 1975 *Topics in Algebra.* New York: Wiley.

Holgate, P. 1975 Genetic algebras satisfying Bernstein's stationary principle. *J. Lond. Math. Soc.* (2) **9,** 613–23.

Lyubich, Yu. I. 1973 Analogues of the Hardy–Weinberg Law. *Sov. Genet.* **9,** 1321–5.

Lyubich, Yu. I. 1978 Algebraic methods in evolutionary genetics. *Biomet. J.* **20,** 511–29.

Lyubich, Yu. I. 1987 A classification of some types of Bernstein algebras. *Sel. Math. Sov.* **6,** 1–14.

Micali, A. & Revoy, P. 1986 Sur les algèbres gamétiques. *Proc. Edinb. Math. Soc.* (2) **29,** 187–97.

Wörz-Busekros 1980, Algebras in genetics. *Lecture Notes in Biomathematics 36.* New York: Springer.