J. Math. Biology 6, 197–206 (1978)

Journal of Mathematical Biology

Selfing in Genetic Algebras

P. Holgate

Department of Statistics, Birkbeck College, University of London, London, WC1E 7HX, England

Summary. The effect of self fertilization on the distribution of genetic types in a population can be represented algebraically by a linear transformation. In this paper the relationship of the transformation to the genetic algebra governing the population is investigated. In particular, the problems of multiple alleles, polyploidy and linked loci are studied.

Key words: Selfing — Genetic algebras

1. Introduction

The use of the theory of genetic algebra has so far been confined to random mating populations. In many treatments of population genetics the next mating system to be considered is self fertilization, which occurs mainly among plants. A further elaboration is to suppose that in each generation a fixed proportion θ of the population undergoes random mating while the remaining proportion $1 - \theta$ is self fertilized. This is again relevant to plants where both self pollination and cross pollination take place. Mathematically, self fertilization is equivalent to complete assortative mating by genotype, and hence the mixed scheme also provides a model for the important phenomenon of partial assortative mating by genotype.

This raises the problem of how far it is possible to extend the theory of genetic algebras to cover the mixture of random mating and selfing.

In a wide variety of cases which has been characterized by Schafer [8], genetic algebras of non-selective systems can be put into a simple canonical form. It is shown in Section 2 that this is still possible for the genetic algebra of the mixed mating system provided that a certain criterion of compatibility, which is specified algebraically, is satisfied.

The fundamental difficulty of population genetics arises from the fact that the transformation from gene or genotype frequencies in one generation to those in the next is quadratic and not therefore immediately amenable to matrix methods. One of the most important results of genetic algebra is to establish that if the mode

0303–6812/78/0006/0197/$02.00

of inheritance leads to a Schafer algebra the quadratic transformation can be represented by a linear transformation on a higher dimensional space, whose matrix can be calculated by a systematic procedure. The minimal polynomial of this matrix is the characteristic equation of the recurrence relation between the vectors of genotype frequencies in successive generations.

The basic result of this paper is that when selfing is compatible with random mating in the sense defined, the linearization procedure can also be carried out for the algebra representing mixed random mating and selfing.

In Section 3 the theory developed in Section 2 is illustrated by applying it to three frequently studied systems of inheritance: multiple alleles at a single locus, polyploidy and linked loci. It is shown that for any multi-allelic or polyploid system, selfing is compatible with random mating and the application to tetraploidy is calculated in detail. The situation is not so simple when linkage is involved. In general selfing is not compatible, but it is in the special situation where independent loci are considered and where all the coupling-repulsion combinations involving the same allele set are identified. The two locus case is calculated in detail.

Let $\mathfrak{A}$ be a commutative Schafer genetic algebra with baric function β, and let $a = (a_0, \ldots, a_n)$ be a heavy basis, namely one for which $\beta(a_0) = \cdots = \beta(a_n) = 1$. Let its multiplication table relative to a be

$$a_i a_j = \sum \gamma_{ijk} a_k.$$

The vector space underlying $\mathfrak{A}$ will be called $\mathfrak{V}$ and a typical element in it will be denoted by $x = \sum x_i a_i$. Although it has not been done in previous work on the subject, it seems convenient in view of the non-linear aspects of the problem, to maintain a notational distinction between $\mathfrak{V}$ and $\mathfrak{V}^*$, the space of row vectors of coefficients $(x_0, \ldots, x_n)$. Its basis consisting of elements $(0, \ldots, 1, \ldots, 0)$ will be called a^*.

The operation 'multiplication by a_j' on $\mathfrak{V}$ is represented on $\mathfrak{V}^*$ by right multiplication by the matrix $\Gamma_j = (\gamma_{ijk})$, where $i, k = 0, \ldots, n$ label the rows and columns. Consider the linear operator S defined on $\mathfrak{V}$ by

$$xS = \left(\sum x_i a_i\right) S = \sum x_i a_i^2 = \sum \sum x_i \gamma_{iik} a_k. \tag{1}$$

The dual, or contragredient operator S^* acting on $\mathfrak{V}^*$ has the matrix $G = (\gamma_{iik})$ when referred to a^*. It can be expressed as

$$G = \sum P_i \Gamma_i \tag{2}$$

where P_i is the square matrix with 1 in its ith diagonal position and 0 everywhere else.

The operator S will be called the selfing of $\mathfrak{A}$ with respect to a. If $\mathfrak{A}$ corresponds to an actual genetic system in which a_i stands for a population composed entirely of genetic type A_i, the basis a is called a natural basis and elements for which $x_i \geqslant 0$, $\sum x_i = 1$ are called population elements. In this case, the action of S on a population element represents the replacement of the population by its filial generation under self fertilization. The selfing with respect to the natural basis will be called the natural selfing of $\mathfrak{A}$.

2. An Algebra for Mixed Selfing and Random Mating

Suppose now that a new product is defined on $\mathfrak{B}$ by

$$x \circ y = \theta xy + (1 - \theta)\beta(y)xS. \tag{3}$$

The corresponding algebra $\mathfrak{A}^0$ is clearly baric, with the same function β as $\mathfrak{A}$, but it is non-commutative. When x, y are population elements the right hand side of (3) represents a filial generation of which a proportion θ is formed from the offspring of random mating between members of x and members of y, and a proportion $1 - \theta$ by self fertilization of members of x.

In a Schafer genetic algebra it is possible to find a canonical basis c, with $a = cT'$ such that if the multiplication table with respect to the new basis is

$$c_i c_j = \sum \gamma_{ijk} c_k \tag{4}$$

then

$$\begin{aligned} \gamma_{0jk} &= \gamma_{j0k} = 0 \quad \text{for } k < j \\ \gamma_{ijk} &= 0 \qquad\qquad \text{for } k \leqslant \max(i, j) \text{ when } i, j > 0. \end{aligned} \tag{5}$$

It follows that if $\Lambda_j = T^{-1}\Gamma_j T$ denotes the right multiplication matrix with respect to the new basis, of the element a_j in the original basis, then (i) Λ_j is upper triangular for $j = 0, \ldots, n$ and (ii) the diagonals of the Λ_j are identical. The order of the components of a is immaterial, therefore T may without loss of generality be multiplied by an arbitrary permutation matrix. Consider the standard factorization $T = NM$ with N lower and M upper triangular matrices. Then $a = cM'N'$. In view of (5), cM' is also a canonical basis. Thus given any arbitrary basis the canonical basis can always be chosen in such a way that the matrix T involved is lower triangular.

Genetic algebras in general are discussed in [3] and the characteristic properties of Schafer algebras in [11, 5, 10].

When referred to the basis c^* the selfing operator has the matrix

$$L = T^{-1}GT = \sum T^{-1}P_i T\Lambda_i = \sum Q_i \Lambda_i, \tag{6}$$

where $Q_i = (u_{ji} t_{ik})$, u_{ji} being the (j, i)th element in T^{-1}. If T is lower triangular, Q_i has non-zero elements only in the rectangle where rows i to n meet columns 0 to i.

In $\mathfrak{A}^0$ the operator 'multiplication on the right by a_j' is represented by right multiplication of $\mathfrak{B}^*$ by the matrix

$$\Gamma_{\theta j} = \theta\Gamma_j + (1 - \theta)G. \tag{7}$$

When referred to the canonical basis the matrix takes the form

$$\Lambda_{\theta i} = T^{-1}\Gamma_{\theta i}T = \theta\Lambda_i + (1 - \theta)L. \tag{8}$$

Equations (7) and (8) exhibit the multiplication constants of $\mathfrak{A}^0$ in the natural and canonical bases respectively.

If L is upper triangular the set of matrices $\Lambda_{\theta i}$ will be upper triangular with identical diagonals. Thus, extending the definition in a straightforward way to the non-commutative case, $\mathfrak{A}^0$ can be called a right Schafer genetic algebra when this is true. In a Schafer algebra the subspaces $\mathfrak{N}^{(i)}$ spanned by $(c_i, \ldots, c_n)$ are ideals. The requirement that L be upper triangular is equivalent to the requirement that the $\mathfrak{N}^{(i)}$ are operator ideals in respect of the selfing operator. When this condition holds the selfing with respect to a will be said to be compatible with the canonical basis c. When there is no danger of confusion the statement that in a certain genetic algebra, selfing is compatible, will mean that a canonical basis c can be found with respect to which the natural selfing is compatible.

When T is lower triangular the effect of S on the elements of c is

$$\begin{aligned} c_i S &= \left(\sum_{j=0}^{i} a_j u_{ij}\right) S = \sum_{j=0}^{i} a_j^2 u_{ij} \\ &= \sum_{j=0}^{i} t_{ij} \sum_{s=0}^{j} \sum_{l=0}^{j} c_s c_l t_{js} t_{jl} = \sum_{s=0}^{i} \sum_{l=0}^{i} c_s c_l \sum_{j=\max s,l}^{i} u_{ij} t_{is} t_{jl} \\ &= \sum_{s=0}^{i} \sum_{l=0}^{i} \sigma(i; s, l) c_s c_l \end{aligned} \tag{9}$$

where $\sigma(i; s, l) = \sum_{j=\max(s,1)}^{i} u_{ij} t_{js} t_{jl}$.

In view of (5), S will be compatible with c if $\sigma(i; s, l) = 0$ whenever $\max(s, l) < i$. An alternative criterion, obtainable from (6) is that

$$l_{ij} = \sum_{s=0}^{i} \sum_{l=0}^{s} t_{is} u_{sl} \lambda_{lsj} = 0 \quad \text{when } j < i.$$

In an algebra representing random mating the evolutionary operator E is defined by $xE = x^2$. When x is a population element it represents the replacement of the population by its offspring under random mating. In a similar way on setting $x = y$ in (3) an operator E_θ may be defined by

$$xE_\theta = x \circ x = \theta xE + (1 - \theta)\beta(x)xS. \tag{10}$$

It represents a generation of evolution under a mixture of random mating and selfing.

In a Schafer algebra the operator E^* corresponding to E, acting on $\mathfrak{B}^*$, can be linearized [8, 1] by representing the points of $\mathfrak{B}^*$ on a surface in a higher dimensional space $\mathfrak{B}^*$. The quadratic operator E^* on $\mathfrak{B}^*$ then corresponds to a linear operator $\hat{E}^*$ on $\hat{\mathfrak{B}}^*$. The representation is obtained by augmenting the coefficient vector $(y_0, \ldots, y_n)$ with respect to the canonical basis by a finite set of monomials in its components. A fundamental result in the theory is that the augmented set of components can be so ordered that the matrix of $\hat{E}^*$ is also upper triangular.

When selfing is compatible with the algebra, the operator E_θ may be linearized, since the construction of $\mathfrak{B}^*$ and $\hat{E}^*$ (or $\hat{E}_\theta^*$) does not depend on commutativity.

3. Single Locus Algebras

The proofs of Theorems 1 and 2 have been designed to illustrate respectively the direct study of the ideal structure and the analysis of the matrix of S^* with respect to c^*.

Theorem 1. *In the zygotic algebra for a single diploid locus with multiple alleles, the natural selfing is compatible.*

Proof. The natural basis comprises the set $\{a_{ij}\}$, $i \leqslant j$, where a_{ij} symbolizes the genotype A_iA_j. Its multiplication table is $a_{ij}a_{kl} = \frac{1}{4}(a_{ik} + a_{il} + a_{jk} + a_{jl})$. A canonical basis with lower triangular T is provided by $c_{00} = a_{00}$, $c_{0i} = a_{00} - a_{0i}$, $c_{ij} = a_{00} - a_{0i} - a_{0j} + a_{ij}$, and the multiplication table in terms of this basis is $c_{00}^2 = c_{00}$, $c_{00}c_{0i} = \frac{1}{2}c_{0i}$, all other products zero. The effect of S is

$$c_{00}S = a_{00}S = a_{00} = c_{00}$$

$$c_{0i}S = (a_{00} - a_{0i})S = a_{00}^2 - a_{0i}^2$$

$$= \tfrac{3}{4}a_{00} - \tfrac{1}{2}a_{0i} - \equiv a_{ii} = c_{0i} - \tfrac{1}{4}c_{ii}$$

$$c_{ij}S = (a_{00} - a_{0i} - a_{0j} + a_{ij})S = a_{00}^2 - a_{0i}^2 - a_{0j}^2 + a_{ij}^2$$

$$= \tfrac{1}{2}(a_{00} - a_{0i} - a_{0j} + a_{ij}) = \tfrac{1}{2}c_{ij}.$$

The elements c_{ij} are ordered lexicographically to provide a canonical basis, and it may be seen directly that selfing is compatible with the ideal structure.

Theorem 2. *In the zygotic algebra for polyploidy, with chromosome or chromatid segregation or a mixture of the two, the natural selfing is compatible.*

Proof. In [7] it is shown that the transformation

$$c_i = \sum_{j=0}^{i} (-1)^j \binom{i}{j} a_j$$

provides a canonical basis for all the relevant gametic algebras, where a_j represents the gamete A^jB^{n-j}. This induces the transformation

$$(c_i, c_j) = \sum \sum (-1)^{k+l} \binom{i}{k} \binom{j}{l} (a_k, a_l) \tag{10}$$

in the duplicate. It is however possible consistently to identify with each other all natural basis elements for which $k + l$ takes a fixed value, say u, and also all canonical basis elements for which $i + j = t$ say. It is biologically natural and mathematically advantageous to make this identification, setting $(a_k, a_l) = b_{k+l} = b_u$ and $(c_i, c_j) = d_{i+j} = d_t$. Then (10) becomes

$$d_t = \sum_{u=0}^{t} (-1)^u \binom{t}{u} b_u. \tag{11}$$

The matrix $T = (t_{ij})$ then has $t_{ij} = (-1)^j\binom{i}{j}$ and it is lower triangular and self reciprocal. The coefficient σ in (9) is then

$$\begin{aligned}\sigma(i; s, u) &= (-1)^{s+u}\sum_{j=u}^{i}(-1)^j\binom{i}{j}\binom{j}{u}\binom{j}{s}\\ &= \frac{(-1)^{s+u}}{s!}\binom{i}{u}\sum_{j=u}^{i}(-1)^j\binom{i-u}{j-u}j^{(s)}\\ &= \frac{(-1)^{s}}{s!}\binom{i}{u}\sum_{j=0}^{i-u}(-1)^j\binom{i-u}{j}(u+j)^{(s)}\\ &= \frac{(-1)^{s+u-i}}{s!}\binom{i}{u}\Delta^{i-u}z^{(s)}\Big|_{z=u}.\end{aligned}$$

Now $z^{(s)}$ is a polynominal of degree s and hence this expression is zero when $i - u > s$, that is when $s + u < i$. The condition required for compatibility is only that $\sigma(i; s, u) = 0$ for $\max(s, u) < i$.

The linearization of E_θ will be exemplified for the case of the tetraploid algebra with chromosome segregation studied in [7]. The multiplication table for the gametic algebra is, with $n = 2$

$$a_ia_j = \sum\left\{\binom{i+j}{s}\binom{2n-i-j}{n-s}\Big/\binom{2n}{n}\right\}a_s.$$

With respect to the canonical basis given above it is

$$c_0^2 = c_0, \qquad c_0c_1 = \tfrac{1}{2}c_1, \qquad c_0c_2 = c_1^2 = \tfrac{1}{6}c_2.$$

Thus for the zygotic algebra, after setting $(c_i, c_j) = d_{i+j}$ the multiplication table is

$$d_0^2 = d_0, \qquad d_0d_1 = \tfrac{1}{2}d_1, \qquad d_0d_2 = \tfrac{1}{6}d_2, \qquad d_1^2 = \tfrac{1}{4}d_2$$

$$d_1d_2 = \tfrac{1}{12}d_3, \qquad d_2^2 = \tfrac{1}{36}d_4, \qquad \text{other products zero.}$$

The matrices of the selfing operator acting on $\mathfrak{Z}^*$, referred to the natural basis b^* dual to $(b_0, \ldots, b_4)$ and the canonical basis d^* dual to $(d_0, \ldots, d_4)$ respectively are

$$G = \begin{bmatrix} 1 & 0 & 0 & 0 & 0\\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & 0 & 0\\ \frac{1}{36} & \frac{2}{9} & \frac{1}{2} & \frac{2}{9} & \frac{1}{36}\\ 0 & 0 & \frac{1}{4} & \frac{1}{2} & \frac{1}{4}\\ 0 & 0 & 0 & 0 & 1\end{bmatrix}, \qquad L = T^{-1}GT = \begin{bmatrix} 1 & 0 & 0 & 0 & 0\\ 0 & 1 & -\frac{1}{4} & 0 & 0\\ 0 & 0 & \frac{5}{6} & -\frac{1}{3} & \frac{1}{36}\\ 0 & 0 & 0 & \frac{1}{2} & -\frac{1}{6}\\ 0 & 0 & 0 & 0 & \frac{1}{6}\end{bmatrix}.$$

The details of the linearization procedure are computed according to the method used in [8].

The effect of E^* on the canonical coordinates of a population element, for which $y_0 = 1$ is obtained from the identity

$$\left(d_0 + \sum y_id_i\right)E = d_0 + \sum (y_iE^*)d_i.$$

The results may be summed up as follows, where y_0 is taken to be 1:

	E^*	S^*
1	1	1
y_1	y_1	y_1
y_2	$\frac{1}{3}y_2 + \frac{1}{4}y_1^2$	$\frac{5}{6}y_2 - \frac{1}{4}y_1$
y_3	$\frac{1}{6}y_1y_2$	$\frac{1}{2}y_3 - \frac{1}{3}y_2$
y_4	$\frac{1}{36}y_2^2$	$\frac{1}{6}y_4 - \frac{1}{6}y_3 + \frac{1}{36}y_2.$

The effect of $E_\theta^* = \theta E^* + (1 - \theta)S^*$ can be obtained from the above table. It can be seen from the first column that in order to linearize E^*, a further set of coordinates corresponding to y_1^2, y_1^3, y_1^4, y_2y_1, $y_2y_1^2$, y_2^2 must be introduced. The lexicographic ordering of the augmented set is based on (i) ascending order of the greatest suffix occurring in the monomical, (ii) ascending powers of the letter suffixed by it, (iii) the same criteria disregarding the letter already considered. The augmented vector is thus

$$(1, y_1, y_1^2, y_1^3, y_1^4, y_2, y_2y_1, y_2y_1^2, y_2^2, y_3, y_4).$$

It transpires that no further coordinates need to be added to achieve the linearization of E_θ^*. Its matrix takes the form $\begin{pmatrix} I & P \\ 0 & Q \end{pmatrix}$ where I is a 5×5 identity matrix, 0 a 6×5 zero matrix and

$$\begin{bmatrix} P \\ Q \end{bmatrix} =$$

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ -\frac{1}{4}(1-\theta) & 0 & 0 & 0 & 0 & 0 \\ \theta & -\frac{1}{4}(1-\theta) & 0 & \frac{1}{16}(1-\theta) & 0 & 0 \\ 0 & \theta & -\frac{1}{4}(1-\theta) & -\frac{1}{2}\theta(1-\theta) & 0 & 0 \\ 0 & 0 & \theta & \theta^2 & 0 & 0 \\ \frac{5}{6}-\frac{1}{2}\theta & 0 & 0 & 0 & -\frac{1}{3}(1-\theta) & \frac{1}{36}(1-\theta) \\ 0 & \frac{5}{6}-\frac{1}{2}\theta & 0 & -\frac{1}{2}(\frac{5}{6}-\frac{1}{2}\theta)(1-\theta) & \frac{1}{6}\theta & 0 \\ 0 & 0 & \frac{5}{6}-\frac{1}{2}\theta & 2\theta(\frac{5}{6}-\frac{1}{2}\theta) & 0 & 0 \\ 0 & 0 & 0 & (\frac{5}{6}-\frac{1}{2}\theta)^2 & 0 & \frac{1}{36}\theta \\ 0 & 0 & 0 & 0 & \frac{1}{2}(1-\theta) & \frac{1}{6}(1-\theta) \\ 0 & 0 & 0 & 0 & 0 & \frac{1}{6}(1-\theta) \end{bmatrix}.$$

This matrix retains the phenomenon pervasive in genetic algebras that the algebraic multiplicities of its eigenvalues are not geometric. Its minimal polynomial, which is thus the characteristic equation of the recurrence relation between vectors of genotype proportions in successive generations is

$$(z - 1)(z - \tfrac{5}{6} + \tfrac{1}{2}\theta)(z - \tfrac{25}{36} + \tfrac{5}{6}\theta - \tfrac{1}{4}\theta^2)(z - \tfrac{1}{2} + \tfrac{1}{2}\theta)(z - \tfrac{1}{6} + \tfrac{1}{6}\theta) = 0.$$

It is a characteristic of a Schafer genetic algebra that the Lie algebra generated by the matrices $\Gamma_0, \ldots, \Gamma_n$ is soluble. If S is compatible then the Lie algebra generated by the Γ_i and G will still be soluble. The increase in the degree of solubility provides an indication of the incongruity between random mating and selfing. In the case studied above it is increased from 2 to 3.

4. Several Loci

When linked loci are involved selfing is not in general compatible, but some limited results can be obtained.

If k loci segregate independently the gametic algebra is the direct product of those corresponding to the individual loci [9]. The zygotic algebra $\mathfrak{Z}_1$ is then obtained by commutative duplication. Consider now the direct product $\mathfrak{Z}_2$ of the duplicates of the algebras for the separate loci. Contrary to part of Theorem 5 of [4], $\mathfrak{Z}_1 \neq \mathfrak{Z}_2$. Indeed with two alleles per locus $\mathfrak{Z}_1$, $\mathfrak{Z}_2$ have dimensions $2^{k-1}(2^k+1)$, 3^k respectively. In the discussion of zygotic algebras in [8] $\mathfrak{Z}_1$ and $\mathfrak{Z}_2$ are erroneously taken to be identical. This question is also discussed in [6].

The natural basis elements of the gametic algebra can be written $a(i_1, \ldots, i_k)$ where each i_j is 0 or 1, coding the alleles at locus j. The basis elements of $\mathfrak{Z}_1$ can be written $a(i_1, \ldots, i_k; j_1, \ldots, j_k)$ where the order of the sets separated by a semicolon is immaterial. Those of $\mathfrak{Z}_2$ can be written $a(i_1, j_1; \ldots; i_k, j_k)$ where the order within each of the pairs is immaterial. The correspondence

$$a(i_1, \ldots, i_k; j_1, \ldots, j_k) \rightarrow a(i_1, j_1; \ldots; i_k, j_k) \tag{12}$$

establishes a homomorphism of $\mathfrak{Z}_1$ onto $\mathfrak{Z}_2$. This follows from the fact that when the loci segregate independently, the gametic output of all the inverse images of $a(i_1, j_1; \ldots; i_k, j_k)$ is the same, and that this output specifies the product. It can be seen that in this case $\mathfrak{Z}_2$ represents the zygotic system when genotypes are classified according to the allelic content at each locus without distinguishing between the various possible partitions among the chromosomes.

Theorem 3. *In the zygotic algebra for k independently segregating loci with no distinction between the partitions of genes between chromosomes, the natural selfing is compatible.*

Proof. The property that selfing is compatible is inherited by direct products, as is clear on considering a lexicographic ordering of the elements of the canonical basis. Compatibility at one locus is established for the diploid zygotic algebra by either Theorem 1 or Theorem 2, and the result follows.

When there is non-trivial linkage the mapping (12) is no longer a homomorphism. Consider two loci with alleles A, B and α, β respectively and recombination fraction r. Put $1 - r = s$. The gametes $A\alpha$, $A\beta$, $B\alpha$, $B\beta$ will be denoted by a_1, a_2, a_3, a_4, the zygotes by a_{ij}, the canonical basis elements of the gametic algebra by $c_0 = a_0$, $c_1 = a_0 - a_1$, $c_2 = a_0 - a_2$, $c_3 = a_0 - a_1 - a_2 + a_3$ and the duplicate canonical basis elements by c_{ij}, $i \leqslant j$.

A typical population element referred to the canonical basis is $\sum y_{ij}c_{ij}$ with $y_{00} = 1$. The following table gives the effect on the vector $(y_{00}, \ldots, y_{33})$ of the operations corresponding to multiplication by $c_{00} = a_{00}$, of E^* and of S^*.

	R	E^*	S^*
1	1	1	1
y_{01}	$\frac{1}{2}y_{01}$	y_{01}	y_{01}
y_{02}	$\frac{1}{2}y_{02}$	y_{02}	y_{02}
y_{03}	$\frac{1}{2}(sy_{03}+ry_{12})$	$sy_{03}+ry_{12}$	$sy_{03}+ry_{12}$
y_{11}	0	$\frac{1}{4}y_{01}^2$	$\frac{1}{4}(y_{11}-\frac{1}{2}y_{01})$
y_{12}	0	$\frac{1}{2}y_{01}y_{02}$	$\frac{1}{2}(y_{12}+y_{02})$
y_{13}	0	$\frac{1}{2}y_{01}(sy_{03}+ry_{12})$	$\frac{1}{2}(y_{13}-sy_{03}-ry_{12})$
y_{22}	0	$\frac{1}{4}y_{02}^2$	$\frac{1}{4}(y_{22}-\frac{1}{2}y_{02})$
y_{23}	0	$\frac{1}{2}y_{02}(sy_{03}+ry_{12})$	$\frac{1}{2}(y_{23}-sy_{03}-ry_{12})$
y_{33}	0	$\frac{1}{4}(sy_{03}+ry_{12})^k$	$\frac{1}{2}(r^2+s^2)y_{33}-\frac{1}{4}(1-r^2-s^2)(y_{13}+y_{23})$ $+\frac{1}{4}(r^2y_{12}+s^2y_{03})$

The compatibility of the selfing depends on the possibility of transforming the R_{ij} and the matrix of S^* simultaneously into upper triangular form by a similarity transformation. It can be seen from the above table that the subspace (y_{03}, y_{12}) is invariant for R_{00} and S^*. Their restrictions to this subspace have matrices respectively

$$\begin{bmatrix} \frac{1}{2}s & 0 \\ \frac{1}{2}r & 0 \end{bmatrix}, \quad \begin{bmatrix} s & \frac{1}{2} \\ r & \frac{1}{2} \end{bmatrix}$$

These matrices cannot simultaneously be put into triangular form by a similarity transformation unless $s = r = \frac{1}{2}$. Thus selfing is not compatible. This is in conformity with the result in [2].

References

1. Abraham, V. M.: Linearising quadratic transformations in genetic algebras. Unpublished Ph.D. thesis. Univ. of London 1976
2. Bennett, J. H., Binet, F. E.: Association between Mendelian factors with mixed selfing and random mating. Heredity **10**, 51–55 (1956)
3. Etherington, I. M. H.: Genetic algebras. Proc. Royal Soc. Edinburgh **59**, 242–258 (1939)
4. Etherington, I. M. H.: Duplication of linear algebras. Proc. Edinburgh Math. Soc. (2) **6**, 222–230 (1941)
5. Gonshor, H.: Contributions to genetic algebras. Proc. Edinburgh Math. Soc. (2) **17**, 289–298 (1971)
6. Heuch, I.: Genetic algebras for systems with linked loci. Math. Biosciences **34**, 35–47 (1977)
7. Holgate, P.: Genetic algebras associated with polyploidy. Proc. Edinburgh Math. Soc. (2) **15**, 1–8 (1966)
8. Holgate, P.: Sequences of powers in genetic algebras. J. London Math. Soc. **42**, 489–496 (1967)

9. Holgate, P.: The genetic algebra of *k* linked loci. Proc. London Math. Soc. (3) **18**, 315–327 (1968)
10. Holgate, P.: Characterisations of genetic algebras. J. London Math. Soc. (2) **6**, 169–174 (1972)
11. Schafer, R. D.: Structure of genetic algebras. American J. Math. **71**, 121–135 (1949)

Received November 29, 1977/Revised January 1, 1978