PROPERTIES OF THE LINEARISATION OF THE QUADRATIC TRANSFORMATION OF GENETIC ALGEBRAS

A thesis submitted for the degree of Master of Philosophy. March 1982.

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Ackowledgements

I would like to thank my supervisor, Dr. V.M. Abraham, for continued encouragement and for suggesting several ideas developed here and Professor P. Holgate for reading and commenting on the manuscript and for useful discussions at earlier stages.

I am grateful to the School of Mathematics, Statistics and Computing for employment as a research assistant while carrying out this work.

ABSTRACT

Properties of the Linearisation of the Quadratic Transformation of Genetic Algebras

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In this thesis we study the linearisation of the quadratic transformation of commutative baric algebras due to Holgate (44), elaborated and applied by Abraham (1-5).

Holgate studied the quadratic transformation $\phi : A \rightarrow A$, $x\phi = x^2$ in special train algebras and showed that they possess a plenary train. In the proof he shows that ϕ can be linearised over a higher dimensional space B in the sense that there exist a map $R : A \rightarrow B$ and a linear map $\tilde{\phi}$ on B such that $x\phi = xR\tilde{\phi}\pi$ (π the projection B onto A). Abraham applies this linearisation to give explicit formulae for plenary sequences in Schafer genetic algebras for polyploidy.

Following remarks of both Abraham and Holgate our aim was to investigate the application of the linearisation to algebras corresponding to more complex modes of inheritance and to investigate the properties of algebras in which this linearisation exists with a view to obtaining a more natural characterisation of algebras arising in genetics.

Our achievements are to have extended the linearisation to continuous time models, to have exhibited limitations to its further extension, to have given a method of constructing algebras possessing the linearisation and to have given an alternative technique that achieves the same ends by more standard linear algebraic methods.

We decided to include a survey of all relevant work that was scattered amongst papers ranging over some forty years when we commenced work. This year a text, Wörz-Busekros (58), has been published which does a very complete job of bringing the subject within the confines of a single volume. However she only briefly mentions linearisation and our survey is restricted to what we need to discuss this.

Contents

1. GENETIC ALGEBRA

The mechanisms of inheritance have been expressed symbolically since Mendel (48) (1869). Hardy (35) in 1908 introduced elementary algebra in proving an equilibrium theorem, the 'Hardy-Weinberg Principle'. Bernstein (9) (1922) used algebraic methods to determine and classify all quadratic transformations representing systems of inheritance which achieve equilibrium after one generation, in 3 dimensions. We are concerned with 'genetic algebras' related to systems of nonassociative algebras which were first defined by Etherington (21) in 1939 and extended thereafter by Schafer, Gonshor, Holgate and others. The basic papers are Etherington (21), Schafer (54), Gonshor (29). See also Raffin (52) for a brief axiomatic treatment.

In the first section we give a review of some basic points from general nonassociative algebra. The next five sections outline the basic theory of genetic algebras and compare the different approaches of Etherington, Gonshor and Schafer.

1.1. Note on nonassociative algebras

We consider only the points we shall need in our presentation of genetic algebras. Our main reference for general nonassociative algebra is Schafer (55).

Algebras arising from genetic formalism regardless of special structure will be termed 'genetic algebras'. Etherington (25) gives several examples with their derivations. The denotation GA is used later for a special class. In most cases genetic algebras are finite dimensional commutative nonassociative algebras over the real or complex fields. The commutativity arises since we do not distinguish the order in which the alleles of a genetic type are taken, i.e. we assume symmetric inheritance. That they are in general nonassociative follows from the simplest examples (see (1.3.1.)), and reflects the nonassociativity of crossing in genetics.

For our purposes the following definition suffices although of course more general definitions (over general fields) are possible.

1.1.1. A is a (commutative) nonassociative algebra (NAA) if A is a finite dimensional vector space over a field F ($F = \mathbb{R}$ or $\mathbb{C}$), together with a bilinear map $\mu : A \times A \longrightarrow A$, $\mu(x,y) = xy$, satisfying $\mu(x,y) = \mu(y,x)$. μ defines a multiplication satisfying:

$$xy = yx$$

$$(x+y)z = xz + yz$$

$$\alpha(xy) = (\alpha x)y = x(\alpha y)$$

for all $\alpha \in F$ and $x,y,z \in A$.

Well known examples of NAA's are the 3-dimensional vector algebra with the cross product and Cayley's 8-dimensional real division algebra.

Various subclasses of NAA have been defined by postulating some alternative to associativity. Let A be an NAA then we have the following.

1.1.2. A is a Jordan algebra if every x,y in A satisfies the Jordan identity

$$(xy)x^2 = x(yx^2).$$

Given any associative algebra A we can associate with it a Jordan algebra by defining the Jordan multiplication

$$x \cdot y = \tfrac{1}{2}(xy + yx).$$

1.1.3. A is a Lie algebra if for all x,y,z in A the anti-commutativity and Jacobi identities hold i.e. respectively

$$x^2 = 0$$

(over fields of characteristic zero this is equivalent to

$$xy = -yx)$$

$$(xy)z + (yz)x + (zx)y = 0.$$

1.1.4. Given any associative algebra A we obtain a Lie algebra L(A) by replacing the given multiplication by the commutator product,

$$[x,y] = xy - yx.$$

Holgate (46) uses properties of a related Lie algebra in characterising genetic algebras.

1.1.5. A is an alternative algebra if for all a,x in A the alternative laws hold i.e.

$$ax^2 = (ax)x$$

$$x^2a = x(xa).$$

1.1.6. A is a power associative algebra if for every x in A, $\langle x \rangle$ is an associative subalgebra of A, where $\langle x \rangle$ denotes the algebra generated by the element x.

In a NAA powers are ambiguous. Etherington (20) has given a theory of products using a notion he calls 'shape' which gives the association or bracketing of the product regardless of the different elements entering into it. The degree of a product (or shape) is the number of elements in it and the altitude is the highest nesting of brackets occuring. Products in which factors are absorbed one at a time e.g.,

$$(a((bc)d))e$$

are called primary products. Products generated by repeated squaring of an element (or having the same shape) are called plenary. Primary and plenary products are in a sense extreme forms between which all other products lie. The following are of particular importance to us.

1.1.7. Let A be a NAA and let $x \in A$. The principal powers x^n are defined by

$$x^1 = x$$
$$x^n = x.x^{n-1}$$

and the plenary powers $x^{[n]}$ are defined

$$x^{[1]} = x$$
$$x^{[n]} = (x^{[n-1]})^2.$$

1.1.8. x is principally nilpotent of index k if the principal power $x^k = 0$ for some integer k and k is minimal for this. More generally nilpotency may be defined with respect to shape. A useful stronger form of nilpotency was defined by Albert (6); x is strongly nilpotent if there exists an integer k such that all products of degree k are zero independent of association. For commutative algebras these are equivalent (Etherington (23)).

These definitions of nilpotency carry over to algebras in the obvious way. In associative (or power associative) algebras these definitions coincide with usual nilpotency.

Several properties of nilpotency true in the associative case fail in general, e.g. every associative non-nilpotent algebra possesses an idempotent but this fails for non-associative algebras.

We note that the definitions of subalgebra, ideal, homomorphism, kernel and quotient algebra do not involve associativity and hence are carried over without modification.

1.1.9. The <u>derived series</u> of A is the series of subalgebras,

$$A^{(1)} \geq A^{(2)} \geq \ldots$$

defined by

$$A^{(1)} = A$$
$$A^{(i+1)} = (A^{(i)})^2$$

where A^2 is the subalgebra of A generated by all pairwise products in A. A is said to be <u>soluble</u> if there exists an integer r such that $A^{(r)} = 0$.

An ideal I of A is soluble if I = 0 or it is a soluble subalgebra of A. All soluble ideals of an algebra are contained in the unique maximal soluble ideal S and the only soluble ideal of the quotient A/S is the zero ideal.

Any nilpotent subalgebra I of A is soluble. This follows from the fact that if I is an ideal of A and T(A) is the associative algebra of multiplications $R_x: A \to A$, $yR_x = yx$ then I is nilpotent iff T(I) is nilpotent. In fact any nilpotent algebra is soluble.

Since, for us, the underlying vector space of a NAA is of finite dimension n it is determined up to isomorphism by n, i.e. is isomorphic to $\mathbb{R}^n$ or $\mathbb{C}^n$.

1.1.10. Let A be a NAA and have basis $a_1, \ldots, a_n$. Then the multiplication of A is completely determined by n^3 multiplication or <u>structure constants</u> λ_{ijk} $i,j,k = 1,\ldots,n$ given by the basic products

$$a_i a_j = \sum_k \lambda_{ijk} a_k.$$

These n^2 equations form the <u>multiplication table</u> of A.

We conclude this section with a brief note on structure.

1.1.11. If A is 1-dimensional then A is associative.

For, $A = \langle a_1 \rangle$ and $a_1^2 = \lambda_{111} a_1$. If $\lambda_{111} = 0$ then $xy = 0$ for all x,y in A. In this case A is called the (1-dimensional) <u>zero algebra</u>. If $\lambda_{111} \neq 0$ then taking $b_1 = \lambda_{111}^{-1} a_1$ as basis, $b_1^2 = b_1$ and A is isomorphic to F under $\alpha \mapsto \alpha b_1$. In both cases we clearly have associativity.

Even in the next dimension (n = 2) there are a great variety of possible NAA's.

1.1.12. Structure of associative algebras

For associative algebras there is a well developed structure theory depending largely on the notion of the 'radical' ideal. In any associative algebra A there exists an ideal R , the <u>radical</u> of A , which is the unique maximal ideal of all nilpotent elements of A. Algebras with zero radical are called <u>semisimple</u>. Any semisimple algebra is a direct sum of <u>simple</u> algebras i.e. not the zero algebra and having no proper ideals. Any simple algebra is a ~~sum~~ direct product of the total matrix algebra of dimension n^2 (n = dimA) and a division algebra. A/R is semisimple. Thus up to a determination of all division algebras the structure of A/R is determined. If the underlying field is $\mathbb{R}$ it is well known that $\mathbb{R}$, $\mathbb{C}$, $\mathbb{H}$ (quaternions) and $\mathbb{O}$ (Cayley numbers) are the only division algebras. Since A is isomorphic to A/R + R, knowledge of the radical completes the structure. Proof of these theorems uses the "Peirce decomposition' relative to an idempotent.

For NAA the situation is far from well developed. Lie algebras have been given an analogous structure theory, although since there are no idempotents different arguments are used. But this is not the case in general.

1.1.13. Structure of nonassociative algebras

While the notions of subalgebra, ideal, iso-, homomorphism, simplicity, factor algebra and direct sum are independent of associativity that of radical is not. The following definition was given by Albert (6). If A is a NAA homomorphic to a semisimple algebra then the radical R of A is the minimal ideal of A such that A/R is semisimple. However there the analogy ends. NAA's are just too general for a complete structure theory, in the sense that it is possible to constuct NAA's with almost any undesirable property.

Progress has been made only for restricted classes e.g. Lie, alternative, Jordan and power associative algebras. This difficulty with structure vanishes for 'Schafer genetic algebras' (see (1.4.7.)) but recurs whenever we consider wider classes e.g. 'train algebras'.

The definition of some classes of genetic algebras employs the notion of rank equation.

1.1.14. The principal (plenary) rank equation of a NAA is the (unique) monic polynomial equation in the principal (plenary) powers satisfied by the general element x of A of minimal degree whose coefficients are homogeneous polynomials in the coordinates of x.

The existence of the principal rank equation is proved by Dickson (19).

1.2. Baric algebras

Every linear associative algebra possesses a matrix representation i.e. is isomorphic to a subalgebra of the matrix algebra of the underlying vector space. NAA's on the other hand may not have a representation. 'Baric algebras' are those that have the simplest kind of representation. The following ideas are due to Etherington (21).

1.2.1. An algebra A over a field F ($\mathbb{R}$ or $\mathbb{C}$) is said to be baric iff it has a non-trivial homomorphism $\beta : A \rightarrow F$.

Genetic algebras for systems in which selection does not occur are baric. The zero algebra and any algebra for which a basis consisting entirely of nilpotent elements exists are not baric.

In a baric algebra A there exists $x \in A$ such that $\beta(x) \neq 0$. β is called the baric (or weight) function and $\beta(x)$ the baric value or weight of x. $x \in A$ such that $\beta(x) \neq 0$ can be normalised by taking $X = x/\beta(x)$ with unit weight.

1.2.2. If A is baric then $\ker\beta$ is an invariant subalgebra of A i.e. $A(\ker\beta) \subseteq \ker\beta$ and $A/\ker\beta$ is isomorphic to F. $\ker\beta$ is called the <u>nilalgebra</u> of A.

1.2.3. $\beta(x)$ is a root of the principal rank equation of (A, β).

1.2.4. Weight functions are not in general unique. (But as we shall see they are unique for important classes of genetic algebras.)

1.2.5. Any commutative NAA R of dimension n-1 over F gives rise to a baric algebra A of dimension n by adjunction of an element u to R such that $u^2 - u$, $uz \in R$ for all $z \in R$, (Schafer (54)).

1.2.6. If A has multiplication

$$a_i a_j = \sum_k \lambda_{ijk} a_k$$

where

$$\sum_k \lambda_{ijk} = 1 \text{ , for all } i,j$$

then A is baric with weight function

$$\beta(x) = \beta(\sum_i x_i a_i) = \sum_i x_i .$$

1.2.7. If A is baric with basis (a_i) and $\beta(a_j) = 1$ and if for every linear map $L : A \to A$ such that $\beta(x) = \beta(xL)$ we have $(xy)L = (xL)(yL)$ then

$$a_i a_j = \tfrac{1}{2}(a_i + a_j)$$

is the unique multiplication (see Gonshor (29)).

If A is a baric algebra we have the following.

There exists $x \in A$ such that $\beta(x) = 1$ and hence x may be taken as a basis element.

Any u in a basis of A such that $\beta(u) \neq 0$ can be replaced by $v = x - u$ with $\beta(v) = 0$.

Any u in a basis of A such that $\beta(u) \neq 0$ can be replaced $v = u/\beta(u)$ with $\beta(v) = 1$.

Thus we have (Etherington (22)):

1.2.8. There exists a linear transformation taking a given basis of A into one having any desired number (≥ 1) of base elements with weight 1 and the rest with weight 0.

Such a basis with p elements of weight 1 and q of weight 0 with $p+q = \dim(A)$ will be called an <u>Etherington canonical basis</u>. In such a basis $\beta(x)$ is the sum of the 'heavy' coefficients.

1.2.9. Etherington (22) has defined the <u>nilproduct</u> for baric algebras:

$$x \,.\, y = xy - \tfrac{1}{2}\beta(x)y - \tfrac{1}{2}\beta(y)x.$$

The set of nilproducts is a subalgebra P of A and we have

$$A \supset \ker\beta \supset P \supset (\ker\beta)^2.$$

Using these ideas Etherington proves that:

$$a_i a_j = \tfrac{1}{2}\beta(a_i)a_j + \tfrac{1}{2}\beta(a_j)a_i + \sum_k \lambda_{ijk}a_k$$

where $\lambda_{ijk} = \lambda_{jik}$ and the a_k are nilsquares of unit weight.

1.2.10. Let (A,β) be a baric algebra with canonical basis (c_i), (see 1.5.1.) $i = 0,1,\ldots,n$ then,

$$K_1 = \ker\beta = \operatorname{span}\{c_1,\ldots,c_n\},\ K_2 = \operatorname{span}\{c_2,\ldots,c_{n-1}\},$$
$$\ldots,\ K_{n-1} = \operatorname{span}\{c_{n-1}\}$$

are a decreasing sequence of ideals of A and

$$A \xrightarrow{\pi_{n-1}} A/K_{n-1} \xrightarrow{\pi_{n-2}} A/K_{n-2} \xrightarrow{\pi_{n-3}} \ldots \xrightarrow{\pi_1} A/K_1 \xrightarrow{\cong} F$$

where π_i is the projection of the cosets of K_{i+1} onto the cosets of K_i and the multiplication of A/K_i is identical to that of A omitting c_i as necessary. The composition $\pi_1 \pi_2 \dots \pi_{n-1} = \beta$, the baric function (see Fortini and Barakat (28)).

1.3 Train algebras and special train algebras

The following definitions are due to Etherington (21).

1.3.1. An algebra A is a train algebra (TA) of A is baric and if the coefficients of the principal rank equation are functions of $\beta(x)$ only. The equation is then called the (principal) train equation and the principal powers are said to form a train.

1.3.2. Example. Let $\mathcal{A}$ be the algebra with basis $\{A, a\}$ over $\mathbb{C}$ and multiplication

$$A^2 = A, \ Aa = \tfrac{1}{2}(A + a), \ a^2 = a.$$

$\beta : A \to \mathbb{C}$, $(x_1 A + x_2 a) = x_1 + x_2$ is a baric function. The principal rank equation is

$$x^2 - (x_1 + x_2)x = 0.$$

$\mathcal{A}$ is a train algebra since the coefficients of this equation are 1 and $\beta(x)$.

Let (A, β) be a baric algebra over $\mathbb{C}$. If

$$f(x) = x^r + \lambda_1 x^{r-1} + \dots + \lambda_{r-1} x = 0$$

is the rank equation then in general the λ_i are homogeneous polynomials of degree i in the coordinates of x, and $\beta(x)$ satisfies $f(x)=0$. If A is TA then since the λ_i are homogeneous we have

$$\lambda_i = \sigma_i \beta(x)^i, \text{ for some } \sigma_i \in \mathbb{C}.$$

After normalisation the equation becomes

$$F(X) = X^r + \theta_1 X^{r-1} + \ldots + \theta_{r-1} X = 0$$

where the θ_i are constants independent of x. This last equation may be regarded as a linear recurrence relation with constant coefficients connecting the principal powers

$$X^r = - \theta_1 X^{r-1} - \ldots - \theta_{r-1} X.$$

For our purposes the rank equation will usually be the train equation.

We have the following sufficient conditions for TA given by Etherington (21).

1.3.3. If (A, β) is a baric algebra, $\ker\beta$ is nilpotent and $(\ker\beta)^m$ are all ideals of A for m = 1,2,... then A is TA. (Where nilpotent means principally nilpotent and $(\ker\beta)^m = (\ker\beta)(\ker\beta)^{m-1}$).

1.3.4. The converse is true for A of <u>rank</u> 1, 2 or 3 (degree of rank equation) but not true in general for higher rank.

1.3.5. A <u>special train algebra</u> (STA) is a TA satisfying (1.3.3.).

Etherington proved (1.3.3.) assuming that the roots of the rank equation do not include $\frac{1}{2}$. Abraham (1) relaxed this and proved (1.3.4.) by giving an example of a TA that is not STA of rank 4.

1.3.2.' In example (1.3.2.) take the Etherington canonical basis

$$c_o = \tfrac{1}{2}(A + a), \quad c_1 = A - a.$$

$$c_0^2 = c_0, \quad c_0c_1 = \tfrac{1}{2}c_1, \quad c_1^2 = 0.$$

And the baric function is

$$\beta(c_0) = 1, \quad \beta(c_1) = 0.$$

Now $\ker\beta = \langle c_1 \rangle$, $(\ker\beta)^2 = 0$, i.e. this algebra satisfies (1.3.3.) and hence is STA.

In STA's many sequences, in addition to the principal powers, may form trains. In particular the plenary powers.

The genetic significance of the principal and plenary trains are that the sequence of principal powers represent successive generations under backcrossing with the initial population and the sequence of plenary powers that of successive generations under random mating (given also the genetic assumptions (G) see p. 107).

1.3.6. Let A have basis $a_1, \ldots, a_n$ and multiplication

$$a_ia_j = \sum_k \lambda_{ijk}a_k.$$

The <u>duplicate</u> A' of A is defined by the multiplication

$$(a_ia_j)(a_ka_l) = \sum_{m,n} \lambda_{ijm}\lambda_{kln}a_{mn}.$$

We consider the genetic significance of duplication below; here we simply distinguish it from the <u>direct product</u> $A \times A$ which has multiplication

$$a_{ij}a_{kl} = \sum_{m,n} \lambda_{ikm}\lambda_{jln}a_{mn}, \quad (a_{rs} = a_ra_s).$$

Consider autopolyploid n-loci multiple allelic symmetric inheritance under the assumptions (G). We now define the 'fundamental genetic algebras'.

Let a_i, $i = 1,2, \ldots, n$ be the set of gametic types in a population x. Each zygote produces a gametic series

$$a_i a_j = \sum_k \lambda_{ijk} a_k, \quad (\sum_k \lambda_{ijk} = 1).$$

1.3.7. Taking the a_i as basis and the gametic series as multiplication defines a commutative NAA, G, called the <u>gametic algebra</u> . G is baric with $\beta(a_i) = 1$. (e.g. (1.3.1.)).

A population expressed in terms of the frequencies of the gametic types it produces is represented by an element x of unit weight in G i.e.

$$x = \sum_i x_i a_i, \quad \text{where } \sum_i x_i = 1.$$

If x,y are populations then

$$xy = \sum_{i,j} x_i y_j a_i a_j = \sum_{i,j,k} x_i y_j \lambda_{ijk} a_k$$

is the distribution of gametes after random mating of x with y. The product left in quadratic form gives the distribution of zygotes in xy.

Putting $a_i a_j = a_{ij}$ we obtain $\{a_{ij},\ i,j = 1,2, \ldots, n\}$ the set of zygotic types. Each couple produces a zygotic series

$$a_{ij} a_{kl} = \sum_{m,n} \lambda_{ijm} \lambda_{kln} a_{mn}.$$

1.3.8. Taking the a_{ij} as basis and the zygotic series as multiplication defines a commutative NAA, Z, called the <u>zygotic algebra</u>.

A population is represented in terms of its zygotic types by an element of unit weight in Z,

$$x = \sum_{i,j} x_{ij} a_{ij}, \quad \text{where } (\sum_{i,j} x_{ij} = 1).$$

The gametic and zygotic representations are related by the gametic series since, given $x = \sum_{i,j} x_{ij} a_{ij} =$ $= \sum_{i,j} x_{ij} a_i a_j$ and $a_i a_j = \sum_k \lambda_{ijk} a_k$ we have,

$$x = \sum_{i,j,k} x_{ij} \lambda_{ijk} a_k.$$

It follows that it is sufficient to consider only the gametic algebras, noting that the gametic representation determines the next generation's zygotic representation.

1.3.9. Example. Zygotic algebra for a diallelic diploid locus.

Let $\mathcal{Z}$ be the algebra with basis AA, Aa, aa and multiplication

$$AA^2 = AA,\ AA.Aa = \tfrac{1}{2}(AA+Aa),\ AA.aa = Aa,$$

$$Aa.Aa = \tfrac{1}{4}AA+\tfrac{1}{2}Aa+\tfrac{1}{4}aa,\ Aa.aa = \tfrac{1}{2}(Aa+aa),\ aa^2 = aa.$$

i.e. Z is the duplicate of (1.3.2.). Take an Etherington canonical basis

$$c_o = AA,\ c_1 = A(A-a),\ c_2 = (A-a)^2.$$

Then the multiplication becomes

$c_o^2 = c_o$, $c_oc_1 = \tfrac{1}{2}c_1$, $c_1^2 = \tfrac{1}{4}c_2$, $c_2^2 = c_oc_2 = c_1c_2 = 0$.

Define $\beta(c_o) = 1$, $\beta(c_i) = 0$ for $i > 0$ (i.e. $\beta(AA) = \beta(Aa) = \beta(aa) = 1$). Then $\ker\beta = \langle c_1, c_2\rangle$, $(\ker\beta)^2 = \langle c_2\rangle$ and $(\ker\beta)^m = 0$ for all $m > 2$. Thus Z is STA.

Putting $x = x_oc_o + x_1c_1 + x_2c_2$ we find that the principal train equation is

$$x^3 - x^2 = 0.$$

(Genetically this tells us that there is equilibrium from the second generation under backcrossing to the initial population x.) Similarly we have the plenary train equation

$$x^{[3]} - x^{[2]} = 0$$

(which tells us that there is equilibrium after one generation of random mating; this is Hardy-Weinberg equilibrium).

Repeated duplication yields the copular algebra and so on; elements of unit weight in each of these algebras represent populations in terms of the couples that produce its zygotes and so on.

The direct product has the following genetic significance. If a population is classified into genetic types in two ways then the distribution of genetic types is represented by an element of unit weight in the direct product of the corresponding algebras. In particular the genetic algebra depending on several autosomal linkage groups is the direct product of the genetic algebras of each linkage group.

1.4. Schafer genetic algebras

Let A be an NAA of dimension n+1 over $\mathbb{C}$. For a fixed $x \in A$ there exist linear maps

$$R_x : A \longrightarrow A, \quad aR_x = ax$$

$$L_x : A \longrightarrow A, \quad aL_x = xa$$

called respectively the right and left multiplications of A. If A is commutative $R_x = L_x$.

Although only the $x \in A$ with non-negative real coefficients x_i such that $\sum_i x_i = 1$ have a probability interpretation, it is inconvenient to restrict ourselves to real algebras since while a real STA is a real TA, it is not necessarily a real 'Schafer genetic algebra' (see Heuch (36)). For this reason we shall henceforth assume that our underlying field is that of the complex numbers.

1.4.1. The transformation algebra (or multiplication algebra) T(A) of A is the algebra of all polynomials in the maps R_x $(x \in A)$ with coefficients in $\mathbb{C}$.

We have for all $L \in T(A)$

$$L = \alpha I + f(R_x, R_y, \ldots), \quad (x,y,\ldots \in A).$$

In general the characteristic polynomial $\det(\alpha I - L)$ of $L \in T(A)$ has coefficients which are polynomials in ~~and~~ the coordinates of the $x,y,\ldots$.

1.4.2. A (Schafer) genetic algebra (GA) is a commutative baric algebra (A,β) over $\mathbb{C}$ such that the coefficients of $\det(\alpha I - L)$ depend on the $x,y,\ldots$ only through $\beta(x)$, $\beta(y)$, ... i.e. if $S, T \in T(A)$ and $S = \alpha I + f(R_{y_0}, R_{y_1}, \ldots)$ and $T = \alpha I + f(R_{x_0}, R_{x_1}, \ldots)$ such that $\beta(x_i) = \beta(y_i)$, then T and S have identical characteristic polynomials.

The following results are due to Schafer (54).

1.4.3. The class of GA is closed under duplication.

1.4.4. If A is GA then A is TA. (The converse is false by an example of Abraham (1)).

1.4.5. If A is STA then A is GA. (The converse is false, a counter example being the copular algebras of simple Mendelian inheritance, e.g. (1.4.6.)

1.4.6. Example.

Starting with the algebra G (1.3.2.), take a canonical basis

$$c_0 = a_1, \; c_1 = a_2 - a_1 \quad \text{where } a_1 = A, \; a_2 = a$$

we obtain the multiplication for G

$$c_0^2 = c_0, \quad c_0c_1 = \tfrac{1}{2}c_1, \quad c_1^2 = 0.$$

Duplicating this gives the algebra Z. Writing its basis

$$d_0 = c_0c_0, \; d_1 = c_0c_1, \; d_2 = c_1c_1$$

we obtain the multiplication for Z

$$d_0^2 = d_0, d_0d_1 = \tfrac{1}{2}d_1, d_1^2 = \tfrac{1}{4}d_2, d_0d_2 = d_1d_2 = d_2^2 = 0.$$

Duplicating again gives the copular algebra C. With the same convention for the basis as for Z we obtain the multiplication for C

$$e_o^2 = e_o,\ e_oe_1 = \tfrac{1}{2}e_1,\ e_oe_2 = \tfrac{1}{4}e_3$$
$$e_1^2 = \tfrac{1}{4}e_2,\ e_1e_2 = \tfrac{1}{8}e_4$$
$$e_2^2 = 1/16e_5$$

and $e_oe_j = e_ie_j = 0$ for $i = 1,\ldots,5;\ j = 3,4,5.$

The baric function is defined by

$$\beta(e_o) = 1,\ \beta(e_i) = 0 \text{ for } i > 0.$$

$\ker\beta = \langle e_1,\ldots,e_5\rangle$, $(\ker\beta)^2 = \langle e_2,e_4,e_5\rangle$, $(\ker\beta)^3 = \langle e_4,e_5\rangle$, and $(\ker\beta)^4 = 0$.

Now since duplication preserves GA, C is GA. However C is not STA since not all the $(\ker\beta)^m$ are ideals of C. In particular, $C(\ker\beta)^2$ contains $e_oe_2 = \tfrac{1}{4}e_3$ which is not a member of $(\ker\beta)^2$ i.e. $(\ker\beta)^2$ is not an ideal of C.

As the title of his paper (54) indicates, Schafer's main concern is the formal structure of GA's. Taking the nonassociative radical R of a GA A, a structure theory must exhibit the nature of R and the quotient A/R. For GA the situation is, as Schafer shows, very simple.

1.4.7. If A is GA then $R = \ker\beta$ and A/R is isomorphic to the field of complex numbers.

1.5. Gonshor's definition of GA

1.5.1. A (Gonshor) genetic algebra is a commutative baric algebra over $\mathbb{C}$ such that there exists a basis (c_i), i=0,1, ,...,n such that the structure constants relative to this basis satisfy

(G1) $\lambda_{ooo} = 1$

(G2) $\lambda_{ojk} = 0$ if $k < j$

(G3) $\lambda_{ijk} = 0$ if $i, j > 0$ and $k \leq \max(i,j)$.

Any basis satisfying (1.5.1.) will be called a (Gonshor) canonical basis.

Such bases are not unique. This can be seen as follows. Let (A, β) be an n+1 dimensional GA with canonical basis (c_i) and structure constants λ_{ijk}. Let $c'_o \in A$ such that $\beta(c'_o) = 1$. Since $\beta(c_o) = 1$, $\beta(c_i) = 0$ $(i > 0)$ and β is linear we have $(c'_o, c_1, \ldots, c_n)$ is a basis of A. (G3) is not affected by the change of basis. On setting $c'_o = \sum_i x_i c_i$ we find

$$c'^2_o = (\sum_i x_i c_i)(\sum_j x_j c_j)$$
$$= c_o + \sum_{k=1}^{n} (\sum_{i,j=o}^{n} \lambda_{ijk} x_i x_j) c_k.$$

So $\lambda'_{ooo} = 1$ i.e. (G1) holds. And,

$$c'_o c_j = (\sum_i x_i c_i) c_j$$
$$= \sum_{k=j}^{n} \lambda_{ojk} c_k + \sum_{k=j+1}^{n} (\sum_{i=1}^{n} x_i \lambda_{ijk}) c_k.$$

So $\lambda'_{ojk} = 0$ if $k < j$ i.e. (G2) holds. Now since $\lambda'_{ijk} = \lambda_{ijk}$ for $i > 0$ $(c'_o, c_1, \ldots, c_n)$ is a distinct Gonshor canonical basis.

Let A be an algebra with basis (c_i), dimension n and multiplication, $c_i c_j = \sum_k \lambda_{ijk} c_k$. Let $N = \text{card}\{\lambda_{ijk} : \lambda_{ijk} = 0\}$ and $M = \text{card}\{c_i c_j : c_i c_j = 0\}$. Then $N \leq n^3$ and $M \leq n^2$. For genetic algebras, relative to the natural basis, $N = M = 0$. For GA clearly N is a canonical basis invariant. And, for example,

$$N \geq \tfrac{1}{2}(n^2 - n) + n(n-1) + (n-1)(n-2) + \ldots + 2.1$$

is a lower bound. The first term arising from (G2) and the second from (G3). Thus $N \geqslant \sum_{r=1}^{n} r^2$. It is an open question whether amongst all bases, canonical bases give maximal N.

Let A be a (Gonshor) genetic algebra with the notation of (1.5.1.), then the following results hold and are due to Gonshor (29).

1.5.2. If $I = \langle c_1, \ldots, c_n \rangle$ and I^r is an ideal of A for all $r = 1,2,\ldots$ then A is STA.

Corresponding to a choice of canonical basis in an STA A with $K = \ker\beta$ we have the following decomposition of A

$$A \cong F + K/K^2 + \ldots + K^{r-1}/K^r$$

where r is the nilpotency index of K. For, $(\ker\beta)^r = 0$ and $(\ker\beta)^s$ is an ideal of A for all integers $0 < s < r$. Now $0 = K^r \subset K^{r-1} \subset \ \ldots \subset K \subset A$. And $A \cong \langle c_o \rangle + K$, while $\langle c_o \rangle \cong F$. Thus $K/K^2 \cong \langle c_1 \rangle$, $K^2/K^3 \cong \langle c_2 \rangle, \ldots,$ $K^{r-1}/K^r \cong \langle c_{r-1} \rangle$. Since A is STA the nilpotency index of K is equal to the dimension of A.

We note that GA is insufficient for the above result. For example in the copular algebra C of (1.4.6.): dim(C)=6, $K = \langle e_1, \ldots, e_5 \rangle$, $K^2 = \langle e_2, e_4, e_5 \rangle$, $K^3 = \langle e_4, e_5 \rangle$ and $K^4 = 0$. In this case we have the decomposition

$$C \cong \langle e_o \rangle + \langle e_1, e_3 \rangle + \langle e_2 \rangle + \langle e_4, e_5 \rangle$$

which does not correspond with the canonical basis.

1.5.3. The baric function is unique, i.e. $\beta(\sum_i x_i c_i) = x_o$ is the only non-trivial homomorphism into $\mathbb{C}$. (This result was stated by Gonshor and proved in a more general form by Holgate (46).)

Thus an Etherington canonical basis with $p = 1$ and $q = n$ is a Gonshor canonical basis.

1.5.4. The principal train roots of A are among the λ_{ojj}, i.e. the λ_{ojj} are the train roots possibly with repetition.

1.5.5. A is a (Schafer) GA iff A is a (Gonshor) genetic algebra.

Henceforth we shall use the denotation GA for either definition noting that (1.5.5.) requires the base field to be algebraically closed as we have specified.

Using definition (1.5.1.) Gonshor proved the following stability theorem for STA's.

1.5.6. The sequence of plenary powers of an element of unit weight in an STA whose train roots other than λ_{ooo} satisfy $|\lambda_i| < \frac{1}{2}$ tends to an idempotent, where $\lambda_i = \lambda_{oii}$.

It is to the problem of determining formulae for these sequences that much of the sequel is devoted.

Gonshor (29) gives the canonical multiplications for several more general modes of inheritance.

For one diallelic 2n-ploid locus with gametic types $a_o, \ldots, a_n$ where a_i has i dominant, n-i recessive genes the genetic multiplication is

$$a_i a_j = \binom{2n}{n}^{-1} \sum_k \binom{i+j}{k}\binom{2n-i-j}{n-k} a_k$$

where $\binom{n}{r} = 0$ if $r < 0$ or $r > n$.

A canonical basis is obtained by the transformation

$$c_j = \sum_{i=o}^{j} (-1)^i \binom{j}{i} a_{n-i}, \text{ where } 0 \leq j \leq n.$$

The multiplication relative to this basis is

1.5.7. $$c_i c_j = \begin{cases} \binom{2n}{i+j}^{-1}\binom{n}{i+j} c_{i+j}, & \text{if } i+j \leq n \\ 0, & \text{otherwise.} \end{cases}$$

If in addition we have mutation with rates r, s dominant to recessive and vice versa respectively then

1.5.8. $$c_i c_j = \begin{cases} \binom{2n}{i+j}^{-1}\binom{n}{i+j} \cdot (1-r-s)^{i+j}\left(c_{i+j} - \binom{n-i-j}{1} r c_{i+j+1} \right. \\ \qquad \left. + \binom{n-i-j}{2} r^2 c_{i+j+2} + \ldots \right) & \text{if } i+j \leq n \\ 0 & \text{otherwise.} \end{cases}$$

The extension to multiple alleles is carried out in (30) and in (31) Gonshor proves that

1.5.9. The gametic algebra for one multiple allelic 2n-ploid locus with mutation is a GA.

1.5.10. Example. Gametic algebra for one tetraploid diallelic locus.

Let AA, Aa, aa be the gametic types. The genetic multiplication is

$$AA^2 = AA,\quad AA.Aa = \tfrac{1}{2}(AA+Aa),\quad AA.aa = 1/6AA+2/3Aa+1/6aa$$

$$Aa.Aa = AA.aa \qquad Aa.aa = \tfrac{1}{2}(Aa+aa)$$

$$aa^2 = aa.$$

A Gonshor basis is obtained using (1.2.8.)

$$c_o = AA,\quad c_1 = A(A-a),\quad c_2 = (A-a)^2.$$

This gives the multiplication

$$c_o^2 = c_o,\ c_o c_1 = \tfrac{1}{2}c_1,\ c_o c_2 = c_1^2 = 1/6c_2,\ c_1 c_2 = c_2^2 = 0.$$

1.6. Comparison of the definitions of genetic algebra

Etherington (21) gives a basis free definition of the class of baric algebras; the subclass of train algebras is defined in terms of a property of the principal rank equation and a subclass of train algebras TA, special train algebras STA, is defined by their structure. The latter two classes are genetic algebras in the sense of Etherington. Duplication of linear algebras is introduced and shown to be genetically significant. While this 'product' is not normally considered in algebra, since it does not preserve associativity, interpreted algebras, gametic, zygotic etc. are each the duplicate of the preceding one. Particular examples of these, corresponding to given modes of inheritance are given and shown to be STA in the gametic cases and only TA in the case of the duplicates. STA is therefore shown not to be closed under duplication.

Schafer (54) defines genetic algebras GA, in a basis free manner using the transformation algebra generated by the multiplication matrices, in fact by a condition on the characteristic equation of elements in this associative algebra. The GA unlike the STA are preserved under duplication. GA are in a sense intermediate between TA and STA. Like the TA but unlike the STA they do not have their structure postulated. Unlike the TA whose structure seems intractable for ranks greater than 3, the GA have a transparent structure (1.4.7.).

Gonshor (29) gives a basis dependent definition of STA which is well suited to calculation. The canonical multiplication imposed by Gonshor is proved equivalent to GA. Many of the extensions of genetic algebra and in particular the linear solution of the n'th generation problem (see 2.1.0.)) are based on the Gonshor formulation. This formulation is a consequence of the nilpotency of the kernel of the baric function. Dickson (18) proved that, for any nilpotent algebra A there exists a basis (a_i) of A such that

$$a_i a_j = \sum_{k > \max(i,j)} \alpha_{ijk} a_k .$$

STA's are nilpotent algebras $(\ker \beta)$ with an idempotent adjoined. The Gonshor multiplication is the required modification of Dickson's result.

Finally we remark that while the NAA that have received extensive study, Jordan, Lie etc., all have some alternative identity postulated and have significant links with the mainstream of mathematics, GA occupy a rather isolated position. Their lack of an alternative to the associative law makes them rather too general, while the baric property makes them rather too special. This conflict is a source of interest.

2. DEVELOPMENTS OF GENETIC ALGEBRA

In this chapter we are concerned with two developments. A 'linearisation' of the quadratic transformation of a genetic algebra due to Holgate (44) and applied by Abraham (1) and Holgate. The 'mixture' of algebras also due to Holgate (45) and considered by Heuch (41). Throughout this chapter we employ the notation of Abraham and Holgate. In chapters 3 and 4 some of this material will be considered in a different way using the notation of operators.

2.1. Linearisation

2.1.0. The n'th generation (or evolution) problem

Genetically the problem is, given an initial population vector x_o, to determine the n'th generation vector x_n, under a given mating system. More specifically we consider x_o under the assumptions (G) in a GA.

Let A be a GA and let $\phi : A \to A$, $x\phi = x^2$. The problem becomes that of obtaining a formula for the n'th plenary power of $x \in A$,

$$x(n) = x^{[n]} = x\phi^{n-1}$$

in terms of n and the coordinates of x.

The quadratic transformation ϕ is nonlinear in general in the sense that the coordinates of $x\phi$ contain nonlinear functions of the coordinates of x.

Haldane (34) solved the problem for autotetraploids by introducing new coordinates to linearise ϕ . Moran (49) asked under what conditions such a linearisation was possible. Although we do not have a complete answer to this question, Holgate has shown (see (2.1.1.)) that GA is sufficient. And we will show that while GA is not necessary and sufficient the conditions required are unlikely to be much wider than GA. Holgate (44) developed the linearisation of ϕ in GA's, in proving that GA's possess a plenary train (see (2.1.1.)). This theorem is the basis of the present section. Abraham (1) studied this linearisation with special reference to polyploid algebras, obtaining explicit formulae up to dodecaploids.

2.1.1. Holgate's linearisation theorem (HLT)

For our purposes the following is the essential part of HLT.

Let (A,ϕ) be a GA together with its quadratic transformation. Then A possesses a plenary train. Let (c_i), $i = 0,1,\ldots,n$ be a canonical basis for A and let U be the set $\{x \in A : \beta(x) = 1\}$ where β is the baric function of A. Then there exists a vector space B isomorphic to $\mathbb{R}^m$ for some m and maps $R:A \longrightarrow B$, $\tilde{\phi}:B \longrightarrow B$ such that the following diagram commutes

$$\begin{tikzcd} B \arrow[r, "\tilde{\phi}"] & B \arrow[d, "\pi"] \\ U \arrow[u, "R"] \arrow[r, "\phi"] & U \end{tikzcd}$$

where π is the projection $\mathbb{R}^m \longrightarrow \mathbb{R}^{n+1}$ $(m \geqslant n)$, i.e.

$$x\phi = xR\tilde{\phi}\pi .$$

(Holgate also proves that matrix($\tilde{\phi}$) is upper triangular and gives expressions for the plenary train roots in terms of the structure constants of A.)

The theorem is proved by induction on the dimension of

A and the key to the proof is that if λ_{ijk} $(i,j,k=0,1,\ldots,n)$ are the structure constants of A_n (the general GA of dimension n+1) then λ_{oii} give the train roots of A_n and these include the squares of the roots of A_{n-1} and correspond to the eigenvalues of $\tilde{\phi}_n$ (the linear map corresponding to $\phi : A_n \longrightarrow A_n$) which in turn are among those of the tensor product $\tilde{\phi}_{n-1} \otimes \tilde{\phi}_{n-1}$. A reduced tensor product (Kronecker product) of matrices (see Bellman (7)) is used having the same properties to obtain a space B of minimal dimension.

Abraham (1) exploits this theorem, or rather its proof, to solve the n'th generation problem for polyploid algebras by iterating $\tilde{\phi}$ instead of plenary powers, i.e. ϕ .

HLT thus provides the partial solution to Moran's question, i.e. the sufficiency of GA for linearisation. In fact Holgate assumed STA, but as Abraham noted he only uses GA. Necessary and sufficient conditions in terms of the coordinates occurring in $x\phi$ are given below (4.2.4.), but coordinate free conditions are still unknown.

The map R in HLT takes the coefficient vector $(1,x_1,\ldots,x_n)$ of a vector x in the affine space U of A_n with respect to the canonical basis, into a coefficient vector $(1,y_1,\ldots,y_{m-1})$ of a vector y in the variety V = ImR. The y_i correspond to the x_i augmented by any higher degree monomials occurring in the coordinates of $x\phi$ and any additional monomials generated by the 'linearising relation',

2.1.2. $$(x_1^{\alpha_1} \ldots x_n^{\alpha_n})\tilde{\phi} = (x_1\phi)^{\alpha_1} \ldots (x_n\phi)^{\alpha_n}.$$

The derivation of this relation is given in (3.1.4.).

2.1.3. Example. We illustrate HLT by applying it to the algebra C of (1.4.6.). Let $x \in C$ then

$$x\phi = e_0 + x_1 e_1 + \tfrac{1}{4}x_1^2 e_2 + \tfrac{1}{2}x_2 e_3 + \tfrac{1}{4}x_1 x_2 e_4 + (1/16)x_2^2 e_5 .$$

Hence we have the coordinate equations

$$1\phi = 1, \quad x_1\phi = x_1, \quad x_2\phi = \tfrac{1}{4}x_1^2, \quad x_3\phi = \tfrac{1}{2}x_2, \quad x_4\phi = \tfrac{1}{4}x_1 x_2,$$
$$x_5\phi = (1/16)x_2^2.$$

Applying the relation (2.1.2.) we obtain the linear system

$1\tilde{\phi} = 1$, $x_1\tilde{\phi} = x_1$, $x_1^2\tilde{\phi} = x_1^2$, $x_1^3\tilde{\phi} = x_1^3$, $x_1^4\tilde{\phi} = x_1^4$,
$x_2\tilde{\phi} = \tfrac{1}{4}x_1^2$, $x_1x_2\tilde{\phi} = \tfrac{1}{4}x_1^3$, $x_2^2\tilde{\phi} = (1/16)x_1^4$, $x_3\tilde{\phi} = \tfrac{1}{2}x_2$,
$x_4\tilde{\phi} = \tfrac{1}{4}x_1x_2$, $x_5\tilde{\phi} = (1/16)x_2^2$.

Thus here the map R is defined by

$$(1,x_1,x_2,x_3,x_4,x_5)R = (1,x_1,x_1^2,x_1^3,x_1^4,x_2,x_1x_2,x_2^2,x_3,x_4,x_5)$$

from the vector space $\mathbb{R}^6$ isomorphic to that underlying the algebra C to the vector space $\mathbb{R}^{11}$.

The selected ordering of the monomials of the image coordinates is defined in (4.1.2.).

Thus $\tilde{\phi}$ is the linear map with matrix

$$\begin{bmatrix} P_{11} & P_{12} \\ P_{21} & P_{22} \end{bmatrix}$$

where $P_{11} = I_5$, $P_{21} = 0_{6\times 5}$,

$$P_{12} = \left[\begin{array}{cccc} 0 & 0 & 0 & \\ 0 & 0 & 0 & \\ \tfrac{1}{4} & 0 & 0 & 0_{5\times 3} \\ 0 & \tfrac{1}{4} & 0 & \\ 0 & 0 & 1/16 & \end{array}\right] \qquad P_{22} = \left[\begin{array}{cccc} & \tfrac{1}{2} & 0 & 0 \\ & 0 & \tfrac{1}{4} & 0 \\ 0_{6\times 3} & 0 & 0 & 1/16 \\ & 0 & 0 & 0 \\ & 0 & 0 & 0 \end{array}\right]$$

The relation $x\phi = xR\tilde{\phi}\pi$ is easily verified.

With the notation of (2.1.1.) we next consider the assertion that the plenary train polynomial, p say, of A is identical to the minimal polynomial m of $\tilde{\phi}$. Holgate

(44) stated that, if $p(\tilde{\Phi})$ annihilates B then $p(\Phi)$ annihilates A and hence p divides m. Abraham (4) stated the identity, p = m, but his proof has shortcomings. The approach used is to prove p divides m and m divides p.

2.1.4. (i) $xRk\tilde{\Phi}^n = xk\Phi^n R$ (k constant)

(ii) $xp(\Phi) = xRp(\tilde{\Phi})\Pi$

(iii) p divides m.

(i) is a simple manipulation and (ii) is proved in Abraham (4). The proof of (iii) follows.

Assume that for all $x \in A$, $xRm(\tilde{\Phi}) = 0$. Then

$$xRm(\tilde{\Phi})\Pi = 0$$

since Π is linear. Thus $xm(\Phi) = 0$, by (ii) and hence since p is minimal, p divides m.

However (ii) is insufficient to prove m divides p for if we proceed as Abraham does by assuming that for all $x \in A$ $xp(\Phi) = 0$, then $xRp(\tilde{\Phi})\Pi = 0$, by (ii). This does not imply $xRp(\tilde{\Phi}) = 0$ since Π is one-one on ImR but not off this set and $xRp(\tilde{\Phi}) \notin$ ImR in general (e.g. $\tilde{\Phi} + \tilde{\Phi}^2$ in the tetraploid algebra). Thus Abraham's proof assumes that $xRp(\tilde{\Phi}) \in$ ImR.

We now turn to a method of obtaining the plenary train equation of a GA. The method is described by Etherington (23) and employed by Abraham (1). Abraham uses the method on the linearised transformation rather than directly on the quadratic transformation. That these processes are equivalent, both producing the plenary train polynomial, is due to the multiplicative property of the linear shift operator (see (3.1.4).

2.1.5 From HLT it follows that the coordinate equations of the linearised transformation $\tilde{\Phi}$ are triangular in form:

$$x_o\tilde{\Phi} = \alpha_{oo}x_o$$
$$x_1\tilde{\Phi} = \alpha_{o1}x_o + \alpha_{11}x_1$$
$$\cdots$$
$$x_n\tilde{\Phi} = \alpha_{on}x_1 + \ldots + \alpha_{nn}x_n$$

i.e. $\tilde{\Phi}$ has a triangular matrix representation:

$$A = \begin{bmatrix} \alpha_{oo} & \alpha_{o1} & \alpha_{on} \\ & \alpha_{11} & \alpha_{1n} \\ & \ddots & \vdots \\ & & \alpha_{nn} \end{bmatrix}$$

Hence if no α_{ij} are zero, min (A) = $\prod_i(A-\alpha_{ii}I)$. If some α_{ij} are zero ($i \geqslant j$) then min (A) is a factor of $\prod_i(A-\alpha_{ii}I)$.

Thus if no α_{ij} are zero the polynomial in $\tilde{\Phi}$ which kills all coordinates is $\prod_i(\tilde{\Phi}-\alpha_{ii}I)$.

2.1.6. $\prod_{i=1}^{q}(\tilde{\Phi}-\alpha_{ii}I)$ is termed the <u>annulling polynomial</u> of x_q in this case. If some α_{ij} are zero ($i \geqslant j$) the annulling polynomial of x_q is the lcm of those that annul the coordinate functions in the image of x_q under $\tilde{\Phi}$.

Thus in our 'triangular algebras' the plenary train equation is found either by obtaining the annulling polynomials for the coordinates of x under Φ or by applying essentially the same process to obtain the minimal polynomial of the linearised transformation.

2.1.7. Example. The algebra of (1.5.10.) gives

$$x_o\tilde{\Phi} = x_o$$
$$x_1\tilde{\Phi} = x_1$$
$$x_1^2\tilde{\Phi} = x_1^2$$
$$x_2\tilde{\Phi} = \tfrac{1}{6}x_1^2 + \tfrac{1}{3}x_2$$

Thus $(\tilde{\Phi}-1)$ annuls x_o, x_1 and x_1^2.

Now $(\tilde{\Phi}-\frac{1}{3})x_2 = \frac{1}{6}x_1^2$, hence $(\tilde{\Phi}-1)(\tilde{\Phi}-\frac{1}{3})x_2 = 0$. Thus the polynomial $(\tilde{\Phi}-1)(\tilde{\Phi}-\frac{1}{3})$ annuls all coordinates and the plenary train equation is

$$(\tilde{\Phi}^2 - 4/3\tilde{\Phi} + \tfrac{1}{3})x = 0$$

We consider next the application of HLT to the n'th generation or evolution problem. Let A be a GA with genetic basis $a_o,\ldots,a_n$ and canonical basis $c_o,\ldots,c_n$. Let $\Phi: A \to A$, $x\Phi = x^2$. With the notation of (2.1.1.) let x_o be the initial vector. Then by HLT

2.1.8. $x_n = x_o\Phi^n = x_oR\tilde{\Phi}^n\Pi$.

This maps the nonlinear problem of computing a sequence of plenary powers to the linear one of iterating an upper triangular matrix, $\mathrm{mat}(\tilde{\Phi})$. This in itself does not necessarily lead directly to explicit formulae for x_n, unless $\tilde{\Phi}^n$ can be expressed in terms of $\tilde{\Phi}$ and n. If $\tilde{\Phi}$ is sparse it may be easy to determine $\tilde{\varphi}^n$ by inspection. In general if we bring mat($\tilde{\varphi}$) to Jordan canonical form (JCF) over $\mathbb{C}$, $J = P\mathrm{mat}(\tilde{\varphi})P^{-1}$ and hence $\mathrm{mat}(\tilde{\varphi})^n = P^{-1}J^nP$, then since n'th iterate algorithms for J^n are known we have Abraham's explicit equation

2.1.9. $x_n = x_o RP^{-1}J^nP\,\Pi$.

Thus the problem of obtaining formulae for sequences of plenary powers (by some inductive process) is transfered to that of computing $\tilde{\varphi}^n$, which if $\tilde{\varphi}$ is not very simple or sparse, is reduced to computation of the JCF of $\tilde{\varphi}$. In practice the matrices are often sparse. If they are not, it is not clear that any advantage is gained since computation of J may be lengthy. Moreover an 'inductive' calculation (see (2.1.18.) is more efficient.

2.1.10. Example. Consider the algebra C in (2.1.2.). From the set of linear equations we obtain the annulling polynomial

$$\tilde{\varphi}(\tilde{\varphi}(\tilde{\varphi} - 1)) = \tilde{\varphi}^3 - \tilde{\varphi}^2.$$

Alternatively consider the matrix of $\tilde{\varphi}$. Since this matrix is sparse one easily sees that $P_{ij} = P^2_{ij}$ except for $(i,j) = (2,2)$, $(i,j) = (1,2)$ and $P^2_{22} = 0$. Also $P^2_{ij} = P^3_{ij}$ for all i,j. Hence $\tilde{\varphi}^3 = \tilde{\varphi}^2$. Again if we compute plenary powers we find

$$x^{[4]} - x^{[3]} = 0.$$

2.1.11. The 'inverse n'th generation problem' is to determine an initial population vector x_o given the n'th generation vector x_n.

2.1.12. If mat($\tilde{\varphi}$) is nonsingular then from (2.1.9.) there follows

$$x_o = x_n R P^{-1} J^{-n} P \,\Pi .$$

We illustrate this approach to the solution of the n'th generation problem and the inverse problem on the simplest nontrivial polyploid algebra.

2.1.13. Example. Consider the algebra of (1.5.10.). The quadratic transformation gives the coordinate equations

$$1\phi = 1,\ x_1\phi = x_1,\ x_2\phi = (1/3)x_2 + (1/6)x_1^2.$$

Linearising via equation (2.1.2.) we obtain

$$1\tilde{\phi} = 1,\ x_1\tilde{\phi} = x_1,\ x_1^2\tilde{\phi} = x_1^2,\ x_2\tilde{\phi} = (1/3)x_2+(1/6)x_1^2. \quad (*)$$

So

$$\mathrm{mat}(\tilde{\phi}) = \begin{bmatrix} & & & 0 \\ & I_3 & & 0 \\ & & & 1/6 \\ 0 & 0 & 0 & 1/3 \end{bmatrix}$$

This matrix is (as are all the $\mathrm{mat}(\tilde{\phi})$ for polyploid algebras computed by Abraham (1)) diagonaliseable and nonsingular.

$$\mathrm{mat}(\tilde{\phi}) \sim \begin{bmatrix} 1 & & & \\ & 1 & & \\ & & 1 & \\ & & & 1/3 \end{bmatrix} = P\mathrm{mat}(\tilde{\phi})P^{-1} = J$$

where P is the matrix of left row eigenvectors

$$\begin{bmatrix} 1 & & & \\ & 1 & & \\ & & 1 & \tfrac{1}{4} \\ & & & 1 \end{bmatrix}$$

Hence the n'th generation equation is

$$x_n = x_o R P^{-1} J^n P \,\Pi$$

where $x_n = x^{[n]}$, $x_o = x$. Now there easily follows

$$P^{-1}J^nP = \begin{bmatrix} 1 & & & \\ & 1 & & \\ & & 1 & \tfrac{1}{4}(1-1/3^n) \\ & & & 1/3^n \end{bmatrix}$$

and hence

$$x_n = (x_{no}, x_{n1}, x_{n2}) = (1, x_{o1}, (1/3^n)x_{o2} + \tfrac{1}{4}(1-1/3^n)x_{o1}^2).$$

Now consider the inverse problem. Writing the linear equations (*) in the form

$$x_{1o} = x_{oo} \ (=1)$$
$$x_{11} = x_{o1}$$
$$x_{11}^2 = x_{o1}^2$$
$$x_{12} = (1/3)x_{o2} + (1/6)x_{o1}^2$$

Regard these as equations for x_{oi} given the x_{1i}. We have

$$x_{oo} = x_{1o} \ (=1)$$
$$x_{o1} = x_{11}$$
$$x_{o1}^2 = x_{11}^2$$
$$x_{o2} = 3x_{12} - \tfrac{1}{2}x_{o1}^2.$$

Also $J^{-1} = \mathrm{diag}(1,1,1,3)$ and $A^{-1} = P^{-1}J^{-1}P$ i.e.

$$\begin{bmatrix} 1 & & & \\ & 1 & & \\ & & 1 & -\tfrac{1}{2} \\ & & & 3 \end{bmatrix}$$

Thus given x_n,

$$x_o = x_n R(A^{-1})^n \Pi \, .$$

If A is singular then the inverse problem does not have a unique solution. In this case 'generalised inverses' may be applied to obtain either a unique x_o or the set of all x_o yielding the given x_n. The appropriate inverses are respectively the Penrose or g-inverse and the g_1-inverse (see Penrose (51), Pearl(50)).

2.1.14. The <u>Penrose</u> <u>generalised</u> <u>inverse</u>, A^g, of a real or complex matrix A (not necessarily square) is the unique solution of the equations

$$AXA = A$$
$$XAX = X$$

$$(AX)^* = AX$$

$$(XA)^* = XA$$

where A^* is the conjugate transpose of A.

If A is nonsingular then $A^g = A^{-1}$.

Let A be $m \times n$ of rank r then there exist matrices B, C such that A = BC. Namely, let B be the matrix of any set of r linearly independent columns of A; since these form a basis of the column space of A, each column of A is uniquely expressible as a linear combination of the columns of B. Let C be the coefficient matrix of this combination. Then we have the explicit formulation of A^g,

$$A^g = C^*(CC^*)^{-1}(BB^*)^{-1}B^*.$$

2.1.15. Example. Consider the algebra $\mathcal{B}_{12}$ given by Holgate (47) with multiplication

$$b_o^2 = b_o,\ b_ob_1 = \tfrac{1}{2}(1-\alpha)b_2,\ b_ob_2 = \tfrac{1}{2}b_2$$

$$b_1^2 = -\alpha b_2,\qquad b_1b_2 = -\tfrac{1}{2}\alpha b_2$$

$$b_2^2 = 0$$

where α is a scalar parameter. The baric function is defined by $\beta(b_o) = 1$, $\beta(b_i) = 0\ (i > 0)$. $\mathcal{B}_{12}$ is not STA. For, $\ker\beta = \langle b_1, b_2\rangle$, $(\ker\beta)^2 = \langle b_2\rangle$ and $(\ker\beta)^m = \langle b_2\rangle$ for all $m \geq 2$. Thus $\ker\beta$ is not nilpotent. $\mathcal{B}_{12}$ is not TA, and hence not GA since each principal power increment introduces new monomials. Also $\lambda_{122}, \lambda_{212} \neq 0$. Nevertheless we can linearise the quadratic transformation ϕ on $\mathcal{B}_{12}$.

$$x\phi = b_o + ((1-\alpha)x_1 - \alpha x_1^2 + x_2 - \alpha x_1x_2)b_2.$$

Hence we have

$$1\tilde{\phi} = 1,\ x_1\tilde{\phi} = 0,\ x_2\tilde{\phi} = 0,\ x_1x_2\tilde{\phi} = 0,$$

$$x_2\tilde{\phi} = ((1-\alpha)x_1 - \alpha x_1^2 + x_2 - \alpha x_1x_2).$$

With respect to the ordering of the monomials:

$$(1,\ x_1,\ x_1^2,\ x_1x_2,\ x_2)$$

(which we discuss below, see (4.2.1.)) we have

$$\mathrm{mat}(\tilde{\Phi}) = \begin{bmatrix} 1 & & 0 \\ 0 & & 1-\alpha \\ 0 & 0_{5\times 3} & -\alpha \\ 0 & & 1 \\ 0 & & -\alpha \end{bmatrix}$$

Now for simplicity let $\alpha = 1$ so that $A = \mathrm{mat}(\tilde{\Phi})$ is the matrix

$$\begin{bmatrix} 1 & & 0 \\ 0 & & 0 \\ 0 & 0_{5\times 3} & -1 \\ 0 & & 1 \\ 0 & & -1 \end{bmatrix}$$

which is clearly singular, rank 2 and order 5. We compute the Penrose generalised inverse. Put

$$B = \begin{bmatrix} 1 & 0 \\ 0 & 0 \\ 0 & -1 \\ 0 & 1 \\ 0 & -1 \end{bmatrix}$$

Let $A = BC$ where C is the matrix of coefficients of the unique linear combination of columns of B representing A

$$C = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}.$$

Now $A^g = C^*(CC^*)^{-1}(B^*B)^{-1}B^*$

$$= \begin{bmatrix} 1 & & & & \\ 0 & & & & \\ 0 & & 0_{4\times 4} & & \\ 0 & & & & \\ 0 & 0 & -1/3 & 1/3 & -1/3 \end{bmatrix}$$

Let x_n be the n'th generation vector then

$$\begin{aligned} x_n &= x_o R A^n \pi \\ &= (1, x_1, x_1^2, x_1 x_2, x_2) A^n \\ &= (1, 0, (-1)^n x_1^2 + (-1)^{n+1} x_1 x_2 + (-1)^n x_2). \end{aligned}$$

And

$$\begin{aligned} x_o &= (1, 0, (-1)^n x_1^2 + (-1)^{n+1} x_1 x_2 + (-1)^n x_2) R (A^g)^n \\ &= (1, 0, 0, 0, (-1)^n x_1^2 + (-1)^{n+1} x_1 x_2 + (-1)^n x_2) (A^g)^n \\ &= (1, 0, (1/3)^n (x_1^2 - x_1 x_2 + x_2)) \end{aligned}$$

is a solution to the inverse problem.

2.1.16. A g_1-inverse of a real or complex $m \times n$ matrix A is an $n \times m$ matrix A^{g_1} such that

$$A A^{g_1} A = A.$$

A^{g_1} is not unique. The general g_1-inverse may be written

$$A^{g_1} = P_2 \begin{bmatrix} I_r & U \\ V & W \end{bmatrix} P_1$$

where P_1, P_2 are nonsingular matrices such that

$$P_1 A P_2 = \begin{bmatrix} I_r & 0 \\ 0 & 0 \end{bmatrix}$$

and U, V, W are arbitrary.

2.1.17. Example. Consider the algebra $\mathcal{B}_{12}$ again, we find

$$P_1 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 & 0 \\ 0 & 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 1 & 1 \end{bmatrix} \qquad P_2 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 & 0 \end{bmatrix}$$

satisfying the above condition and hence

$$A^{g_1} = P_2 \begin{bmatrix} I_2 & U \\ V & W \end{bmatrix} P_1 .$$

An alternative approach to the solution of the n'th generation problem is usually computationally more economical. Etherington (21) pointed out that the plenary train equation may be regarded as a difference equation. Abraham (1) stated that the matrix solution of the n'th generation equation can be extremely cumbersome and that in practice one solves the nonlinear equations arising from $x_n\phi = x_{n+1}$ successively.

Suppose A is a GA and $x_o \in A$ is the initial population vector. Then we may write $x_o\phi = x_o^2 = x_1$ and in general $x_n\phi = x_o\phi^n = x_o^{[n+1]} = x_{n+1}$.

With respect to a canonical basis

$$\begin{aligned}(x_{no}, \ldots, x_{nm})\phi &= (x_n\phi_o, \ldots, x_n\phi_m) \\ &= (x_{n+1,o}, \ldots, x_{n+1,m})\end{aligned}$$

i.e. ϕ gives rise to a system of difference equations,

2.1.18.
$$\begin{aligned} x_{n+1,o} &= x_n\phi_o \\ &\cdots \\ x_{n+1,m} &= x_n\phi_m. \end{aligned}$$

Thus ϕ is regarded as the shift operator for the sequence of plenary powers of x_o. In general the functions ϕ_i are nonlinear in the coordinates of x_n, but the difference equations are first order and the i'th equation involves only x_j for $j \leq i$. This is a consequence of the canonical multiplication (see (4.2.)), hence they can be solved successively with substitutions. The method is used by Abraham (1) to compute n'th generation formulae for polyploid algebras of dimension greater than 4 (hexaploids) where the matrices become excessively large. We illustrate its use in (2.1.20.) below and consider it further in chapter 3.

Consider now a polyploid diallelic locus under the genetic assumptions (G) except that we will allow mutation

ABSTRACT

Properties of the Linearisation of the Quadratic Transformation of Genetic Algebras

W.D. Willcox

In this thesis we study the linearisation of the quadratic transformation of commutative baric algebras due to Holgate (44), elaborated and applied by Abraham (1-5).

Holgate studied the quadratic transformation $\phi : A \longrightarrow A$, $x\phi = x^2$ in special train algebras and showed that they possess a plenary train. In the proof he shows that ϕ can be linearised over a higher dimensional space B in the sense that there exist a map $R: A \rightarrow B$ and a linear map $\tilde{\phi}$ on B such that $x\phi = xR\tilde{\phi}\Pi$ (Π the projection B onto A). Abraham applies this linearisation to give explicit formulae for plenary sequences in Schafer genetic algebras for polyploidy.

Following remarks of both Abraham and Holgate our aim was to investigate the application of the linearisation to algebras corresponding to more complex modes of inheritance and to investigate the properties of algebras in which this linearisation exists with a view to obtaining a more natural characterisation of algebras arising in genetics.

Our achievements are to have extended the linearisation to continuous time models, to have exhibited limitations to its further extension, to have given a method of constructing algebras possessing the linearisation and to have given an alternative technique that achieves the same ends by more standard linear algebraic methods.

We decided to include a survey of all relevant work that was scattered amongst papers ranging over some forty years when we commenced work. This year a text, Wörz-Busekros (58), has been published which does a very complete job of bringing the subject within the confines of a single volume. However she only briefly mentions linearisation and our survey is restricted to what we need to discuss this.

with rates r, s between the two alleles.

If the genetic basis is (a_i) $(i=0,1,\dots,n)$, a_i having i dominant and n-i recessive alleles, then the Gonshor basis is

$$c_j = \sum_{i=0}^{j}(-1)^i\binom{j}{i}a_{n-i} \qquad (0 \leq j \leq n)$$

with the multiplication (1.5.7.). If the dominant allele mutates to the recessive and vice versa with rates r, s respectively, then the multiplication is given by (1.5.8.). This defines a polyploid mutation algebra, which is GA (Gonshor (29)) and hence we can solve the n'th generation equation (2.1.9.) of these algebras.

Let A be a polyploid GA, then mutation also leads to a <u>mutation</u> <u>map</u> $m: A \longrightarrow A$ defined on a canonical basis by

2.1.19. $m(c_i) = (1-r-s)^i\left(c_i\binom{n-i}{1}rc_{i+1}+\binom{n-i}{2}r^2c_{i+2}+\dots\right).$

m is a linear map on A. In practice it is simpler to define the appropriate mutation algebra and work within this, than to incorporate m in equation (2.1.9.).

2.1.20. Example. Consider the tetraploid algebra (1.5.10.). Suppose that the alleles A, a mutate into one another with rates r, s respectively. The corresponding mutation algebra has multiplication,

$$c_o^2 = c_o-2rc_1+r^2c_2,\quad c_oc_1 = \tfrac{1}{2}\alpha(c_1-rc_2),\quad c_oc_2 = (1/6)\alpha^2c_2,$$
$$c_1^2 = (1/6)\alpha^2c_2,\qquad c_1c_2 = 0\,;$$
$$c_2^2 = 0\,;$$

where $\alpha = (1-r-s)$.

Let $x_o = c_o+x_{o1}c_1+x_{o2}c_2$ then

$$x_o^2 = c_o+(\alpha x_{o1}-2r)c_1+(r^2-r\alpha x_{o1}+(1/6)\alpha^2x_{o1}^2+(1/3)\alpha^2x_{o2})c_2$$

i.e.

$$1\phi = 1,\ x_{o1}\phi = \alpha x_{o1} - 2r.1$$

$$x_{o2}\phi = r^2.1 - r\alpha x_{o1} + (1/6)\alpha^2 x_{o1}^2 + (1/3)\alpha^2 x_{o2}.$$

We have then, the difference equations

$$x_{n+1,o} = x_{no} = 1 \tag{1}$$

$$x_{n+1,1} = \alpha x_{n1} - 2rx_{no} \tag{2}$$

$$x_{n+1,2} = r^2.1 - r\alpha x_{n1} + (1/6)\alpha^2 x_{n1}^2 + (1/3)\alpha^2 x_{n2} \tag{3}$$

Equation (1) implies

$$x_{no} = 1$$

and equation (2) that

$$x_{n1} = \alpha^n x_{o1} - \sum_{i=0}^{n-1} \alpha^i (2r).$$

Substituting for x_{n1} in equation (3) we have

$$x_{n+1,2} = (1/3)\alpha^2 x_{n2} + \beta$$

where

$$\beta = r^2 - r\alpha(\alpha^n x_{o1} - \sum_{i=0}^{n-1}(\alpha^i)(2r)) + (1/6)\alpha^2(\alpha^n x_{o1} - \sum_{i=0}^{n-1}(\alpha^i)(2r))^2.$$

Hence

$$x_{n2} = ((1/3)\alpha^2)^n x_{o2} + \sum_{i=0}^{n-1}((1/3)\alpha^2)^i \beta .$$

Putting $r = s = 0$, so that $\alpha = 1$ and $\beta = (1/6)x_{o1}^2$ we obtain

$$x_n = (x_{oo},\ x_{o1},\ (1/3^n)x_{o2} + \sum_{i=0}^{n-1}(1/3)^i(1/6)x_{o1}^2)$$

which is the solution without mutation.

2.2. Mixtures of Algebras

In this section we discuss an extension of genetic algebra, using linear combinations of algebras, that lead to its being applicable to two new genetic situations. In polyploids, apart from chromosome segregation, chromatid segregation plays an important role. Linear combinations of algebras for each extreme form of segregation model arbitrary segregation. Secondly we consider k linked loci.

Here we again assume simple Mendelian inheritance. The simplest case is the gametic algebra for two linked autosomal loci each with two alleles. The general case of k linked autosomal loci with multiple alleles is modelled by linear combinations of tensor products of 'linked products'. We do not pursue this topic far since our interest is in linearisation and these algebras turn out to be GA.

Using the Gonshor formulation of GA, Holgate (42) defined n-ploid segregation algebras of degree s, A(n,s) of dimension n+1, $s \in \mathbb{Z}$.

Let a_i be a gametic locus containing i dominant, n-i recessive genes (i=0,1,...,n). For chromosome segregation we have

$$a_i a_j = \binom{2n}{n}^{-1} \sum_{k=0}^{n} \binom{i+j}{k}\binom{2n-i-j}{n-k} a_k .$$

For chromatid segregation

$$a_i a_j = \binom{4n}{n}^{-1} \sum_{k=0}^{n} \binom{2i+2j}{k}\binom{4n-2i-2j}{n-k} a_k .$$

These formulae are derived in Moran (49).

2.2.1. For n, $s \in \mathbb{Z}$ the <u>n-ploid segregation algebra</u> A(n,s) of degree s is defined by the multiplication

$$a_i a_j = \binom{2sn}{n}^{-1} \sum_{k=0}^{n} \binom{si+sj}{k}\binom{2sn-si-sj}{n-k} a_k .$$

2.2.2. A(n,1) are the previous polyploid algebras. A(n,2) are the n-ploid algebras for chromatid segregation only.

Transforming to a canonical basis (2.2.1.) becomes

$$c_i c_j = \binom{2sn}{n}^{-1} \sum_{k=0}^{n} \binom{2sn-k}{n-k} (-1)^k c_k \sum_{l=0}^{i+j} (-1)^l \binom{i+j}{l}\binom{sl}{k} .$$

In genetics both types of segregation occur in proportions depending on the distance of the loci concerned from the centromere.

2.2.3. Let A_1, A_2 be two algebras over the same vector space with products o, . respectively. Define

$$a \times b = \alpha(a \circ b) + (1-\alpha)(a \,.\, b)\ ,\quad (0 \leq \alpha \leq 1)$$

where $a \in A_1$, $b \in A_2$.

This product defines a new algebra called the <u>mixture</u> of A_1 and A_2 and the mixture is independent of the choice of basis in A_1, A_2.

If A_1, A_2 are GA then so is the mixture.

The A(n,1), n = 1,2,...,12 have been computed by Abraham (1). The A(n,2) follow from (2.2.1.) and by (2.2.3.) we may compute the multiplication tables for the mixtures with a proportion α of chromosome and $1-\alpha$ of chromatid segregation. These algebras are GA and hence explicit formulae for the n'th generation of a given population vector may be obtained as outlined in section (2.1.).

2.2.4. Example. Tetraploid algebra with arbitrary segregation. Take A(2,2), it has multiplication

$$c_o^2 = c_o,\ c_oc_1 = \tfrac{1}{2}c_1 - 1/28c_2,\ c_oc_2 = 1/7c_2,$$
$$c_1^2 = 1/7c_2,\qquad c_1c_2 = 0,$$
$$c_2^2 = 0.$$

Take A(2,1) it has multiplication

$$c_o^2 = c_o,\ c_oc_1 = \tfrac{1}{2}c_1,\ c_oc_2 = 1/6c_2,$$
$$c_1^2 = 1/6c_2,\ c_1c_2 = 0,$$
$$c_2^2 = 0.$$

Then the multiplication table of the mixture $\mathcal{A}$ of A(2,1) and A(2,2) is

$$c_o^2 = c_o,\ c_oc_1 = \tfrac{1}{2}c_1 + (\alpha-1)1/28c_2,\ c_oc_2 = (\alpha/42+1/7)c_2,$$
$$c_1^2 = (\alpha/42+1/7)c_2,\qquad c_1c_2 = 0,$$
$$c_2^2 = 0.$$

For $x = c_o + x_1c_1 + x_2c_2$ in $\mathcal{A}$ we have

$$x\Phi = c_o+x_1c_1+(1/14(\alpha-1)x_1+1/21(\alpha+6)x_2+1/42x_1^2(\alpha+6))c_2.$$

From this we obtain the matrix of $\tilde{\Phi}$

$$\begin{bmatrix} 1 & & \\ & 1 & (1/14)(\alpha-1) \\ & & 1 \quad (1/42)(\alpha+6) \\ & & (1/21)(\alpha+6) \end{bmatrix}.$$

On putting $\alpha = 1$ we retrieve the induced map of the tetraploid algebra (2.1.13.).

The minimal polynomial is

$$(\tilde{\Phi} - 1)(\tilde{\Phi} - (1/21)(\alpha + 6))$$

and the plenary train equation is

$$x^{[3]} - (1 + (1/21)(\alpha + 6))x^{[2]} + (1/21)(\alpha + 6)x = 0.$$

The genetic algebra for k linked loci was first formulated by Etherington (21) and subsequently by Bertrand (14), Rieirsöl (53), Holgate (45) and Heuch (38,40). We shall follow the approach of Holgate.

2.2.5. An algebra A_r is said to be an <u>elementary STA</u> (ESTA) if it is the gametic algebra of simple Mendelian inheritance for one diploid locus with r+1 alleles i.e. having genetic basis $a_o,\ldots,a_r$ and multiplication

$$a_ia_j = \tfrac{1}{2}(a_i+a_j).$$

Transforming to a canonical basis

$$c_o = a_o,\ c_i = a_o-a_i \quad (i\neq 0)$$

gives multiplication

$$c_o^2 = c_o,\ c_oc_i = \tfrac{1}{2}c_i,\ c_ic_j = 0 \quad \text{if } i,j > 0.$$

2.2.6. (Holgate (45)). If A is an ESTA then A and its duplicate A' are STA, A is a Jordan algebra and the general element x in A satisfies

$$x^{[2]} - x = 0$$

i.e. Hardy-Weinberg equilibrium is reached in one generation.

Now consider k unlinked loci with $r_1+1, \ldots, r_k+1$ alleles respectively.

2.2.7. The tensor product $A = \bigotimes_{j=1}^{k} A_{r_j}$ of ESTA's A_{r_j} is defined in the standard way (e.g. Greub (33)). Thus if $(c_{i_1}), \ldots, (c_{i_k})$ are bases of $A_{r_1}, \ldots, A_{r_k}$ then dropping the $\otimes$ notation for products of elements, $c_{i_1} \ldots c_{i_k}$ is a basis of A and the multiplication is given by

$$(c_{i_1} \ldots c_{i_k})(c_{j_1} \ldots c_{j_k}) = (c_{i_1} c_{j_1}) \ldots (c_{i_k} c_{j_k})$$

where the products within the brackets on the r.h.s. are those of the factor algebras.

A is an STA.

2.2.8. Let $A_1, \ldots, A_k$ be k ESTA's and let A_i have genetic basis $a_{i_0}, \ldots, a_{i_{k_i}}$. Define the linked product

$$A = A_1 * \ldots * A_k$$

to be the algebra with basis $\{ a_{1i_1} \ldots a_{ki_k} : 0 \leq i_j \leq r_j \}$ and multiplication

$$(a_{1i_1} \ldots a_{ki_k})(a_{1j_1} \ldots a_{kj_k}) = \tfrac{1}{2}(a_{1i_1} \ldots a_{ki_k} + a_{1j_1} \ldots a_{kj_k})$$

i.e. the tensor product with 'half sum multiplication'.

A is an ESTA with weight function $\beta(a_{1i_1} \ldots a_{ki_k}) = 1$ for all basis elements. A represents k linked loci with no recombination.

2.2.9. Let $A_1, \ldots, A_k$ be ESTA's. Let $I = (i_1, \ldots, i_q)$ be a partition of k in q parts. Define the recombination algebra A(I) of the A_i by

$$A(I) = (A_1 * \dots * A_{i_1}) \otimes (A_{i_1+1} * \dots * A_{i_1+i_2})$$
$$\otimes (A_{i_1+i_2+1} * \dots * A_{i_1+i_2+i_3})$$
$$\dots$$
$$\otimes (A_{i_1+\dots+i_{q-1}+1} * \dots * A_{i_1+\dots+i_q}).$$

It follows that

$$\mathop{\ast}_i A_i = A(k)$$
$$\bigotimes_i A_i = A(1,\dots,1).$$

An element x in A(I) represents a population in which loci fall into groups of $i_1, \dots, i_q$ such that (1) there is no recombination between loci in each group and (2) the groups are unlinked.

Holgate shows that the A(I) are STA. Finally he constructs specified linear combinations (mixtures) of the A(I) representing k linked loci with arbitrary recombination

2.2.10. $$A = \sum_I \alpha(I) A(I)$$

where the coefficients $\alpha(I)$ are determined by the recombination distribution. These mixtures are shown to be STA and expressions for their plenary roots are obtained.

Since the entire construction preserves STA, HLT holds in all these algebras so we do not pursue them further here.

2.2.11. Example. Consider two diallelic loci (k=2). Take an ESTA for each locus $A_{r_1} = A_{r_2} = A_1$. Write $A = A_{r_1}$, $B = A_{r_2}$. Both have basis a_1, a_2 and multiplication : $a_i a_j = \frac{1}{2}(a_i + a_j)$. Let $I_1 = (1,1)$ and $I_2 = (2)$. Let $\{\alpha(I)\}$ be a set of $2^{k-1} = 2$ real numbers μ, ν such that $\mu + \nu = 1$. Now $A(I_1) = A \otimes B$ and $A(I_2) = A * B$ and

$$A = \sum_I \alpha(I)A(I) = \mu(A \otimes B) + \nu(A * B).$$

For x, y in A, $xy = \mu\, x \otimes y + \nu\, x*y$.

All the A(I) have the same number of factors and have a common canonical basis $(a_1a_1, a_1a_2, a_2a_1, a_2a_2)$. Thus A has the same basis.

In order to have a framework in which to discuss the question of the uniqueness of various mixtures of algebras Heuch (41) regarded the mixtures as elements in vector spaces of algebras. These ideas lead to a geometric description of the algebras over $\mathbb{C}$ arising in the genetics of randomly mating populations (see (4.1.) below).

We consider n-dimensional algebras A over $\mathbb{C}$ for fixed n. Within isomorphism the underlying vector space is $\mathbb{C}^n$. Since we shall employ several algebras A_i we distinguish their multiplications by writing $xy(A_i)$ for the product of x and y in A_i.

2.2.12. Let A_1, A_2 be two algebras; we define their sum and scalar multiples by the rules

$$xy(A_1 + A_2) = xy(A_1) + xy(A_2)$$
$$xy(\alpha A_i) = \alpha\, xy(A_i).$$

Under these operations a collection $\{A_i\}$ of algebras of the same dimension generates a vector space over $\mathbb{C}$ which we shall denote by $\mathbb{C}^n_A$.

2.2.13. Let $c_1, \ldots, c_n$ be a basis of $\mathbb{C}^n$. Then $A_1, \ldots, A_m$ each isomorphic to $\mathbb{C}^n$, are said to be <u>linearly independent</u> if

$$\sum_{k=1}^{m} \alpha_k c_i c_j (A_k) = 0 \quad (i,j = 1, \ldots, n)$$

implies $\alpha_k = 0$ for all k.

This will hold if there exist x, $y \in \mathbb{C}^n$ such that $xy(A_1)$,

..., $xy(A_m)$ are linearly independent in $\mathbb{C}^n$.

We may now define a general mixture of algebras (redefining 2.2.3.):

2.2.14. A mixture of algebras A_i each isomorphic to $\mathbb{C}^n$ as a vector space is alinear combination of algebras in $\mathbb{C}^n_A$ and a mixture $\sum_i \alpha_i A_i$ such that $\sum_i \alpha_i = 1$ where $\alpha_i \geq 0$ are real, i.e. a convex combination, will be called a proper mixture.

2.2.15. Let $c_1, \ldots, c_n$ be a fixed basis of A isomorphic to $\mathbb{C}^n$ as a vector space, then the multiplication in any A in $\mathbb{C}^n_A$ is defined by

$$c_i c_j (A) = \sum_{k=1}^{n} \lambda_{ijk} c_k.$$

Thus the elements of $\mathbb{C}^n_A$ are labelled by their structure tensors λ^k_{ij}, (see (4.1.21.)).

2.2.16. $A \in \mathbb{C}^n_A$ is commutative iff $\lambda_{ijk} = \lambda_{jik}$ for all k. Let $\mathbb{C}^n_C = \{C \in \mathbb{C}^n_A : C \text{ is commutative}\}$ then $\mathbb{C}^n_C$ is a subspace of $\mathbb{C}^n_A$.

2.2.17. Let $\mathbb{C}^n_B = \{B \in \mathbb{C}^n_A : B \text{ is baric}\}$. For a suitable choice of $c_1, \ldots, c_n$, $\lambda_{111} = 1$, $\lambda_{ij1} = 0$ $(i,j \neq 1)$. Hence $\mathbb{C}^n_B$ is a flat in $\mathbb{C}^n_A$.

2.2.18. Let $\mathbb{C}^n_G = \{G \in \mathbb{C}^n_A : G \text{ is GA}\}$ then $\mathbb{C}^n_G$ forms a flat in $\mathbb{C}^n_A$.

The dimensions of these flats or spaces is in some sense a measure of the size of the subclass of corresponding algebras. As we might expect

$$\dim \mathbb{C}^n_G < \dim \mathbb{C}^n_B < \dim \mathbb{C}^n_C < \dim \mathbb{C}^n_A$$

for all $n > 1$, since the corresponding dimensions are $(1/6)(n^3+5n-6) < \frac{1}{2}(n^3-n) < \frac{1}{2}(n^3+n^2) < n^3$.

Heuch (41) has shown that the class of all n-dimensional algebras over $\mathbb{C}$ arising in genetics of random mating populations, strictly containing GA, can be characterised as a polyhedron in the vector space of algebras $\mathbb{C}^n_A$ and that $\mathbb{C}^n_B$ is the smallest flat containing this polyhedron. We return to this and other characterisations in (4.1.).

More complex modes of inheritance have been represented by mixtures of algebras from a subset $S \subset \mathbb{C}^n_G$. Such mixtures for example for k-linked loci have been constructed by Holgate (45) and Heuch (41) using different subsets S. Heuch (41) shows that these mixtures may be written uniquely from a well defined subset of $\mathbb{C}^n_B$. This is summarised in:

2.2.19. Let T be the smallest subspace of $\mathbb{C}^n_A$ containing a given subset S of algebras in $\mathbb{C}^n_A$. Then all the algebras in S may be written as a unique mixture of algebras in a set U iff U is a basis of T and $U \subset \mathbb{C}^n_B$.

2.2.20. Example. Consider the gametic tetraploid algebra for arbitrary segregation. Let $a_1, \ldots, a_t$ be the possible alleles. The algebra is a mixture of an algebra A_1 for chromosome segregation and an algebra A_2 for chromatid segregation with multiplications

$$(a_i a_j)(a_k a_l)(A_1) = 1/6(a_i a_j + a_i a_k + a_i a_l + a_j a_k + a_j a_l + a_k a_l)$$

$$(a_i a_j)(a_k a_l)(A_2) = 1/28(a_i a_i + a_j a_j + a_k a_k + a_l a_l) + \\ + 1/7(a_i a_j + a_i a_k + a_i a_l + a_j a_k + a_j a_l + a_k a_l)$$

where $i,j,k,l = 1,2, \ldots, t$ respectively.

The mixture is given by

$$(1 - \alpha)A_1 + \alpha A_2$$

where α is the proportion of chromatid segregation. Now A_1, A_2 form a basis for the smallest subspace K of the space of algebras concerned.

Since with t = 2 the subspace of $\mathcal{C}^n_A$ generated by $\mathcal{C}^n_G$ is of dimension 13, (see Heuch (41)), and 13 is very much greater than dim K = 2, we see that the polyploid algebras are a very special class, as has already been noted, with respect to the form of their linearised quadratic transformations.

3. LINEARISATION

Let (A, Φ) be a GA together with its quadratic transformation. In this chapter we discuss the linearisation of Φ from several points of view.

We recall that (2.1.1.) gives sufficient but not necessary and sufficient conditions for the existence of a linearisation of Φ and also that Abraham (1) has proved that the order of a linearisation (i.e. the dimension of the 'induced linear space') is independent of the basis in the case that A is GA.

HLT (2.1.1.) maps the nonlinear problem of iterating Φ into the linear one of iterating $\tilde{\Phi}$ (in the notation of Abraham). The map is not functorial. Φ is not an algebra homomorphism, though it is related to the tensor functor. We have already presented the results of Abraham and Holgate on linearisation in (2.1.). In particular we considered only plenary sequences in A i.e. given $x_o \in A$

$$x_1 = x_o^2$$
$$x_n = x_{n-1}^2$$

or in terms of Φ

$$x_n = x_o \Phi^n$$

and by HLT

$$x_n = x_o R \tilde{\Phi}^n \Pi .$$

In (3.1.) we consider the difference and differential operators E, D acting on sequences or functions in A and generalise the notion of train. In (3.2.) we consider the matrix form of the solution of linear vector difference and differential equations. In (3.3.) we apply this to the solution of the n'th generation equation in the plenary case. In so doing we formulate the solution for the continuous time model of Heuch (39). In (3.4.) we consider some algebras with discrete only or discrete and continuous plenary linearisation. In (3.5.) we show a limitation of linearisation by considering its extension to the case of overlapping generations.

3.1. Discrete and continuous trains

Let (A, β) be a baric algebra over $\mathbb{R}$, with basis (c_i).

3.1.1. An arbitrary sequence in A will be denoted by

$$x: \mathbb{Z} \to A,\ x(m) = \sum_i x_i(m) c_i$$

where x_i is a real sequence.

An arbitrary function of a real variable on A will be denoted by

$$x: \mathbb{R} \to A,\ x(t) = \sum_i x_i(t) c_i$$

where x_i is a real function.

3.1.2. The <u>shift</u> and (forward) <u>difference</u> <u>operators</u> E, Δ respectively are defined as usual

$$Ex(m) = x(m+1)$$

$$\Delta x(m) = x(m+1) - x(m)$$

and the <u>differential</u> <u>operator</u> D

$$Dx(t) = \lim_{h \to 0} (x(t+h) - x(t))/h.$$

Since the x are vector functions of a scalar variable we have:

3.1.3. $$Ex(m) = \sum_i Ex_i(m) c_i$$

$$Dx(t) = \sum_i Dx_i(t) c_i.$$

We shall assume that the x are such that Ex_i, Dx_i are defined for all i.

If x(n) and y(n) are two sequences on A we may form the product sequence

$$z(n) = x(n)y(n).$$

Then

$$Ez(n) = z(n+1) = x(n+1)y(n+1) = Ex(n)Ey(n).$$

Thus we have the product rules:

3.1.4. $$E(xy) = ExEy$$
$$D(xy) = (Dx)y + x(Dy).$$

Equations for Δ may be obtained from the relation $\Delta = E - I$, where I is the identity operator.

If $\beta(c_i) = 1$ for each i then both E and D commute with β. Also E, D satisfy the distributive laws.

Let F(A) be the class of sequences $f_x : \mathbb{Z} \longrightarrow A$, $f_x(m) = \sum_i x_i(m)c_i$ such that $E^r x_i(m)$ are defined for all $r = 0,1,2,\dots$. Then $E^r f_x(m) = \sum_i E^r x_i(m)c_i$ independently of the basis. Let $\Phi : A \longrightarrow F(A)$, $\Phi(x) = f_x$ and suppose further that $f_x(0) = x$ and $\beta(x) = 1$ for all $m \geqslant 0$.

3.1.5. If for all $f_x \in \Phi(A)$ such that $\beta(x) = 1$, f_x satisfies a linear equation with constant coefficients:

$$E^{(s)}f_x(m) + \theta_1 E^{(s-1)}f_x(m) + \dots + \theta_s f_x(m) = 0$$

then Φ is said to be a (discrete) <u>train</u> on A.

Replacing $f_x : \mathbb{Z} \longrightarrow A$ by $f_x : \mathbb{R} \longrightarrow A$ and E by D in the above we obtain the definition of a <u>continuous train</u> on A. The equations are called <u>train equations</u>. This definition of a train differs from (1.3.1.) only in requiring the θ_i to be constant, it is due to Heuch (39).

3.2. Linear equations

The theories of linear difference and differential equations with constant coefficients are parallel, the parallelism lies in the following.

3.2.1. If $\Delta x(n) = ax(n)$ then $x(n) = (a+1)^n x(0)$, while if $Dx(t) = ax(t)$ then $x(t) = e^{at}x(0)$, where a is constant.

Generalising to systems of linear equations i.e. for vector equations we have,

3.2.2. Given a system of first order linear difference equations with constant coefficients

$$Ex(n) = x(n)A$$

$$x(0) = (x_1(0),\dots,x_m(0))$$

where A is an $m \times m$ matrix, the solution is given by

$$x(n) = x(0)A^n.$$

To give an explicit formula for $x(n)$ in terms of n and $x(0)$ we have to express A^n in terms of the a_{ij} (the entries of A) and n. If A is sparse this may not be difficult. Otherwise we may put A in JCF and use known n'th iterate algorithms. Say $J = PAP^{-1}$ is the JCF of A then

$$x(n) = x(0)P^{-1}J^nP$$

and J decomposes to a sum $D + N$ of a diagonal and a nilpotent matrices D, N respectively. Hence we have an explicit formula for $x(n)$ in terms of n and the initial coordinates.

3.2.3. Similarly given a system of first order linear differential equations

$$Dx(t) = x(t)A$$
$$x(0) = (x_1(0),\dots,x_m(0))$$

the solution (t starting from zero) is

$$x(t) = x(0)e^{tA}$$

where $$e^A = \sum_{r=0}^{\infty} A^r/r!$$

is the exponential matrix.

Again to compute e^{tA} requires calculation of r'th powers of A, which unless A is sparse may be achieved by use of the JCF of A. Thus

$$x(t) = x(0)P^{-1}e^{t[\mathrm{diag}(\lambda_1,\dots,\lambda_n)+N]}P$$

where the λ_i are the eigenvalues of A and N = 0 if these are all distinct.

The following example shows the role of the JCF in determining the form of the general solution.

3.2.4. Example. Consider the equation

$$(D^3 - D^2 - D + I)x = 0.$$

We transform this third order equation to three first order equations. Put

$$y_1 = x,\ y_2 = Dy_1,\ y_3 = Dy_2$$

then

$$Dy_1 = y_2$$
$$Dy_2 = y_3$$
$$Dy_3 = -y_1 + y_2 + y_3.$$

Put $Y = (y_1,y_2,y_3)$ and

$$A = \begin{bmatrix} 0 & 0 & -1 \\ 1 & 0 & 1 \\ 0 & 1 & 1 \end{bmatrix}$$

then the equation may be written

$$DY = YA.$$

The characteristic equation of A is

$$(\lambda - 1)^2 (\lambda + 1) = 0$$

with roots $\lambda_1 = 1$ with multiplicity $m_1 = 2$ and $\lambda_2 = -1$ with $m_2 = 1$.

This determines the JCF of A

$$J = \begin{bmatrix} 1 & 1 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & -1 \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & -1 \end{bmatrix} + \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} = D + N$$

say, where N is nilpotent of index 2 and D is diagonal.

Now the solution is of the form

$$Y(t) = Y(0)e^{t(D+N)}$$

where

$$e^{tD} = \begin{bmatrix} e^t & & \\ & e^t & \\ & & e^t \end{bmatrix} \text{ and } e^{tN} = \begin{bmatrix} 1 & t & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

Thus

$$Y(t) = \begin{bmatrix} e^t & te^t & 0 \\ 0 & e^t & 0 \\ 0 & 0 & e^{-t} \end{bmatrix}$$

and the solution vector is any linear combination of the column vectors i.e.

$$Y(t) = (ae^t, (at+b)e^t, ce^{-t})$$

where $a = e^{t_o}$, $b = at_o$, $c = e^{-t_o}$. If $t_o = 0$ then $a = b = c = 1$.

Thus it is N that gives the form of the solution corresponding to multiple roots of the auxiliary equation.

3.3. Plenary trains and continuous trains

3.3.1. Let A be GA and let $x = x(0)$ represent a population in its initial state

$$x(0) = \sum_i x_i(0) c_i .$$

Suppose that in passing from generation m to generation m+1 the population x(m) dies and is replaced by the offspring of random mating between individuals of x(m). With (c_i) as basis of A let

$$c_i c_j = \sum_k \lambda_{ijk} c_k.$$

Let $f_x : \mathbb{Z} \to A$, $f_x(m) = x(m) = \sum_i x_i(m) c_i$. Then under the genetic assumptions (G)

$$Ef_x(m) = (f_x(m))^2$$
$$f_x(0) = x$$

or equivalently

$$\Delta f_x(m) = (f_x(m))^2 - f_x(m)$$
$$f_x(0) = x.$$

The sequence f_x satisfying this first order second degree difference equation is

$$f_x(n) = x^{[n]}$$

the <u>plenary sequence</u>. Heuch (39) has shown that varying x the function $\Phi : A \to F(A)$, $\Phi(x) = f_x$ is the (discrete) <u>plenary train</u> of A i.e. for all $x \in A$ such that $\beta(x) = 1$, $\Phi(x)$ satisfies an equation of the form

3.3.2. $E^{(s)} f_x(n) + \theta_1 E^{(s-1)} f_x(n) + \ldots + \theta_s f_x(n) = 0,$

called the <u>plenary train equation</u> (c.f. (3.1.5.)).

3.3.3. In direct analogy let x = x(0) represent a population at time t = 0 (t real). Again

$$x(0) = \sum_i x_i(0) c_i.$$

Now suppose that in a time interval (t,t+h) a proportion d_h of the population x(t) dies and is replaced by the offspring of random mating between individuals alive at time t. Again suppose

$$c_i c_j = \sum_k \lambda_{ijk} c_k$$

and let $f_x: \mathbb{R} \to A$, $f_x(t) = x(t) = \sum_i x_i(t)c_i$. Then under the assumptions (G) we find the continuous analogue is

$$Df_x(t) = (f_x(t))^2 - f_x(t).$$

The function satisfying this differential equation with initial condition

$$f_x(0) = x$$

we call the plenary function. Varying x, we have Φ is the continuous plenary train of A if $\Phi(x)$ satisfies

3.3.4. $D^{(s)}f_x(t) + \theta_1 D^{(s-1)}f_x(t) + \dots + \theta_s f_x(t) = 0.$

Heuch (39) has shown this to be the case.

We note that for the plenary case the evolution function is a solution of a 'Bernoulli equation'. In the scalar case over real functions these equations ($Df + f = f^2$) are, as is well known, lineariseable (putting $g = f^{-1}$ gives $-Dg + g + 1 = 0$). We shall see below that when the equations are not so nice the Holgate linearisation is not possible.

A similar account to that given for plenary trains may be given for principal trains. Suppose given a population x in which individuals dying in the time interval (t,t+h) are replaced by the offspring of matings between individuals of x(t) and the individuals in a constant population identical to x(0). Then the evolution function is a solution of

$$Df_x(t) = -f_x(t) + f_x(0)f_x(t).$$

If $(f_x(0)) = 1$ and $f_x(0) = x(0) = x$ then Heuch (39) shows that this defines a continuous principal train.

3.4. Continuous and discrete linearisation

We would like basis independent necessary and sufficient conditions for the quadratic transformation of an algebra to be lineariseable. We have not been able to give these. Short of this the present section exhibits some limitations of linearisation which lead us to suspect that the conditions sought are not much wider than GA.

Let (A, ϕ) be a fixed GA of dimension n+1 together with its quadratic transformation. Consider the difference equation

3.4.1. $$Ex(m) = (x(m))^2$$
$$x(0) = x$$

where $x \in A$. If

$$x(m) = (x_o(m), \ldots, x_n(m))$$

relative to a basis (c_i) of A, then we have the system of equations

$$Ex_i(n) = (x(n))^2 \Pi_i$$

where $i = 0, 1, \ldots, n$ and Π_i is the projection on the i'th coordinate.

Now the r.h.s. is a sum of monomials

$$m_{ij}(x) = x_i^{\alpha j_i} \ldots x_l^{\alpha j_l}$$

where $j = 1, 2, \ldots, r$, Hence

$$Ex_i(n) = \sum_j m_{ij}(x).$$

Since A is GA this system involves only first order equations and hence may be solved by 'forward recursion' as in (3.4.3.) below. Or, for each nonlinear monomial we may define via (3.1.4.)

$$Em_{ij}(x) = E(x_i^{\alpha j_i} \ldots x_l^{\alpha j_l}) = (Ex_i)^{\alpha j_i} \ldots (Ex_l)^{\alpha j_l}.$$

Again since A is GA (sufficient but not necessary and sufficient), and hence (2.1.1.) holds, this product rule generates only finitely many additional equations and repeated application eventually leads to the linear system

3.4.1'. $$Ey(n) = y(n)A$$

where the coordinates y_i of y are those of x, x_i, augmented by a finite set of monomials in the x_i and A is a matrix. The solution of this system is

$$y(n) = y(0)A^n.$$

Similarly considering the differential equation

3.4.2. $$Dx(t) = (x(t))^2 - x(t)$$
$$x(0) = x$$

we obtain the system of equations

$$Dx_i(t) = (x(t))^2\pi_i - x(t)\pi_i.$$

Again these equations are first order for $x \in A$, A a GA and may be solved by forward recursion. Or, we may define a system of linear equations, corresponding to a Holgate linearisation, applying the D product rule to any non-linear monomials on the r.h.s. We obtain a matrix equation

3.4.2.' $$Dy(t) = y(t)A$$

with solution

$$y(t) = y(0)e^{tA}.$$

The following example illustrates the various solutions mentioned above for the first non-trivial polyploid algebra.

3.4.3. Example. Consider the tetraploid algebra with canonical multiplication

$$c_o^2 = c_o,\ c_oc_1 = \tfrac{1}{2}c_1,\ c_oc_2 = c_1^2 = (1/6)c_2. \qquad (*)$$

Given this multiplication and the equation

$$Ex(n) = (x(n))^2$$
$$x(0) = (1, x_1, x_2)$$

we obtain the nonlinear vector difference equation for $x = x(0)$ such that $\beta(x) = 1$,

$$Ex(n) = c_o + x_1(n)c_1 + ((1/3)x_2(n) + (1/6)x_1^2(n))c_2$$
$$x(0) = c_o + x_1c_1 + x_2c_2.$$

And hence the system of nonlinear scalar equations

$$Ex_o(n) = 1, \ x_o(0) = 1 \qquad (1.1)$$
$$Ex_1(n) = x_1(n), \ x_1(0) = x_1 \qquad (1.2)$$
$$Ex_2(n) = (1/3)x_2(n) + (1/6)x_1^2(n), \ x_2(0) = x_2 \qquad (1.3)$$

Solving these by forward recursion, from (1.1), (1.2) we obtain

$$x_o(n) = 1$$
$$x_1(n) = x_1(0).$$

Substituting in (1.3) we obtain a linear equation

$$Ex_2(n) = (1/3)x_2(n) + (1/6)x_1^2(0).$$

Solving this by recursion

$$\begin{aligned} x_2(n) &= (1/3^n)x_2(0) + \textstyle\sum_{i=0}^{n-1} 1/3^i . (1/6)x_1^2(0) \\ &= (1/3^n)x_2(0) + \tfrac{1}{4}(1 - 1/3^n)x_1^2(0). \end{aligned}$$

Thus

$$x(n) = (1, \ x_1(0), \ (1/3^n)x_2(0) + \tfrac{1}{4}(1-1/3^n)x_1^2(0)).$$

Alternatively we may (following Abraham (1)) linearise equations (1) and solve by matrix methods. Equations (1) are linearised by introducing an equation for x_1^2 giving

$$\left.\begin{aligned} Ex_o(n) &= 1 \\ Ex_1(n) &= x_1(n) \\ Ex_1^2(n) &= (Ex_1(n))^2 = x_1^2(n) \\ Ex_2(n) &= (1/3)x_2(n) + (1/6)x_1^2(n). \end{aligned}\right\} \qquad (2)$$

The order chosen for these equations is discussed in

(4.2.2.) below, it corresponds to the lexicographic ordering of the monomials in the x_i $(i = 0,1,2)$ with identities removed.

In matrix form (2) becomes

$$Ey(n) = (x_o(n), x_1(n), x_1^2(n), x_2(n)) \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1/6 \\ 0 & 0 & 0 & 1/3 \end{bmatrix} \qquad (2)$$

$$= y(n)A \text{ say}$$

with solution $y(n) = y(0)A^n$.

Writing $y(0) = x(0)R$ we have Abraham's equation

$$x(n) = x(0)RA^n\Pi$$

where Π is the projection.

Obtaining the JCF, J, of A we have

$$x(n) = x(0)RP^{-1}J^nP\Pi$$

where $J = PAP^{-1}$, P being the matrix of left row eigenvectors since A is diagonaliseable. Thus

$$P = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & \frac{1}{4} \\ 0 & 0 & 0 & 1 \end{bmatrix} \qquad P^{-1} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & -\frac{1}{4} \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

and

$$J = \begin{bmatrix} 1 & & & \\ & 1 & & \\ & & 1 & \\ & & & 1/3 \end{bmatrix}$$

The n'th power of J is easily evaluated and hence we have

$$y(n) = (x_o(0), x_1(0), x_1^2(0), x_2(0)) \begin{bmatrix} 1 & & & \\ & 1 & & \\ & & 1 & \frac{1}{4}(1-1/3^n) \\ & & & 1/3^n \end{bmatrix}$$

and hence

$$x(n) = (x_o(0), x_1(0), \tfrac{1}{4}(1-1/3^n)x_1^2(0)+(1/3^n)x_2(0))$$

as in the first solution.

We now obtain the analogous solutions for the continuous case.

Given the multiplication (*) as before and the equation

$$Dx(t) = (x(t))^2 - x(t)$$

$$x(0) = (1, x_1, x_2)$$

we obtain the nonlinear vector differential equation

$$Dx(t) = 0.c_o + x_1(t)(x_o(t)-1)c_1 + (-x_2(t)+(1/3)x_o(t)x_2(t) + (1/6)x_1^2(t))c_2$$

$$x(0) = x_o(0)c_o + x_1(0)c_1 + x_2(0)c_2.$$

Hence we have the system

$$Dx_o(t) = 0 \qquad (1.1)'$$

$$Dx_1(t) = x_1(t)(x_o(t)-1) \qquad (1.2)'$$

$$Dx_2(t) = (-2/3)x_2(t)+(1/6)x_1^2(t) \qquad (1.3)'$$

We may solve these by forward recursion, by direct integration

$$x_o(t) = 1$$

$$x_1(t) = x_1(0).$$

Substituting in (1.3)' gives the linear equation

$$Dx_2(t) = (-2/3)x_2(t)+(1/6)x_1^2(0).$$

Multiplying through by the integrating factor $e^{\int 2/3dt}$

$$x_2(t) = (x_2(0)-\tfrac{1}{4}x_1^2(0))e^{(-2/3)t}+\tfrac{1}{4}x_1^2(0).$$

Thus

$$x(t) = (1, x_1(0), x_2(0)e^{(-2/3)t}+\tfrac{1}{4}(1-e^{(-2/3)t})x_1^2(0)).$$

Alternatively we may linearise equations (1)' and solve by matrix methods. Equations (1)' are linearised by introducing an equation for x_1^2 via the D product rule.

$$\begin{aligned} Dx_o(t) &= 0 \\ Dx_1(t) &= x_1(t)(x_o(t)-1) = 0 \\ Dx_1^2(t) &= 2x_1(t)(Dx_1(t)) = 0 \\ Dx_2(t) &= (-2/3)x_2(t)+(1/6)x_1^2(t) \end{aligned} \qquad (2')$$

In matrix form

$$Dy(t) = (x_o(t),x_1(t)x_1^2(t),x_2(t)) \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1/6 \\ 0 & 0 & 0 & -2/3 \end{bmatrix}$$

$$= y(t)A \text{ say.}$$

This has solution

$$y(t) = y(0)e^{tA}.$$

Hence

$$x(t) = x(0)Re^{tA}\Pi \ .$$

Again computation of e^{tA} may be facilitated by taking the JCF of A. If P is such that $J = P^{-1}Ap$ is the JCF of A then

$$\begin{aligned} y(t)P &= y(0)e^{tA}P \\ &= y(0)PP^{-1}e^{tA}P \\ &= y(0)Pe^{tP^{-1}AP} \\ &= y(0)Pe^{t[diag(\lambda_1,\ldots,\lambda_n)+N]} \end{aligned}$$

where the λ_i are the eigenvalues of A. Thus

$$x(t) = x(0)Re^{t[diag(\lambda_1,\ldots,\lambda_n)+N]} \ .$$

However in the present case this is unnecessary for we have

$$y(t) = y(0) \sum_{r=0}^{\infty} t^r A^r/r!$$

$$=y(0)(I_4 + \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & t^r/r!.(1/6)(-2/3)^{r-1} \\ 0 & 0 & 0 & t^r/r!.(-2/3)^r \end{bmatrix})$$

which is easily seen to be equal to

$$(1, x_1(0), x_1^2(0), x_2(0))\begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & \frac{1}{4}(1-e^{(-2/3)t}) \\ 0 & 0 & 0 & e^{(-2/3)t} \end{bmatrix}$$

giving the solution obtained by forward recursion.

We next show that the possibility of linearisation of the discrete equation does not imply that of the continuous equation, even if the latter may be solved by successive substitution.

3.4.4. Example. Let A be the algebra with multiplication

$$\begin{aligned} c_o^2 = c_o,\ c_oc_1 = 0,\ c_oc_2 &= \tfrac{1}{2}c_2,\ c_oc_3 = \tfrac{1}{2}c_3, \\ c_1^2 = c_2,\ c_1c_2 &= 0,\ c_1c_3 = \tfrac{1}{2}c_3, \\ c_2^2 &= c_3,\ c_2c_3 = 0, \\ c_3^2 &= 0. \end{aligned}$$

A is not GA, however the equations corresponding to (3.4.1.) yield a finite system corresponding to (3.4.1.') i.e. the discrete equation linearises. On the other hand the equations corresponding to (3.4.2.) do not yield a finite system corresponding to (3.4.2.')

A smaller dimension example with the same property is the algebra $\mathcal{B}_{12}$.

3.4.5. Example. Consider the algebra $\mathcal{B}_{12}$ (2.1.15.) with the parameter $\alpha = 1$. The multiplication is

$b_o^2 = b_o,\ b_ob_1 = 0,\ b_ob_2 = \frac{1}{2}b_2,\ b_1^2 = -b_2,\ b_1b_2 = -\frac{1}{2}b_2,$
$b_2^2 = 0.$

The discrete equation linearises (2.1.15.). The plenary function is defined by

$$Dx(t) = (x(t))^2 - x(t)$$

where

$$x(0) = (1, x_1, x_2).$$

This gives

$$Dx_o(t) = 0$$
$$Dx_1(t) = 0$$
$$Dx_2(t) = -x_1^2(t) - x_1(t)x_2(t).$$

Integrating the first two equations we have

$$x_o(t) = 1$$
$$x_1(t) = x_1.$$

Substituting for $x_1(t)$ in the third equation,

$$Dx_2(t) = -x_1^2 - x_1(x_2(t))$$

a first order linear equation. Hence

$$x_2(t) = -x_1^3 + Ce^{-x_1 t}$$

which with the initial conditions gives

$$x_2(t) = -x_1^3 + (x_1^3 + x_2)e^{-x_1 t}.$$

Thus

$$x(t) = (1, x_1, (x_1 + x_2)e^{-x_1 t} - x_1^3).$$

However if we attempt to linearise, the D operator applied to the monomial $x_1(t)x_2(t)$ generates an infinite system of equations,

$$D((x_1(t))^n x_2(t)) = -(x_1(t))^{n+2} - (x_1(t))^{n-1} x_2(t).$$

3.4.6. For an arbitrary baric algebra together with its quadratic transformation (A, ϕ) we shall say that A is Eϕ -lineariseable if the system of equations (3.4.1.') derived from (3.4.1.) is finite and that A is Dϕ -lineariseable if the system (3.4.2.') derived from (3.4.2.) is finite.

From (3.4.4.) or (3.4.5.) we see that

3.4.7. A is Eϕ -lineariseable does not imply that A is

$D\phi$ -lineariseable.

We note that all examples we know of are not GA. We shall also show, see (4.1.15), that mixture can destroy the property - $E\phi$ -lineariseable. This result casts some doubt on the usefulness of the class of $E\phi$-lineariseable algebras in comparison with GA or STA, the former having a form of closure under mixture (providing a basis for the mixtures can be chosen in the same way).

3.5. Sequences for overlapping generations

In this section we consider linearisation of the transformations defined by Heuch (36) which model the evolution of populations with some overlapping of generations.

Given an n-dimensional GA with canonical basis and a function defining a sequence: x(0), x(1), ... , whose terms satisfy an equation with constant coefficients i.e. a train equation, we express the sequence in terms of n difference equations giving x(m) in terms of the coordinates of x(r) where $r \leq n$. This system of difference equations is in general r'th order nonlinear. The structure of GA's, in particular the nilpotency of the (n-1)-dimensional subalgebra $\ker\beta$, implies that the first and second equations are linear, the third is nonlinear in terms from the second and so on. For principal or plenary sequences, constructed from a single element of the algebra all the equations are first order. It follows that solving the equations successively with successive substitution of the solution of the i'th equation in the i+1'th equation, the system may be solved by solving only linear first order equations. Or, as we have seen, Holgate's linearisation applies. By the introduction of new variables for the nonlinear terms and for any generated by the shift operator product rule we obtain a system of first order linear equations.

The sequences we now consider are not so 'nice' and even in simple cases our third equation is second order second degree. For these sequences the Holgate linearisation depends on m, the sequence index, different linearisations being required to evaluate different points in the evolution. It follows that this linearisation is not useful to obtain explicit formulae for the m'th term. It would be useful to prove that for a class of sequences more general than principal or plenary and for a given class of algebras, e.g. GA, the system of difference equations is solvable successively with substitutions, as seems to be the case at least for the sequences considered here.

3.5.1. Let A be GA and x(1), ..., x(p) be given elements of A. Following Heuch (36) define a sequence

$$x(j+p) = \sum_{k=0}^{p-1} \sum_{h=0}^{p-1} \alpha_{hk} x(j+h)x(j+k)$$

where $j = 1,2,\ldots$; $\alpha_{hk} = \alpha_{kh}$ and $\sum_{h,k} \alpha_{hk} = 1$.

Thus we are now concerned with sequences constructed from p initial and not necessarily related vectors instead of the sequences of single 'powers' considered so far.

We note that Etherington's definition of a train could be generalised to this context by requiring that the coefficients be functions of the weights of the p initial vectors only. We prefer to follow Heuch (36) and define a train by the condition that the coefficients be constant.

We shall also work entirely within the plane of unit weight, $U = \{x \in A : \beta(x) = 1\}$. For, while in the case of plenary powers it follows that if every $x \in U$ satisfies a train equation then every $y \in A$ does too, this does not follow for the more general sequences used here. This is not restrictive in applications since only those vectors in U have a probability distribution interpretation.

The sequence (3.5.1.) models the evolution of populations satisfying (G) except that mating which takes place at given times may be between overlapping generations in the sense that the individuals participate in mating for the last time when they reach an age of p generations. Each generation a proportion $2\alpha_{hk}$ $(h \neq k)$ or α_{hh} of the crosses are made between individuals of age p-h and p-k. Apart from this mating is random. x(j) gives the distribution for individuals born in generation j given the distributions of the first p generations.

A 'pure overlap' sequence is constructed as follows. In (3.5.1.) let p=2 so that

$$x = \alpha_{oo}(x(j))^2 + 2\alpha_{o1}x(j)x(j+1) + \alpha_{11}(x(j+1))^2.$$

Suppose further that $\alpha_{oo} = \alpha_{11} = 0$, hence $\alpha_{o1} = \frac{1}{2}$. Then we have

3.5.2. $$x(j+2) = x(j+1)x(j).$$

3.5.3. Example. Let A be the tetraploid algebra (1.5.10.), then with x(1), x(2) given vectors in A we have

$$x(3) = x(2)x(1) = c_o + \tfrac{1}{2}(x_1(1)+x_2(1))c_1 + (1/6)((x_1(2) + x_2(2) + x_1(1)x_2(1))c_2.$$

For n = 2,3,...

$$Ex(n) = x(n-1+2) = x(n)x(n-1)$$

i.e. for $x(n) = c_0+x_1(n)c_1+x_2(n)c_2$

$$Ex(n) = c_0+\tfrac{1}{2}(x_1(n)+x_1(n-1))c_1+(1/6)(x_2(n)+x_2(n-1)+x_1(n)x_1(n-1))c_2$$

Hence we obtain the system

$$Ex_0(n) = x_0(n)$$

$$Ex_1(n) = \tfrac{1}{2}(x_1(n)+x_1(n-1))$$

$$Ex_2(n) = (1/6)(x_2(n)+x_2(n-1)) + x_1(n)x_1(n-1)$$

with initial conditions given by $x(1)$, $x(2)$.

We note that this system is second order, second degree.

It is non-lineariseable. If we attempt to linearise by introducing new equations for $x_1(n)x_1(n-1)$ and any further monomials generated by the E product rule,

$$Ex_1(n)x_1(n-1) = Ex_1(n)Ex_1(n-1)$$

$$= \tfrac{1}{4}(x_1(n)x_1(n-1)+x_1(n)x_1(n-2)+x_1^2(n-1)+x_1(n-1)x_1(n-2))$$

This generates new higher order monomials, which in a solution by forward recursion would already have solutions.

In general

$$Ex_1(n)x_1(n-r) = \tfrac{1}{4}(x_1(n)x_1(n-r)+x_1(n)x_1(n-r-1)+ \\ +x_1(n-1)x_1(n-r)+x_1(n-1)x_1(n-r-1)).$$

Now for each finite n, r is finite, the process generates only finitely many linear equations, N say. But for large n, N is large, the linearisation depends on n. For arbitrary n we require an infinite dimensional space i.e. there does not exist a Holgate linearisation (see (4.2.8.). Thus we have,

3.5.4. Sequences giving rise to systems of difference equations with nonlinear terms of order greater than 1 may not be linearised by Holgate's method.

Such systems may however be solved by forward recursion.

3.5.5. Example. (3.5.3.) continued.

We have

$$Ex_0(n) - x_0(n) = 0$$

$$E^2x_1(n-1) - \tfrac{1}{2}Ex_1(n-1) - \tfrac{1}{2}x_1(n-1) = 0$$

$$E^2x_2(n-1) - (1/6)Ex_2(n-1) - (1/6)x_2(n-1) = x_1(n)x_1(n-1).$$

The first two equations are linear homogeneous of first and second order respectively and hence given two initial conditions are solved immediately. For the first the complementary function is $x_0^C(n) = k$ and with $x_0(0) = 1$ we have

$$x_0(n) = 1.$$

For the second the complementary function is

$$x_1^C(n-1) = k_1\tfrac{1}{4}(1+\sqrt{5})^n + k_2\tfrac{1}{4}(1-\sqrt{5})^n$$

k_1, k_2 may be determined from the initial conditions $x(1)$, $x(2)$ and the equations for $x(3)$, $x(4)$. We obtain

$$x_1(n-1) = f(n, x_1(1), x_1(2)).$$

Now the nonlinear term in the third equation involves only $x_1(r)$ which has already been solved. On substituting this solution in the third equation we obtain a second order linear nonhomogeneous equation

$$E^2x_2(n-1)-(1/6)Ex_2(n-1)-(1/6)x_2(n-1) = f(n,x_1(1),x_1(2)).f(n-1,x_1(1),x_1(2))$$

By standard operator methods we obtain a solution of the form

$$x_2(n) = g(n,f(n,x_1(1),x_1(2)),x_2(1),x_2(2)).$$

Thus with $p=2$, $\alpha_{00} = \alpha_{11} = 0$ in (3.5.1.) we have two linear homogeneous equations of first and second order respectively and one second order, second degree equation which reduces to a linear non-homogeneous second order equation on solution of the preceding equations (with the given ordering). Unlike the non-overlapping case, where all the equations are first order, here linearisation depends on n and hence is not a useful technique for obtaining explicit formulae for the general term.

For arbitrary α_{ij} subject to the conditions (3.5.1.), to linearise the equation corresponding to (3.5.4.) over even the tetraploid algebra requires linearisation of an equation of the form

$$X_{n+1} + \alpha X_n + \beta X_{n-1} + \gamma X_n^2 + \delta X_n X_{n-1} + \varepsilon X_{n-1}^2 = 0$$

where α, β, γ, δ, ε, are constant.

The nonlinearity increases if we increase p. For arbitrary p a sequence of the form (3.5.1.) which satisfies a train equation will give a system of nonlinear difference equations which while solvable by the method of (3.5.5.) will not in general be lineariseable.

4. CHARACTERISATION OF GENETIC ALGEBRAS

In (1.1.12) we indicated that the structure of associative algebras A depends on the nature of the radical R, since A is isomorphic to A/R + R where the structure of A/R is known up to a determination of all division algebras over the base field. We also mentioned the intractability of the structure of nonassociative algebras in general. For GA's (1.4.7.) gives a simple structure, R = kerβ and A/R is isomorphic to $\mathbb{C}$. While this is simple it has no clear genetic interpretation. We also noted the intractability of the structure of TA's.

The problem we consider in this chapter is that of finding a class of algebras sufficiently wide for algebras arising in gentics, having a simple characterisation or structure theory that is genetically meaningful. GA is at present the best such class and we shall consider some solutions of the latter part of the problem for this class.

It has been suggested (Abraham (1)) that the existence of a Holgate linearisation of the quadratic transformation (ϕ) of an algebra might provide such a characterisation. The class of algebras required is ideally wider than GA but having a simpler structure than TA. GA was defined in this spirit with respect to STA and the property of closure under duplication, STA not being closed under this genetically natural operation.

We first consider existing characterisations of GA, then we investigate the applicability of linearisation to the problem. In (4.2.) we give necessary and sufficient coordinate conditions for linearisation of ϕ . We also show that there are algebras of genetic significance not satisfying these conditions. This together with our remark that the class of algebras for which φ has a Holgate linearisation is unlikely to be much wider than GA, lead us to suspect that GA is probably the 'best' solution to the characterisation problem of genetic algebras.

In (4.3.) we consider the basis free approach of Holgate's characterisation theorem. As already mentioned, basis free necessary and sufficient conditions for the linearisation of φ is still an open problem. On the basis of the results here we believe that they are equivalent to the existence of a plenary train.

4.1. Some characterisations of GA

Several characterisations of the class GA have been given. Gonshor (32) considered characterisation and proved the following result.

Let (A, β) be a baric algebra and let $N = \ker \beta$. Then N is an ideal of A but in general N^r $(= N^{r-1}N)$ are not, nor in general is $N^{r+s} = N^r N^s$.

Let $N^{[n]}$ be the set of all linear combinations of products in A with at least n terms in N. $N^{[n]}$ is an ideal of A and,

4.1.1. A is GA iff there exists $n \in \mathbb{Z}$ such that $N^{[n]} = 0$.

This theorem gives a simple criterion for GA as a subclass of baric algebras related to the nilpotency of the kernel of the baric function. However it neither relates GA to more familiar classes nor has a clear genetic significance.

Algebras arising in genetics do not lie, as a whole, in any of the better known classes of nonassociative algebras. Both Schafer (54) and Holgate (43,46) have related certain subclasses of GA to more familiar classes. Schafer proved the following result.

4.1.2. If A is the gametic or zygotic algebra for one diploid diallelic locus with simple Mendelian inheritance then A is a Jordan algebra.

Holgate (43) proved the same result without using the transformation algebra and hence was able to generalise to multiple alleles.

4.1.3. If A is the gametic algebra corresponding to n+1 alleles $a_o, \ldots, a_n$ at a diploid locus with multiplication

$$a_i a_j = \tfrac{1}{2}(a_i + a_j)$$

then for $x = \sum_i x_i a_i$ and $\beta(x) = \sum_i x_i$ we have

$$x^2 = \beta(x)x.$$

Thus for all x such that $\beta(x) = 1$, x is idempotent and since

$$(\beta(x)y)x = \beta(x)(yx)$$

A is a Jordan algebra.

4.1.4. An STA is a Jordan algebra if its train roots all have values among 1, $\frac{1}{2}$, 0.

This excludes GA's corresponding to polyploidy or several loci. In fact includes only those algebras corresponding to the simplest forms of inheritance. Holgate remarks that for a GA to be a Jordan algebra seems dependent on Hardy-Weinberg equilibrium being reached in one generation.

Bernstein (10,11,12) attempted to classify all quadratic forms which could represent non-selective systems of inheritance in which a stationary distribution is reached in a single generation. He achieved this in 3 dimensions. Holgate (47) presented Bernstein's results in terms of a classification of algebras. Among these classes of algebras there is a one parameter family whose members are neither STA, GA or even TA. We have already introduced this, example (2.1.15.), without reference to the Bernstein property which we now define.

4.1.5. A commutative baric algebra (A, β) over $\mathbb{C}$ is said to be a <u>Bernstein</u> <u>algebra</u> (BA) if for all $x \in A$ such that $\beta(x) \neq 0$

$$x^{[3]} - \beta(x)^2 x^{[2]} = 0.$$

Holgate (47) formulated this definition and proved the following two results.

4.1.6. If A is BA then it contains an idempotent.

4.1.7. If (A, β) is BA such that $(\ker\beta)^3 = 0$ then A is STA.

Bernstein classified the 3-dimensional systems by the number of idempotent basis elements. Holgate (47) derives the corresponding algebras B_o, B_{11}, B_{12}, B_2, B_3 which contain 0, 1, 2, 3 idempotents in a basis. Thus Bernstein showed that there are just 5 laws of inheritance of 3 genetic types satisfying Hardy-Weinberg equilibrium.

We have considered the algebra B_{12} in some detail since it provides a useful test case.

4.1.8. Example. B_{12} (see (2.1.15.)) is a Bernstein algebra with

$$x^{[2]} = b_o + (1-\alpha + x_2 - \alpha x_1^2 - x_1x_2)b_2 = x^{[3]}.$$

Bertrand (13,15a) introduced a notion she calls 'grade' which allows some characterisation. In (15a) she also shows that NAA's satisfying certain conditions can be associated to a Jordan algebra.

Let A be a commutative NAA. Let $e_1,\ldots,e_n$ be a basis of A and let T(A) be the transformation algebra, generated by I_n and $R_{x_1},\ldots,R_{x_r}$ say. Now T(A) is a subspace of M(A) the algebra of all linear transformations on A. So we have putting $N = \dim T(A)$ and $n = \dim A$, $N \leq n^2$. If $N = r+1$ then there exists a basis of T(A)

$$I,\ R_{e_1},\ \ldots,\ R_{e_r} \qquad (b_1)$$

If $N > r+1$ then there exists $s > 0$ products $R_{e_i}R_{e_j}$ linearly independent among themselves and among the elements of the basis (b_1). If $N = r+1+s$ then a basis of T(A) is

$$I, R_{e_1}, \ldots, R_{e_r}, R_{e_{i_1}}R_{e_{j_1}}, \ldots, R_{e_{i_s}}R_{e_{j_s}} \qquad (b_2)$$

Again if $N > r+1+s$ then there exists $t > 0$ independent products $R_{e_i}R_{e_j}R_{e_k}$. Proceeding in this way, since the dimension of T(A) is finite, we obtain a basis of T(A),

$$(I,\ R_{e_i},\ R_{e_i}R_{e_j},\ \ldots,\ R_{e_{i_1}}R_{e_{i_2}}\ldots R_{e_{i_q}}).$$

4.1.9. The number q in the above basis of T(A) is independent of the basis of A and is called the <u>grade</u> of A.

4.1.10. Example. (1). Let G be the gametic algebra of simple Mendelian inheritance (see (1.3.2.)). The principal and plenary rank equations are both

$$x^2 - x_o x = 0.$$

Kerβ is nilpotent of index 2. G is STA. Bertrand (13) shows that any such algebra has grade 1.

(2). Let Z be the duplicate of G (see (1.3.9.)). This algebra has principal and plenary rank equations

$$x^3 - (x_1+2x_2+x_3)x^2 = 0$$
$$x^{[3]} - (x_1+2x_2+x_3)^2 x^{[2]} = 0$$

respectively.

Kerβ is nilpotent of index 3 and Z is STA. Consider all products of the R_{c_i} of order less than 3, where (c_i) is a canonical basis for Z. We find writing $R_i = R_{c_i}$:

$$R_1R_1R_1 = R_1R_1R_o = R_2 = 0$$
$$R_1R_oR_1 = \tfrac{1}{2}R_oR_1R_1 = \tfrac{1}{2}R_1R_1$$
$$R_1R_oR_o = \tfrac{1}{2}R_oR_1R_o = \tfrac{1}{4}R_1R_o$$
$$R_oR_oR_1 = \tfrac{1}{2}R_1 - \tfrac{1}{2}R_oR_1 + 2R_1R_o$$
$$R_oR_oR_o = 3/2R_oR_o - \tfrac{1}{2}R_o$$
$$R_iR_jR_k = 0 \text{ for the remaining triples } (i,j,k).$$

Thus the transformation algebra has basis

$$\{I, \{R_i\}, \{R_iR_j\} : (i,j = 0,1,2)\}$$

with dimension 13. So Z has grade 2.

Bertrand (15a) established a connection between grade, STA and degree of principal rank equation. STA's possess a unique non zero idempotent if no train root equals $\frac{1}{2}$ (Gonshor (29)).

4.1.11. Let (A,β) be an STA with unique idempotent and principal rank equation of degree k+1. Then (1) if kerβ

is nilpotent of index 1 then grade $A \leq k$; (2) if $\ker \beta$ is nilpotent of index 2 then grade $A \leq 2k-1$.

The same remarks as those following Gonshor's characterisation (4.1.1.) apply to this result.

Bertrand's result concerning Jordan algebras is:

4.1.12. If A is an NAA such that 1) for all $x \in A$ there exists $x' \in A$ such that $R_x R_x = R_{x'}$, and 2) if there exists $x_o \in A$ such that $R_{x_o} = 0$ then $x_o = 0$; then there is an associated Jordan algebra A* differing from A only in its multiplication * which is defined by the relation $2R_{x*y} = 2R_{xy} + R_y R_x$.

If A* is not nilpotent then it is possible using the Pierce decomposition relative to an idempotent e of A*, (see Schafer (55)), to write A as a direct sum $A = A_o + A_1 + A_2$ such that

$$R_{x_o} R_e = R_e R_{x_o} = 0 \text{ if } x_o \in A_o$$
$$R_{x_1} R_e = R_e R_{x_1} = R_{x_1} \text{ if } x_1 \in A_1$$
$$R_e R_{x_2} R_e = 0 \text{ if } x_2 \in A_2.$$

As we have already seen (2.2.12.) Heuch (41) introduced spaces of algebras in order to discuss various mixtures, in particular to consider their uniqueness. This leads to a geometric characterisation of genetic algebras.

For fixed dimension n we have the following chain of spaces of algebras (c.f. (2.2.18.)

$$\mathbb{C}^n_G \subset \mathbb{C}^n_B \subset \mathbb{C}^n_C \subset \mathbb{C}^n_A.$$

$\mathbb{C}^n_G$ is constructed using a fixed canonical basis (these are not unique (see (1.5.2.)). There exist algebras arising in genetics that are not GA. Heuch gives the following geometric description of algebras over the complex numbers arising in the genetics of randomly mating populations.

4.1.13. Let $\mathbb{C}^n_{\mathcal{G}}$ be the class of all n-dimensional baric algebras with a fixed genetic basis. Then $\mathbb{C}^n_{\mathcal{G}}$ forms a polyhedron P in $\mathbb{C}^n_A$ and $\mathbb{C}^n_B$ is the smallest flat containing P.

Not all algebras arising in genetics are even baric, e.g. (4.2.8.(2)) below, however baric algebras seem to be the largest class that it is useful to consider. Unfortunately as Heuch showed,

4.1.14. $\mathbb{C}^n_G$ (and hence also $\mathbb{C}^n_B$) is not closed under mixture.

That $\mathbb{C}^n_B$ is not closed under mixture follows from the result that any mixture of baric algebras with different nilalgebras is not baric. We also show that mixture does not preserve the linearisability of the quadratic transformation.

4.1.15. If two algebras A, B in $\mathbb{C}^n_A$ have lineariseable quadratic transformations, the quadratic transformation of a mixture of A and B may not be lineariseable.

As an example take the algebras A, B over the complex numbers defined by

$$c_1^2 = c_1,\ c_2^2 = c_3,\ c_i c_j\ 0 \text{ for } (i,j) \neq (1,1),(2,2)$$
$$c_1^2 = c_1,\ c_3^2 = c_2,\ c_i c_j = 0 \text{ for } (i,j) \neq (1,1),(3,3)$$

respectively. Then take the mixture $\frac{1}{2}(A + B)$ with multiplication

$$c_1^2 = c_1,\ c_2^2 = \tfrac{1}{2}c_3,\ c_3^2 = \tfrac{1}{2}c_2,\ c_ic_j = 0 \text{ if } i \neq j.$$

In A for x such that $\beta(x) = 1$ i.e. $x = c_o + x_1c_1 + x_2c_2$, $x^2 = c_o + x_1^2c_2$. In B $x^2 = c_o + x_2^2c_1$. We obtain the linear equations for A,

$$1\widetilde{\Phi} = 1,\ x_1\widetilde{\Phi} = 0,\ x_1^2\widetilde{\Phi} = 0,\ x_2\widetilde{\Phi} = x_1^2$$

and for B,

$$1\widetilde{\Phi} = 1,\ x_1\widetilde{\Phi} = x_2^2,\ x_2\widetilde{\Phi} = 0,\ x_2^2\widetilde{\Phi} = 0.$$

But for the mixture we obtain the infinite set of equations,

$$1\widetilde{\Phi} = 1,\ x_1\widetilde{\Phi} = \tfrac{1}{2}x_2^2,\ x_2\widetilde{\Phi} = \tfrac{1}{2}x_1^2,\ \ldots$$

$$x_1^{2^n}\widetilde{\Phi} = (1/2^n)x_2^{2^n},\ x_2^{2^n}\widetilde{\Phi} = (1/2^n)x_2^{2^n},\ldots\ .$$

This result shows a limitation of the application of linearisation to the problem of characterisation.

We next consider a characterisation theorem given by Holgate (46). Holgate introduced Lie algebras into the study of GA's. The characterisation he achieved is, unlike Schafer's structure theorem (1.4.7.), amenable to some genetic interpretation. (As Schafer stated in his paper his interest was purely formal.) We first introduce various algebras associated with a given commutative baric algebra (A,β).

4.1.16. The transformation algebra $T(A) = \langle I, R_x : x \in A \rangle$. $T(A)$ is a subalgebra of the total matrix algebra $M(A)$ of A. These algebras are associative.

4.1.17. Let $L(A)$ be the Lie multiplication algebra of A i.e. the algebra generated by the R_x $(x \in A)$ with the commutator product

$$[R_x, R_y] = R_xR_y - R_yR_x.$$

We note that if R(A) is the right multiplication algebra, generated by the R_x $(x \in A)$ then

$$\dim L(A) = \dim R(A).$$

L(A) is a subset of M(A) and a subalgebra of L(M(A)).

4.1.18. Let L'(A) be the first derived algebra of L(A). Thus L'(A) consists of the set of all commutator products $[R_x, R_y]$ in L(A).

4.1.19. If every element of L(A) is nilpotent then L'(A) is nilpotent and hence L(A) is solvable.

Holgate's characterisation theorem (HCT) gives the following necessary and sufficient conditions for GA.

4.1.20. A baric algebra (A, β) is GA iff L(A) is solvable and $\ker\beta$ is (principally) nilpotent.

We shall assume A is commutative but nonassociative. Otherwise the associator (x,y,z) and the commutator $[x,y]$ vanish and $R_xR_y = R_{xy}$ or $[R_x, R_y] = 0$ so that L(A) is a zero algebra, $L(A)^2 = 0$ i.e. L(A) is solvable.

Holgate gives in his paper an example possessing a high degree of symmetry to illustrate HCT, namely the gametic algebra for 1 diploid multiple allelic locus. The symmetry is exploited to show that L(A) is solvable. In less symmetric cases we are forced to use direct calculations as in (4.3.3.) below.

Another possible approach to the characterisation problem is to use the 'structure tensors' of the algebras concerned. For algebras defined in terms of conditions on their structure constants, as in the Gonshor definition of GA, we might expect properties of the class defined to show up more clearly as properties of the corresponding set of structure tensors in the appropriate space of tensors or tensor algebra.

Let A be a GA with basis $c_o, \ldots, c_{n-1}$ and multiplication

$$c_i c_j = \sum_k \lambda_{ijk} c_k.$$

If A* is the dual space of A as a vector space, then to each triple (c^k, c_i, c_j) of $A^* \times A \times A$ is associated the scalar λ_{ijk} since

$$\begin{aligned} c^k(c_i c_j) &= c^k(\sum_l \lambda_{ijl} c_l) \\ &= \sum_l \lambda_{ijl} c^k(c_l) \\ &= \sum_l \lambda_{ijl} \delta^k_l \\ &= \lambda_{ijk} \end{aligned}$$

where δ^k_l is the Kronecker delta.

Thus the n^3 scalars λ_{ijk} form the components of a tensor, λ^k_{ij}, in the tensor space $\bigotimes^2_1(A^*, A)$, (see Greub (33)). Equivalently the λ_{ijk} define a (1+2)-linear function $A^* \times A \times A \to \mathbb{C}$ i.e. a scalar valued tensor of order (1,2) (a mixed tensor).

4.1.21. The tensor λ^k_{ij} is called the <u>structure tensor</u> of A.

Little has yet been obtained from this approach apart from a derivation of the result that given two GA's with structure tensors λ^k_{ij}, μ^k_{ij} we obtain a new GA with structure tensor $\lambda^k_{ij} \otimes \mu^k_{ij}$, a result that is easily verified without recourse to tensors. Since, if the structure constants of two algebras satisfy G1-G3 then so too do their products.

4.2. Basis dependent characterisation

The algebra B_{12} (2.1.15.) shows that GA is sufficient but not necessary and sufficient for a Holgate linearisation. B_{12} breaks the GA conditions G1-G3 only in the removal of the possible equality in G3, since $\lambda_{122} = -\frac{1}{2}$ (not zero).

Let (A, β) be a baric algebra. Take an Etherington canonical basis (c_i) such that $\beta(c_o) = 1$ and $\beta(c_i) = 0$ for $i > 0$ (c.f.(1.2.8.)). Let U be the plane of unit weight in A i.e. $U = \{ x \in A : x = c_o + x_1 c_1 + \dots + x_n c_n \}$. Let M_r be the set of monomials in the x_i $(i = 0,1,\dots,n)$ with $x_o = 1$, of degree less than r, with associative and commutative identities removed and such that the representative monomial has its terms of highest degree on the left. We now define an order on M_r.

4.2.1. If $m_{ij}(x) = x_i^{\alpha_{j_i}} \dots x_1^{\alpha_{j_1}}$ and $m_{kl}(x) = x_k^{\alpha_{l_k}} \dots x_1^{\alpha_{l_1}}$ define

$$m_{ij}(x) \leq m_{kl}(x)$$

iff $i < k$ or $i = k$ and $\alpha_{j_i} < \alpha_{l_i}$, where $x_{i'}^{\alpha_{j_{i'}}}, x_{k'}^{\alpha_{j_{k'}}}$ are the first non-identical terms from the left, i.e. if $m_{ij}(x)$ precedes or is identical to $m_{kl}(x)$ in the lexicographical order.

For example taking all monomials of degree less than or equal to 2 in $\{1, x_1\}$ we have $\{1.1, 1.x_1, x_1.1, x_1.x_1\}$ and removing identities gives $\{1.1, x_1.1, x_1.x_1\}$. Ordering this set and writing the monomials in the usual way we have $1 \leq x_1 \leq x_1^2$.

Now suppose we have a nonlinear transformation ψ of A. We may express $x\psi$ relative to a fixed basis by a set of equations

$$x_i\psi = f(x_o, x_1, \ldots, x_n)$$

in the coordinates x_i of x.

4.2.2. If $x \in U$, then a set of equations

$$x_i\psi = \sum_j m_{ij}(x)$$

$$m_{ij}(x) = x_1^{\alpha_{j_i}} \ldots x_n^{\alpha_{j_n}}\psi = (x_1\psi)^{\alpha_{j_i}} \ldots (x_n\psi)^{\alpha_{j_n}}$$

where $i = 0,1,\ldots,n$; $j = 1,2,\ldots,m$ $m \leq \text{card } M_r$ such that the $m_{ij}(x) \in M_r$ satisfy

$$m_{ij}(x) \leq x_i \text{ or } m_{ij}(x)\psi = 0$$

will be called a <u>formal linearisation of ψ of degree</u> r. (We have adopted the left hand convention for the monomial functions.)

4.2.3. The class of baric algebras whose coordinate equations arising from $x\phi = x^2$ $(x \in U)$ satisfy the conditions for a formal linearisation will be denoted <u>L1</u>.

4.2.4. Let (A,ϕ) be a baric algebra together with its quadratic transformation then A is in L1 iff A is E_ϕ-lineariseable.

First assume A is in L1 and suppose $m_{ij}(x) \leq x_i$ $j=1,2,\ldots,s$ where $s = \text{card } M_r$. Then an arbitrary equation in the system for $x\phi$ is

$$m_{ij}(x)\phi = x_i^{\alpha_{j_i}} \ldots x_1^{\alpha_{j_1}}\phi = (x_i\phi)^{\alpha_{j_i}} \ldots (x_1\phi)^{\alpha_{j_1}}.$$

Now each $(x_k\phi)^{\alpha_{j_k}} = (\sum_l m_{kl}(x))^{j_k}$ where $k \leq i$, and $l = 1,\ldots,s$. Thus $m_{kl}(x) \leq x_i$. Hence all the monomials generated by $m_{ij}(x)$ are less than or equal to x_i. Hence they are finite in number and so A is E_ϕ - lineariseable.

Suppose now some $m_{ij}(x) > x_i$. Then since A is in L1, $m_{ij}(x)\phi = 0$ and hence all such monomials only generate zeroes. So again only a finite number of distinct monomials is generated and A is $E\phi$-lineariseable.

Conversely if A is $E\phi$-lineariseable then the monomials generated are finite in number and all are less than or equal to x_n. This is only possible if the conditions for A to be in L1 are satisfied. For, otherwise there exists $m_{ij}(x) > x_i$ and $m_{ij}(x)\phi \neq 0$. Hence $m_{ij}(x) = x_i^{\alpha_{j_i}} \ldots x_1^{\alpha_{j_1}}$ where $\alpha_{j_i} > 1$. Thus we have a system of equations for $x\phi$ with terms in $x_i^{\alpha_{j_i}} = (x_i\phi)^{\alpha_{j_i}}$, which in turn involves terms in $x_i^{2\alpha_{j_i}}$. Therefore the system contains an infinite sequence of monomials of increasing degree

$$\left\{ x_i^{2n\alpha_{j_i}} : n = 1,2, \ldots \right\}.$$

Hence A is not $E\phi$-lineariseable. This is a contradiction completing the proof.

4.2.5. Construction of algebras in L1

Suppose given a formal linearisation of ϕ of finite degree. We assume x to belong to the plane of unit weight of a commutative baric algebra A with baric function defined by $\beta(c_0)=1$, $\beta(c_i)=0$ for $i > 0$ where (c_i) is a basis of A and quadratic map ϕ. Compare coefficients of $x\phi$ given by the equations of the formal linearisation with those of the formal expansion of $x^{[2]}$. A solution of the basic product equations, $c_i c_j = \sum_k \lambda_{ijk} c_k$ for the λ_{ijk} gives the structure constants of an algebra in L1. The algebra so obtained is of course not unique.

Examples constructed in this way are necessarily

$E\phi$-lineariseable. We shall see that they are not in general GA.

By starting with a formal linearisation having an infinite system of equations we construct algebras in which the quadratic map is not lineariseable, e.g. (4.2.7.).

4.2.6. Example. Let M_4 consist of all monomials in 1, x_1, x_2, x_3 of degree less than or equal to 4 ordered by (4.2.1.). We arbitrarily define subject to (4.2.2.):

$$1\phi = 1, \quad x_1\phi = 0, \quad x_2\phi = x_2+x_1^2,$$
$$x_3\phi = x_3+x_2^2+x_1x_3.$$

Then by (3.1.4.)

$$x_1^2\tilde{\phi} = 0, \quad x_2^2\tilde{\phi} = x_2^2+2x_2x_1^2+x_1^4, \quad x_1^4\tilde{\phi} = 0,$$
$$x_2x_1^2\tilde{\phi} = 0, \quad x_3x_1\tilde{\phi} = 0.$$

The ordered set of monomials is

$$(1,\ x_1,\ x_1^2,\ x_1^4,\ x_2,\ x_2x_1^2,\ x_2^2,\ x_3,\ x_3x_1).$$

Let $x = c_0 + \sum_{i=1}^{3} x_i c_i$ the formal expansion of x^2 is $x^2 = \sum_i x_i^2 c_i^2 + 2\sum_{i,j} x_i x_j c_i c_j$. From our formal linearisation we have

$$x\tilde{\phi} = c_0 + (x_2+x_1^2)c_2 + (x_3+x_2^2+x_3x_1)c_3.$$

On solving the basic product equations for the structure constants we have

$$c_0^2 = c_0,\ c_0c_1 = 0,\ c_0c_2 = \tfrac{1}{2}c_2,\ c_0c_3 = \tfrac{1}{2}c_3,$$
$$c_1^2 = c_2, c_1c_2 = 0, \quad c_1c_3 = \tfrac{1}{2}c_3,$$
$$c_2^2 = c_3, \quad c_2c_3 = 0,$$
$$c_3^2 = 0.$$

This defines an algebra A in L1. A is not GA. The linear transformation $\tilde{\phi}$ corresponding to ϕ has a sparse matrix with minimal equation

$$\tilde{\phi}^3 - 2\tilde{\phi}^2 + \tilde{\phi} = 0.$$

Computing plenary powers verifies that the plenary train equation is

$$x^{[4]} - 2x^{[3]} + x^{[2]} = 0.$$

This is in fact the construction of example (3.4.4.).

Abraham (1) proved that the dimension of the linearising space is independent of the choice of basis in A. The following is an immediate corollary.

4.2.7. If a system of linearising equations is infinite with respect to one basis then it is with respect to any basis.

Thus to show that ϕ cannot be linearised in a given algebra it is sufficient to show that in a given basis an infinite number of linearising equations are generated. We have tacitly assumed this in some previous examples.

4.2.8. Example. (1) Let A be a commutative baric algebra defined by

$$c_o^2 = c_o, \quad c_oc_1 = c_1, \quad c_1^2 = 2c_1$$

and $\beta(c_o) = 1$, $\beta(c_1) = 0$.

Any x such that $\beta(x) = 1$ satisfies

$$1\phi = 1, \; x_1\phi = 2x_1(1+x_1)$$

Now

$$x_1^2\tilde{\phi} = 4x_1^2(1+x_1)^2$$

hence ϕ generates an infinite sequence of monomials of increasing degree. So A is not E_ϕ-lineariseable. Similarly A does not possess a (finite) plenary train equation. We note that $\ker\beta$ is not nilpotent.

(2) A more complex example is the non baric algebra for

zygotic sex linkage and multiple alleles given by Wörz-Busekros (57). The multiplication table is

$$
\begin{array}{c|ccccc}
 & a_{11} & a_{12} & a_{22} & a_1 & a_2 \\
\hline
a_{11} & & & & \frac{1}{2}(a_{11}+a_1) & \frac{1}{2}(a_{11}+a_2) \\
a_{12} & & 0_{3\times 2} & & \frac{1}{2}(a_{12}+a_1) & \frac{1}{2}(a_{12}+a_2) \\
a_{22} & & & & \frac{1}{2}(a_{22}+a_1) & \frac{1}{2}(a_{22}+a_2) \\
a_1 & \frac{1}{2}(a_{11}+a_1) & \frac{1}{2}(a_{12}+a_1) & & & \\
 & & & & 0_{2\times 2} & \\
a_2 & \frac{1}{2}(a_{11}+a_2) & \frac{1}{2}(a_{12}+a_2) & & &
\end{array}
$$

From this there follows in the given basis

$$
\begin{aligned}
x_{11}\phi &= x_{11}x_1 + x_{11}x_2 \\
x_{12}\phi &= x_{12}x_1 + x_{12}x_2 \\
x_{22}\phi &= x_{22}x_1 + x_{22}x_2 \\
x_1\phi &= x_{11}x_1 + x_{12}x_1 + x_{22}x_2 \\
x_2\phi &= x_{11}x_2 + x_{12}x_2 + x_{22}x_2
\end{aligned}
$$

and application of the E product rule now generates an infinite system of equations for monomials of increasing degree (e.g. $x_{11}^n x_1^n$, $n=1,2,\ldots$).

(3) As a final example we give one of Heuch (39) which represents two genetic types such that like matings produce only one type and unlike matings produce only the other type. Let A be the algebra defined by

$$a_o^2 = a_o = a_1^2 \ , \ a_oa_1 = a_1a_o = a_1$$

with $\beta(x) = x_o+x_1$. Then $\ker\beta$ is the set $\{x \in A : x_1=-x_o\}$. Hence $(\ker\beta)^2 = \ker\beta$. i.e. $x \in \ker\beta$ implies $x = x_oa_o-x_oa_1$. So $x^2 = 2x_o^2(a_o-a_1)$. In general

$$x^n = 2^{n-1}x_o^n(a_o - a_1) \neq 0, \ (x_o\neq 0).$$

Thus $\ker\beta$ is not nilpotent and hence A is not GA. The principal train equation is

$$x^3 - 2x_ox^2 + (x_o^2-x_1^2)x = 0.$$

Since the coefficients are not functions of $\beta(x)$ only A is not TA. The coordinate equations for $x\phi$ are

$$x_o\phi = x_o^2+x_1^2, \quad x_1\phi = 2x_ox_1.$$

This generates an infinite system of equations

$$x_o^n\tilde{\phi} = (x_o+x_1^2)^n, \quad x_1^n\tilde{\phi} = 2nx_o^nx_1^n.$$

We next consider the duplicate of the algebra B_{12} and show that linearisation is preserved in this case and that the conditions for linearisation must be wider than GA in ways other than those previously encountered.

4.2.10. Example. B_{12}'.

From the multiplication of B_{12}, (2.1.15.), we obtain the duplicate B_{12}'. Writing the duplicate basis $b_{oo}, \ldots, b_{22}$ as $c_o, \ldots, c_5$ we have

	c_o	c_1	c_2	c_3	c_4	c_5
c_o	c_o	0	$\frac{1}{2}c_2$	$-c_2$	$-\frac{1}{2}c_2$	0
c_1		0	0	0	0	0
c_2			$\frac{1}{4}c_5$	$-\frac{1}{2}c_5$	$-\frac{1}{4}c_5$	0
c_3				c_5	$\frac{1}{2}c_5$	0
c_4					$\frac{1}{4}c_5$	0
c_5						0

Let $x = c_o + \sum_i x_ic_i$ then

$$x^2 = c_o+(x_2-2x_3-x_4)c_2+(\tfrac{1}{4}x_2^2-x_2x_3-\tfrac{1}{2}x_2x_4+x_3^2+x_3x_4+\tfrac{1}{4}x_4^2)c_5.$$

Hence we obtain the coordinate equations

$$1\phi = 1, \quad x_1\phi = 0, \quad x_2\phi = x_2-2x_3-x_4, \quad x_3\phi = 0, \quad x_4\phi = 0,$$

$$x_5\phi = \tfrac{1}{4}x_2^2-x_2x_3-\tfrac{1}{2}x_2x_4+x_3^2+x_3x_4+\tfrac{1}{4}x_4^2.$$

Linearising via (2.1.2.) these equations are extended by

$$x_2^2\tilde{\phi} = x_2^2-4x_3x_2-2x_4x_2+4x_3^2+4x_4x_3+x_4^2, \quad x_2x_3\tilde{\phi} = x_2x_4\tilde{\phi} =$$

$$= x_3^2\tilde{\phi} = x_3x_4\tilde{\phi} = x_4^2\tilde{\phi} = 0.$$

Ordering the monomials occuring in these equations by

(4.1.1.) we have:

$$(1,x_1,x_2,x_2^2,x_3,x_3x_2,x_3^2,x_4,x_4x_2,x_4x_3,x_4^2,x_5)$$

giving the sparse induced linear transformation whose only non zero columns are 1, 3, 4 and 12. The minimal polynomial is easily found to be $\tilde{\varphi}^2 - \tilde{\varphi}$. The plenary train polynomial is identical to min $\tilde{\varphi}$ and hence B_{12}' is a Bernstein algebra.

This example together with (4.2.6.) illustrate several facts about linearisation. The class of algebras L1 is wider than GA. Both B_{12} and B_{12}' are in L1 and both break the Gonshor conditions in different ways. B_{12} breaks only G3, B_{12}' only G2 (λ_{032}, $\lambda_{042} \neq 0$). Both these algebras are Bernstein algebras but not TA, having plenary train equation $x^{[3]} - x^{[2]} = 0$. Example (4.2.6.) is also in L1 but is neither GA nor a Bernstein algebra. It breaks both conditions G2 and G3 of GA while possessing the plenary train equation, $x^{[4]} - 2x^{[3]} + x^{[2]} = 0$. There exist TA that are not in L1, e.g. Abraham's counter-example to a conjecture of Suttles (56) of a TA that is not a GA (see (1)). This does not possess a plenary train.

These results indicate that linearisability of the quadratic transformation is equivalent to the existence of a plenary train equation. We note that this is stronger than the identity of the plenary train polynomial and the minimal polynomial of the induced linear map. This identity is equivalent to the assertion that the existence of a plenary train equation $xp(\varphi) = 0$ implies the existence of an Holgate linearisation with minimal polynomial p. Our assertion implies the converse too.

4.3. Basis free characterisation

Holgate's characterisation theorem (4.1.21.) provides necessary and sufficient conditions for GA and by his theorem (2.1.1.) GA is sufficient for the linearisation of the quadratic transformation. In this section we consider the relationship between the basis dependent linearisation and the basis free conditions of HCT. In particular we consider algebras satisfying one or other of the conditions of HCT. We note that known examples of algebras in L1 but not in GA are not TA.

4.3.1. We denote by L2 the class of baric algebras satisfying either the solvability condition (S) or the nilpotency condition (N) of (4.1.21.) i.e. (A, β) such that either $L(A)$ is solvable or $\ker\beta$ is comprised wholly of (principally) nilpotent elements.

4.3.2. L2 is closed under duplication.

Let (c_i) be a basis of A. A' is isomorphic to $A^2 + K$ where K is the kernel of the homomorphism $h: A' \longrightarrow A^2$, $c_{ij}h = c_ic_j$ and $L(A^2)$ is a Lie subalgebra of $L(A)$. The solvability of $L(A)$ implies that of $L(A^2 + K)$ and hence of $L(A')$. Also if β is the baric function of A then $\ker\beta|_{A^2}$ is a subset of $\ker\beta$. This together with the homomorphism h implies the nilpotency of the kernel of the baric function of A' given that of A.

4.3.3. Example. B_{12} ($\alpha = 1$) is in L2, (satisfying S but not N).

The multiplication table is

$$b_o^2 = b_o, \quad b_ob_1 = 0, \quad b_ob_2 = \tfrac{1}{2}b_2,$$
$$b_1^2 = -b_2, b_1b_2 = -\tfrac{1}{2}b_2,$$
$$b_2^2 = 0.$$

The baric function is defined by $\beta(b_o) = 1$, $\beta(b_i) = 0$ for $i > 0$. Let $x = x_ob_o+x_1b_1+x_2b_2$ then

$$x^2 = x_o^2b_o + (x_ox_2-x_1^2-x_1x_2)b_2.$$

Now $\ker\beta = \langle b_1,b_2\rangle$, $(\ker\beta)^2 = \langle b_1,b_2\rangle\langle b_1,b_2\rangle = \langle b_2\rangle$ and $(\ker\beta)^3 = \langle b_1,b_2\rangle\langle b_2\rangle = \langle b_2\rangle$. So $\ker\beta$ is not nilpotent, and any x in $\ker\beta$ of the form $x_1b_1+x_2b_2$ is not principally nilpotent. Thus N is not satisfied.

We show that B_{12} satisfies condition S of L2. We must do this directly since B_{12} does not possess the symmetry of Holgate's example.

$L(B_{12})$ is the algebra generated by the R_x $(x \in B_{12})$ with the commutator product. We have

$$R_{b_o} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & \tfrac{1}{2} \end{bmatrix} \quad R_{b_1} = \begin{bmatrix} 0 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & -\tfrac{1}{2} \end{bmatrix} \quad R_{b_2} = \begin{bmatrix} 0 & 0 & 0 \\ 0 & -\tfrac{1}{2} & 0 \\ \tfrac{1}{2} & 0 & 0 \end{bmatrix}$$

Computing basic products,

$$[R_{b_i},R_{b_i}] = 0, \quad [R_{b_i},R_{b_j}] = -[R_{b_j},R_{b_i}]$$

and

$$[R_{b_o},R_{b_1}] = 0, \quad [R_{b_o},R_{b_2}] = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ -\tfrac{1}{4} & 0 & 0 \end{bmatrix}, \quad [R_{b_1},R_{b_2}] = [R_{b_o},R_{b_2}].$$

Now $[R_{b_2},R_{b_o}]$ is linearly independent among the R_{b_i} $(i=0,1,2)$. For, writing $R_i = R_{b_i}$ and $R_{ij} = [R_i,R_j]$ and setting

$$\alpha_0R_0 + \alpha_1R_1 + \alpha_2R_2 + \alpha_{20}R_{20} = 0$$

we find on solving the linear system that all the coefficients must be zero.

Thus a basis of $L(B_{12})$ contains at least

$$\left\{ R_0,\ R_1,\ R_2,\ [R_2,R_0] \right\}. \qquad (*)$$

This is a basis providing all products among these are linearly dependent on this set. We have

$$R_0,R_{20} = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ -\frac{1}{8} & 0 & 0 \end{bmatrix} = \tfrac{1}{2}R_{02}$$

$$[R_1,R_{20}] = [R_2,R_{20}] = [R_{20},R_{20}] = 0.$$

So (*) is a basis of $L(B_{12})$ and hence its multiplication is

	R_0	R_1	R_2	R_{02}
R_0	0	0	R_{02}	$\frac{1}{2}R_{02}$
R_1	0	0	R_{02}	0
R_2	$-R_{02}$	$-R_{02}$	0	0
R_{02}	$-\frac{1}{2}R_{02}$	0	0	0

Now $L(B_{12})^{(2)}$ is generated by R_{02} and $[R_{02},R_{02}] = 0$. So $L(B_{12})^{(2)}$ is a zero algebra of dimension 1 and hence $L(B_{12})^{(3)} = 0$. Thus $L(B_{12})$ is solvable.

4.3.4. Example. B_{12}' is in L2 , (satisfying N but not S). The multiplication is given in (4.2.10.) where it is shown that B_{12}' is in L1. B_{12}' is not GA since $\lambda_{032}, \lambda_{042} \neq 0$. Ker$\beta$ is nilpotent for $\ker\beta = \langle c_1,c_2,c_3,c_4,c_5\rangle$, $(\ker\beta)^2 = \langle c_5\rangle$ and $(\ker\beta)^3 = 0$. Now since B_{12} is not GA and $\ker\beta$ is nilpotent it follows from HCT that $L(B_{12}')$ is not solvable.

4.3.5. Example. A 3-dimensional nonassociative baric algebra in L2 but not in L1. We define the algebra from an infinite formal linearisation:

$1\phi = 1$, $x_1\phi = x_1$, $x_2\phi = x_1+x_1x_2$,

$x_1x_2\tilde{\phi} = x_1^2+x_1^2x_2$, $x_1^2\tilde{\phi} = x_1^2$, $x_1^2x_2\tilde{\phi} = x_1^3x_2$, ...

Note that $x_1x_2 > x_2$ by our order (4.2.1.) and $x_1x_2\tilde{\phi} \neq 0$.

For a basis (c_i) and $x = c_o+x_1c_1+x_2c_2$ formally we have

$$x\phi = c_o + x_1c_1 + (x_1+x_1x_2)c_2.$$

Solving the basic product equations for a set of structure constants we obtain

$$\begin{aligned} c_o^2 &= c_o, \quad c_oc_1 = \tfrac{1}{2}c_1, \quad c_oc_2 = 0,\\ c_1^2 &= 0, \quad c_1c_2 = \tfrac{1}{2}c_2,\\ c_2^2 &= 0. \end{aligned}$$

This gives an algebra A whose quadratic transformation satisfies the given equations. A is baric with $\beta(c_o) = 1$, $\beta(c_i) = 0$ for $i > 0$, since $\beta(xy) = x_oy_o = \beta(x)\beta(y)$.

A is not GA since $\lambda_{122} \neq 0$. Moreover $\ker\beta$ is not nilpotent. Any x of the form $x_1c_1+x_2c_2$ is not principally nilpotent. The associator is non zero i.e. A is not associative. Next consider the Lie multiplication algebra L(A) of A. We have basic right multiplications

$$R_{c_o} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 \end{bmatrix} \quad R_{c_1} = \begin{bmatrix} 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2} \end{bmatrix} \quad R_{c_2} = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2} \\ 0 & 0 & 0 \end{bmatrix}$$

R_0, R_1, R_2 say. Then writing $R_{ij} = [R_i,R_j]$ we have

$$R_{01} = \begin{bmatrix} 0 & \frac{1}{4} & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \quad R_{02} = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & \frac{1}{4} \\ 0 & 0 & 0 \end{bmatrix} \quad R_{12} = \begin{bmatrix} 0 & 0 & \frac{1}{4} \\ 0 & 0 & -\frac{1}{4} \\ 0 & 0 & 0 \end{bmatrix}$$

$R_{02} = \frac{1}{2}R_2$, so R_{02} is linearly dependent on the R_i. Solving the linear system

$$\alpha_0R_0 + \alpha_1R_1 + \alpha_2R_2 + \alpha_{01}R_{01} + \alpha_{12}R_{12} = 0$$

we find $\alpha_0 = \alpha_1 = \alpha_2 = \alpha_{01} = \alpha_{12} = 0$

i.e. that R_{01}, R_{12} together with R_0, R_1, R_2 form a maximally linearly independent set thus far. So a basis of L(A) contains at least

$$\{ R_0, R_1, R_2, R_{01}, R_{12} \}.$$

That no further linearly independent elements are generated i.e. that this set is maximal follows from:

$[R_{01},R_{01}] = \frac{1}{2}R_{01}$, $[R_0,R_{12}] = R_{12} + \frac{1}{4}R_2$, $[R_1,R_{01}] = 0$,
$[R_1,R_{12}] = -R_{12} - \frac{1}{4}R_2$, $[R_2,R_{01}] = -\frac{1}{2}(\frac{1}{2}R_2 + R_{12})$,
$[R_{01},R_{12}] = [R_2,R_{01}]$ and $[R_2,R_{12}] = 0$.

Thus L(A) is of dimension 5 with multiplication

	R_0	R_1	R_2	R_{01}	R_{12}
R_0	0	R_{01}	$\frac{1}{2}R_2$	$\frac{1}{2}R_{01}$	$R_{12}+\frac{1}{4}R_2$
R_1		0	R_{12}	0	$-(R_{12}+\frac{1}{4}R_2)$
R_2			0	$-(\frac{1}{4}R_2+\frac{1}{2}R_{12})$	0
R_{01}				0	$-(\frac{1}{4}R_2+\frac{1}{2}R_{12})$
R_{12}					0

Now consider the derived series. $L(A)^{(2)}$ consists of all pairwise products of L(A) and hence is generated by the matrices R_2, R_{01}, R_{12}. Since these are linearly independent among themselves they form a basis for $L(A)^{(2)}$ giving

	R_2	R_{01}	R_{12}
R_2	0	$-(\frac{1}{4}R_2+\frac{1}{2}R_{12})$	0
R_{01}	$\frac{1}{4}R_2+\frac{1}{2}R_{12}$	0	$-(\frac{1}{4}R_2+\frac{1}{2}R_{12})$
R_{12}	0	$-(\frac{1}{4}R_2+\frac{1}{2}R_{12})$	0

Thus $L(A)^{(2)} \neq 0$. Again $L(A)^{(3)}$ is generated by R_2, R_{12} and $[R_2,R_{12}] = 0$. So $L(A)^{(3)}$ is a zero algebra of dimension 2. Hence $L(A)^{(4)} = 0$ and L(A) is solvable.

Summarising these results we have

Algebra	GA	L1	L2	
			S	N
GA	1	1	1	1
B_{12}	0	1	1	0
B_{12}'	0	1	0	1
(4.3.5.)	0	0	1	0

It is clear that linearisation of the quadratic transformation in a commutative baric algebra does not depend in any simple way on the structure as it is given by the characterisation theorem of Holgate.

APPENDIX 1

Evolution of Trains in Baric Algebras by Standard Linear Algebraic Methods

0. Abstract

Let $\{x(n) : n = 0,1, \ldots\}$ be a train in a baric algebra over the complex field. This paper considers the problem of obtaining an explicit formula for x(n) in terms of n and the initial coordinates. In particular it considers the 'linearisation' of the quadratic transformation in genetic algebras due to Holgate (10) and its application to the explicit solution of the evolution of sequences of plenary powers by Abraham (1-4). It is shown that classical methods give a lower dimensional linear algebraic solution over a more general class of algebras and for a more general class of trains than Holgate's linearisation.

1. Introduction

Etherington (6) introduced the following three classes of nonassociative algebras and applied them to problems in genetics. An algebra over the complex field is said to be baric if there exists a non trivial homomorphism β into $\mathbb{C}$. If the rank equation for principal powers,

$$x^n = x.x^{n-1}$$

in a baric algebra $\mathcal{A}$ has coefficients which are functions of $\beta(x)$ only, so that for $x \in \mathcal{A}$ such that $\beta(x) = 1$ the coefficients are constants, then $\mathcal{A}$ is said to be a train algebra and the principal powers are said to form a train.

Baric algebras satisfying (1) $\ker\beta$ is principally nil-potent and (2) $(\ker\beta)^m$ are ideals of $\mathcal{A}$ for $m = 1,2,\ldots$ are necessarily train algebras and algebras satisfying these conditions are called <u>special train algebras</u>. In special train algebras other 'powers' may form trains, in particular the <u>plenary powers</u>,

$$x^{[n]} = (x^{[n-1]})^2.$$

Etherington showed that train algebras of rank 1, 2 or 3 possess plenary trains. Bernstein algebras are defined by their plenary trains (11). But otherwise, converse conditions have not been considered.

Schafer (12) defined a further class which was subsequently given the following definition by Gonshor (8). A commuative baric algebra is said to be a <u>genetic algebra</u> if the multiplication for a basis (c_i), $c_i c_j = \sum_k \lambda_{ijk} c_k$ satisfies (1) $\lambda_{000} = 1$, (2) $\lambda_{0jk} = 0$ if $k < j$ and (3) $\lambda_{ijk} = 0$ if $i,j > 0$ and $k \leq \max(i,j)$.

Holgate (10) studied the quadratic transformation $\phi : \mathcal{A} \to \mathcal{A}$, $x\phi = x^2$ in genetic algebras and showed that all genetic algebras possess a plenary train. In proving this theorem he shows that ϕ can be linearised over a higher dimensional space $\mathcal{B}$ in the sense that there exists a map $R : \mathcal{A} \to \mathcal{B}$ and a linear map $\tilde{\phi}$ such that

$$x\phi = xR\tilde{\phi}\pi \qquad (1)$$

where π is the projection $\mathcal{B} \to \mathcal{A}$. $\mathcal{B}$ is in fact a 'reduced' tensor power of $\mathcal{A}$. The theorem gives the plenary train roots in terms of the structure constants λ_{ijk}.

Abraham (1-4) applies Holgate's linearisation (1) to give explicit solutions for the evolution of $x^{[n]} = x\phi^n$ i.e. of plenary sequences in genetic algebras for polyploidy and to obtain the 'linearising functions' for those in which none of the $\lambda_{ijk} = 0$ unless defined to be so by the Gonshor conditions. His solutions are obtained from the equation

$$x\tilde{\Phi}^n = xRP^{-1}J^nP\pi \qquad (2)$$

derived from (1), where J is the Jordan canonical form of the matrix of $\tilde{\Phi}$, A say, and $J = PAP^{-1}$. Since J^n can be written down in terms of J and n this equation gives $x^{[n]}$ in terms of n and the coordinates of x.

Etherington (7) gives a method of obtaining the plenary train equation of a commutative baric algebra.

In this paper we shall use the shift operator E on vector sequences in an algebra and scalar sequences in the coefficient field, $Ex(n) = x(n+1)$. We also apply the standard method of reduction of an r'th order difference or differential equation to r 1'st order equations.

By the 'Holgate/Abraham linearisation method' we shall mean the construction of $\tilde{\Phi}$ in equation (1) and its use in equation (2).

We show that classical methods suffice for a linear algebraic solution of the evolution equation $Ex(n) = x(n)^2$ in a commutative baric algebra possessing a plenary train. The class of such algebras is strictly wider than genetic algebras. x(n) is obtained in terms of n and the coordinates of x(0), ..., x(r) where r+1 is the plenary rank. The solution is carried out in dimension r without recourse to Holgate's linearisation and the higher dimensional spaces of the Holgate/Abraham method.

2. Plenary Trains

Let $(\mathcal{A},\beta)$ be a commutative baric (nonassociative) algebra of arbitrary finite dimension m+1 over the complex field possessing a plenary train of rank r+1. Let

$$x^{[r+1]} + \theta_1 x^{[r]} + \ldots + \theta_r x = 0$$

be the plenary train for x such that $\beta(x) = 1$. Then we have for all $x(n)$, $\beta(x(0)) = 1$ implies $\beta(x(n)) = 1$ and hence

$$(E^r + \theta_1 E^{r-1} + \ldots + \theta_r)x(n) = 0$$

where the θ_i are constant and $Ex(n) = x(n)^2$.

Since the θ_i are complex the polynomial in E is obtained as a product of linear factors.

Put $y_1(n) = x(n)$, $y_i(n) = Ey_{i-1}(n)$ for $i = 1,2, \ldots, r$; then

$$Ey_1(n) = y_2(n)$$

$$\ldots$$

$$Ey_{r-1}(n) = y_r(n)$$

$$Ey_r(n) = -\theta_r y_1(n) - \ldots - \theta_1 y_r(n).$$

Let

$$A = \begin{bmatrix} 0 & 1 & 0 & \ldots & 0 \\ 0 & 0 & 1 & \ldots & 0 \\ 0 & 0 & 0 & \ldots & 0 \\ \cdot & \cdot & \cdot & \ldots & \cdot \\ \cdot & \cdot & \cdot & \ldots & 1 \\ -\theta_1 & -\theta_2 & -\theta_3 & \ldots & -\theta_r \end{bmatrix}$$

A is the companion matrix of the plenary train polynomial over the algebra $\mathcal{A}$.

Let

$$Y(n) = (y_1(n), \ldots, y_r(n))^t$$

then

$$EY(n) = Y(n)A \tag{3}$$

with solution

$$Y(n) = A^nY(0) \tag{4}$$

(We revert to the left hand convention as is more usual in this context.)

The advantage of phrasing the problem in this way is that the companion matrices have the property that their characteristic and minimal polynomials are identical and equal to the plenary train polynomial. Moreover the eigenvectors and the generalised eigenvectors and hence the Jordan form are easily obtainable. And, the inverse matrix can be written down immediately (see Brand (5)).

Now, unless A is very sparse when we may proceed directly with the preceding equation, there exists a nonsingular matrix P such that $J = P^{-1}AP$ is the Jordan form of A, hence

$$Y(n) = PJ^nP^{-1}Y(0)$$

where J^n can be given in terms of J and n. P is the matrix of row eigenvectors or generalised eigenvectors in the case of multiple roots of the plenary train equation.

Thus

$$(x(n), Ex(n), \ldots, E^{r-1}x(n)) = (x(0), Ex(0), \ldots, E^{r-1}x(0))M$$

where say

$$M = \begin{bmatrix} \alpha_{11} & \cdots & \alpha_{1r} \\ \cdot & & \cdot \\ \cdot & & \cdot \\ \cdot & & \cdot \\ \alpha_{r1} & & \alpha_{rr} \end{bmatrix}$$

and so

$$x(n) = (\alpha_{11}x(0) + \alpha_{21}Ex(0) + \ldots + \alpha_{r1}E^{r-1}x(0)).$$

In terms of coordinates

$$(x_o(n), \ldots, x_m(n)) = ((\alpha_{11}x(0) + \ldots + \alpha_{r1}E^{r-1}x(0))\Pi_o, \ldots, (\alpha_{11}x(0) + \ldots + \alpha_{r1}E^{r-1}x(0))\Pi_m)$$

where Π_i is the projection on the i'th coordinate.

If we put

$$Ex(0) = (Ex_o(0), \ldots, Ex_m(0))$$

where on the l.h.s. E is the shift operator of the vector sequence defined by $Ex(n) = x(n)^2$ while on the r.h.s. the E's are each shift operators of different scalar sequences defined by the particular algebra $\mathcal{A}$, then we may write

$$(x_o(n), \ldots, s_m(n)) = (\alpha_{11}x_o(0) + \ldots + \alpha_{r1}E^{r-1}x_o(0), \ldots, \alpha_{11}x_m(0) + \ldots + \alpha_{r1}E^{r-1}x_m(0)).$$

Thus x(n) is obtained explicitly in terms of n and the coordinates of x(0), ..., x(r-1) where r is the plenary rank of $(\mathcal{A}, \beta)$ from the vector equation

$$x(n) = PJ^nP^{-1} \cdot Y(0). \qquad (5)$$

The calculations in Abraham (1,4) can be achieved in this way in dimension r, generally much less than the dimension of the Holgate linearisation.

3. Example

Consider the algebra for tetraploidy given in (1.5.10.). The plenary train equation is

$$x^{[3]} - 4/3x^{[2]} + 1/3x = 0.$$

Equivalently in the operator $E = 1 + \Delta$, $f(E)x(n) = 0$, where $f(E) = E^2 - 4/3E + 1/3$.

We replace this second order linear equation by two first order equations.

Put $y_1(n) = x(n)$, $y_2(n) = Ey_1(n)$. Then

$$Ey_1(n) = y_2(n)$$
$$Ey_2(n) = -1/3y_1(n)+4/3y_2(n).$$

Let $Y(n) = (y_1(n),y_2(n))^t$ then we have

$$EY(n) = AY(n) \qquad (*)$$

where

$$A = \begin{bmatrix} 0 & 1 \\ -1/3 & 4/3 \end{bmatrix}.$$

A is the companion matrix of f(E). The characteristic (= minimal) equation of A is identical to the plenary train equation.

Now the equation (*) has solution

$$Y(n) = A^nY(0).$$

To obtain A^n explicitly we use the Jordan canonical form. The eigenvalues of A are 1, 1/3 with corresponding eigenvectors (1,1) and (1,1/3).

Now

$$J = B^{-1}AB$$

where B is the matrix of row eigenvectors, e_i, and B^{-1} is the matrix of column vectors of the reciprocal set, e^j, such that $e_i \cdot e^j = d_i^j$ (Kronecker delta).

We have

$$J = B^{-1}AB = \begin{bmatrix} -\frac{1}{2} & 3/2 \\ 3/2 & -3/2 \end{bmatrix} \begin{bmatrix} 0 & 1 \\ -1/3 & 4/3 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 1 & 1/3 \end{bmatrix}$$
$$= \begin{bmatrix} 1 & 0 \\ 0 & 1/3 \end{bmatrix}.$$

So $J^n = \begin{bmatrix} 1 & 0 \\ 0 & 1/3^n \end{bmatrix}$

Hence

$$Y(n) = BJ^nB^{-1}Y(0)$$
$$= \begin{bmatrix} \frac{1}{2}(1/3^{n-1} - 1) & \frac{1}{2}(3-1/3^{n-1}) \\ \frac{1}{2}(1/3^n - 1) & \frac{1}{2}(3-1/3^n) \end{bmatrix} Y(0)$$

from which there follows

$$x(n) = \tfrac{1}{2}(1/3^{n-1}) \ , \ \tfrac{1}{2}(3-1/3^{n-1}) \ . \begin{bmatrix} x(0) \\ Ex(0) \end{bmatrix}$$

which gives

$$x(n) = c_0+x_1(0)c_1+((1/3^n)x_2(0)+\tfrac{1}{4}(1-1/3^n)x_1^2(0))c_2.$$

This agrees with the solution obtained in (2.1.13.).

4. Other Trains

Finally we mention that, since our derivation of (5) for the plenary case does not depend on the plenary property but only on the property of trains, the standard method outlined here applies to any train in a single indeterminate whose terms preserve baric value. Thus we have the following.

Let $\{X(n)\}$ be a train in a commutative baric algebra with $\beta X(n) = 1$ and train equation

$$T(E)X(n) = 0.$$

Then

$$X(n) = PJ^nP^{-1} \ . \ Y(0)$$

where $Y(0) = (X(0), EX(0), \ldots, E^rX(0))$, J is the Jordan canonical form of the companion matrix of $T(E)$, P is the matrix of generalised eigenvectors and $r+1$ is the rank of the train equation.

The method also applies to 'continuous trains' (see Heuch (9)). The 'continuous theorem' is obtained by replacing n by t and E by D in the discrete theory, where t is a continuous parameter and D is the differential operator. The equations corresponding to (3), (4) here will be

$$DY(t) = AY(0) \qquad (6)$$

$$Y(t) = e^{tA}Y(0) \qquad (7)$$

where e^{tA} is an exponential matrix.

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APPENDIX 2

In genetic algebra as a model several genetic conditions are assumed. In our presentation we shall frequently wish to refer to these conditions so we collect them together here for convenience . If we are relaxing some of the conditions we will specify only those that are not supposed to apply, otherwise we shall simply refer to the genetic assumptions G.

G. (i) infinite population

(ii) even ploidy

(iii) diallelic loci

(iv) chromosome segregation only

(v) no linkage

(vi) random mating

(vii) non overlapping generations

(viii) no mutation

(ix) no selection.

(iii), (iv), (vii) and (viii) are relaxed in some cases here. (v) implies all alleles segregate. It has been relaxed by several authors. (vi) implies the statistical independence of the gene frequencies. (i) is necessary for (vi). (ii) is connected with the form of polyploidy assumed - autopolyploidy.

(ix) is universally imposed in genetic algebra (to date at least). The reason for this is that the introduction of the 'selection coefficient' destroys 'normalisation'. For example if A, a are alleles of an initial population $xA + ya$ $(x+y=1)$ and the fitness of A is 1 and of a is $1-s$ $(0 \leq s \leq 1)$, so A has selective advantage over a. Then after selection we have $xA + (1-s)ya$ where $x + y - sy \neq 1$ unless $s = 0$.

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