JORDAN ALGEBRAS ARISING IN POPULATION GENETICS

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The non-associative algebras arising in genetics (**1**), are rather isolated from other branches of non-associative algebra (**6**). However, in a paper (**5**), in which he studied these algebras in terms of their transformation algebras, Schafer proved that the gametic and zygotic algebras for a single diploid locus are Jordan algebras.

In this note I prove these results by methods which do not make use of transformation algebras, and which therefore accommodate the multiallelic case more easily, and in which the main object is to maximise the interplay between the algebraic formalism and the genetic situation to which it corresponds.

The gametic algebra $\mathscr{G}$ corresponding to $n+1$ alleles $a_0, \ldots, a_n$ at a locus has multiplication table

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

For a typical element $x = \sum_0^n \alpha_i a_i$, the weight w is defined by $w(x) = \sum_0^n \alpha_i$, and it follows by calculation using (1) that

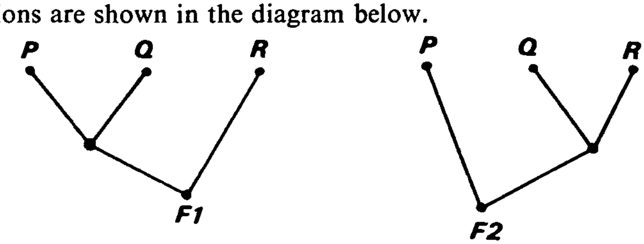
$$x^2 = w(x)x. \tag{2}$$

Proposition 1 (Algebraic). *Every element of unit weight in $\mathscr{G}$ is idempotent.*

(Genetic). *In the absence of selection, the gametic proportions remain constant from generation to generation.*

Proof. The algebraic result is immediate from (2), while the genetic formulation is axiomatic.

As frequently happens, the algebraic result is more comprehensive, since only those elements of unit weight for which all the α_i are non-negative correspond to populations. The non-associativity of genetic algebras corresponds to the fact that if P, Q and R are populations, and if P and Q mate and the offspring mate with R, the final result is in general different from that arising from mating between P, and the offspring of mating between Q and R. The two situations are shown in the diagram below.



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A Jordan algebra is one in which for any elements x, y

$$(x^2y)x = x^2(yx), \; xy = yx. \tag{4}$$

Proposition 2 (Algebraic). *$\mathscr{G}$ is a Jordan algebra.*

(Genetic). *In the mating schemes shown in* (3), *the populations F_1 and F_2 have the same genetic proportions if P is the offspring of mating of R with itself.*

Proof. Algebraically, (4) follows from (2) and (1). Genetically, the condition implies that P and R contain the same gametic proportions.

The genetic algebra $\mathscr{Z}$ corresponding to proportions of zygotic types is formed by duplicating $\mathscr{G}$ (see (1), (2)). Its basis elements are pairs (x, y) of basis elements of $\mathscr{G}$ with the multiplication rule $(x, y)(u, v) = (xy, uv)$. A canonical basis may be taken in $\mathscr{G}$ by setting $c_0 = a_0$, $c_i = a_0 - a_i (i \neq 0)$, for which the multiplication table is

$$c_0^2 = c_0, \; c_0 c_i = \tfrac{1}{2} c_i, \; c_i c_j = 0, \; (i, j \neq 0).$$

Then on writing $d_{ij} = (c_i, c_j)$ the multiplication table for the duplicate $\mathscr{Z}$ can be written

$$\begin{aligned} &d_{00}^2 = d_{00}, \; d_{00} d_{0i} = \tfrac{1}{2} d_{0i}, \; d_{0i} d_{0j} = \tfrac{1}{4} d_{ij}, \\ &\text{other products zero, } (i, j \neq 0). \end{aligned} \tag{5}$$

The weight of a typical element $x = \sum_{i=0}^{n} \sum_{j=i}^{n} \alpha_{ij} d_{ij}$ is $w(x) = \alpha_{00}$.

Proposition 3 (Algebraic). *Every element of the form $y = x^2 - w(x)x$ annihilates $\mathscr{Z}$.*

(Genetic). *The extent to which the zygotic proportions in a population differ from the Hardy-Weinberg equilibrium state has no effect on the offspring distribution produced by mating between this population and any other.*

Proof. Algebraically, for x defined immediately above the statement, computation using (5) gives

$$x^2 - w(x)x = \tfrac{1}{4} \sum_{i=1}^{n} \sum_{j=1}^{n} (\alpha_{0i}\alpha_{0j} - \alpha_{00}\alpha_{ij}) d_{ij}.$$

Using (5) again this element annihilates $\mathscr{Z}$. Again, the genetic formulation is obvious on biological grounds and the relationship can be seen on noting that since by the Hardy-Weinberg law equilibrium is attained after a single generation of mating, $x^2 - x$ represents the amount of departure from equilibrium when x is an element of $\mathscr{Z}$ representing a population.

Proposition 4. *Proposition* 2 *holds for $\mathscr{Z}$.*

Proof. In algebraic terms, let $u = x^2 - w(x)x$. Then since any product involving u is zero, use of the distributive and commutative laws gives

$$\begin{aligned} (x^2y)x &= (uy)x + \{w(x)\}(xy)x \\ &= u(yx) + \{w(x)\}x(yx) \\ &= x^2(yx). \end{aligned}$$

Hence $\mathscr{Z}$ is a Jordan algebra. Genetically, P and R have the same gametic proportions, and the result follows from the genetic formulation of Proposition 3.

Let $\mathscr{A}$ be an algebra in which multiplication (denoted by a dot) is associative. Let $\mathscr{A}^+$ be the algebra obtained by replacing multiplication by " Jordan multiplication " (denoted by juxtaposition), defined by

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

$\mathscr{A}^+$ is clearly commutative and (4) is easily verified (see (4), p. 152), hence it is a Jordan algebra. Any algebra isomorphic to $\mathscr{A}^+$ or a sub-algebra of it is called a special Jordan algebra. Not all Jordan algebras however are special Jordan algebras.

Consider the algebra $\mathscr{A}$ whose basis elements are $a_0, \ldots, a_n$, with multiplication table

$$a_i \,.\, a_j = a_i. \tag{6}$$

This is clearly associative and $\mathscr{A}^+$ is isomorphic to $\mathscr{G}$. If it were possible to know in advance that the genes of a given one of two populations mating together would be transmitted to the offspring, it could be written first in the product, and the system would correspond to the multiplication table (6). The fact that $\mathscr{G}$ is a special Jordan algebra thus appears as a consequence of inheritance being symmetric in the parents.

Schafer also proved in the diallelic case that $\mathscr{Z}$ is a special Jordan algebra (5, p. 333), but I have been unable to find a biological parallel to this result. It follows readily from Theorem 5 of (5) that a special train algebra can only be a Jordan algebra if its train roots, as defined in (3, § 2) all have values among 1, $\frac{1}{2}$, 0, since they are the proper values of a transformation corresponding to multiplication by the canonical basis element of unit weight (3, § 2), and this corresponds in Schafer's equation 12, to the case where $\alpha = 0$ and f is the identity function. This excludes the genetic algebras corresponding to polyploidy or several loci. The appearance of Jordan algebras therefore seems to be bound up with the property of attaining equilibrium after a single generation of mating.

Finally, consider the case of two unlinked diallelic loci with alleles a_0, a_1, b_0, b_1 for which the multiplication table is

$$(a_i b_j)(a_r b_s) = \tfrac{1}{4}(a_i b_j + a_i b_s + a_r b_j + a_r b_s).$$

Let

$$x = \sum_{i=0}^{1} \sum_{j=0}^{1} g_{ij} a_i b_j, \quad y = \sum_{i=0}^{1} \sum_{j=0}^{1} f_{ij} a_i b_j$$

be two population elements in the gametic algebra. Then by routine computation

$$\begin{aligned} x^2 &= x - \tfrac{1}{2}(g_{00} g_{11} - g_{01} g_{10})(a_0 b_0 - a_0 b_1 - a_1 b_0 + a_1 b_1) \\ &= x - \tfrac{1}{2}\alpha u, \quad \text{(say)}, \end{aligned}$$

and after further calculation

$$uy = \tfrac{1}{4}u.$$

To see to what extent Proposition 2 fails in this case, consider the " associator " x^2, y and x,

$$\begin{aligned}(x^2y)x - x^2(yx) &= \tfrac{1}{2}\alpha\{u(yx)-(uy)x\}\\ &= \tfrac{1}{2}\alpha\{\tfrac{1}{4}u-\tfrac{1}{4}ux\}\\ &= \tfrac{3}{32}\alpha u.\end{aligned}$$

It is thus a scalar multiple of a fixed element, is independent of y, and depends on x only through $\alpha = g_{00}g_{11}-g_{01}g_{10}$. This is, in genetic terminology, the coefficient of linkage disequilibrium.

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