XXIII.—Genetic Algebras.

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CONTENTS.

§ 1. Introduction.

Two classes of linear algebras, generally non-associative, are defined in § 3 (*baric algebras*) and § 4 (*train algebras*), and the process of *duplication* of a linear algebra in § 5. These concepts, which will be discussed more fully elsewhere, arise naturally in the symbolism of genetics, as shown in §§ 6–15. Many of their properties express facts well known in genetics; and the processes of calculation which are fundamental in many problems of population genetics can be expressed as manipulations in the genetic algebras. In cases where inheritance is of a simple type (*e.g.* §§ 10–13, 15) this constitutes a new point of view, but perhaps amounts to little more than a change of notation as compared with existing methods. § 14, however, indicates the possibility of generalisations which would seem to be impossible by ordinary methods.

The occurrence of the genetic algebras may be described in general terms as follows. The mechanism of chromosome inheritance, in so far as it determines the probability distributions of genetic types in families and filial generations, and expresses itself through their frequency distributions, may be represented conveniently by algebraic symbols. Such a symbolism is described, for instance, by Jennings (1935, chap. ix); many applications are given by Geppert and Koller (1938). It is shown in the present paper that the symbolism is equivalent to the use of a system of related linear algebras, in which multiplication (equivalent to the procedure of "chessboard diagrams") is commutative ($PQ=QP$) but non-associative ($PQ.R \neq P.QR$). A population (*i.e.* a distribution of genetic types) is represented by a normalised hypercomplex number in one or other algebra, according to the point of view from which it is specified. If P, Q are populations, the filial generation $P \times Q$ (*i.e.* the statistical population of offspring resulting from the random mating of individuals of P with individuals of Q) is obtained by multiplying two corresponding representations of P and Q; and from this requirement of the symbolism it will be obvious why multiplication must be non-associative. It must be understood that a population may mean a single individual, or rather the information which we may have concerning him in the form of a probability distribution.

Inheritance will be called *symmetrical* if the sex of a parent does not affect the distribution of gametic types produced. Paying attention only to the inheritance of gene differences (not of phenotypes), every regular mode of symmetrical inheritance in theoretical genetics has its fundamental *gametic algebra*, from which other algebras (*zygotic*, etc.) are deduced by duplication. From the nature of the symbolism these are of necessity baric algebras; but it appears on closer examination that they belong in all cases to the narrower category of train algebras.

(The fundamental algebras can be modified to take account of various kinds of selection. They are then no longer train algebras, although the baric property and the relation of duplication sometimes persist.)

Symmetry of inheritance may be disturbed by unequal crossing over in male and female, by sex linkage, or by gametic selection. These cases are not discussed at all in the present paper; but it may be stated briefly that in the absence of selection the corresponding genetic algebras (of order n, say) possess train subalgebras (of order $n-1$).

The occurrence of a non-associative linear algebra in the simplest case of Mendelian inheritance was pointed out by Glivenko (1936).

§ 2. Notation.

By *principal powers* in a non-associative algebra, I mean powers in which the factors are absorbed one at a time always on the right or always on the left (see (3.6)). Otherwise, for the notation and nomenclature for non-associative products and powers, see my paper "On Non-Associative Combinations" (1939). The word *pedigree* which occurs there can now be interpreted almost in its ordinary biological sense.

Elements of a linear algebra (*i.e.* hypercomplex numbers) will be called *elements* and denoted by Latin letters, generally small ($a, b, \ldots$); but normalised elements, *i.e.* elements of unit weight (§ 3), will be denoted by Latin capitals ($A, B, \ldots$). The letters m, n, r, however, denote positive integers.

Elements of the field F over which a linear algebra is defined will be called *numbers* and denoted by small Greek letters ($\alpha, \beta, \ldots$). Thus, an *element* is determined by its coefficients, which are *numbers*. In the genetical applications, F may be taken as the field of real numbers. The enumerating indices (subscripts and superscripts) take positive integer values, either 1 to m, 1 to n, or 1 to r, according to the context.

Block capitals ($\mathsf{A}, \mathsf{B}, \ldots$) denote algebras.

The symbol Σ indicates summation with respect to repeated indices, *e.g.* with respect to σ in (3.3), with respect to σ and τ in (5.3).

The symbol 1^n stands for a set of 1's. Thus the formula (6.3) means the same as

$$\sum_{\sigma=1}^{n} \gamma_\sigma^{\mu\nu} = 1.$$

The advantage of this notation is that such formulæ retain their form under linear transformations of the basis of a genetic algebra, 1^n being replaced by the vector ξ^n (*cf.* (6.12)).

§ 3. Baric Algebras.

It is well known that a linear associative algebra possesses a matrix representation. Non-associative algebras in general do not, but may. The simplest such representation would be a scalar representation on the field F over which the algebra is defined. A linear algebra X, associative or not, which possesses a non-trivial representation of this kind, will be called *baric*.

The definition means that to any element x of X there corresponds a number $\xi(x)$ of F, not identically zero, such that

$$\xi(x+y)=\xi(x)+\xi(y), \quad \xi(\alpha x)=\alpha\xi(x), \quad \xi(xy)=\xi(x)\xi(y). \quad (x, y<\mathsf{X},\ \alpha<\mathsf{F}) \quad (3.1)$$

$\xi(x)$ will be called the *weight* of x, or the *weight function* of X. If $\xi(x)\neq 0$, x can be *normalised*—that is, replaced by the element

$$X=x/\xi(x) \quad . \quad . \quad . \quad . \quad . \quad . \quad (3.2)$$

of unit weight. Elements of zero weight will be called *nil elements*. The set U of all nil elements is evidently an invariant subalgebra of X; *i.e.* $\mathsf{XU} \leqslant \mathsf{U}$: it will be called the *nil subalgebra*.

Let the multiplication table of a linear algebra X be

$$a^\mu a^\nu = \Sigma\gamma_\sigma^{\mu\nu} a^\sigma, \quad (\mu, \nu, \sigma = 1, \ldots, n) \quad . \quad . \quad . \quad (3.3)$$

and let the general element be denoted

$$x=\Sigma\alpha_\mu a^\mu. \quad . \quad . \quad . \quad . \quad . \quad . \quad (3.4)$$

For X to be a baric algebra, it is necessary and sufficient that the equations (3.3), *regarded as ordinary simultaneous equations in* F *for the unknowns* a^μ, *should possess a non-null solution* $a^\mu=\xi^\mu$. For this is obviously necessary, the ξ^μ being the weights of the basic elements a^μ. Conversely, if the condition is satisfied and we take

$$\xi(x)=\Sigma\alpha_\mu\xi^\mu, \quad . \quad . \quad . \quad . \quad . \quad . \quad (3.5)$$

then (3.1) are at once deducible. The basic weights ξ^μ form the *weight vector* of X. In the genetical applications, $\xi^\mu=1^\mu$.

Let the right rank equation (Dickson, 1914, § 19), or equation of lowest degree connecting the right principal powers,

$$x, x^2, x^3, \ldots, \quad x^m = x^{m-1}x, \ldots, \quad . \quad . \quad . \quad (3.6)$$

be

$$f(x) \equiv x^r + \theta_1 x^{r-1} + \theta_2 x^{r-2} + \ldots + \theta_{r-1}x = 0, \quad . \quad . \quad (3.7)$$

where each coefficient θ_m is a homogeneous polynomial of degree m in the co-ordinates α_μ of x. Then $f(x)$, being zero, is of zero weight. Hence the equation is satisfied when we substitute $\xi(x)$ for x; consequently $x-\xi(x)$ must be a factor of $f(x)$. The same is true for the left rank equation. Thus

$\xi(x)$ is a root of the right and left rank equations. . . (3.8)

The weight function of an algebra is not necessarily unique. In fact, a commutative associative linear algebra for which the determinant $|\Sigma\gamma_\sigma^{\mu\nu}\gamma_\tau^{\sigma\rho}|$ does not vanish has n independent weight functions; and its rank equation is hence completely determined by (3.8) (Dickson, 1914, § 55, and the references given there).

§ 4. Train Algebras.

A baric algebra with the weight function $\xi(x)$ and right rank equation (3.7) will be called a *right train algebra* if the coefficients θ_m, in so far as they depend on the element x, depend only on $\xi(x)$. A *left train algebra* is defined similarly. For simplicity, suppose multiplication commutative, so that we may drop "left" and "right."

Since θ_m is homogeneous of degree m in the co-ordinates of x, it must in a train algebra be a numerical multiple of $\xi(x)^m$. Hence (if the field F

be sufficiently extended, *e.g.*, to include complex numbers) the rank equation can be factorised:

$$f(x) \equiv x(x-\xi)(x-\lambda_1\xi)(x-\lambda_2\xi)\ldots=0. \quad . \quad . \quad . \quad (4.1)$$

(It is implied that when the left side is expanded, powers of x are interpreted as principal powers.) The numbers $1, \lambda_1, \lambda_2 \ldots$ are the *principal train roots* of the algebra.

For a normalised element (3.7) becomes

$$f(X) \equiv X^r+\theta_1X^{r-1}+\theta_2X^{r-2}+\ldots+\theta_{r-1}X=0, \quad . \quad (4.2)$$

where now the θ's are constant (*i.e.* independent of X); and (4.1) becomes

$$f(X) \equiv X(X-1)(X-\lambda_1)(X-\lambda_2)\ldots=0. \quad . \quad . \quad (4.3)$$

Since (4.2) can be multiplied by X any number of times, it can be regarded as a linear recurrence equation with constant coefficients connecting the principal powers of the general normalised element X. Solving the recurrence relation for $X^m (m > r)$ in the usual way, we obtain $1, \lambda_1, \lambda_2 \ldots$ as the roots of the auxiliary equation; hence a formula for X^m can be written down in terms of $X, X^2, \ldots X^{r-1}$. Hence also for the general non-nil element $x=\xi X$, the value of $x^m=\xi^mX^m$ is known; while for a nil element u, $u^m=0 (m > r)$.

The properties of train algebras will be studied elsewhere, and the following theorem proved:—

If (1) X *is a baric algebra*; (2) *its nil subalgebra* U *is nilpotent* (Wedderburn, 1908 *a*, p. 111); (3) *for* $m=1, 2, 3, \ldots$, *the subalgebra* $U^{(m)}$, *consisting of all products of altitude m* (Etherington, 1939, p. 156) *formed from nil elements is an invariant subalgebra of* X (*as it necessarily is of* U); *then* X *is a train algebra.*

For train algebras of rank $r=2$ or 3, provided that the principal train roots do not include $\frac{1}{2}$, the conditions are necessary as well as sufficient; but I cannot say whether this converse holds more generally or not. I will call X a *special train algebra* if it satisfies the conditions (1), (2), (3). In such algebras it can be shown that there are many other sequences which have properties like those of the sequence of principal powers; *i.e.* sequences of elements derived from the general element, which satisfy linear recurrence equations whose coefficients, being functions of the weight only, become constants on normalisation. Such sequences will be called *trains*. For example, the sequence of plenary powers

$$x, x^2, x^{2+1}, x^{2^2}, \ldots, \quad . \quad . \quad . \quad . \quad . \quad (4.4)$$

and the sequence of primary products

$$x, Vx, V.Vx, V:V.Vx, \ldots, \quad . \quad . \quad . \quad (4.5)$$

form trains in a special train algebra.

It is convenient to denote the mth element of a train as $x^{[m]}$, and to regard it as a symbolic mth power of x. Let the normalised recurrence equation, or *train equation*, be

$$g[X] \equiv X^{[r]}+\phi_1X^{[r-1]}+\phi_2X^{[r-2]}+\ldots+\phi_{r-1}X=0, \quad . \quad (4.6)$$

where the ϕ's are numerical constants. It is implied that the equation may be symbolically "multiplied all through" by X any number of times. It may also be symbolically factorised:

$$g[X] \equiv X[X-1][X-\mu_1][X-\mu_2]\ldots=0. \quad . \quad . \quad (4.7)$$

The square brackets indicate that after expansion powers of X are to be interpreted as symbolic powers. The expansion being performed as in ordinary algebra, multiplication of the symbolic factors is commutative and associative. Extra factors may be introduced without destroying the validity of the train equation; but assuming that all superfluous factors have been removed, s is the *rank* of the train, and the numbers $1, \mu_1, \mu_2, \ldots$ are the *train roots*, by means of which a formula for $X^{[m]}$ $(m > s)$ can be written down.

In the applications to genetics, it will be found that all the fundamental symmetrical genetic algebras are special train algebras. Various trains have genetical significance; the $X^{[m]}$ represent successive discrete generations of an evolving population or breeding experiment, and the train equation is the recurrence equation which connects them.

Thus, for example, plenary powers (4.4) refer to a population with random mating; principal powers (3.6) to a mating system in which each generation is mated back to one original ancestor or ancestral population; and the primary products (4.5) to the descendants of a single individual or subpopulation X mating at random within a population Y. Other mating systems are described by other sequences, and in various well-known cases these have the train property—that is, the determination of the mth generation depends ultimately on a linear recurrence equation with constant coefficients. It usually happens that the train roots are real, distinct, and not exceeding unity. Hence it may be shown that $X^{[m]}$ tends to equilibrium with increasing m; the rate of approach to equilibrium is ultimately that of a geometrical progression with common ratio equal to the largest train root excluding unity; but it may be some generations (depending on the number of train roots) before this rate of approach is manifest.

Train roots may be described as the eigen-values of the operation of symbolic multiplication by X, or in genetic language, the operation of passing from one generation to the next.

Train algebras of (principal) rank 3, which occur in several contexts

in genetics, have certain special properties. For example, *if the train equation for principal powers is* $X(X-1)(X-\lambda)=0$, *then the train equation for plenary powers is* $X[X-1][X-2\lambda]=0$; *and* vice versa. Examples may be seen below in (10.12), (12.4, 5), (15.3), where respectively $\lambda=0, \frac{1}{2}(1-\omega), \frac{1}{8}$.

§ 5. Duplication.

Let

$$a^\mu a^\nu=\Sigma\gamma_\sigma^{\mu\nu}a^\sigma \quad . \quad . \quad . \quad . \quad . \quad (5.1)$$

be the multiplication table of a linear algebra X with basis a^μ $(\mu=1, \ldots, n)$. Then

$$a^\mu a^\nu . a^\rho a^\phi=\Sigma\gamma_\sigma^{\mu\nu}a^\sigma . \Sigma\gamma_\tau^{\rho\phi}a^\tau.$$

Writing

$$a^\mu a^\nu=a^{\mu\nu}, \quad . \quad . \quad . \quad . \quad . \quad (5.2)$$

this becomes

$$a^{\mu\nu}a^{\rho\phi}=\Sigma\gamma_\sigma^{\mu\nu}\gamma_\tau^{\rho\phi}a^{\sigma\tau}, \quad . \quad . \quad . \quad . \quad (5.3)$$

which may be regarded as the multiplication table of another linear algebra, isomorphic with the totality of quadratic forms in the original algebra. It will be called the *duplicate* of X, and denoted X′. It is commutative and of order $\frac{1}{2}n(n+1)$ if X is commutative; non-commutative and of order n^2 if X is non-commutative. It is generally non-associative, even if X is associative. It is not to be confused with what may be called the *direct square* of X, or direct product of two algebras isomorphic with X: this would be an algebra of order n^2, having the multiplication table

$$a^{\mu\nu}a^{\rho\phi}=\Sigma\gamma_\sigma^{\mu\rho}\gamma_\tau^{\nu\phi}a^{\sigma\tau}, \quad . \quad . \quad . \quad . \quad (5.4)$$

differing from (5.3) in the arrangement of indices.

Some theorems on duplication will be proved elsewhere. It will be shown that the duplicates (i) of a linear transform of an algebra, (ii) of the direct product of two algebras, (iii) of a baric algebra with weight vector ξ^μ, (iv) of a train algebra with principal train roots $1, \lambda, \mu, \ldots$, are respectively (i) a linear transform of the duplicate algebra, (ii) the direct product of the duplicates, (iii) a baric algebra with weight vector $\xi^\mu\xi^\nu$, (iv) a train algebra with principal train roots $1, 0, \lambda, \mu, \ldots$ These theorems are relevant as follows: (iii) in view of §§ 7, 8; (ii) in view of § 9; (i) in connection with the method used in § 14; (iv) in deriving equations such as (10.10), (12.6).

Duplication of an algebra may be compared with the process of forming the second induced matrix of a given matrix (Aitken, 1935; *cf.* also Wedderburn, 1908 *b*).

§ 6. Gametic Algebras.

Consider the inheritance of characters depending on any number of gene differences at any number of loci on any number of chromosomes in a diploid or generally autopolyploid species. Assume that inheritance is symmetrical in the sexes: the sex chromosomes are thus excluded, and crossing over if present must be equal in male and female.

Let $G^1, G^2, \ldots, G^n$ denote the set of gametic types determined by these gene differences. Then there will be

$$m=\tfrac{1}{2}n(n+1) \quad . \quad . \quad . \quad . \quad . \quad (6.1)$$

zygotic types $G^\mu G^\nu (=G^\nu G^\mu)$. The formulæ giving the series of gametic types produced by each type of individual, and their relative frequencies, may be written

$$G^\mu G^\nu=\Sigma\gamma_\sigma^{\mu\nu}G^\sigma, \quad . \quad . \quad . \quad . \quad . \quad (6.2)$$

with the normalising conditions

$$\Sigma\gamma_\sigma^{\mu\nu}1^\sigma=1; \quad . \quad . \quad . \quad . \quad . \quad (6.3)$$

$\gamma_\sigma^{\mu\nu}$ is then the probability that an arbitrary gamete produced by an individual of zygotic type $G^\mu G^\nu$ is of type G^σ.

(I speak of *zygotic types*—individuals distinguished by the gametes from which they were formed—rather than *genotypes*—individuals distinguished by the gametes which they produce—because the $G^\mu G^\nu$ are not all distinct genotypes if more than one chromosome is involved: the zygotic algebra, § 7, will have the same train equation if genotypes are used, but will then not be a duplicate algebra.)

A population P which produces gametes G^μ in proportions α_μ may be represented by writing

$$P=\Sigma\alpha_\mu G^\mu. \quad . \quad . \quad . \quad . \quad . \quad (6.4)$$

Imposing the normalising condition

$$\Sigma\alpha_\mu 1^\mu=1, \quad . \quad . \quad . \quad . \quad . \quad (6.5)$$

α_μ denotes the probability that an arbitrary gamete produced by an arbitrary individual of P is of type G^μ.

A population may also be described by the proportions of the zygotic types $G^\mu G^\nu$ which it contains; thus we may write

$$P=\Sigma\alpha_{\mu\nu}G^\mu G^\nu, \quad . \quad . \quad . \quad . \quad . \quad (6.6)$$

with the normalising condition

$$\Sigma\alpha_{\mu\nu}1^\mu 1^\nu=1, \quad . \quad . \quad . \quad . \quad . \quad (6.7)$$

and a similar probability interpretation. We may suppose without loss of generality that $\alpha_{\mu\nu}=\alpha_{\nu\mu}$, so that in (6.6) the coefficient of $G^\mu G^\nu$ is

$2a_{\mu\nu}$ if $\mu \neq \nu$. The two representations are connected by the gametic series formulæ (6.2); that is to say, from the zygotic representation (6.6) follows the gametic representation

$$P = \Sigma a_{\mu\nu}\gamma_\sigma^{\mu\nu}G^\sigma. \quad . \quad . \quad . \quad . \quad . \quad . \quad (6.8)$$

If two populations P, Q intermate at random, representations of the first filial generation are obtained by multiplying the gametic representations of P and Q; *i.e.* if

$$P = \Sigma\alpha_\mu G^\mu, \quad Q = \Sigma\beta_\mu G^\mu, \quad . \quad . \quad . \quad . \quad (6.9)$$

the population of offspring is

$$PQ = \Sigma\alpha_\mu\beta_\nu G^\mu G^\nu \quad . \quad . \quad . \quad . \quad . \quad (6.10)$$

$$= \Sigma\alpha_\mu\beta_\nu\gamma_\sigma^{\mu\nu}G^\sigma. \quad . \quad . \quad . \quad . \quad (6.11)$$

In particular, the population of offspring of random mating of P within itself is given by P^2.

We may now view the situation abstractly. The gametic series (6.2) form the multiplication table of a commutative non-associative linear algebra with basis $G^\mu(\mu = 1, \ldots, n)$. It will be called the *gametic algebra* for the type of inheritance considered, and denoted **G**. The equations (6.3) show that **G** is a baric algebra with weight vector

$$\xi^\mu = 1^\mu. \quad . \quad . \quad . \quad . \quad . \quad . \quad (6.12)$$

With regard to its gametic type frequencies, a population is represented by a normalised element (6.4) of **G**. Multiplication in **G** has the significance described in § 1, and it follows from the multiplicative property of the weight in a baric algebra that PQ will be automatically normalised if P and Q are.

§ 7. Zygotic Algebras.

When individuals of types $G^\mu G^\nu$, $G^\sigma G^\delta$ mate, the probability distribution of zygotic types in their offspring can be obtained by multiplying the gametic representations (given by (6.2)) together, and leaving the product in quadratic form (as in (6.10)). We obtain

$$G^\mu G^\nu \cdot G^\sigma G^\delta = \Sigma\gamma_\alpha^{\mu\nu}\gamma_\tau^{\sigma\delta}G^\alpha G^\tau;$$

or, writing

$$Z^{\mu\nu} = G^\mu G^\nu \quad . \quad . \quad . \quad . \quad . \quad . \quad (7.1)$$

to emphasise the union of paired gametes into single individuals,

$$Z^{\mu\nu}Z^{\sigma\delta} = \Sigma\gamma_\alpha^{\mu\nu}\gamma_\tau^{\sigma\delta}Z^{\alpha\tau}. \quad . \quad . \quad . \quad . \quad (7.2)$$

These $\frac{1}{2}m(m+1)$ equations, then, are the formulæ giving the series of zygotic types produced by the mating type or *couple* $Z^{\mu\nu} \times Z^{\sigma\delta}$, the probability of $Z^{\alpha\tau}$ being the corresponding coefficient $\gamma_\alpha^{\mu\nu}\gamma_\tau^{\sigma\delta} + \gamma_\tau^{\mu\nu}\gamma_\alpha^{\sigma\delta}$ (if $\alpha \neq \tau$) or $\gamma_\alpha^{\mu\nu}\gamma_\tau^{\sigma\delta}$ (if $\alpha = \tau$).

The linear algebra with basis $Z^{\mu\nu}$ and multiplication table (7.2) will be called the *zygotic algebra* for the type of inheritance considered. It is a baric algebra with weight vector $1^\mu 1^\nu$, the duplicate of the gametic algebra **G**, and will be denoted

$$\mathbf{Z} = \mathbf{G}'. \quad . \quad . \quad . \quad . \quad . \quad (7.3)$$

A population, regarded as a distribution of zygotic types, is represented by a normalised element

$$P = \Sigma a_{\mu\nu}Z^{\mu\nu}, \quad \text{where} \quad \Sigma a_{\mu\nu}1^\mu 1^\nu = 1;$$

and multiplication in **Z**, as in **G**, has the significance described in § 1. A product left in quadratic form in the Z's gives now the probability distribution of couples $Z^{\mu\nu}Z^{\sigma\delta}$ among the parents; or, as I shall call it, the *copular representation* of the population of offspring.

§ 8. Further Duplicate Genetic Algebras.

The process of duplication can be applied repeatedly. Thus the $\frac{1}{2}m(m+1)$ types of paired zygotes, or couples,

$$K^{\mu\nu\cdot\sigma\delta} = Z^{\mu\nu}Z^{\sigma\delta}, \quad . \quad . \quad . \quad . \quad . \quad (8.1)$$

can be taken as the basis of a new linear algebra

$$\mathbf{K} = \mathbf{Z}' = \mathbf{G}''. \quad . \quad . \quad . \quad . \quad . \quad (8.2)$$

Call it the *copular algebra*. A normalised element with positive coefficients

$$P = \Sigma a_{\mu\nu\cdot\sigma\delta}K^{\mu\nu\cdot\sigma\delta}, \quad \text{where} \quad \Sigma a_{\mu\nu\cdot\sigma\delta}1^\mu 1^\nu 1^\sigma 1^\delta = 1,$$

is the copular representation of a population—the probability distribution of couples in the parents of the individuals comprised in the population.

Similarly, in the next duplicate algebra $\mathbf{K}'$, the basic symbols would classify tetrads of grandparents.

In all these algebras, multiplication has the significance described in § 1.

§ 9. Combination of Genetic Algebras.

Consider two distinct genetic classifications referring to the same population P, firstly into a set of m genetic types

$$A^1, A^2, \ldots, A^m;$$

secondly into a set of n genetic types

$$B^1, B^2, \ldots, B^n$$

of the same kind (gametic, zygotic, etc.). Let the corresponding genetic algebras be **A**, **B** with multiplication tables

$$A^\mu A^\nu = \Sigma\gamma_\alpha^{\mu\nu}A^\alpha, \qquad B^\beta B^\delta = \Sigma\delta_\tau^{\beta\delta}B^\tau.$$

By taking account of both classifications at once, we obtain a third classification which may be called their *product*, into mn genetic types

$$C^{\mu\beta} = A^\mu B^\beta.$$

The type $C^{\mu\beta}$ comprises all individuals (gametes, zygotes, etc.) who are of type A^μ in the first classification, B^β in the second.

If the characters of the two classifications are inherited independently, *i.e.* if they involve two quite distinct sets of chromosomes, then the probabilities $\gamma_\alpha^{\mu\nu}$, $\delta_\tau^{\beta\delta}$ refer to independent events. Hence the genetic algebra with basis $C^{\mu\beta}$ is the direct product

$$\mathbf{C} = \mathbf{AB};$$

i.e. its multiplication table is

$$C^{\mu\beta}C^{\nu\delta} = \Sigma\gamma_\alpha^{\mu\nu}\delta_\tau^{\beta\delta}C^{\alpha\tau}.$$

It follows that a genetic algebra which depends on several autosomal linkage groups must be a direct product **ABC** . . . of genetic algebras, one factor algebra for each linkage group.

If, however, the A and B classifications are independent but genetically linked, *i.e.* if they involve two quite distinct sets of gene loci but not distinct sets of chromosomes, then the probabilities $\gamma_\alpha^{\mu\nu}$, $\delta_\tau^{\beta\delta}$ are not independent. Regarded as a linear set, **C** is still the product of the linear sets **A** and **B**; but the algebra **C** will not be the direct product of the algebras **A** and **B** (except in the very exceptional case when all crossing over values between A and B are precisely 50 per cent.). It is, however, still the case that **C** contains subalgebras isomorphic with **A** and **B**. For example, if these algebras are gametic, and if we keep the first index of $C^{\mu\beta}$ constant, we are virtually disregarding all the A-loci, so we obtain a subalgebra isomorphic with **B**; and this can be done in m ways.

Hence a genetic algebra based on the allelomorphs of several autosomal loci possesses numerous automorphisms.

It will be shown in § 14 that even when linkage is involved the gametic algebra can be symbolically factorised, and regarded as a symbolic direct product of non-commutative factor algebras, one for each locus (see (14.12)).

§§ 10–15. Examples of Symmetrical Genetic Algebras.

A more detailed description of practical applications will be given elsewhere. My object here is simply to show that the genetic algebras are

train algebras. I give in each case the principal and plenary train equations, *i.e.* the identities of lowest degree connecting respectively the sequences of principal and plenary powers of a normalised element. As explained in § 4, these are really recurrence equations, and have a special significance in genetics.

§ 10. Simple Mendelian Inheritance.

For a single autosomal gene difference (D, R), the gametic multiplication table is

$$DD = D, \quad DR = \tfrac{1}{2}D + \tfrac{1}{2}R, \quad RR = R. \quad . \quad . \quad (10.1)$$

Writing

$$A = DD, \quad B = DR, \quad C = RR, \quad . \quad . \quad . \quad (10.2)$$

we find, *e.g.*,

$$B^2 = (\tfrac{1}{2}D + \tfrac{1}{2}R)^2 = \tfrac{1}{4}A + \tfrac{1}{2}B + \tfrac{1}{4}C.$$

Hence and similarly the zygotic multiplication table is

$$A^2 = A, \quad B^2 = \tfrac{1}{4}A + \tfrac{1}{2}B + \tfrac{1}{4}C, \quad C^2 = C,$$
$$BC = \tfrac{1}{2}B + \tfrac{1}{2}C, \quad CA = B, \quad AB = \tfrac{1}{2}A + \tfrac{1}{2}B. \quad . \quad . \quad (10.3)$$

Call these two algebras $\mathbf{G}_2$, $\mathbf{Z}_2$ ($\mathbf{Z}_2 = \mathbf{G}_2'$), and denote their general elements

$\mathbf{G}_2$: $x = \delta D + \rho R, \quad . \quad . \quad . \quad . \quad . \quad (10.4)$

$\mathbf{Z}_2$: $x = \alpha A + 2\beta B + \gamma C. \quad . \quad . \quad . \quad . \quad (10.5)$

The principal rank equations are

$\mathbf{G}_2$: $x^2 - (\delta + \rho)x = 0, \quad . \quad . \quad . \quad . \quad (10.6)$

$\mathbf{Z}_2$: $x^3 - (\alpha + 2\beta + \gamma)x^2 = 0; \quad . \quad . \quad . \quad . \quad (10.7)$

and the plenary rank equations (or identities of lowest degree connecting plenary powers of the general elements) are (10.6) and

$\mathbf{Z}_2$: $x^{2\cdot 2} - (\alpha + 2\beta + \gamma)^2x^2 = 0. \quad . \quad . \quad . \quad . \quad (10.8)$

A population P is represented by an element of unit weight in either algebra, *i.e.* (10.4) or (10.5) with

$$\delta + \rho = 1, \quad \alpha + 2\beta + \gamma = 1,$$

the ratios $\delta : \rho$, $\alpha : 2\beta : \gamma$ giving the relative frequencies of the gametic types which it produces or genotypes which it contains. In this case (10.6), (10.7), (10.8) become the train equations

$\mathbf{G}_2$: $P^2 = P, \quad . \quad . \quad . \quad . \quad . \quad . \quad (10.9)$

$\mathbf{Z}_2$: $P^3 = P^2, \quad P^{2\cdot 2} = P^2, \quad . \quad . \quad . \quad . \quad (10.10)$

expressing facts well known in genetics. It is convenient to write these equations in the form (*cf.* 4.7)

$$\mathbf{G_2}: \quad P(P-1)=0, \quad . \quad . \quad . \quad . \quad . \quad (10.11)$$

$$\mathbf{Z_2}: \quad P^2(P-1)=0, \quad P^2[P-1]=0. \quad . \quad . \quad (10.12)$$

§ 11. Multiple Allelomorphs.

For n allelomorphs $G^\mu(\mu=1, \ldots, n)$, the gametic and zygotic multiplication tables are

$$G^\mu G^\nu = \tfrac{1}{2}G^\mu + \tfrac{1}{2}G^\nu, \quad . \quad . \quad . \quad . \quad (11.1)$$

$$Z^{\mu\nu}Z^{\rho\sigma} = \tfrac{1}{4}Z^{\mu\rho} + \tfrac{1}{4}Z^{\mu\sigma} + \tfrac{1}{4}Z^{\nu\rho} + \tfrac{1}{4}Z^{\nu\sigma}, \quad . \quad . \quad . \quad (11.2)$$

where $Z^{\mu\nu}=G^\mu G^\nu$. The algebras $\mathbf{G}_n$, $\mathbf{Z}_n$ so determined reduce to $\mathbf{G}_2$, $\mathbf{Z}_2$ when $n=2$; and they have in general the same train equations (10.11), (10.12).

§ 12. Linked Allelomorphs.

For two linked series of multiple allelomorphs, respectively m and n in number, with crossing over probability ω, the gametic multiplication table is

$$G^{\mu\alpha}G^{\nu\beta} = \tfrac{1}{2}(1-\omega)(G^{\mu\alpha}+G^{\nu\beta}) + \tfrac{1}{2}\omega(G^{\mu\beta}+G^{\nu\alpha}), \quad . \quad . \quad (12.1)$$

where $G^{\mu\alpha}(\mu=1, \ldots, m;\ \alpha=1, \ldots, n)$ are the mn gametic types. Denote this gametic algebra $\mathbf{G}_{mn}(\omega)$. The principal and plenary rank equations are

$$x^3 - \tfrac{1}{2}(3-\omega)\xi_2 x^2 + \tfrac{1}{2}(1-\omega)\xi^2 x = 0, \quad . \quad . \quad . \quad (12.2)$$

$$x^{2^2} - (2-\omega)\xi^2 x^2 + (1-\omega)\xi^2 x = 0, \quad . \quad . \quad . \quad (12.3)$$

giving for a normalised element P the train equations

$$P^3 - \tfrac{1}{2}(3-\omega)P^2 + \tfrac{1}{2}(1-\omega)P \equiv P(P-1)\left(P - \frac{1-\omega}{2}\right) = 0, \quad . \quad (12.4)$$

$$P^{2^2} - (2-\omega)P^2 + (1-\omega)P \equiv P[P-1][P-(1-\omega)] = 0. \quad . \quad (12.5)$$

In the duplicate algebra $\mathbf{Z}_{mn}(\omega)=\mathbf{G}_{mn}(\omega)'$ the corresponding equations are

$$P^2(P-1)\left(P - \frac{1-\omega}{2}\right) = 0, \qquad P^2[P-1][P-(1-\omega)] = 0. \quad . \quad (12.6)$$

§ 13. Independent Allelomorphs.

Consider two series of multiple allelomorphs in separate autosomal linkage groups. This being indistinguishable from the case of § 12 with $\omega=\frac{1}{2}$, the gametic algebra is $\mathbf{G}_{mn}(\frac{1}{2})$. As in § 9, it may also be expressed as the direct product $\mathbf{G}_m\mathbf{G}_n$.

§ 14. Linkage Group.

I will first rewrite equations (12.1) with a change of notation. I will then write down the analogous equations for the case of three linked loci, and examine the structure of the corresponding algebra. This will be a sufficient indication of the procedure which can be followed out quite generally for a complete linkage group comprising any number of loci on one autosome, with any number of allelomorphs at each locus. The method may be extended to include any number of linkage groups.

Equations (12.1) may be written

$$AB\,.\,A'B' = \tfrac{1}{2}(1-\omega)(AB+A'B') + \tfrac{1}{2}\omega(AB'+A'B). \quad . \quad . \quad (14.1)$$

Here A and B refer to the two gene loci. $A^\alpha B^\alpha$ would mean the same as $G^{\mu\alpha}$—a gamete with the μth allelomorph at the A-locus and the αth at B; but dropping the indices AB and A′B′ stand for any particular gametic types, the same or different.

(14.1) may again be rewritten

$$AB\,.\,A'B' = \tfrac{1}{2}\varpi(A+\chi A')(B+\chi B'), \quad . \quad . \quad . \quad (14.2)$$

where $\varpi=1-\omega$ and χ is an operator which interchanges ω and ϖ, so that $\chi^2=1$ and $\varpi\chi=\omega$.

Now consider the case of three loci A, B, C, having respectively m, n, r allelomorphs, and crossing over probabilities ω_{AB}, ω_{BC}, ω_{AC}. The gametic algebra may be symbolised conveniently as $\mathbf{G}_{mnr}(\omega)$, where ω is the symmetrical matrix of the crossing over values, with diagonal zeros. Its multiplication table, comprising $\frac{1}{2}mnr(mnr+1)$ formulæ, is

$$ABC\,.\,A'B'C' = \tfrac{1}{2}\lambda(ABC+A'B'C') + \tfrac{1}{2}\mu(A'BC+AB'C') + \tfrac{1}{2}\nu(AB'C+A'BC') + \tfrac{1}{2}\rho(ABC'+A'B'C), \quad (14.3)$$

where

$$\lambda+\mu+\nu+\rho=1, \quad . \quad . \quad . \quad . \quad . \quad (14.4)$$

$$\mu+\nu=\omega_{AB}, \qquad \nu+\rho=\omega_{BC}, \qquad \mu+\rho=\omega_{AC}. \quad . \quad . \quad (14.5)$$

The ω's are not independent, but are connected only by an inequality (Haldane, 1918):

$$\omega_{AC} = \omega_{AB} + \omega_{BC} - \kappa\omega_{AB}\omega_{BC}, \quad \text{where } 0 \leqslant \kappa \leqslant 2, \quad . \quad . \quad (14.6)$$

from which may be deduced

$$\mu\rho \geqslant \nu\lambda. \quad . \quad . \quad . \quad . \quad . \quad (14.7)$$

Now introduce the following operators:—

$$\left.\begin{array}{llll} \chi_1 \text{ interchanges } \lambda \text{ with } \mu, & & \nu \text{ with } \rho, \\ \chi_2 \quad ,, & \lambda \quad ,, & \nu, & \rho \quad ,, \quad \mu, \\ \chi_3 \quad ,, & \lambda \quad ,, & \rho, & \mu \quad ,, \quad \nu. \end{array}\right\} \quad . \quad . \quad (14.8)$$

Together with 1, they form an Abelian group, having the relations

$$\left.\begin{array}{llll} \chi_2\chi_3=\chi_1, & \chi_3\chi_1=\chi_3, & \chi_1\chi_2=\chi_3, \\ \chi_1^2=\chi_2^2=\chi_3^2=\chi_1\chi_2\chi_3=1. \end{array}\right\} \quad . \quad . \quad (14.9)$$

(14.3) may then be rewritten:

$$ABC\,.\,A'B'C' = \tfrac{1}{2}\lambda(A+\chi_1A')(B+\chi_2B')(C+\chi_3C'). \quad . \quad . \quad (14.10)$$

This symbolism can be manipulated with considerable freedom. For example, an expression such as $(\alpha ABC+\beta A'BC)$ can be written $(\alpha A+\beta A')BC$; and when two such expressions are multiplied, the distributive law works. The interchange symbols co-operate in the same way.

(14.10) may again be rewritten

$$ABC\,.\,A'B'C' = (\chi_0A+\chi_1A')(\chi_0B+\chi_2B')(\chi_0C+\chi_3C'), \quad . \quad (14.11)$$

where $\chi_0=1$, and the operand $\frac{1}{2}\lambda$ is implied. Finally, (14.11) may be analysed into

$$AA'=\chi_0A+\chi_1A', \qquad BB'=\chi_0B+\chi_2B', \qquad CC'=\chi_0C+\chi_3C'. \quad (14.12)$$

This separation of the symbols, or factorisation of the algebra (*cf.* end of § 9), will evidently yield valid results, provided that after recombination and application of (14.9). χ_0 is interpreted as $\frac{1}{2}\lambda$, χ_1 as $\frac{1}{2}\mu$, χ_2 as $\frac{1}{2}\nu$, χ_3 as $\frac{1}{2}\rho$. It must be noted that the symbols when separated in this way are non-commutative; *e.g.* $AA'\neq A'A$, since $ABC\,.\,A'B'C'\neq A'BC\,.\,AB'C'$.

Select a particular gametic type ABC, and write

$$A-A=u, \qquad B-B=v, \qquad C-C=w, \quad . \quad . \quad (14.13)$$

where $A\neq\mathbf{A}$, $B\neq\mathbf{B}$, $C\neq\mathbf{C}$. Thus the symbols u, v, w are nil elements having respectively $m-1$, $n-1$, $r-1$ possible values. We have from (14.12):

$$\begin{aligned} A^2&=(\chi_0+\chi_1)A,\\ Au&=A^2-AA=(\chi_0+\chi_1)A-(\chi_0A+\chi_1A)=\chi_1u,\\ uA&=A^2-AA=(\chi_0+\chi_1)A-(\chi_0A+\chi_1A)=\chi_0u,\\ u^2&=A^2-AA-AA+A^2=(\chi_0+\chi_1)A-(\chi_0A+\chi_1A)-(\chi_0A+\chi_1A)+(\chi_0+\chi_1)A=0, \end{aligned}$$

and eight similar equations.

Now write

$$\left.\begin{array}{llll} \mathbf{ABC}=\mathrm{I}, & u\mathbf{BC}=\bar{u}, & \mathbf{A}v\mathbf{C}=\bar{v}, & \mathbf{AB}w=\bar{w}, \\ \mathbf{A}vw=\overline{vw}, & u\mathbf{B}w=\overline{uw}, & uv\mathbf{C}=\overline{uv}, & uvw=\overline{uvw}. \end{array}\right\} \quad . \quad (14.14)$$

The symbols I, $\bar{u}$, $\bar{v}$, $\bar{w}$, $\overline{vw}$, $\overline{uw}$, $\overline{uv}$, $\overline{uvw}$ thus introduced are linear and linearly independent in the gametic type symbols; and their number is

$$1+(m-1)+(n-1)+(r-1)+(n-1)(r-1)+(r-1)(m-1)+(m-1)(n-1)+(m-1)(n-1)(r-1)=mnr,$$

which is equal to the number of gametic type symbols. They may thus be taken as a new basis for the gametic algebra. The transformed multiplication table is then easily deduced. We find, for example,

$$\mathrm{I}^2=\mathrm{I},$$

$$\mathrm{I}\bar{u}=A\bar{u}\,.\,B\bar{u}\,.\,C\bar{u}=\chi_1(\chi_0+\chi_2)(\chi_0+\chi_3)\bar{u}=(\chi_0+\chi_1+\chi_2+\chi_3)\bar{u}=\tfrac{1}{2}\bar{u},$$

since $\chi_0+\chi_1+\chi_2+\chi_3$ is to be interpreted as $\frac{1}{2}\lambda+\frac{1}{2}\mu+\frac{1}{2}\nu+\frac{1}{2}\rho=\frac{1}{2}$. Similarly:

$$\begin{aligned} \mathrm{I}\overline{vw}&=\tfrac{1}{2}(\lambda+\mu)\overline{vw}, & \mathrm{I}\overline{uvw}&=\tfrac{1}{2}\lambda\overline{uvw},\\ \bar{u}\bar{v}&=\tfrac{1}{2}(\nu+\rho)\overline{uv}, & \bar{u}\overline{vw}&=\tfrac{1}{2}\mu\overline{uvw}, & \bar{u}^2&=\bar{u}\overline{uv}=\bar{u}\overline{uvw}=0. \end{aligned}$$

These results are typical, all other products in the transformed multiplication table being obtainable from them by cyclic permutation of u, v, w and μ, ν, ρ and 1, 2, 3.

It is now readily verifiable that the algebra has the structure of a special train algebra as defined in § 4, with

$$\mathbf{U}=(\bar{u}, \bar{v}, \bar{w}, \overline{vw}, \overline{uw}, \overline{uv}, \overline{uvw}), \qquad \mathbf{U}^{(1)}=(\overline{vw}, \overline{uw}, \overline{uv}, \overline{uvw}),$$
$$\mathbf{U}^{(2)}=(\overline{uvw}), \qquad \mathbf{U}^{(3)}=0.$$

Many of its properties can be most easily deduced from this transformed form. It can be shown that its principal and plenary train roots, other than unity, are the results of

$$\chi_0, \qquad \chi_0+\chi_1, \qquad \chi_0+\chi_2, \qquad \chi_0+\chi_3,$$

operating respectively on $\frac{1}{2}\lambda$ and λ. Further details are postponed until the properties of special train algebras have been studied elsewhere.

§ 15. Polyploidy.

A single example—the simplest possible—will illustrate the occurrence of special train algebras in this connection. The gametic algebra with multiplication table

$$\left.\begin{array}{llll} A^2=A, & B^2=AC=\tfrac{1}{2}A+\tfrac{1}{2}B+\tfrac{1}{2}C, \\ C^2=C, & BC=\tfrac{1}{2}B+\tfrac{1}{2}C, & AB=\tfrac{1}{2}A+\tfrac{1}{2}B, \end{array}\right\} \quad . \quad (15.1)$$

refers to the inheritance of a single autosomal gene difference in autotetraploids. (*Cf.* Haldane, 1930, the case $m=2$, with A, B, C written for A^2, Aa, a^2.)

This is a special train algebra, as may be seen by performing the transformation

$$A=A, \qquad A-B=u, \qquad A-2B+C=p. \quad . \quad . \quad (15.2)$$

It has the principal and plenary train equations

$$P(P-1)(P-\tfrac{1}{2})=0, \qquad P[P-1][P-\tfrac{1}{2}]=0. \quad . \quad . \quad (15.3)$$

SUMMARY.

A population can be classified genetically at various levels, according to the frequencies of the gametic types which it produces, of the zygotic types of individuals which it contains, of types of mating pairs in the preceding generation, and so on. It is represented accordingly by means of hypercomplex numbers in one or other of a series of linear algebras (gametic, zygotic, copular, . . .), each algebra being isomorphic with the quadratic forms of the preceding algebra. Such a series of *genetic algebras* exists for any mode of genetic inheritance which is symmetrical in the sexes. (Genetic algebras for unsymmetrical inheritance also exist, but are not considered here.) Many calculations which occur in theoretical genetics can be expressed as manipulations within these algebras.

The algebras which arise in this way are all commutative non-associative linear algebras of a special kind. Firstly, they are *baric algebras*, *i.e.* they possess a scalar representation; secondly, they are *train algebras*, *i.e.* the rank equation of a suitably normalised hypercomplex number has constant coefficients. Some theorems concerning such algebras are enunciated.

REFERENCES TO LITERATURE.

AITKEN, A. C., 1935. "The normal form of compound and induced matrices," *Proc. Lond. Math. Soc.* (2), vol. xxxviii, pp. 354–376.

DICKSON, L. E., 1914 (reprinted 1930). *Linear algebras*, Cambridge Tract, No. 16.

ETHERINGTON, I. M. H., 1939. "On non-associative combinations," *Proc. Roy. Soc. Edin.*, vol. lix, pp. 153–162.

GEPPERT, H., and KOLLER, S., 1938. *Erbmathematik*, Leipzig.

GLIVENKO, V., 1936. "Algèbre mendelienne," *Moscow Acad. Sci. C.R.*, vol. iv, pp. 385–386.

HALDANE, J. B. S., 1918. "The combination of linkage values," *Journ. Gen.*, vol. viii, pp. 299–309.

——, 1930. "Theoretical genetics of autopolyploids," *Journ. Gen.*, vol. xxii, pp. 359–372.

JENNINGS, H. S., 1935. *Genetics*, London.

WEDDERBURN, J. H. M., 1908 (*a*). "On hypercomplex numbers," *Proc. Lond. Math. Soc.* (2), vol. vi, pp. 77–118.

——, 1908 (*b*). "On certain theorems in determinants," *Proc. Edin. Math. Soc.* (1), vol. xxvii, pp. 67–69.

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OBITUARY NOTICES.

Henry Edward Armstrong, Ph.D., LL.D., F.R.S., Hon. F.R.S.E.

HENRY EDWARD ARMSTRONG, who was elected an Honorary Fellow in 1934, died on July 13, 1937, in his ninetieth year. Although his connection with our Society was brief, he had been a Fellow of the Chemical Society since 1870 and of the Royal Society of London since 1876. For many years, indeed, he had been recognised as the "grand old man" of British Chemistry.

He first studied chemistry under Hoffmann at the Royal College of Chemistry in 1865; Tyndall and Huxley were also his scientific instructors. In 1868 he left the private laboratory of Frankland to obtain his Ph.D. degree with Kolbe at Leipzig. He inherited there Kolbe's gift of provocative criticism, for the skilful employment of which he will always be remembered.

There followed a long teaching and research career at the London Institution, Finsbury Square, and at the City and Guilds College, South Kensington. As a teacher, Armstrong was characteristically unorthodox, and he disturbed his complacent colleagues for decades by his constant advocacy of what became known as the "neuristic method" of presenting science experimentally in schools, as opposed to the traditional "didactic method." In research Armstrong was pre-eminent in organic chemistry, and his inspiration is evident by the large number of research students who worked under his direction and later became leaders in chemical industry or education.

As a controversialist, Armstrong knew no equal. For fifty years he never ceased to attack the Arrhenius theory of ionization in solution with almost religious fervour. He had himself carried out a most extensive study of the physical properties of sulphuric acid just before the ionic hypothesis came into prominence, and his communications frequently read as if he were still dipping his pen into that liquid. Never, however, was there any personal rancour in his polemics; he could be just as genial in conversation as vituperative in writing.

There can be no doubt that as *laudator temporis acti* he frequently failed to appreciate the significance of new lines of chemical advance, but there can also be no doubt that he frequently acted as a most efficient and salutary brake on over-fanciful speculations.

J. K.