

PANMIXIA WITH TETRASOMIC AND HEXASOMIC INHERITANCE *

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Received June 20, 1953

BECAUSE of the greater number of genotypes and of modes of gamete formation, any genetic analysis is much more complex when the nature of inheritance is polysomic rather than disomic. Consequently, whilst random mating in populations of disomic organisms has been considered in some detail (for a list of references see BENNETT 1954), there have been few parallel discussions for polysomic forms. HALDANE (1930) first considered random mating with a single polysomic locus under the assumption of random chromosome segregation. The nature of polysomic inheritance at a single locus has since been clarified (FISHER and MATHER 1943) and recently, GEIRINGER (1949) has given a complex treatment of random mating at a single polysomic locus taking account of double reduction. I have also given an independent approach for the case of a tetrasomic locus (BENNETT 1949). In the present article, I consider random mating with linkage in tetrasomic and hexasomic inheritance. The assumptions made are that the generations do not overlap, that the same conditions exist for the two sexes and that there is neither mutation nor selection.

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For a single factor, the effect of a generation of random mating can be expressed as a linear transformation of the gametic frequencies. The results for tetrasomic inheritance may be summarized as follows. Suppose that there are any number of alleles A, a, a', \dots at the given locus and that these are present in the original population with frequencies $p(A), p(a), p(a')$, etc. These frequencies are constant in the absence of selection and mutation. If p_n denotes the frequency of occurrence of a given gametic genotype in the pooled gametic output of the n th generation of random mating and α is the amount of double reduction at the given locus, typical principal components of frequency (FISHER 1949, p. 30) are as follows.

$$L_n = (2 + \alpha) p_n(A^2) - 2(1 - \alpha) p(A)^2 - 3\alpha p(A) \quad (1)$$

$$M_n = (2 + \alpha) p_n(Aa) - 4(1 - \alpha) p(A) p(a) \quad (2)$$

Each of these principal components corresponds with the latent root $(1 - \alpha)/3$, i.e.,

$$L_n = [(1 - \alpha)/3]^n L_0 \text{ and } M_n = [(1 - \alpha)/3]^n M_0$$

* Part of the cost of the accompanying mathematical formulae has been paid by the GALTON and MENDEL MEMORIAL FUND.

These results are equivalent to Geiringer's equations (21) but there is a slight difference in expression. In the present article no distinction is made between genotypes Aa and aA , and $p(Aa)$ is used to denote the total frequency of both these genotypes.

With a single locus and disomic inheritance, the distribution of zygotic genotypes reaches the equilibrium state after one generation of random mating (HARDY 1908). This is not the case with tetrasomic inheritance. Not only is the rate of approach to equilibrium dependent upon the amount of double reduction but so are the equilibrium distributions themselves. It is only in the case of no double reduction that the distribution of gametes approaches the state of independence in which $p(A^2) = p(A)^2$, $p(Aa) = 2p(A)p(a)$, etc. To compare the rates of approach to equilibrium at different loci we may compare the values of $\log_e[3/(1-\alpha)]$.

The equilibrium distribution of zygotic genotypes is given by the expansion of

$$\left\{ 3\alpha \sum_a p(a)a^2 + 2(1-\alpha) \left[\sum_a p(a)a \right]^2 \right\}^2 / (2+\alpha)^2 \quad (3)$$

where the summations are taken over all alleles at the given locus (cf. GEIRINGER's equations (23)). If $\alpha = 0$, this is

$$\left[\sum_a p(a)a \right]^4$$

(cf. HALDANE 1930, p. 363).

Now consider the result of random mating for a single hexasomic locus. If β denotes the amount of double reduction at the given locus, typical principal components of frequency are as follows (cf. GEIRINGER's equations (28)).

$$L_n = (9 + \beta)(9 + 2\beta)p_n(A^3) - 27(1 - \beta)(3 - \beta)p(A)^3 - 45\beta(3 - \beta)p(A)^2 - 20\beta^2p(A) \quad (4)$$

$$M_n = (9 + \beta)(9 + 2\beta)p_n(A^2a) - 81(1 - \beta)(3 - \beta)p(A)^2p(a) - 45\beta(3 - \beta)p(A)p(a) \quad (5)$$

$$N_n = (9 + \beta)(9 + 2\beta)p_n(Aaa') - 162(1 - \beta)(3 - \beta)p(A)p(a)p(a') \quad (6)$$

Each of these principal components corresponds with the latent root $(6 - 2\beta)/15$ and so to compare the rates of approach to equilibrium at different loci, we may compare the values of $\log_e[15/(6 - 2\beta)]$. At equilibrium, the genotypic distribution of zygotes is given by the expansion of

$$\left\{ 27(1 - \beta)(3 - \beta) \left[\sum_a p(a)a \right]^3 + 45\beta(1 - \beta) \left[\sum_a p(a)a^2 \right] \sum_a p(a)a + 20\beta^2 \sum_a p(a)a^3 \right\}^2 / \left[(9 + \beta)(9 + 2\beta) \right]^2 \quad (7)$$

each summation being taken over all alleles at the locus.

LINKAGE WITH TETRASOMIC INHERITANCE

With disomic inheritance, the genotypes of all individuals which are heterozygous at a given number of linked loci can be transformed into one another by gene substitutions. Whilst this is not the case with polysomic inheritance, the heterogenic genotypes may be classified into a number of isomorphic sets such that each genotype of a set can be transformed into any other of the same set by a number of gene substitutions. All genotypes of any isomorphic set have equivalent gametic frequencies. This is in accordance with the generalized form of the Mendelian law of heredity, "The gametic frequencies are invariant in respect of any gene substitution applied systematically to the genic content of an organism and of the gametes it produces" (FISHER 1947, p. 58).

TABLE 1

*Modes of gamete formation for two loci in a tetrasomic organism.
Parental genotype $a_1b_1/a_2b_2/a_3b_3/a_4b_4$.*

| Mode of formation | Typical gamete |
|-------------------|-----------------|
| 1 | a_1b_1/a_2b_2 |
| 2 | a_1b_1/a_1b_1 |
| 3 | a_1b_1/a_2b_3 |
| 4 | a_1b_1/a_1b_2 |
| 5 | a_1b_1/a_2b_1 |
| 6 | a_1b_2/a_3b_4 |
| 7 | a_2b_1/a_3b_1 |
| 8 | a_1b_2/a_1b_3 |
| 9 | a_1b_2/a_2b_3 |
| 10 | a_1b_2/a_1b_2 |
| 11 | a_1b_2/a_2b_1 |

Taking together the isomorphic sets of genotypes which are related by permutation of loci, we have a classification according to genera (loc. cit., p. 70).

With two linked loci and disomic inheritance, there are only two modes of gamete formation and these correspond to recombinant and non-recombinant gametes. The gametic output of an individual heterozygous at each of two linked loci can therefore be specified in terms of a single parameter, the recombination fraction. With tetrasomic inheritance at two linked loci, eleven modes of gamete formation can be distinguished. We shall adopt FISHER'S (1947) classification of these modes of formation (table 1). The respective frequencies of occurrence of these modes of gamete formation will be denoted by f_i ($i = 1, 2, \dots, 11$) where

$$\sum_{i=1}^{11} f_i = 1.$$

The gametic output of any tetrasomic individual heterogenic at two linked loci can therefore be specified linearly in terms of these eleven parameters.

We shall now consider the chromosome or gene-combination frequencies upon random mating. Suppose that two alleles are available at both of the linked loci and let these be denoted by A, a and B, b . For those genotypes with

only one allele at either locus, the frequency of occurrence of any pair of genes at these two loci on one chromosome is, of course, the same in the gametic output as it is in the parental genotype itself. With one exception, this is not true of genotypes with two alleles at both loci. The exceptional genotype is biduplex neutral, $AB/Ab/aB/ab$. For all other genotypes with two alleles at both loci, the frequency of occurrence of any pair of genes on one chromosome in the gametes is some linear function of the recombination fraction. These frequencies relevant to the gametic output from one representative genotype of each of the five genera are shown in table 2. The recombination fraction is denoted by y .

Any gene-combination has the same frequency of occurrence in the zygotes of a given generation as in the gametic output of the preceding generation. The relations between the frequencies of gene-combinations in the gametic output of a given generation and in the zygotes of the preceding generation are contained in table 2. If w_n denotes the frequency of a given zygotic genotype in the n th generation of random mating and p_n that of a given gametic genotype,

TABLE 2

Frequencies of gene-combinations in gametic output of tetraploids.

| Typical parental genotype | Number of genotypes in genus | Frequencies of gene-combinations in the gametic output | | | | ÷ |
|---------------------------|------------------------------|--|----------|----------|---------|----|
| | | AB | Ab | ab | aB | |
| $AB/ab/ab/ab$ | 4 | $1 - y$ | y | $3 - y$ | y | 4 |
| $Ab/aB/ab/ab$ | 4 | y | $3 - y$ | $6 + y$ | $3 - y$ | 12 |
| $AB/Ab/ab/ab$ | $4 + 4$ | $3 - 2y$ | $3 + 2y$ | $6 - 2y$ | $2y$ | 12 |
| $AB/AB/ab/ab$ | 2 | $3 - 2y$ | $2y$ | $3 - 2y$ | $2y$ | 6 |
| $AB/Ab/aB/ab$ | 1 | 1 | 1 | 1 | 1 | 4 |

or of a given gene-combination (chromosome), amongst the total gametic output of this same generation, then from table 2 we can immediately obtain the following relation.

$$\begin{aligned}
 p_{n+1}(AB) - p_n(AB) = & \\
 & (y/12) [-3w_{n+1}(AB/ab/ab/ab) + 3w_{n+1}(Ab/Ab/Ab/aB) \\
 & - 3w_{n+1}(AB/AB/AB/ab) + 3w_{n+1}(Ab/aB/aB/aB) \\
 & - w_{n+1}(AB/Ab/Ab/ab) + w_{n+1}(Ab/aB/ab/ab) \\
 & - w_{n+1}(AB/aB/aB/ab) + w_{n+1}(AB/AB/Ab/aB) \\
 & - 2w_{n+1}(AB/Ab/ab/ab) + 2w_{n+1}(Ab/Ab/aB/ab) \\
 & - 2w_{n+1}(AB/AB/aB/ab) + 2w_{n+1}(AB/Ab/aB/aB) \\
 & - 2w_{n+1}(AB/aB/ab/ab) + 2w_{n+1}(AB/Ab/Ab/aB) \\
 & - 2w_{n+1}(AB/AB/Ab/ab) + 2w_{n+1}(Ab/aB/aB/ab) \\
 & - 4w_{n+1}(AB/AB/ab/ab) + 4w_{n+1}(Ab/Ab/aB/aB)]. \quad (8)
 \end{aligned}$$

As the zygotes of the $(n + 1)$ th generation are formed by the random union of gametes produced from the n th generation, the zygotic frequencies are expressible as quadratic functions of the gametic frequencies of the previous generation. For example,

$$\begin{aligned}
 w_{n+1}(AB/ab/ab/ab) &= 2p_n(AB/ab)p_n(ab/ab) \\
 w_{n+1}(AB/Ab/ab/ab) &= 2p_n(AB/Ab)p_n(ab/ab) \\
 &\quad + 2p_n(AB/ab)p_n(Ab/ab) \quad (9) \\
 w_{n+1}(AB/AB/ab/ab) &= 2p_n(AB/AB)p_n(ab/ab) \\
 &\quad + p_n(AB/ab)p_n(AB/ab).
 \end{aligned}$$

Making these substitutions in (8), we arrive, after some simplification, at the following equation.

$$p_{n+1}(AB) = p_n(AB) + (y/6) [4p(A)p(B) - 4p_n(AB) + p_n(Ab/aB) - p_n(AB/ab)] \quad (10)$$

If $y = 0$, then $p_n(AB) = p_0(AB)$ as for a single locus. Now gametes of genotypes AB/ab and Ab/aB can be formed only from individuals that are digenic at both loci. From the gametic matrices for such individuals (FISHER 1947) we find that

$$\begin{aligned}
 p_n(Ab/aB) - p_n(AB/ab) = & \\
 (1/12) [2(f_1 - f_{11}) + f_3 - f_9] [-3w_n(AB/ab/ab/ab) + 3w_n(Ab/Ab/Ab/aB) & \\
 - 3w_n(AB/AB/AB/ab) + 3w_n(Ab/aB/aB/aB) & \\
 - w_n(AB/Ab/Ab/ab) + w_n(Ab/aB/ab/ab) & \\
 - w_n(AB/aB/aB/ab) + w_n(AB/AB/Ab/aB) & \\
 - 2w_n(AB/Ab/ab/ab) + 2w_n(Ab/Ab/aB/ab) & \\
 - 2w_n(AB/AB/aB/ab) + 2w_n(AB/Ab/aB/aB) & \\
 - 2w_n(AB/aB/ab/ab) + 2w_n(AB/Ab/Ab/aB) & \\
 - 2w_n(AB/AB/Ab/ab) + 2w_n(Ab/aB/aB/ab) & \\
 - 4w_n(AB/AB/ab/ab) + 4w_n(Ab/Ab/aB/aB)] \quad (11)
 \end{aligned}$$

Hence, by reason of (8),

$$p_n(Ab/aB) - p_n(AB/ab) = [2(f_1 - f_{11}) + f_3 - f_9] \times [p_n(AB) - p_{n-1}(AB)]/y \quad (12)$$

Hence from (10) we obtain the following relation.

$$p_{n+1}(AB) = p_n(AB) + (1/6) [2(f_1 - f_{11}) + f_3 - f_9] [p_n(AB) - p_{n-1}(AB)] + (2y/3) [p(A)p(B) - p_n(AB)] \quad (13)$$

Putting $r_n(AB) = p(A)p(B) - p_n(AB)$

then $r_{n+1}(AB) - (1 + \delta)r_n(AB) + (\gamma + \delta)r_{n-1}(AB) = 0$

where $\gamma = 2y/3$

and $\delta = -\gamma + [2(f_1 - f_{11}) + f_3 - f_9]/6$.

The solution of this recurrence equation is

$$r_n(AB) = -(C_n + D_n)r_0(AB) + D_n[p_0(Ab/aB) - p_0(AB/ab)]$$

where C_n and D_n are given by

$$\begin{bmatrix} C_n \\ D_n \end{bmatrix} = \begin{bmatrix} 1 & 1 \\ \delta & -\gamma \end{bmatrix}^n \begin{bmatrix} -1 \\ 0 \end{bmatrix}$$

The matrix $\begin{bmatrix} 1 & 1 \\ \delta & -\gamma \end{bmatrix}$ has positive latent roots,

$$\lambda = (\frac{1}{2})\{1 + \delta + [(1 + \delta)^2 - 4(\gamma + \delta)]^{1/2}\}$$

$$\mu = (\frac{1}{2})\{1 + \delta - [(1 + \delta)^2 - 4(\gamma + \delta)]^{1/2}\}$$

These latent roots correspond with principal components

$$L_n = 2\gamma C + \{1 - \delta - [(1 + \delta)^2 - 4(\gamma + \delta)]^{1/2}\} D_n \tag{14}$$

$$M_n = 2\gamma C + \{1 - \delta + [(1 + \delta)^2 - 4(\gamma + \delta)]^{1/2}\} D_n \tag{15}$$

such that

$$L_n = -2\gamma\lambda^n$$

$$M_n = -2\gamma\mu^n$$

If $4(\gamma + \delta)$ is less than $(1 + \delta)^2$, there will be a real value for θ such that $4(\gamma + \delta) \cosh^2\theta = (1 + \delta)^2$ and we may then write

$$\lambda^n = (\gamma + \delta)^{n/2} \exp(n\theta)$$

$$\mu^n = (\gamma + \delta)^{n/2} \exp(-n\theta).$$

It follows that

$$C_n = -\frac{1}{2}(1 - \delta)(\gamma + \delta)^{(n-1)/2} \frac{\sinh n\theta}{\sinh \theta} - (\gamma + \delta)^{n/2} \cosh n\theta$$

$$D_n = \gamma(\gamma + \delta)^{(n-1)/2} \frac{\sinh n\theta}{\sinh \theta}$$

As $(\gamma + \delta)^{n/2} \exp\theta$ is less than unity for all possible values of γ other than $\gamma = 0$, it follows that

$$\lim_{n \rightarrow \infty} C_n = 0$$

$$\lim_{n \rightarrow \infty} D_n = 0.$$

$$\text{Hence } \lim_{n \rightarrow \infty} p_n(AB) = p(A) p(B). \tag{16}$$

A comparison of the rates of approach to equilibrium at different pairs of linked loci may be made by comparing the values of

$$-\log_e \lambda = \log_e \left\{ (\frac{1}{2}) (1 + \delta) + [(\frac{1}{4}) (1 - \delta)^2 - \gamma]^{1/2} \right\}.$$

For two closely linked loci in chromosomes which form only bivalents

$$f_1 = 1 - 2y, f_3 = 2y,$$

$$f_2 = f_4 = f_5 = f_6 = f_7 = f_8 = f_9 = f_{10} = f_{11} = 0.$$

In this case, we have approximately, when n is large,

$$C_n = -\exp(-ny)$$

$$D_n = y \exp(-ny)$$

so that

$$p_n(AB) = p(AB) + g(0) [1 - \exp(-ny)] + y h(0) \exp(-ny).$$

It follows that the equilibrium frequencies are the products of the equilibrium frequencies for the separate loci, i.e., at equilibrium, the factors are associated at random. For example,

$$\lim_{n \rightarrow \infty} p_n(AB/AB) = [9/(2 + \alpha)(2 + \alpha')] [\alpha p(A) + 2(1 - \alpha)p(A)^2/3]$$

$$\times [\alpha' p(B) + 2(1 - \alpha')p(B)^2/3]$$

$$\lim_{n \rightarrow \infty} p_n(AB/Ab) = [9/(2 + \alpha)(2 + \alpha')] [\alpha p(A) + 2(1 - \alpha)p(A)^2/3]$$

$$\times [4(1 - \alpha')p(B)p(b)/3]$$

and so on, where $\alpha = f_2 + f_4 + f_8 + f_{10}$ and $\alpha' = f_2 + f_5 + f_7 + f_{10}$, are the frequencies of double reduction at the first and second loci respectively.

LINKAGE WITH HEXASOMIC INHERITANCE

An analysis similar to that of the preceding section may be carried out for hexasomic inheritance. There are sixty hexasomic genotypes digenic at both of two linked loci and these may be classified into twelve genera (FISHER 1947, p. 69). The inheritance is characterized by forty modes of gamete formation. The enumeration which will be adopted for these is the same as I have used elsewhere (BENNETT 1953).

TABLE 3

Frequencies of gene-combinations in gametic output of hexaploids.

| Typical parental genotype | Number of genotypes in genus | Frequencies of gene-combinations in the gametic output | | | | ÷ |
|---------------------------|------------------------------|--|---------|---------|--------|----|
| | | AB | Ab | ab | aB | |
| AB/ab/ab/ab/ab/ab | 4 | 1 - y | y | 5 - y | y | 6 |
| Ab/aB/ab/ab/ab/ab | 4 | y | 5 - y | 20 + y | 5 - y | 30 |
| AB/Ab/ab/ab/ab/ab | 4 + 4 | 5 - 4y | 5 + 4y | 20 - 4y | 4y | 30 |
| Ab/Ab/aB/ab/ab/ab | 4 + 4 | 2y | 10 - 2y | 15 + 2y | 5 - 2y | 30 |
| AB/Ab/Ab/ab/ab/ab | 4 + 4 | 5 - 3y | 10 + 3y | 15 - 3y | 3y | 30 |
| AB/AB/ab/ab/ab/ab | 4 | 5 - 4y | 4y | 10 - 4y | 4y | 15 |
| AB/Ab/aB/ab/ab/ab | 4 | 5 - 2y | 5 + 2y | 15 - 2y | 5 + 2y | 30 |
| Ab/Ab/aB/aB/ab/ab | 4 | 2y | 5 - 2y | 5 + 2y | 5 - 2y | 15 |
| AB/AB/Ab/ab/ab/ab | 4 + 4 | 10 - 6y | 5 + 6y | 15 - 6y | 6y | 30 |
| AB/Ab/Ab/aB/ab/ab | 2 + 2 | 1 | 2 | 2 | 1 | 6 |
| AB/AB/AB/ab/ab/ab | 2 | 5 - 3y | 3y | 5 - 3y | 3y | 10 |
| AB/AB/Ab/aB/ab/ab | 2 | 10 - 3y | 5 + 3y | 10 - 3y | 5 + 3y | 30 |

As before, we suppose that there are two alleles available at both loci. These will be denoted by A, a and B, b . Using y for the recombination fraction between the loci, the frequencies of the various gene-combinations in the gametic output are shown in table 3 for one representative genotype from each of the twelve genera. Comparing this with table 2, we see that corresponding with the unique neutral tetrasomic genotype, namely biduplex neutral, there are four neutral hexasomic genotypes. These are all duplo-triplex and comprise a conjugate pair of isomorphic sets, each of two genotypes. From table 3, in a parallel manner to that outlined previously for tetrasomic inheritance, we can arrive at the following relation which is analogous to (10).

$$\begin{aligned}
 p_{n+1}(AB) = & p_n(AB) + (y/15) [9p_n(Ab)p_n(aB) - 9p_n(AB)p_n(ab) \\
 & + 2p_n(Ab/Ab/aB) - 2p_n(AB/ab/ab) \\
 & + 2p_n(Ab/aB/aB) - 2p_n(AB/AB/ab) \\
 & + p_n(AB/Ab/aB) - p_n(AB/aB/ab) \\
 & + p_n(Ab/aB/ab) - p_n(AB/Ab/ab)]. \quad (17)
 \end{aligned}$$

From the gametic matrices for digenic hexasomic genotypes with two linked loci (BENNETT 1953) it can be shown that

$$\begin{aligned}
 y[2p_n(Ab/Ab/aB) - 2p_n(AB/ab/ab) + 2p_n(Ab/aB/aB) - 2p_n(AB/AB/ab) \\
 + p_n(AB/Ab/aB) - p_n(AB/aB/ab) + p_n(Ab/aB/ab) - p_n(AB/Ab/ab)] \\
 = 15(\gamma' + \delta') [p_n(AB) - p_{n-1}(AB)] \quad (18)
 \end{aligned}$$

where $\gamma' = 3y/5$ and

$$\begin{aligned}
 15(\gamma' + \delta') = & 6f_1 + 4f_2 + 4f_3 + 2f_4 + 2f_5 + 2f_6 + 2f_7 + f_9 - f_{10} \\
 & - 2f_{11} - 2f_{14} - f_{16} - 4f_{17} - f_{18} - 2f_{19} - 3f_{20} \\
 & + 3f_{21} + 3f_{22} + 2f_{23} + 2f_{24} + f_{25} + f_{26} + f_{27} + f_{28} \\
 & - f_{33} - f_{34} - 2f_{35} - 2f_{36} - 3f_{37} - 3f_{38} - 2f_{39} - 2f_{40}. \quad (19)
 \end{aligned}$$

Equation (18) is the analogue of (12). It follows that

$$\begin{aligned}
 p_{n+1}(AB) = & p_n(AB) + (\gamma' + \delta') [p_n(AB) - p_{n-1}(AB)] \\
 & + \gamma' [p(A)p(B) - p_n(AB)] \quad (20)
 \end{aligned}$$

This is of the same form as equation (13). Hence the analysis for two loci showing hexasomic inheritance may be derived from that given earlier in this paper for two tetrasomic loci on replacing γ and δ by γ' and δ' respectively. In particular, it follows that at equilibrium, two hexasomic factors are associated at random, the frequencies being the products of the equilibrium frequencies for the separate loci.

SUMMARY

Random mating with linked factors is considered in a population of organisms which exhibit tetrasomic or hexasomic inheritance.

Tables are presented giving gene-combination frequencies in the gametic

output in terms of the recombination fraction for a pair of linked loci. Recurrence relations are established for these frequencies and solved quite generally.

It is shown that at equilibrium, linked factors are associated at random.

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