SOME EQUILIBRIUM CONDITIONS FOR GENETIC POPULATIONS

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INTRODUCTION

The first and foremost important concept of population genetics which goes as the most important landmark in the subject is genetic equilibrium. By 'equilibrium' we mean that there is no change in genetic constituents in a population from generation to generation. But this does not help one to characterize genetic populations which are in equilibrium. To deal with the case in more details we shall draw distinctions between three types of equilibriums.

Definition 1 : A population is said to be in *genic equilibrium* if there is no change of gene frequencies from generation to generation.

Definition 2 : A population is said to be in *genotypic equilibrium* if there is no change in genotypic proportions from generation to generation.

It is obvious that a population which is under genotypic equilibrium must be also under genic equilibrium. But the other way implication is not valid in general.

Definition 3 : A population is said to be in *phenotypic equilibrium* if there is no change in phenotypic proportions from generation to generation.

It is to be noted that these concepts are defined with reference to one or more genetic character. When the alleles concerned are codominant in nature, genotypic and phenotypic equilibriums are equilivanent.

In the following sections we shall study some implications of these three definitions.

2. GENIC EQUILIBRIUM

Let us consider the case with two alleles (A and a) at an autosomal locus where the different mating types frequencies in the population are given by table 1. Thus, for example, u_{11} represents the frequency of $Aa \times Aa$ mating and so on. Now, in the absence of selection in the form of differential fertility and mortality, the propor-

TABLE 1

Mating frequencies with autosomal genes

Mates	*AA*	*Aa*	*aa*	*Total*
AA	u_{22}	u_{21}	u_{20}	D
Aa	u_{21}	u_{11}	u_{10}	*H*
aa	u_{20}	u_{10}	u_{00}	*R*
Totals	*D*	*H*	*R*	1

tion of three genotypes among the offspring of the above population of couples is seen to be :

$$D' = u_{22} + u_{21} + \tfrac{1}{4}\, u_{11}$$

$$H' = u_{21} + 2u_{20} + u_{10} + \tfrac{1}{2}\, u_{11} \qquad \ldots(1)$$

and

$$R' = u_{10} + u_{00} + \tfrac{1}{4}\, u_{11}$$

The *A*, *a*-gene frequencies in the population of parents, obtained by gene counting from table 1, can be easily seen to be identical with the gene frequencies in the offspring population, obtained from the expressions (1), again by the same gene-count method. We thus have the following :

Proposition 1 : In the absence of mutation, migration and selection, under all systems of mating the gene frequencies remain constant from generation to the next.

Apparently, this was the contention of J.B.S. Haldane, who called it as "Gene Pool Theorem". Therefore, to characterize any mating system, it is not sufficient to consider genic equilibrium. A more general working out of 'gene pool theorem' is given in Adikari, Chakraborty and Sarma (1971).

3. Genotypic Equilibrium

Genetic equilibrium is usually understood in this sense only. One particular such equilibrium condition under random mating (a mating system in the case of bisexual organisms where any one individual of one sex is equally likely to mate with any individual of the opposite sex) is known as Hardy-Weinberg's (or Hardy-Weinberg-Castle's) law. A more general result is known in the two allelic case which can be stated as follows :

Proposition 2 (Li, 1955). A population will be in equilibrium (genotypic) with respect to an autosomal locus with two alleles A and a, if and only if the $Aa \times Aa$ matings are twice as frequent as those between the two different homozygotes ($AA \times aa$ and $aa \times AA$).

This is immediate if one equates $D=D'$, $H=H'$ and $R=R'$ [from expressions of (1)].

Analogous conditions can also be studied in the case of sex-linked characters. As usual, one may take the homogametic XX individuals as females and the heterogametic XY as males, where X denotes the sex-chromosome. Then, with respect to a X-linked locus with two alleles A and a, in case of females we have genotypes AA, Aa and aa whereas the males can be of genotype A or a. With this the mating types and their proportions can be represented by Table 2.

TABLE 2

Mating frequencies with sex-linked genes

Females	*Males*		*Total*
	A	*a*	
AA	u_{21}	u_{20}	Q_2
Aa	u_{11}	u_{10}	Q_1
aa	u_{01}	u_{00}	Q_0
Total	P_1	P_0	1

With this, it is easy to see that the zygotic proportions of the females in the next generation are given by

$$Q_2'=u_{21}+\frac{u_{11}}{2}$$

$$Q_1'=u_{20}+\frac{u_{11}}{2}+\frac{u_{10}}{2}+u_{01}$$

$$Q_0'=\frac{u_{10}}{2}+u_{00}$$

which in turn give the necessary and sufficient conditions for genotypic equilibrium as $u_{11}=2u_{20}$ and $u_{10}=2u_{01}$. It can be verified that these conditions also imply that the genotypic proportions are kept constant in the next generation in male population. Thus we have :

Proposition 3 : A population will be in genotypic equilibrium with respect to a X-linked locus with two alleles A and a if and only if frequency of $Aa \times A$ mating $=2\times$ frequency of $AA \times a$ mating and frequency of $Aa \times a$ mating $=2\times$ frequency of $aa \times A$ mating.

Similar results can also be obtained with more than two alleles at a locus. But as the number of alleles increases, the number of conditions also increases enormously. With three alleles A_1, A_2, A_3 at an autosomal locus, it may be seen that there are as many as six equations which together form a set of necessary and sufficient conditions for genotypic equilibrium. The mating frequencies in such a situation can be designated by Table 3.

TABLE 3

Mating frequencies with 3 alleles at an autosomal locus

Mates	A_1A_1	A_1A_2	A_1A_3	A_2A_2	A_2A_3	A_3A_3	*Total*
A_1A_1	u_{11}	u_{12}	u_{13}	u_{14}	u_{15}	u_{16}	U_1
A_1A_2	u_{12}	u_{22}	u_{23}	u_{24}	u_{25}	u_{26}	U_2
A_1A_3	u_{13}	u_{23}	u_{33}	u_{34}	u_{35}	u_{36}	U_3
A_2A_2	u_{14}	u_{24}	u_{34}	u_{44}	u_{45}	u_{46}	U_4
A_2A_3	u_{15}	u_{25}	u_{35}	u_{45}	u_{55}	u_{65}	U_5
A_3A_3	u_{16}	u_{26}	u_{36}	u_{46}	u_{65}	u_{56}	U_6
Total	U_1	U_2	U_3	U_4	U_5	U_6	1

From this, one easily gets the necessary and sufficient conditions for genotypic equilibrium as

$$
\begin{aligned}
u_{22}&=4u_{14},\ u_{23}=2u_{15}\\
u_{55}&=4u_{46},\ u_{25}=2u_{34}\\
u_{33}&=4u_{16},\ u_{35}=2u_{26}
\end{aligned} \quad \ldots(2)
$$

For a sex-linked locus with three alleles the number of conditions is even more. One can easily see that in such a case there are as many as eight equations which form a set of necessary and sufficient conditions.

The proposition 2 can easily be generalized to obtain a set of necessary and sufficient conditions for k alleles $(k-2)$ at an autosomal locus. In such a case we have $k(k-1)/2$ number of equations of the form

$$\text{Freq. of } A_iA_j \times A_iA_j \text{ matings} = 4\,(\text{Freq. of } A_iA_i \times A_jA_j \text{ matings})$$

$$\text{for all } i\,j\ ;\ i, j = 1, 2, \ldots, k. \quad \ldots(3)$$

and $k(k-1)\,(k-2)/2$ equations of the form

Freq. of $A_iA_j \times A_iA_\lambda$ matings$=2$ (Freq. of $A_iA_i \times A_jA_\lambda$ matings) for all i, j, $\lambda=1, 2, \ldots, k$ such that $j\ \lambda$ and $i=j=\lambda$.

Note that total number of equations in such a set is $k(k-1)^2/2$. Thus putting $k=3$, we have 6 equations, for four allelic case one has 18 equations and so on.

It may be seen, in particular for three allelic case, that although there are in all 21 proportions u_{ij}'s, the number of equations they have to satisfy for genotypic equilibrium is only 6, and that these equations involve only 12 of the u_{ij}'s. Since that leaves a great deal of freedom of choice of the values of the u_{ij}'s, it is obvious that genotypic equilibrium may be obtained under a variety of mating systems. It can be verified, in particular, that mating proportions calculated on the basis of the random mating model (Li, 1967) as well as Wright's model (Wright, 1949) satisfy equations (2) or (3). Incidentally, these are the two models which received major attention in the studies of equilibrium-population since the general class of equilibrium population is very wide.

4. Phenotypic Equilibrium

As is already mentioned, phenotypic equilibrium differs from genotypic equilibrium only when the alleles concerned have dominance relationship between them. We shall study this type of equilibrium only with respect to a specific character (*i.e. ABO* blood group) to illustrate that even otherwise phenotypic and genotypic equilibriums are always equivalent.

Considering the well known three allelic theory of *ABO* blood groups we know that there are three alleles *A*, *B* and *O* forming six genotypes *AA*, *BB*, *OO*, *AB*, *OA* and *OB*. Since both of *A* and *B* alleles are dominant over *O*-allele, there are only four phenotypes *O*, *A*, *B* and *AB*. If we denote by symbols f_{OO} , f_{OA} , f_A ...the proportions of individuals in the population of parents with the genotypes and phenotypes *OO*,*OA*, *A*, . , . ; and by f'_{OO} f'_{OA}, f'_A ,... the corresponding proportions in the population of children, phenotypic equilibrium would mean the following equalities:

$$f'_{OO}=f_{OO}\,, f'_{AB}=f_{AB}\,, f'_A=f_A=f_{OA}+f_{AA}$$

and $$f'_B=f_B=f_{OB}+f_{BB}.$$

The last two equations would convey the impression that the genotype frequencies f_{OA}, f_{AA} , f_{OB} and f_{BB} are free to have different values, only under the restriction shown in the equations, *viz*., that their sums giving phenotype frequencies remain constant. Now, it has already been seen that the gene frequencies (p, q, r of A, B and O respectively) remain constant from one generation to another in the absence of selection, under any arbitrary mating system. It follows that the genotype frequencies of the population of parents must also satisfy the two equations

$$2f_{OO}+f_{OA}+f_{OB}=2r$$

$$f_{OA}+2f_{AA}+f_{AB}=2p$$

and the dependent equation

$$f_{OB}+2f_{BB}+f_{AB}=2q,$$

where p, q and r may be treated as fixed constants. There are thus 4 independent equations which uniquely determine f_{OA}, f_{AA}, f_{OB} and f_{BB}, and these can be written down as simple linear functions of p, q, r and the phenotype frequencies of the offspring population. In other words, we have

Proposition 4 : In the absence of selection, mutation and migration a mating system which leads to phenotypic equilibrium automatically leads to genotypic equilibrium, the reverse implication being always obviously true.

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