GENOTYPIC FREQUENCIES AT EQUILIBRIUM FOR A MULTILOCUS GAMETOPHYTIC INCOMPATIBILITY SYSTEM

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SUMMARY

Equations for the genotypic frequencies at equilibrium in two- and k -locus incompatibility systems are given on the basis of an equal fertility of all genotypes. The number of alleles may be different at each locus. The results are compared with those of Charlesworth (1979), who used another approach with unequal fertility.

1. INTRODUCTION

IN plants gametophytic incompatibility systems are established in many families. In grasses two loci S and Z act together (Lundqvist, 1956; Hayman, 1956; Lundqvist, 1961; Weimarck, 1968). Under natural conditions the pollen is incompatible with every genotype that can produce gametes with the same alleles as the pollen at both loci. Therefore selfing is excluded, and the progenies consist only of genotypes like $S_{ii}Z_{kl}$ and $S_{ij}Z_{kk}$ (single heterozygotes) or $S_{ij}Z_{kl}$ (double heterozygotes). Homozygous genotypes $S_{ii}Z_{kk}$ do not exist. At equilibrium all alleles at one locus have the same frequency.

Lundqvist (1962) tried to estimate the genotypic frequencies at equilibrium, if there are n_1 alleles at locus S and n_2 alleles at locus Z . Charlesworth (1979) reexamined this problem and gave quite different formulae. She stated that for her approach a general solution was only possible for $n_1 = n_2 = n$. Charlesworth calculated the frequency of a genotype $S_{ii}Z_{kl}$ (and since $n_1 = n_2 = n$, the same frequency is given for $S_{ij}Z_{kk}$) in the next generation as the sum of all probabilities that a pollen of type S_iZ_k meets a gamete S_iZ_l at a compatible genotype, plus the sum of all probabilities, that a pollen of type S_iZ_l meets a gamete S_iZ_k at a compatible genotype.

With this approach the probability that a genotype is able to generate a gamete S_iZ_l and is incompatible to the pollen type S_iZ_k is larger for the double heterozygotes than for the single heterozygotes. However pollen usually is produced to such an excess, that no difference in fertility between single and double heterozygotes should be expected.

Therefore in this paper another approach is used, which assumes an equal number of progenies for single and double heterozygotes. Then a general solution for arbitrary allele numbers n_1 and n_2 can be given. The approach can be extended to more than two loci.

2. GENOTYPIC FREQUENCIES AT EQUILIBRIUM FOR TWO LOCI

To calculate the genotypic frequencies three classes have to be distinguished:

class $X_1(S_{ii}Z_{kl})$ with frequency x_1 at equilibrium,

class $X_2(S_{ij}Z_{kk})$ with frequency x_2 at equilibrium and

class $X_3(S_{ij}Z_{kl})$ with frequency x_3 at equilibrium.

$r_1 = n_1n_2(n_2-1)/2$, $r_2 = n_1n_2(n_1-1)/2$ and $r_3 = n_1n_2(n_1-1)(n_2-1)/4$ are the numbers of different genotypes in each class. At equilibrium the frequency of each allele at locus S is $1/n_1$ and at locus Z is $1/n_2$. This is also true within the three classes X_1 , X_2 and X_3 . A genotype of class X_1 produces progenies in the relation $(n_2-2)X_1:(n_1-1)X_2:(n_1-1)(n_2-1)X_3$. Similarly the progenies of a genotype from class X_2 are formed by $(n_2-1)X_1:(n_1-2)X_2:(n_1-1)(n_2-1)X_3$ and progenies of a genotype from class X_3 by $(n_2-2)X_1:(n_1-2)X_2:(n_1n_2-n_1-n_2)X_3$. Now the genotypic frequencies at equilibrium can be found using the generation matrix G , which contains the relative frequencies of the progenies in the different classes:

$$G = \begin{bmatrix} \frac{n_2-2}{n_1n_2-2} & \frac{n_2-1}{n_1n_2-2} & \frac{n_2-2}{n_1n_2-4} \\ \frac{n_1-1}{n_1n_2-2} & \frac{n_1-2}{n_1n_2-2} & \frac{n_1-2}{n_1n_2-4} \\ \frac{(n_1-1)(n_2-1)}{n_1n_2-2} & \frac{(n_1-1)(n_2-1)}{n_1n_2-2} & \frac{n_1n_2-n_1-n_2}{n_1n_2-4} \end{bmatrix}$$

At equilibrium $Gx = x$ with

$$x = \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix}.$$

Only two of the equations are independent. But a third independent equation is given by $x_1 + x_2 + x_3 = 1$. The solution is:

$$x_1 = (n_1n_2 - n_1 - 2)(n_1n_2 - 2)(n_2 - 1)/Z,$$

$$x_2 = (n_1n_2 - n_2 - 2)(n_1n_2 - 2)(n_1 - 1)/Z,$$

$$x_3 = 1 - x_1 - x_2 = (n_1n_2 - 1)(n_1n_2 - 4)(n_1 - 1)(n_2 - 1)/Z$$

and

$$Z = (n_1n_2 - 2)(n_1^2n_2 + n_1n_2^2 - 4n_1n_2 - n_1 - n_2 + 4) \\ + (n_1 - 1)(n_2 - 1)(n_1n_2 - 1)(n_1n_2 - 4).$$

In case of $n_1 = n_2 = n$ (the case considered by Charlesworth) the formulae are reduced to:

$$x_1 = x_2 = (n^2 - 2)/Z,$$

$$x_3 = (n + 2)(n - 1)^2/Z$$

and

$$Z = 2(n^2 - 2) + (n - 1)^2(n + 2).$$

Table 1 contains the frequencies of the three classes at equilibrium. For comparison, the values of Charlesworth are also given for $n_1 = n_2 = n$. Though the deviations are small, they are not due to rounding errors, as is shown in the discussion. The case of $n_1 = n_2 = 2$ is a special case, when double heterozygotes cannot produce progeny (see England, 1974).

3. MORE THAN TWO LOCI

In the case of more than two loci the number of equations is increasing. The calculations can be done in a similar way to that described for two loci. In the case of different allele numbers at the loci, the number of classes and therefore the number of equations is $2^k - 1$. If $n_1 = n_2 = \dots = n_k = n > 2$, k new classes can be formed, since in this case it is not necessary to distinguish between different types of single heterozygotes or double heterozygotes. The case of $n = 2$ at all loci must be excluded, since in this case no seed is set on genotypes heterozygous at all loci. England (1974) gave a general solution for this situation.

First the case of three loci is considered. X_{001} will denote the class of genotypes heterozygous at the third locus only, X_{010} is the class of genotypes heterozygous only at the second locus, X_{111} at all three loci, and so on. x_{001} , x_{010} , x_{111} and so on are the frequencies of the corresponding classes at equilibrium. The equations for x_{001} , x_{011} and x_{111} are given by

$$\begin{aligned} x_{001} &= \frac{(n_3 - 2)x_{001} + (n_3 - 1)(x_{010} + x_{100})}{n_1 n_2 n_3 - 2} + \frac{(n_3 - 2)(x_{011} x_{101}) + (n_3 - 1)x_{110}}{n_1 n_2 n_3 - 4} \\ &\quad + \frac{(n_3 - 2)x_{111}}{n_1 n_2 n_3 - 8} \\ x_{011} &= \frac{(n_2 - 1)(n_3 - 1)(x_{001} + x_{010} + x_{100})}{n_1 n_2 n_3 - 2} \\ &\quad + \frac{(n_2 n_3 - n_2 - n_3)x_{011} + (n_2 - 1)(n_3 - 1)(x_{101} + x_{110})}{n_1 n_2 n_3 - 4} \\ &\quad + \frac{(n_2 n_3 - n_2 - n_3)x_{111}}{n_1 n_2 n_3 - 8} \\ x_{111} &= \frac{(n_1 - 1)(n_2 - 1)(n_3 - 1)(x_{001} + x_{010} + x_{100})}{n_1 n_2 n_3 - 2} \\ &\quad + \frac{(n_1 - 1)(n_2 - 1)(n_3 - 1)(x_{011} + x_{101} + x_{110})}{n_1 n_2 n_3 - 4} \\ &\quad + \frac{((n_1 - 1)(n_2 - 1)(n_3 - 1) - 1)x_{111}}{n_1 n_2 n_3 - 8}. \end{aligned}$$

In a similar way the equations for x_{010} , x_{100} , x_{101} and x_{110} are constructed. Only six equations are independent. The last equation must be replaced by

$$x_{001} + x_{010} + x_{100} + x_{011} + x_{101} + x_{110} + x_{111} = 1.$$

TABLE 1

Frequency of genotypic classes (x_1, x_2, x_3) and number of genotypes in each class (r_1, r_2, r_3) for two loci with n_1 and n_2 alleles at equilibrium

n_1	n_2	x_1	Single heterozygotes			$x_1 + x_2$	Double heterozygotes		Charlesworth (1979)	
			r_1	x_2	r_2		x_3	r_3	single/double	heterozygotes
2	2	0.2500	2	0.2500	2	0.5000	0.5000	1	0.500	0.500
2	3	0.4000	6	0.1000	3	0.5000	0.5000	3	—	—
2	4	0.4286	12	0.0714	4	0.5000	0.5000	6	—	—
3	3	0.2059	9	0.2059	9	0.4118	0.5882	9	0.414	0.586
3	4	0.2448	18	0.1399	12	0.3846	0.6154	18	—	—
4	4	0.1707	24	0.1707	24	0.3415	0.6585	36	0.342	0.657
5	5	0.1456	50	0.1456	50	0.2911	0.7089	100	0.292	0.708
6	6	0.1269	90	0.1269	90	0.2537	0.7463	225	0.254	0.747
8	8	0.1010	224	0.1010	224	0.2020	0.7981	784	0.202	0.798
10	10	0.0839	450	0.0839	450	0.1678	0.8322	2025	0.168	0.833

In case of $n_1 = n_2 = n_3$ the number of different equations is reduced to three.

For k loci only the case of $n_1 = n_2 = \dots = n_k = n > 2$ is considered in more detail. The frequency of a genotype from class $X_{k-m,m}$, heterozygous at m loci and homozygous at $(k-m)$ loci is denoted by $x_{k-m,m}$. At equilibrium this frequency is

$$x_{k-m,m} = \binom{k}{m} \sum_{l=1}^k \frac{\binom{k}{l} (n-1)^m - \binom{k-m}{l-m}}{(n^k - 2^l) \binom{k}{l}} x_{k-l,l}.$$

$\binom{k-m}{l-m}$ is zero for $l < m$. Table 2 contains the genotypic frequencies for two, three and four loci and 5, 10, 15 and 20 alleles at each locus.

4. DISCUSSION

Under natural conditions no genotypes exist that are homozygous at all incompatibility loci, since pollen grains are not compatible if they carry only alleles also present on the female. Charlesworth (1979) calculated the

TABLE 2

Frequency of genotypic classes for n alleles at each locus at equilibrium

No. of loci	Genotypic class	Frequency at equilibrium			
		$n = 5$	$n = 10$	$n = 15$	$n = 20$
2	ho.het = $X_{1,1}$	0.2911	0.1678	0.1181	0.0911
	het.het = $X_{0,2}$	0.7089	0.8322	0.8819	0.9089
3	ho.ho.het = $X_{2,1}$	0.0801	0.0245	0.0116	0.0068
	ho.het.het = $X_{1,2}$	0.3865	0.2422	0.1738	0.1352
	het.het.het = $X_{0,3}$	0.5333	0.7333	0.8145	0.8581
4	ho.ho.ho.het = $X_{3,1}$	0.0208	0.0032	0.0010	0.0005
	ho.ho.het.het = $X_{2,2}$	0.1499	0.0482	0.0231	0.0135
	ho.het.het.het = $X_{1,3}$	0.4133	0.2917	0.2168	0.1715
	het.het.het.het = $X_{0,4}$	0.4160	0.6569	0.7590	0.8146

probability at equilibrium, that a genotype is compatible with a certain pollen type. Since the double heterozygotes are incompatible with four and the single heterozygotes only with two pollen types, her approach is based on the assumption that the stronger selection between pollen types by the double heterozygotes results in a reduced seed set. The percentage of reduction depends on the number of alleles.

Observations on the pollen tube growth in rye indicate that pollen is in excess and several pollen tubes can start to grow. Therefore it seems an unjustified assumption that the seed set of the double heterozygotes is reduced. If the fertility of all types is equal, a general solution can be given for arbitrary numbers n_1 and n_2 of alleles, as was shown in this paper.

In case of $n_1 = n_2 = n$, the deviations from the result of Charlesworth (1979) are small and practically disappear, provided n is large. For large n the differences in fertility are small in the approach of Charlesworth.

In the general case of k loci, the number of equations increases rapidly as k exceeds 2. In the literature, few species with more than two incompatibility loci are known. Till now the highest number of loci has been found in *Beta vulgaris*. Experimental results led to the assumption (Larsen, 1977), that at least four incompatibility loci are involved. Further loci, which are homozygous in his material, cannot be excluded.

The expected genotypic frequency at equilibrium must be known, if the number of alleles at the incompatibility loci is to be estimated experimentally. Experimental results on this topic for rye will be given by us in a future paper.

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