SHORT PAPER

Fitting of a binomial distribution to the number of chiasmata per bivalent

Yasuo UKAI

*National Institute of Agro-Environmental Sciences,
Tsukuba, Ibaraki 305*

(Received December 7, 1987)

ABSTRACT

Statistical tests on the distribution of the number of chiasmata per chromosome, collected from literatures, showed that they can be approximated by binomial distributions with one obligatory chiasma, i.e., $B(N-1, p)$. N is proportional to the average number of chiasmata, while p is nearly constant for the species tested.

1. INTRODUCTION

In spite of the very early finding by Haldane (1931) and subsequent general support (Sybenga, 1975) that occurrence of chiasmata on a particular chromosome pair is not random, Poisson distributions have often been adopted for the number of chiasmata among different chromosomes, and applied to theoretical consideration of mapping function (Owen, 1950), linkage block (Hanson, 1959a) and average recombination frequency (Franklin, 1970). The present study was undertaken with a view to obtaining regularity, if any, involved in the distribution of the number of chiasmata.

2. SOURCE OF DATA

Table 1 shows 14 data (No. 1–14) on the distribution for the number of chiasmata, collected from seven different reports. All but one (No. 3, mosquito) are from plants. No. 1, 11 and 12 are based on a single chromosome, viz. a large median chromosome (called *M*) of *Vicia faba*, a median and a submedian chromosome of *Fritillaria*, respectively. The remaining data are those pooled over two or more chromosomes of similar length and centromere position. No. 14 represents data pooled over five varieties, among which no significant difference was observed. Data on chromosomes of interspecific hybrid plant, and on chromosomes treated with an agent, such as colchicine, were not chosen. No. 16 is data from an abnormal rye plant, which has breakdown of processes governing the distribution

Table 1. *Data of the distributions for the number of chiasmata per chromosome*

No.	Species	Number of chiasmata per chromosome											
		0	1	2	3	4	5	6	7	8	9	10	11 12
1	<i>Vicia faba</i> (M chr.)				1	3	7	13	33	39	41	28	8
2	<i>Vicia faba</i> (S chr.)		2	21	104	106	42	6					
3	<i>Theobaldia longiareolata</i>		5	53	69	36	7						
4	<i>Lilium longiflorum</i>	7	158	302	115	17							
5	<i>Lilium pyrenaicum</i>		1	23	47	37	8	3	1				
6	<i>Lilium regale</i> (plant 1)		4	21	54	38	12	1	1	1			
7	<i>Lilium regale</i> (plant 2)		10	45	62	12	3						
8	<i>Lilium Henryi</i>		1	15	23	16	5						
9	<i>Lilium japonicum</i>		2	20	27	10	1						
10	<i>Lilium speciosum</i>		26	83	81	38							
11	<i>Fritillaria chitralensis</i> (1M)		3	4	3	16	14	5	4	1			
12	<i>Fritillaria chitralensis</i> (1SM)			2	1	6	16	16	7	2			
13	<i>Fritillaria chitralensis</i> (10ST)		1	10	48	68	69	36	12	6			
14	<i>Secale cereale</i> , 5 varieties		76	586	38								
15	<i>Secale</i> interspecific cross (N)	5	92	247	6								
16	<i>Secale</i> interspecific cross (A)	92	125	93	33	7							

Reference: No. 1 and 2, Maeda, 1980; No. 3, Callan and Montalenti, 1947; No. 4, Fogwill, 1958; No. 5, 6, 7, 8 and 9, Mather, 1935; No. 10, Shepard et al., 1974; No. 11, 12 and 13, Bennett, 1938; No. 14, Sax, 1934; No. 15 and 16, Jones, 1967.

of chiasmata in normal genotypes (Jones, 1957). Chiasma occurs at random in this plant, and the number of chiasmata per chromosome follows a Poisson distribution. No. 15 is its normal counterpart. These 15 and 16 were added for comparison of mean and variance relationship with the other data. In No. 4 and 15 about 1 percent of chromosomes lacks chiasmata, while none of the chromosomes lacks chiasma in all the other data. No. 15 derived from an interspecific cross, and hence the presence of chromosomes without chiasma may be due to structural hybridity between a part of homologous chromosomes. The reason for the existence of chromosomes lacking chiasma in No. 4 is not clear.

3. RESULTS AND DISCUSSION

The mean and variance of the number of chiasmata per chromosome were calculated (Table 2). The mean ranges from 1.94 (No. 14) to 8.30 (No. 1), and the variance from 0.160 (No. 14) to 3.093 (No. 1). The variance is much lower than the mean in all cases, in agreement with the early finding by Haldane (1931) using Maeda's (1930) data. The abnormal rye plant No. 16 possesses the variance nearly equal to the mean, showing a characteristic to a Poisson distribution, while its normal counterpart No. 15 shows the variance much lower than the mean. Plotting the variance against the mean (Fig. 1) revealed that, except for No. 11

Table 2. *Mean and variance of the number of chiasmata and the estimated $N-1$ and p of a binomial distribution $B(N-1, p)$ with one obligatory chiasma*

No.	Mean	Variance	$N-1 \pm \text{S.E.}$	$p \pm \text{S.E.}$
1	8.30	3.093	$13 \pm .05$	$.562 \pm .010$
2	3.65	0.849	$4 \pm .01$	$.663 \pm .014$
3	2.92	0.938	$3 \pm .01$	$.641 \pm .021$
4	1.96	0.616	$3 \pm .01$	$.324 \pm .011$
5	3.34	1.050	$4 \pm .02$	$.585 \pm .022$
6	3.34	1.204	$5 \pm .04$	$.468 \pm .019$
7	2.64	0.704	$3 \pm .02$	$.548 \pm .025$
8	3.15	0.909	$4 \pm .05$	$.538 \pm .032$
9	2.80	0.671	$3 \pm .04$	$.600 \pm .037$
10	2.57	0.809	$3 \pm .01$	$.525 \pm .019$
11	4.40	2.531	$13 \pm .73$	$.261 \pm .017$
12	5.44	1.639	$7 \pm .07$	$.634 \pm .026$
13	4.52	1.793	$7 \pm .02$	$.503 \pm .012$
14	1.94	0.160		
15	1.72	0.263		
16	1.25	1.025		

Probability function $f(x) = {}_{N-1}C_{x-1} p^{x-1} q^{N-x}$ ($x=1, 2, \dots, N$) where x is the number of chiasmata.

Fig. 1. Relationship between the mean and variance of the number of chiasmata per bivalent.

and 16, there is a linear regression of the variance on the mean. The regression line crosses the X-axis of abscissa at a point close to 1. In addition the regression coefficient was much lower than 1. These results suggest that one chiasma is obligatory for each bivalent, and that the frequency of the remaining chiasmata may follow a binomial distribution $B(N-1, p)$, where N is an interger.

$N-1$ and p with their standard errors were estimated by maximum likelihood method (Table 2). In No. 4 the class for no chiasma was combined with the class for 1 chiasma. No. 14 and 15 were excluded from the calculation because the number of classes for 1 or more chiasmata was only 3 for these data, and the degree of freedom after fitting a binomial distribution was reduced to zero. $N-1$ thus estimated was found to be proportional to the average number of chiasmata except for No. 11 (Fig. 2), the regression coefficient being 1.78. On the other hand, p was nearly constant except for No. 4 and 11, ranging from 0.46 to 0.65 (Fig. 3).

Excluding No. 4 and 11 which exhibited exceptional behaviour in relation of $N-1$ and p to mean chiasma, χ^2 value for the goodness of fit of the binomial distribution to the observed data was calculated (Table 3). Prior to calculation, the class with observed or expected frequency less than 2 was combined with the neighbouring class. The χ^2 values showed that the observed frequency well agreed with the expected one except No. 2 for which the deviation was significant at the 5% level. Frequency distribution for the number of chiasmata assuming Poisson distribution $Po(\lambda) = e^{-\lambda} \frac{\lambda^x}{x!}$ with one obligatory chiasma was also obtained by putting λ equal to the mean. The χ^2 values were much larger in Poisson distribution than in binomial one, and the deviation was significant at the 1% level in all cases tested. A truncated binomial distribution, excluding class zero, showed no better fit to the

Fig. 2. Estimated $N-1$ of a binomial distribution $B(N-1, p)$, plotted against the mean number of chiasmata per bivalent.

observed data, as compared with a binomial distribution with one obligatory chiasma.

One thing to be noted here is that a binomial distribution with two parameters (N and p) naturally gives χ^2 values smaller than does a Poissonian with only one parameter. So the sole comparison of χ^2 value between the two distributions does not make sense as to which of the two is a better model for the data. Under this situation Akaike Information Criterion (AIC) can be effectively used (Sakamoto *et al.*, 1983). AIC calculated was clearly lower for the binomial model than for Poissonian model, and the difference was much larger than 1 in all data. This indicates a much better fit of the former distribution than the latter.

Thus, it can be concluded that the frequency of the number of chiasmata per bivalent can be better expressed by a binomial distribution, with one obligatory chiasma in the majority of the observed data. The biological significance of the present result is not clear at present. However, Fox (1973) presented a model of chiasma distributions along chromosome length. According to his model(f), chiasma determination is sequential from telomere to centromere, and a given chiasma interferes with the subsequent chiasma initiation only on its centromeric side with a specified distance, within which chiasma initiation is precluded, and the distance follows a truncated normal distribution. A preliminary study by computer simulation was carried out to examine the distribution of the number of chiasmata

Fig. 3. Estimated p of a binomial distribution, plotted against the mean number of chiasmata per bivalent.

Table 3. χ^2 value and Akaike Information Criterion (AIC) to test goodness of fit of the Binomial and Poisson distributions to the observed data

No.	Poissonian			Binomial		
	d.f.	χ^2	AIC	d.f.	χ^2	AIC
1	7	46.36**	754.7	6	5.42	712.5
2	3	95.04**	818.7	2	8.27*	724.1
3	2	29.37**	439.1	1	4.43	409.5
5	2	25.92**	336.3	1	1.00	312.2
6	3	29.19**	394.4	2	4.72	370.2
7	2	39.23**	349.0	1	3.75	315.3
8	2	8.93**	164.8	1	0.13	157.6
9	2	10.67**	157.7	1	1.65	143.8
10	2	21.21**	608.8	1	1.73	590.2
12	4	20.48**	179.5	3	1.25	160.9
13	4	38.25**	862.3	3	3.62	823.8

The number corresponds to the reference in Table 1. * and ** stand for significance levels at 5 and 1%, respectively.

per chromosome under this model. It was found that interference in the sense of his model can be an important cause, which determines the number of chiasmata per chromosome. A detailed results will be published elsewhere.

I thank Dr. T. Miwa and two referees for comments and suggestions which helped to improve the presentation.

REFERENCES

- BENNETT, E. S. (1938) The origin and behaviour of chiasmata XI. *Fritillaria chitralensis*. *Cytologia* **8**, 443-451.
- CALLAN, H. G. and MONTALENTI, G. (1947) Chiasma interference in mosquitoes. *J. Genet.* **48**, 119-134.
- FOGWILL, M. (1958) Differences in crossing over and chromosome size in the sex cells of *Lilium* and *Fritillaria*. *Chromosoma* **9**, 493-504.
- FOX, D. P. (1973) The control of chiasma distribution in the locust, *Schistocerca gregaria* (Foskal). *Chromosoma* **43**, 289-328.
- FRANKLIN, I. R. (1970) Average recombination frequencies. *Genetics* **66**, 709-711.
- HALDANE, J. B. S. (1931) The cytological basis of genetical interference. *Cytologia* **3**, 54-65.
- HANSON, W. D. (1959a) The theoretical distribution of lengths of parental gene blocks in the gametes of an F_1 individual. *Genetics* **44**, 197-209.
- JONES, G. H. (1967) The control of chiasma distribution in rye. *Chromosoma* **22**, 69-90.
- MAEDA, T. (1930) On the configurations of gemini in the pollen mother cells of *Vicia faba* L. *Memoirs of the College of Science, Kyoto Univ. Series B* **2**, 125-135.
- MATHER, K. (1935) Meiosis in *Lilium*. *Cytologia* **6**, 354-380.
- OWEN, A. R. G. (1950) The theory of genetical recombination. *Advances in Genetics* **3**, 117-157.
- SAKAMOTO, Y., ISIGURO, M. and KITAGAWA, G. (1983) "Jouhouryou Toukeigaku (Information Statistics)". Kyouritu Shuppan, Tokyo.
- SAX, K. (1935) Variation in chiasma frequencies in *Secale*, *Vicia* and *Tradescantia*. *Cytologia* **6**, 289-293.
- SHEPARD, J., BOOTHROYD, E. R. and STERN, H. (1974) The effect of colchicine on synapsis and chiasma formation in microsporocytes of *Lilium*. *Chromosoma* **44**, 423-437.
- SYBENGA, J. (1975) Meiotic configurations. Springer-Verlag, Berlin.