Theoretical and Applied Genetics 45, 197–204 (1974)

The Transmission of Rye B Chromosomes in Natural Pollination

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Summary. This paper examines the transmission of B chromosomes in natural (but controlled) pollination, in order to obtain results which can be applied to natural populations of rye. The frequencies of the female gametes in both 2n = = 14 + 1 and 2n = 14 + 2 rye plants have been estimated with reference to their chromatid constitution. From the results obtained on the offspring, it seems that preferential distribution takes place during female meiosis of 2n = = 14 + 2 plants. It has been demonstrated that pollen carrying B chromosomes formed in plants of 2n = 14 + 2 was more competitive than normal pollen. On the contrary, when it was formed from plants 2n = 14 + 1, B chromosome elimination by pollen was total. This process may be considered as sporophytic determination. The genetic significance of the presence of B chromosomes in natural populations is discussed. It is proposed that B chromosomes may be the cytological expression of a complex evolutionary system which results in conservation of population genetic variability.

Introduction

The cytological behaviour of rye B chromosomes during somatic mitosis, meiosis and pollen mitosis has been extensively studied (Kishikawa, 1965; Müntzing, 1966, 1967). However, in the experiments investigating the transmission of B chromosomes the crosses have been manually made. In this paper the transmission of B chromosomes in natural (but controlled) pollination is examined, in order to obtain results which could be applied to natural populations of rye.

Material and Methods

Secale cereale L. var. Caribou was used. Chromosome counts were made on root-tips pretreated in cold water (0–2 °C) for 24 hours and fixed in Farmer's solution (1 : 3). The root-tips were then hydrolyzed in 1N HCl at 60 °C for 12 minutes and stained with fuchsin.

Fertilization was carried out under natural conditions. Groups of plants with determined chromosome constitutions were isolated, so that open pollination between plants of the same group was allowed but the participation of alien pollen excluded. In these crosses almost complete allogamy can be assumed, as rye is characterized by a strong system of incompatibility (Lundqvist, 1956, 1958). Therefore seeds harvested from each plant are formed by their own egg-cells and pollen from other plants of the same pollination group.

Chromosome counts of the offspring were made. Using previous descriptions of meiosis and pollen mitosis, it was possible to deduce the competitive ability of the pollen carrying different numbers of B chromosomes in natural pollination. In addition, the behaviour on the female side was deduced from the offspring obtained.

Results

Table 1 shows the pollination groups under study. In every case, B chromosomes were of the standard type.

In Table 2 the chromosome controls of the offspring obtained from the crosses involving normal and 1 B chromosome rye plants are reported.

The same type of combination could be found several times in the same or in a different pollination group (see asterisks in Table 2). Therefore, the percentages of every chromosome constitution of the offspring could be recorded as the weighted percentages of the same combinations (Table 3). In the cases where deleted-B or B-isochromosomes were found, they were considered as belonging to the standard type. For example, a plant 2n = 14+2 B standard + 1 B-iso was recorded as 2n = 14 + 3.

a) Combination ♀ 14 + 1 × ♂ 14 (Table 3). The frequencies of the chromosome numbers obtained in the progeny of the crosses ♀ 14 + 1 × ♂ 14 could be attributed to the behaviour of the B chromosome during meiosis and postmeiotic mitosis in the embryo sac; in every case the pollen was normal. On this basis, in the plant 2n = 14 + 1, the B chromosome was cytologically eliminated in 86.61% of the cases, conserved in 1.79%, and underwent non-disjunction and preferential distribution in 11.60%.

b) Combination ♀ 14 × ♂ 14 + 1 (Table 3). Since the plant 2n = 14 + 1 produced pollen with 2, 1 or no B chromosomes, which competed in pollination

Table 1. *Pollination groups under isolation*

(14; 14 + 1)
(14; 14; 14 + 1)
(14; 14 + 1; 14 + 1)

(14; 14 + 2)
(14; 14; 14 + 2)
(14; 14 + 2; 14 + 2)

(14 + 1; 14 + 1; 14 + 1)
(14 + 2; 14 + 2; 14 + 2; 14 + 2; 14 + 2)
(14 + 3; 14 + 3; 14 + 3; 14 + 3; 14 + 3)
(14 + 4; 14 + 4; 14 + 4; 14 + 4; 14 + 4)

with each other (certation), it was not possible to deduce, as in the previous case, the cytological behaviour of the B chromosome present in the male side. A greater tendency for B chromosome conservation on the male side than on the female side was observed.

c) Combinations ♀ 14 × ♂ $\left\{\begin{matrix}14 \text{ or}\\ 14+1\end{matrix}\right.$ and ♀ 14 + 1 × ♂ $\left\{\begin{matrix}14 \text{ or}\\ 14+1\end{matrix}\right.$ (Table 3). In the combination ♀ 14 × ♂ $\left\{\begin{matrix}14 \text{ or}\\ 14+1\end{matrix}\right.$ only plants lacking B chromosomes were harvested from the 2n = 14 parent. So B chromosome elimination by pollen was total. Therefore, it might be assumed that when pollen from 2n = 14 and 2n = 14 + 1 plants is in competition, only normal pollen is fertile; thus, B chromosomes are being transmitted exclusively by the female side. This is further confirmed as the offspring obtained from the combination ♀ 14 + 1 × ♂ 14 (see first row in Table 3) was similar to that from the combination ♀ 14 + 1 × ♂ $\left\{\begin{matrix}14 \text{ or}\\ 14+1\end{matrix}\right.$ (3rd row, Table 3). On the other hand, when the plant 2n = 14 + 1 was not in competition, the pollen carrying B chromosomes was fertile, as shown in the combinations ♀ 14 × ♂ 14 + 1 2nd row Table 3) and ♀ 14 + 1 × ♂ 14 + 1 (5th row Table 3).

In Table 4 the chromosome controls of the offspring obtained from the crosses involving normal rye plants and those with 2 B chromosomes are reported. The same type of combination could be found several times in the same or different pollination groups (see asterisks in Table 4). Therefore, the percentages of every chromosome constitution of the offspring can be recorded as weighted percentages of the same combination (Table 5).

d) Combination ♀ 14 + 2 × ♂ 14 (Table 5). The frequencies obtained in the offspring could be attributed to the cytological behaviour of B chromosomes during female gametogenesis. This assumption agrees with that indicated in the combination ♀ 14 + 1 × × ♂ 14. Since no plants 2n = 14 + 1 were obtained, it can be deduced that gametes carrying 1 B chromosome are not formed in the megasporogenesis

Table 2. *Chromosome controls of the offspring obtained from the crosses involving normal and 1 B-chromosome rye plants*

Parents				Offspring								
Pollination groups		female chromosome number	male chromosome number	Number of seeds		Chromosome constitutions of descendants						
				germinated	controlled	14	14 + 1	14 + 2	14 + 4	$14 + 1_s$ iso	$14 + 1_b$ iso	$14 + 2 + 1_b$ iso
(14), (14 + 1)	*	14	14 + 1	24	24	18 75.00	4 16.67	2 8.33				
	**	14 + 1	14	48	41	37 90.24	1 2.44	3 7.32				
(14), (14), (14 + 1)	***	14	14 or 14 + 1	62	37	37 100.00						
	***	14	14 or 14 + 1	27	14	14 100.00						
	**	14 + 1	14	110	71	60 84.51	1 1.41	10 14.08				
(14), (14 + 1), (14 + 1)	*	14	14 + 1	110	93	74 79.57	7 7.53	7 7.53		1 1.07	4 4.30	
	****	14 + 1	14 or 14 + 1	106	100	81 81.00	2 2.00	16 16.00	1 1.00			
	****	14 + 1	14 or (14 + 1	110	87	73 83.91	3 3.45	11 12.64				
(14 + 1), (14+ 1), (14+ 1)	*****	14 + 1	14 + 1	120	93	64 68.82	2 2.15	20 21.50	3 3.22	2 2.15	1 1.07	1 1.07
	*****	14 + 1	14 + 1	13	13	11 84.62	2 15.38					
	*****	14 + 1	14 + 1	8	8	7 87.50	1 12.50					

of 2n = 14 + 2 plants. This fact will be discussed elsewhere.

e) Pollination groups (14, 14, 14 + 2) and (14, 14 + 2, 14 + 2) (Table 5).

By comparing results obtained in the combination ♀ 14 × ♂ 14 + 2 with ♀ 14 × ♂ $\left\{\begin{array}{l}14 \text{ or}\\ 14+2\end{array}\right.$, it can be deduced that pollen carrying B chromosomes has a competitive advantage over normal pollen. This conclusion agrees with that obtained when comparing ♀ 14 + 2 × ♂ 14 with ♀ 14 + 2 × ♂ $\left\{\begin{array}{l}14 \text{ or}\\ 14+2\end{array}\right.$.

Table 3. *Offspring obtained from the crosses involving normal and 1 B chromosome rye plants. Frequencies are expressed as weighted percentages*

Combinations	Chromosome constitution of descendants				
	14	14 + 1	14 + 2	14 + 3	14 + 4
♀ (14 + 1) × ♂ (14)	86.61	1.79	11.60		
♀ (14) × ♂ (14 + 1)	78.63	13.66	7.69		
♀ (14 + 1) × ♂ (14) or (14 + 1)	82.35	2.67	14.44		0.53
♀ (14) × ♂ (14) or (14 + 1)	100				
♀ (14 + 1) × ♂ (14 + 1)	71.93	7.01	17.54	0.87	2.63

Table 6 shows the chromosome controls of the pollination groups (14 + 1 × ··· × 14 + 1) (14 + 2 × × ··· × 14 + 2) (14 + 3 × ··· × 14 + 3) (14 + 4 × ··· × 14 + 4). The frequencies of every chromosome constitution, expressed as weighted percentages, are classified as elimination, reduction, conservation and augmentation in Table 7. This classification was chosen because it shows more clearly the variation in B chromosome frequency transmission. For example, a plant 14 + 2 obtained from the cross 14 + 1 × 14 + 1 would be classified as augmentation (× 2). On the other hand, a plant 14 + 2 obtained from the cross 14 + 3 × 14 + 3 would be classified as reduction (× 2/3).

In the last column of Table 7 the augmentation totals are shown. In every case an augmentation in frequencies was demonstrated, the maximum increase being shown in the pollination group (14 + 2 × × ··· × 14 + 2). This finding is paradoxical because it is known that a high number of B chromosomes is deleterious to populations.

Discussion

Studies carried out by many authors on rye B chromosomes have identified some characteristics of their genetic and cytological behaviour (see review by Müntzing, 1967). At the cytological level the most interesting is an irregular gametogenesis. This is mainly due to asynapsis or desynapsis, formation of laggards, and non-disjunction and preferential distribution to the generative pole during pollen mitosis. Therefore, plants with a given number of B chromosomes form pollen grains of differing chromosome constitution. Moreover, gametes lacking B chromosomes, or having the same, a lower or higher number of B chromosomes than their own sporophyte, can be formed. (As an example see Table 8.)

Table 5. *Offspring obtained from the crosses involving normal and 2 B chromosome rye plants. Frequencies are expressed as weighted percentages*

Combinations	Chromosome constitution of descendants						
	14	14 + 1	14 + 2	14 + 3	14 + 4	14 + 5	14 + 6
♀ (14 + 2) × ♂ (14)	49.48		46.39	3.30	1.03		
♀ (14) × ♂ (14 + 2)	22.22	22.22	52.78		2.78		
♀ (14 + 2) × ♂ 14 or 14 + 2	25.42	7.62	34.82	5.08	21.19		0.85
♀ (14) × ♂ 14 or 14 + 2	32.75	19.54	47.42	0.29			
♀ (14 + 2) × ♂ (14 + 2)	0.79	4.51	23.16	14.75	56.32	0.26	0.26

Table 4. *Chromosome control of the offpring obtained from*

Parents				Offspring							
Pollination groups		female chromosome number	male chromosome number	Number of seeds		Chromosome constitution of descendants					
				Germinated	Controlled	14	14 + 1	14 + 2	14 + 3	14 + 4	14 + 6
(14), (14 + 2)	*	14	14 + 2	22	20	5 25.00	3 15.00	7 35.00			
	**	14 + 2	14	78	77	47 61.04		28 36.36	2 2.60		
(14), (14), (14 + 2)	***	14	14 or 14 + 2	115	89	41 46.07	10 11.24	36 40.45	1 1.12		
	***	14	14 or 14 + 2	417	259	73 28.18	33 12.74	128 49.42			
	**	14 + 2	14	28	20	1 5.00		16 80.00	1 5.00	1 5.00	
(14), (14 + 2), (14 + 2)	*	14	14 + 2	67	52	11 21.15	5 9.61	30 57.70		2 3.85	
	****	14 + 2	14 or 14 + 2	118	103	23 22.33	3 2.91	43 41.74	3 2.91	24 23.30	1 0.97
	****	14 + 2	14 or 14 + 2	33	15	7 46.67		4 26.67	1 6.67	1 6.67	
(14 + 2), (14+ 2) (14 + 2), (14 + 2), (14 + 2)	*****	14 + 2	14 + 2	111	73	2 2.74	3 4.11	15 20.55	5 6.85	44 60.27	
	*****	14 + 2	14 + 2	100	82		2 2.44	14 17.07	14 17.07	50 60.98	
	*****	14 + 2	14 + 2	120	94		1 1.06	17 18.09	12 12.77	60 63.83	1 1.06
	*****	14 + 2	14 + 2	123	94		5 5.32	30 31.91	12 12.76	41 43.61	
	*****	14 + 2	14 + 2	41	34	1 2.94	1 2.94	11 32.35	4 11.76	14 41.18	

Table 6. *Chromosome controls of the offspring obtained from*

Parents			Offspring				
Pollination group	female chromosome number	male chromosome number	Number of seeds		Chromosome constitution of descendants		
			Germinated	Controlled	14	14 + 1	14 + 2
(14 + 1), (14 + 1), (14 + 1)	14 + 1	14 + 1	120	93	64 68.82	2 2.15	20 21.50
	14 + 1	14 + 1	13	13	11 84.62		2 15.38
	14 + 1	14 + 1	8	8	7 87.50		1 12.50
(14 + 2), (14 + 2), (14 + 2), (14 + 2), (14 + 2)	14 + 2	14 + 2	111	73	2 2.74	3 4.11	15 20.55
	14 + 2	14 + 2	100	82		2 2.44	14 17.07
	14 + 2	14 + 2	120	94		1 1.06	17 18.09
	14 + 2	14 + 2	123	94		5 5.32	30 31.91
	14 + 2	14 + 2	41	34	1 2.94	1 2.94	11 32.35
(14 + 3), (14 + 3), (14 + 3), (14 + 3), (14 + 3)	14 + 3	14 + 3	8	8			
	14 + 3	14 + 3	25	13			3 23.08
	14 + 3	14 + 3	20	17	1 5.88		2 11.75
	14 + 3	14 + 3	90	43	2 4.65		5 11.63
	14 + 3	14 + 3	0	0			
(14 + 4), (14 + 4), (14 + 4), (14 + 4), (14 + 4)	14 + 4	14 + 4	0	0			

the crosses involving normal and 2 B-chromosome rye plants

Offspring

Chromosome constitution of descendants

14 + 1_s iso	14 + 2 + 1_s iso	14 + 1_b iso	14 + 2 + 1_b iso	14 + 3 + 1_b iso	14 + 4 + 1_b iso	14 + 1 + 1 dB	14 + 2 + 1 dB	14 + 2 + 1_b iso + 1 dB	14 + 1; 14 + 2	14 + 2; 28 + 4	13 + 2
1		4									
5.00		20.00									
1											
1.12											
9	1	14							1		
3.47	0.39	5.41							0.39		
										1	
										5.00	
		3									1
		5.57									1.92
1	1	3	1								
0.97	0.97	2.91	0.97								
		2									
		13.33									
	1		1				1	1			
	1.37		1.37				1.37	1.37			
			1			1					
			1.22			1.22					
			2		1						
			2.13		1.06						
2		2	2								
2.12		2.12	2.12								
	1	1		1							
	2.94	2.94		2.94							

the crosses involving rye plants with the same number of B-chromosomes

Offspring

Chromosome constitution of descendants

14 + 3	14 + 4	14 + 6	14 + 1_s iso	14 + 2 + 1_s iso	14 + 1_b iso	14 + 2 + 1_b iso	14 + 3 + 1_b iso	14 + 4 + 1_b iso	14 + 1 + 1 dB	14 + 2 + 1 dB	14 + 2 + 1_b iso + 1 dB
	3		2		1	1					
	3.22		2.15		1.07	1.07					
5	44			1		1				1	1
6.85	60.27			1.37		1.37				1.37	1.37
14	50					1			1		
17.07	60.98					1.22			1.22		
12	60	1				2		1			
12.77	63.83	1.06				2.13		1.06			
12	41		2		2	2					
12.76	43.61		2.12		2.12	2.12					
4	14			1	1		1				
11.76	41.18			2.94	2.94		2.94				
2	5	1									
25.00	62.50	12.50									
2	7	1									
15.38	53.84	7.69									
3	6	3		1						1	
17.65	35.29	17.35		5.88						5.88	
11	18	6		1							
25.58	41.88	13.95		2.32							

Table 7. *Variation in B-chromosome frequency transmission*

Pollination groups	Total number of seeds		Elimination	Reduction		Conservation	Augmentation						Total of Augmentation
	germinated	controlled		$\times \frac{1}{2}$	$\times \frac{2}{3}$		$\times \frac{4}{3}$	$\times \frac{3}{2}$	$\times \frac{5}{2}$	× 2	× 3	× 4	
(14 + 1), (14 + 1), (14 + 1)	141	114	71.93			4.39				20.17	0.88	2.63	23.38
(14 + 2), (14 + 2), (14 + 2), (14 + 2), (14 + 2)	445	377	0.79	4.51		23.34		14.85	0.26	55.96	0.26		71.35
(14 + 3), (14 + 3), (14 + 3), (14 + 3), (14 + 3)	143	81	3.70		21.35	25.93	44.44			13.58			54.02
(14 + 4), (14 + 4), (14 + 4), (14 + 4), (14 + 4)	0	0											

Taking into consideration the data of preceding authors, and the results obtained in this present investigation, the following conclusions can be stated.

i) In plants 2n = 14 + 1, the elimination frequency of the B-univalent by the female side was high. Indirect evidence of preferential distribution was found, in agreement with previous reports by Müntzing (1945).

ii) In the offspring harvested from the combinations ♀ 14 × ♂ 14 + 1 and ♀ 14 × ♂ 14 + 2, 13.66% and 22.22% plants having 2n = 14 + 1 respectively were obtained. Therefore, it can be concluded that preferential distribution does not always take place when 1 or 2 B chromosomes are present in the male sporophyte.

iii) In the progeny of the combination ♀ 14 × × ♂ 14 + 1, more plants with 2n = 14 + 1 than 2n = 14 + 2 were found. This could be explained by a favourable certation for pollen carrying the lower number of B chromosomes or by the occurrence of nondisjunction in a small proportion of pollen mitosis in 2n = 14 + 1 plants. These two phenomena could take place simultaneously.

iv) From the offspring obtained in the combination ♀ 14 + 2 × ♂ 14 (Table 5) the constitution of the female gametes was deduced: 49.48% having 7 chromatids, 46.39% having 7 + 1, 3.30% having 7 + 3 and 1.03% having 7 + 4.

The cytological behaviour of B chromosomes during female gametogenesis has not been extensively studied, so it is not known whether preferential distribution occurs during meiosis or post-meiotic mitosis or successively in both. Table 8 shows a theoretical scheme of the cytological behaviour of B chromosomes of a 2n = 14 + 2 B-rye plant during both micro and megasporogenesis. It is based on experimental data for microsporogenesis reported by other authors. In the combination ♀ 14 + 2 × ♂ 14, approximately half of the descendants obtained had B chromosomes while the remainder had none. The absence of 2n = = 14 + 1 can be attributed to preferential distribution of B chromosomes in every case. Thus, the only pathway which makes the theoretical gamete constitutions compatible with the observed results, requires failure of B chromosome pairing and migration of both B-univalents to the same pole (see Table 8). Alternatively, similar results could be obtained if both B chromosomes paired and meiotic non-disjunction took place. This possibility has not been considered in the scheme because it was not observed in microsporogenesis.

v) In some cases, (see 4th row in Table 4) a high number of individuals carrying B isochromosomes was obtained which probably indicates genetic polymorphism of the B centromere.

vi) From comparing the offspring obtained from the combination ♀ 14 × ♂ $\left\{\begin{array}{l}14 \text{ or} \\ 14+1\end{array}\right.$ with ♀ 14 ×

Table 8. *Scheme showing the cytological behaviour of B-chromosomes during gametogenesis of a 2n = 14 + 2 B rye plant*

	Meiosis	Micro or megaspore post-meiotic mitosis		gametes
Pairing	B- and A-chromosomes behaving in a similar manner	B-chromosome undergoing normal disjunction		7 + 1
		B-chromosome undergoing non-disjunction		7 + 2
Failure of pairing	Each of the B-univalents migrating to different pole at AI	B-chromosome undergoing normal disjunction		7 + 1
		B-chromosome undergoing non-disjunction		7 + 2
	Both B-univalents migrating to the same pole	Spore having B-chromosomes	Both B-chromosomes undergoing normal disjunction	7 + 2
			One of the B-chromosomes undergoing non-disjunction	7 + 3
			Both B-chromosomes undergoing non-disjunction	7 + 4
		Spore lacking B-chromosomes		7
	None B-univalent migrating to the poles			7
	Only one B-univalent is included in a pole while the other is not	Spore lacking B-chromosomes		7
		Spore having B-chromosomes	Normal disjunction	7 + 1
			Non-disjunction	7 + 2

The above considered possibilities are based on experimental data of microsporogenesis (see the text).

$\times$ ♂ $\left\{\begin{matrix}14\text{ or}\\ 14+2\end{matrix}\right.$ (Tables 3 and 5) it can be concluded that pollen carrying B chromosomes formed by plants 2n = 14 + 2 was more competitive than normal pollen. This fact could explain in part the existence of B chromosomes in natural populations in spite of their deleterious effects.

When comparing this behaviour with that of plants 14 + 1 in which B chromosome elimination by pollen was total, it can be deduced that the competitive ability of the pollen does not depend on the chromosome constitution of the pollen grain but on the plant in which it was formed. This process may be considered as a sporophytic determination.

vii) When only plants carrying B chromosomes were crossed (Table 7), a general tendency to increase the number of B chromosomes in the offspring was observed. However, pollen with a high number of B chromosomes was not fertile.

viii) Müntzing (1963), Kishikawa (1965) and Moss (1966) demonstrated that in rye there is a negative correlation between seed production and the number of B chromosomes. Therefore, plants having many B chromosomes tend to be eliminated from populations. Unfortunately, this investigation did not include a fertility study. Nevertheless, our data on seed germination of each pollination group (Table 7) are in agreement with those previous investigations, with the exception of the (14 + 1 × · · · × 14 + 1) group. This difference may be accounted for by the smaller number of plants involved in this pollination group.

From all these observations it may be concluded that the permanence of B chromosomes since the oldest rye populations has probably been maintained by a complex equilibrium. On one hand, the tendency to increase the number of B chromosomes by the process of non-disjunction is compensated by the high sterility of pollen carrying too many B chromosomes. On the other hand, normal pollen competes disadvantageously with pollen carrying a small number of B chromosomes produced by 14 + 2 plants.

Although very little is known about the origin of B chromosomes (considered as a unique category), there are two theories which provide an explanation. The first postulates that B chromosomes are subproducts of caryotypic stabilization (Fernandes, 1949; Cleland, 1951; Markarian et al., 1958; Kimura, 1962; Jackson, 1962; Tothil, 1964; Battaglia, 1964; Manna et al., 1965; Jauhar et al., 1968; Kranz, 1968; Tsuchiya, 1969; Hayman et al., 1969; Matsuda, 1970; Favarger et al., 1970; Hazra et al., 1971; Patton, 1972; Stephens et al., 1972). The second theory is mainly based on the lack of pairing between A and B chromosomes, claiming independent origins (Östergren, 1945, 1947; Rhoades et al., 1972).

B chromosomes have been extensively studied in many species, such as corn, rye, grasshoppers, etc. Many other studies refer to the possible presence of B chromosomes. However, it is possible that sometimes A chromosomes, differing in size from the normal complement and originating from structural variations, have been confused with B chromosomes. Actually, it is difficult to decide which chromosomes are genuine B chromosomes when their nature and origin are unknown. Some of their properties have been stated, the most interesting being the process of preferential distribution. This mechanism leads to an increase in the number of B chromosomes in the gametes. Furthermore, pollen carrying a high number of B chromosomes is very sterile, so autogamy would lead to the extinction of the species. Therefore, populations having B chromosomes must be allogamous in order to survive.

Finally, it may be concluded that the genuine B chromosomes may be the cytological expression of a complex evolutionary system which results in the conservation of population genetic variability.

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Received April 2, 1974

Communicated by F. Mechelke

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