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Genetic control of the rate of transmission of rye B chromosomes. I. Effects in 2B × 0B crosses

F. ROMERA, M. M. JIMÉNEZ & M. J. PUERTAS
Departamento de Genética, Facultad de Biología, Universidad Complutense, 28040 Madrid, Spain

Selection for plants showing low or high transmission rates of B chromosomes demonstrates the existence of genotypes which affect this character. The results suggest that the gene or genes involved in this control are located in the A chromosomes. It is shown that plants from the low transmission rate class tend to lose B chromosomes, while plants from the high transmission rate class tend to accumulate Bs. It is therefore concluded that these genotypes can influence the frequency of B chromosomes in different populations.

Keywords: B-chromosome, *Secale cereale*, selection, transmission rate.

Introduction

The inheritance of rye B chromosomes is non-Mendelian with different features on the male and female sides. The mode of transmission is well known on the male side, i.e. the peculiar meiosis (Kishikawa, 1965), pollen mitosis (Müntzing, 1946) and differential fertilization (Puertas *et al.*, 1986, 1988). These three features produce accumulation mechanisms which, together with the harmful effects of Bs on the fitness of carriers (Müntzing, 1963; Puertas *et al.*, 1985; Romera *et al.*, 1989), bring about the maintenance of B chromosome polymorphisms in populations.

The mode of transmission on the female side is less well known, since female meiosis and gametogenesis are difficult to observe, especially using quantitative analysis. However, the existence of accumulation mechanisms in female gametophytes has been demonstrated both cytologically (Håkanson, 1948) and by crosses (Müntzing, 1943, 1945, 1966).

In a previous paper we reported that progenies of crosses involving 2B females and 0B males showed a remarkably large variation in the number of Bs transmitted, with the frequencies of 0B plants ranging from 4 to 76 per cent (Puertas *et al.*, 1990). The pattern of the distribution of Bs in these progenies suggested to us the existence of genotypes affecting the transmission rate of B chromosomes on the female side. In this paper we investigate progenies of 2B × 0B crosses in order to demonstrate the existence of such genotypes in rye.

Genetic control of B chromosome transmission has been previously demonstrated in the grasshopper *Myrmeleotettix maculatus* (Shaw & Hewitt, 1985; Shaw *et al.*, 1985) in the mealybug *Pseudococcus affinis* (Nur & Brett, 1987, 1988) and suggested in the Compositae *Hypochoeris maculata* (Parker *et al.*, 1982).

Materials and methods

The material used was *Secale cereale* with B chromosomes from the Puyo population, which naturally carries B chromosomes at a high frequency.

Plants used as parents for the crosses were obtained from the progenies of 2B × 0B crosses studied in a previous paper (Puertas *et al.*, 1990). In that paper we analysed 18 different 2B × 0B crosses whose progenies were collected plant by plant, and from which 438 descendants were screened for the number of Bs. These progenies showed a remarkable variation for the character 'mean number of Bs per plant' with values ranging from 0.48 to 2.16, and an average mean of 1.37 (Table 1).

From these 18 crosses we used seeds from two crosses selected for their low transmission rate of Bs (marked with a single asterisk in Table 1, and jointly designated as the 'low class') and seeds from two crosses selected for their high transmission rate of Bs (marked with a double asterisk in Table 1, and jointly designated as the 'high class').

Seeds of these crosses were germinated and their chromosomes counted cytologically. Ten 0B and ten 2B seedlings were taken from the low class (five from

Table 1 Distribution of B chromosomes in progenies of 2B × 0B crosses of the parental population. Plants from crosses marked with one asterisk were selected as parents of the low transmission rate class. Those marked with two asterisks were selected as parents of the high transmission rate class

Cross	B frequency in the progeny					Mean number of Bs per plant
	0B	1B	2B	3B	4B	
1*	19		6			0.48
2*	15		5			0.50
3	14		10		1	0.96
4	12		23			1.04
5	12		23			1.04
6	9		11			1.10
7	5		10			1.33
8	8		18			1.38
9	7		18			1.44
10**	5		19			1.58
11	5		20			1.60
12	4	1	18			1.61
13	7		15	1	2	1.64
14	4	1	20			1.64
15	4		21			1.68
16	3		22			1.76
17**	2		12	1		1.80
18	1		21		3	2.16
Total	136	2	292	2	6	1.37

0B and five 2B from crosses 1 and 2 in Table 1) and were planted at random locations in an experimental field plot. Seven 0B (five from cross 10 and two from cross 17) and ten 2B seedlings (five from each of the crosses 10 and 17) were likewise planted in another plot in the same experimental field.

All the 2B plants were emasculated and were open-pollinated by 0B plants from within the same plot. Thus the selected plants with and without Bs in each plot belonged to the same class: either low or high transmission rate. Both plots were isolated to prevent cross-pollination between them.

The offspring were collected plant by plant and 25 seeds of each female were screened for the presence of B chromosomes; i.e. 250 seeds for both the low and high classes.

Since the character 'transmission rate of B chromosomes' has to be measured as progenies we refer to 'parental population' or 'parents' as the low and high class plants grown from seed of the crosses listed in Table 1, and 'descendants' are their progenies.

In all cases the chromosome counts were made in root tips. They were fixed in acetic alcohol 1:3 and stained by the Feulgen method.

Table 2 Descendants obtained from 2B × 0B crosses in the low transmission rate class

Plant	B frequency in the progeny					Mean number of Bs per plant
	0B	1B	2B	3B	4B	
1	25					0
2	25					0
3	21		4			0.32
4	20	1	4			0.36
5	20	1	2		2	0.52
6	18		7			0.56
7	17		8			0.64
8	17		8			0.64
9	10		15			1.20
10	10		14	1		1.24
Total	183	2	62	1	2	0.55

Table 3 Descendants obtained from 2B × 0B crosses in the high transmission rate class

Plant	B frequency in the progeny						Mean number of Bs per plant
	0B	1B	2B	3B	4B	6B	
1	10		15				1.20
2	7	1	17				1.40
3	9		12		4		1.60
4	5		19		1		1.68
5	4		20		1		1.74
6	3		22				1.76
7	3		21		1		1.84
8	0		24		1		2.08
9	2		17		6		2.32
10	2		11	1	10	1	2.84
Total	45	1	178	1	24	1	1.85

Results

Results of the 2B × 0B crosses made with the low and high transmission classes are shown in Tables 2 and 3, respectively.

We first compared, by an ANOVA, the mean number of Bs per plant in the parental population and in the descendants of both low and high classes. We also used *t*-tests to compare the mean of the parents with the descendants of the low class, and the mean of the parents with the descendants of the high class. All these tests showed highly significant differences between the values compared.

From Tables 2 and 3 it can be calculated that the frequency of plants with Bs in the descendants of the low class is 0.27, while in the high class it is 0.82. These

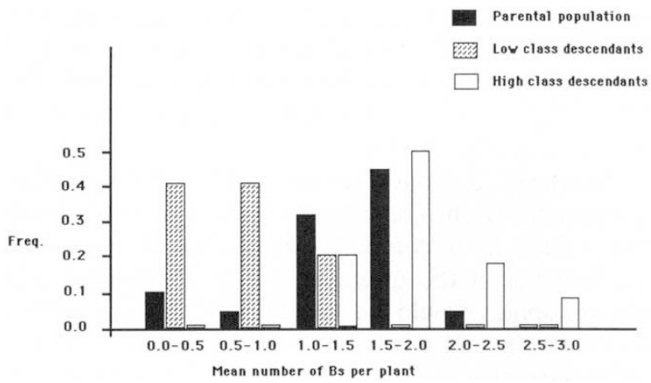

Fig. 1 Distribution of the mean number of Bs per plant in the parental population and in the descendants of both low and high transmission rate classes of B chromosomes.

values were 0.25 and 0.82 in their parents, respectively (Table 1).

Figure 1 compares the distribution of the variable 'mean number of Bs per plant' in the parental population, and in the descendants of both low and high classes. It can be observed that in the parental population there is a continuous distribution of this variable, while the distribution covers only the two extremes in the descendants. The average mean number of Bs per plant in the parental population was 1.37. The average mean of Bs per plant in the plants selected as parents for the low class was 0.49, and in those selected for the high class it was 1.69. So that, the selection differential was $D=0.88$ and 0.32 for the low and high classes, respectively. The mean number of Bs per plant in the descendants of the low class was 0.55, so the selection gain is $G=0.82$, while in the high class $G=1.85-1.37=0.48$.

The heritability of this character, estimated from the quotient G/D, is $H=0.93$ for the low class and 1.5 for the high class. The error of this estimation cannot be calculated, but these high values suggest a high value for the genetic component of the observed variability in this population.

Discussion

In the 2B × 0B crosses made in our previous works a large variation in the number of B chromosomes transmitted from cross to cross was observed. Some progenies showed few plants with Bs, while others showed up to 95 per cent (Puertas *et al.*, 1990). Two out of the 18 progenies of such 2B × 0B crosses shown in Table 1 have a mean number of Bs per plant less than one, indicating a tendency to lose B chromosomes, while others have a high mean, with a continuous distribution between them (Fig. 1). This type of distribution suggested to us the existence of genotypes affecting the transmission rate of B chromosomes. We, therefore, made a mass selection experiment, in which we selected plants from the progenies of both extremes of the distribution: those which showed low and high transmission rates. The assumption was that if the variation was, even partially, due to genetic control over the transmission of Bs, a selection gain would be obtained.

The results of this work are clearly in agreement with this hypothesis. The low class after selection varies from 0 to 1.24 Bs transmitted (Table 2), while the high class varies from 1.20 to 2.84 (Table 3). In both cases, the selection gain was high (Fig. 1).

It is remarkable that the descendants of the low class show values of the mean number of Bs per plant of less than one, in eight out of the ten cases. There were even two cases in which no plant with Bs was obtained (plants 1 and 2, Table 2). Such a result has never been reported before, in spite of the large number of these types of crosses reported in the literature. Similarly, in the high class, there is one case in which all plants of the progeny have Bs (plant 9, Table 3). This rapid selection gain, together with the similarity in the frequency of plants with Bs between the selected parents and their descendants suggests that a low number of loci are involved in this control.

It seems, in all probability, that these loci are located on A chromosomes rather than on Bs. According to the observation of non-disjunction during female post meiotic mitosis (Håkanson, 1948), almost all 2B plants formed in a 2B × 0B cross have to be homozygous for the B chromosome, since both Bs come from a single B chromatid after non-disjunction. Therefore, if the genes existed on the B chromosomes little variation would be observed, while variation for A genotypes is to be expected in an open-pollinated species such as rye. Heterogeneity for A genotypes is further provided by the mode in which we make the crosses, since pollen from various 0B males can fertilize each 2B female.

The phenotypic effect of the gene or genes whose existence is demonstrated in this work, is variation on the transmission rate of B chromosomes in 2B × 0B crosses. These genes have to act in such a way that different 2B plants transmit their Bs at different frequencies. Therefore, these genes must have a differential influence on the formation of the zygotes or gametes.

It is possible that zygotes with different numbers of Bs vary in their viability depending on the plant where they were formed, but this hypothesis is not in agreement with our previous results. The mean number of grains per flower, per spike or per plant formed is significantly different in plants with or without Bs: the higher the number of Bs in a plant, the lower the number of grains formed. This is so regardless of the

variety, the *Secale* species or the year of measurement (Puertas *et al.*, 1985; Romera *et al.*, 1989). So that, the variation does not seem to be a property of individual plants, but rather of the Bs themselves.

It is also possible that different zygotes could be produced by differential fertilization of female gametes, due to some discrimination by the carrier plant. This possibility cannot be tested because of the lack of cytological data about female gametogenesis, although competition among female gametes is difficult to explain.

The variation in the transmission rate of B chromosomes during female gametogenesis could be brought about at various stages: (i) variation in non-disjunction frequency, (ii) loss or unbalanced separation of Bs during meiosis, and (iii) variation in direction rate of Bs towards the nucleus forming the egg-cell. Cytological data are essential in order to discriminate among these three possibilities, although our data seems to rule out the first one.

The behaviour of B chromosomes is different during micro- and megagametogenesis since 1B plants almost never appear in progenies of 2B × 0B crosses, while they are not infrequent in 0B × 2B crosses. In all 0B × 2B crosses reported in the literature, the average frequency of 1B plants is 12 per cent, while in 2B × 0B it is only 1.6 per cent (Puertas, 1990). This indicates a highly efficient mechanism of non-disjunction on the female side. The gene or genes with effect on the transmission rate cannot therefore influence non-disjunction rate since it occurs in almost 100 per cent of the cases. In addition, if the efficiency of non-disjunction was the cause of the difference between low and high transmission rates, we would observe different frequencies of 1B vs. 2B, which is not the case.

The plants 3, 9 and 10 of the high class (Table 3) show a high number of 4B progeny. This is especially so for plant 10, which even shows one having 6B. 4B and 6B plants from a 2B × 0B cross can be formed by a failure of segregation at meiosis, together with postmeiotic non-disjunction, or by normal meiosis followed by various non-disjunction events during megagametogenesis. On the other hand it is also remarkable that progenies with a low mean of Bs transmitted had some plants with many Bs (plant 5, Table 2), and vice versa, progenies with a high mean of Bs transmitted had no plants with many Bs, but many plants with 2 Bs (plant 6, Table 3).

This suggests that the B frequency in the progeny in 2B × 0B crosses can be influenced in two steps, i.e. a regular behaviour during meiosis and postmeiotic mitosis will produce 0B or 2B gametes, whose frequency will depend on the direction rate of Bs towards the nucleus forming the egg cell, while an irregular behaviour will produce 4B, or even 6B gametes. The fact that some 3B and 4B plants appear in the low class, and no plants with 4B appear in some progenies of the high class, suggests that the control over these two steps can be different.

Matthews & Jones (1983) estimated parameters influencing B chromosome transmission and applied the values to a computer simulation model. They showed that if the direction rate is less than 0.5, B chromosomes would be rapidly lost, but concluded, from parameters estimated from observations on the male side, that the direction rate was not important since this parameter was always high and only slightly variable. In our case the rapid loss of Bs in the low transmission class suggests that the direction rate could be important on the female side.

It seems possible that the occurrence of genes which effect transmission rate in a population could influence the frequency of B chromosomes in such a population. All features of Bs previously studied are sufficient to explain the maintenance of the polymorphism in spite of the non-Mendelian transmission of B chromosomes, but they do not explain why different populations have different frequencies of B chromosomes. Populations with a high frequency of genotypes for high transmission rate could have higher frequencies of Bs, and vice versa. It could be that the gene or genes concerned could influence the frequency at which Bs occur in a population, and that the maintenance of the polymorphism then depends on other factors, mainly the effect of Bs on fitness together with the special behaviour of Bs during gametogenesis and fertilization.

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