

LOCALIZATION OF THE GENES CONTROLLING B CHROMOSOME TRANSMISSION RATE IN MAIZE (*ZEA MAYS* SSP. *MAYS*, POACEAE)¹

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In previous papers we found that the frequency of B chromosomes in native races of maize varies considerably in different populations. Moreover, we found genotypes that control high and low transmission rates (TR) of B chromosomes in the Pisingallo race. In the present work crosses were made to determine whether the genes controlling B-TR are located on the normal chromosome set (As) or on the B chromosomes (Bs). We made female f.0B × male m.2B crosses between and within high (H) and low (L) B-TR groups. The Bs were transmitted on the male side in all cases. The mean B-TR from the progeny of f.0B (H) × m.2B (H) and f.0B (H) × m.2B (L) crosses was significantly higher than that from f.0B (L) × m.2B (L) and f.0B (L) × m.2B (H) crosses. The results show that the B-TR of the crosses corresponds to the H or L B-TR of the 0B female parents irrespective of the Bs of the male parent. This indicates that B-TR is genetically controlled by the 0B female parent and that these genes are located on the A chromosomes.

Key words: B chromosome; B transmission rate control; maize; maize native races; Poaceae; *Zea mays* ssp. *mays*.

B chromosomes (Bs) are widely distributed in maize (Longley, 1938; Randolph, 1941; McClintock, Kato-Y, and Blumenschein, 1981). Native populations from northern Argentina exhibit large differences in the frequency of their B chromosomes (Chiavarino et al., 1997a; Rosato et al., 1998). It is reported that Bs are maintained due to various mechanisms of “drive” consisting of (1) the suppression of meiotic loss when they are in single dose, (2) nondisjunction at the second pollen grain mitosis (Roman, 1947; Carlson, 1978; Carlson and Chou, 1981; Carlson and Roseman, 1992), (3) preferential fertilization by the sperm nucleus carrying the Bs produced during the nondisjunction process (Roman, 1948; Carlson, 1969), and (4) a higher competitive ability of B-carrying pollen grains (Beckett, 1982). According to Carlson and Roseman (1992) these accumulation mechanisms are sufficient to account for the maintenance of B polymorphism in maize populations. These mechanisms cannot, however, account for the difference in B-frequency among different populations (Chiavarino et al., 1995; Naranjo et al., 1995).

Variation in B transmission rate (B-TR) is a common feature of B inheritance, in such a way that the Bs tend to be lost in some progenies and to increase in number

in others, compared to Mendelian expectation. The genetic control of this transmission rate has been demonstrated in some animal species, i.e., *Myrmeleotettix maculatus* (grasshopper; Shaw and Hewitt, 1985; Shaw, Hewitt, and Anderson, 1985), *Pseudococcus affinis* (mealybug; Nur and Brett, 1987, 1988), *Eyprepocnemis plorans* (grasshopper; Herrera et al., 1996), and in some plants, i.e., *Hypochoeris maculata* (Parker, Taylor, and Ainsworth, 1982), *Secale cereale* (Romera, Jiménez, and Puertas, 1991; Jiménez et al., 1995, 1997), *Aegilops speltoides* (Cebriá, Navarro, and Puertas, 1994), and *Allium schoenoprasum* (Bougourd and Plowman, 1996).

We have investigated the existence of genetic control of B-chromosome transmission rate (B-TR) selecting H and L B-TR genotypes on the male and female side, from a population of the maize native race Pisingallo. First, we obtained one generation (G0) from f.0B × m.1B (G0m) and f.1B × m.0B (G0f) crosses within a random sample of seeds collected from the original population. Second, we made crosses selecting individuals showing the highest and the lowest B-TR values (G1m and G1f). Selection gain was obtained demonstrating the presence of genotypes controlling B-TR on both male and female sides (Rosato et al., 1996).

The objectives of this paper were: (a) to continue the selection for H and L B-TR in two new generations (G2 and G3) and (b) to locate the genes that control B-TR by making 0B female × 2B male (G3) crosses between selected individuals from G2 with the highest and the lowest B-TR.

MATERIALS AND METHODS

This experiment was carried out with individuals from the maize native race Pisingallo (VAV 6313). The seeds of the primitive population were collected in 1991 in Las Piedras Blancas (Los Tordillos, Am-

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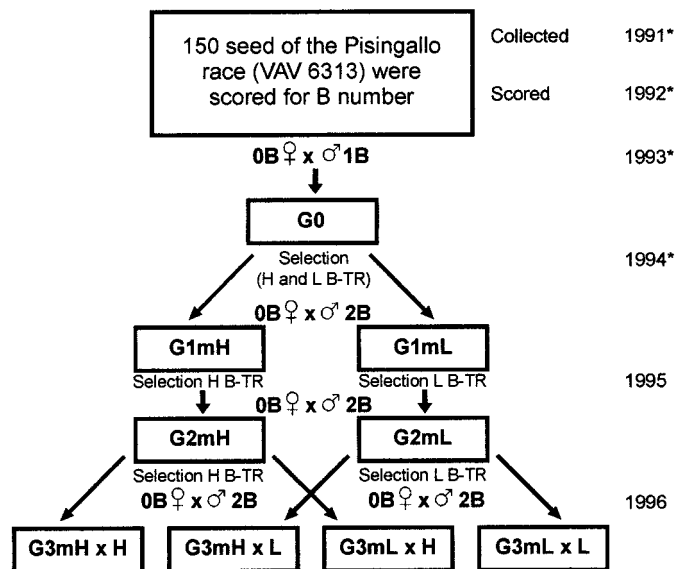


Fig. 1. Schematic representation of the experimental crosses. H = high, L = low. Asterisks indicate results published in Rosato et al. (1996).

TABLE 2. B number and B-TR in the progeny of f.0B × m.2B crosses (G2) within L group. The asterisk marks the selected ear for G3.

Cross	Number of Bs in G2			Total	Mean no. of Bs	B-TR
	0B	2B	4B			
1	14	14		28	1.00	0.50
2	16	16		32	1.00	0.50
3	14	14		28	1.00	0.50
4	18	18		36	1.00	0.50
5	15	14		29	0.97	0.48
6*	43	39		82	0.95	0.48
7	14	9	1	24	0.92	0.46
8	16	13		29	0.90	0.45
Total	150	137	1	288	0.97	B-TR = 0.48 ± 0.01

0B and 2B seedlings under the same conditions in the experimental greenhouse of IFSC. We made four types of f.0B × m.2B crosses between and within both H and L B-TR groups. A total of 22 successful crosses was obtained as following: (1) five f.0B (H) × m.2B (H); (2) six f.0B (H) × m.2B (L); (3) six f.0B (L) × m.2B (H); and (4) five f.0B (L) × m.2B (L) (Fig. 1). The number of Bs in G3 was determined in primary root tips of at least 20 individuals of each of the 22 ears obtained (Tables 3–6).

The H and L B-TR of G1 and G2 were compared with a Kruskal-Wallis test. The male H and L B-TR of G3 were compared with a two-way ANOVA test. The frequencies of progeny with 2B, related to the frequencies of individuals with 0B, were compared with the Mendelian expectation (0.5) using a χ^2 test.

RESULTS

The B-TR of the G2 progeny resulting from f.0B × m.2B crosses within the H B-TR group was: B-TRH ± SE = 0.68 ± 0.03 (Table 1). The frequency of individuals with 2B was significantly higher than the Mendelian expectation (0.5) ($\chi^2 = 57.619, P < 0.00001$). G2 progeny resulting from f.0B × m.2B crosses within the L B-TR group was B-TRL ± SE = 0.48 ± 0.01 (Table 2). The frequency of individuals with 2B was not significantly lower than the Mendelian expectation ($\chi^2 = 0.588, P = 0.443$). The L B-TR and H B-TR obtained in G2 were significantly different according to the results from the Kruskal-Wallis test ($F = 10.691, df = 1, 13, P = 0.0011$).

The mean B-TR of the G3 progeny resulting from f.0B (H) × m.2B (H) crosses was: B-TRH ± SE = 0.71 ± 0.04 (Table 3). The frequency of individuals with 2B was significantly higher than the Mendelian expectation ($\chi^2 = 23.04, P < 0.00001$).

The mean B-TR of the G3 progeny resulting from f.0B (L) × m.2B (L) crosses was: B-TRL ± SE = 0.48 ±

bato Department, Catamarca Province Argentina), 28°01.707'S - 65°56.971' W, situated at the altitude of 1600 m above sea level. The frequency of plants with Bs in this original population was 44% (Rosato et al., 1996). The remaining seeds are deposited in the seedbank of the Laboratorio Vavilov (Facultad de Agronomía, UBA) and in the Instituto Fitotécnico de Santa Catalina (IFSC, Universidad Nacional de La Plata).

Figure 1 shows a schematic representation of the experimental crosses carried out with population VAV 6313 involving three generations of selection for high (H) or low (L) B-TR on the male side. B-TR was estimated as the quotient between the mean number of Bs transmitted to the progeny and the number of Bs of the parental plant that carried them. To score for B number, primary root tips were pretreated with 0.002 mol/L 8-hydroxyquinoleine for 3 h at 20°-22°C and subsequently fixed in ethanol:acetic acid (3:1). Root tips were then squashed in propionic haematoxylin (2%) with ferric citrate as a mordant (Núñez, 1968).

The G2 generation was obtained by making seven successful 0B female × 2B male crosses (Table 1) with those selected G1 plants showing H B-TR (140 plants), and eight successful 0B female × 2B male crosses (Table 2) with those selected G1 plants showing L B-TR (90 plants). B number was scored in at least 23 individuals from each of 15 ears obtained in G2 (Tables 1 and 2).

To obtain G3 we grew a sample of 105 grains from a G2 ear obtained from selection for H B-TR (0.82) and 58 grains from a G2 ear obtained from selection for L B-TR (0.48) (asterisks in Tables 1 and 2). We grew

TABLE 1. B number and B-TR in the progeny of f.0B × m.2B crosses (G2) within H group. The asterisk marks the selected ear for G3.

Cross	Number of Bs in G2				Total	Mean no. of Bs	B-TR
	0B	1B	2B	4B			
1*	23		108		131	1.65	0.82
2	10		18	2	30	1.47	0.73
3	9	1	23		33	1.42	0.71
4	10		19		29	1.31	0.66
5	12		22		34	1.29	0.65
6	13		17	1	31	1.23	0.61
7	10		13		23	1.13	0.57
Total	87	1	220	3	311	1.36	B-TR = 0.68 ± 0.03

TABLE 3. B number and B-TR in the progeny of f.0B (H) × m.2B (H) crosses (G3).

Cross	Number of Bs in G3			Total	Mean no. of Bs	B-TR
	0B	2B	4B			
1	6	20	1	27	1.63	0.82
2	9	27		36	1.50	0.75
3	7	19		26	1.46	0.73
4	8	18		26	1.38	0.69
5	12	15		27	1.11	0.56
Total	42	99	1	142	1.42	B-TR = 0.71 ± 0.04

TABLE 4. B number and B-TR in the progeny of f.0B (L) × m.2B (L) crosses (G3).

Cross	Number of Bs in G3			Mean no. of Bs	B-TR
	0B	2B	Total		
1	10	14	24	1.17	0.58
2	14	16	30	1.07	0.53
3	10	10	20	1.00	0.50
4	15	12	27	0.89	0.44
5	17	8	25	0.64	0.32
Total	66	60	126	0.95	B-TR = 0.48 ± 0.04

0.04 (Table 4). The frequency of individuals with 2B was not significantly lower than the Mendelian expectation ($\chi^2 = 0.286, P = 0.593$).

Mean B-TR values of both H ($F = 0.3680, df = 1, 10, P = 0.5576$) and L ($F = 0.0753, df = 1, 11, P = 0.7888$) selected lines did not show significant differences between G2 and G3 generations.

The mean B-TR of the G3 progeny resulting from f.0B (H) × m.2B (L) crosses was: B-TR ± SE = 0.70 ± 0.05 (Table 5); this value does not significantly differ from the B-TR from f.0B (H) × m.2B (H) ($P = 0.99882$). The frequency of individuals with 2B was also significantly different from Mendelian expectation ($\chi^2 = 21.893, P < 0.00001$).

The mean male B-TR of the G3 progeny resulting from f.0B (L) × m.2B (H) crosses was: B-TR ± SE = 0.48 ± 0.04 (Table 6); this value does not significantly differ from the B-TR from f.0B (L) × m.2B (L) ($P = 0.99906$). The frequency of individuals with 2B was not significantly higher than the Mendelian expectation (0.5) ($\chi^2 = 0.39, P < 0.532$).

In all cases most individuals were 0B or 2B, and the frequency of 1B or 4B plants was very low (Tables 1–6).

There were significant differences in the B-TR between groups (1 vs. 3 and 2 vs. 4; Table 7) when H and L B-TR female progenitors were considered ($F = 26.453, df = 1, 18, P < 0.0001$), whereas no significant difference was found between H and L B-TR groups (1 vs. 2 and 3 vs. 4; Table 7) when male mean B-TR progenitors were considered ($F = 0.040, df = 1, 18, P = 0.8436$) (Table 7).

TABLE 5. B number and B-TR in the progeny of f.0B (H) × m.2B (L) crosses (G3).

Cross	Number of Bs in G3				Mean no. of Bs	B-TR
	0B	2B	4B	Total		
1	6	20	2	28	1.71	0.86
2	5	22		27	1.63	0.81
3	8	19		27	1.41	0.70
4	9	19		28	1.36	0.68
5	11	15		26	1.15	0.58
6	11	14		25	1.12	0.56
Total	50	109	2	161	1.40	B-TR = 0.70 ± 0.05

TABLE 6. B number and B-TR in the progeny of f.0B (L) × m.2B (H) crosses (G3).

Cross	Number of Bs in G3				Mean no. of Bs	B-TR
	0B	2B	4B	Total		
1	11	14		25	1.12	0.56
2	14	16		30	1.07	0.53
3	13	11	1	25	1.04	0.52
4	16	16		32	1.00	0.50
5	14	13		27	0.96	0.48
6	18	8		26	0.62	0.31
Total	86	78	1	165	0.97	B-TR = 0.48 ± 0.04

DISCUSSION

Selection for high (H) and low (L) B-TR in G2 and G3—The B-TR value obtained from the H B-TR selected G2 group (0.68) was significantly higher than that of L B-TR (0.48). G3 progenies from f.0B (H) × m.2B (H) crosses showed a mean B-TR significantly higher than that obtained from f.0B (L) × m.2B (L) crosses (0.71 ± 0.04 and 0.48 ± 0.04, respectively). This indicates that H and L B-TR groups remained different along the three generations of selection (G1, G2, and G3), and therefore the genetic control of B-TR is fully demonstrated.

On the other hand, B-TR values of G2 and both f.0B (L) × m.2B (L) and f.0B(L) × m.2B (H) crosses of G3 were close to 0.5, indicating that in this group the B-TR is Mendelian. On the contrary, the B-TR values in the H B-TR group in G2 and both f.0B (H) × m.2B (H) and f.0B (H) × m.2B (L) crosses of G3 were significantly higher than the Mendelian expectation of 0.5. We therefore conclude that in the L genotype the Bs are randomly transmitted to the progeny in f.0B × m.2B crosses, whereas in the H genotype they show a strong accumulation.

Localization of genes controlling B-TR—The mean B-TR resulting from f.0B (H) × m.2B (H) and f.0B (H) × m.2B (L) crosses was significantly higher than the mean B-TR from f.0B (L) × m.2B (L) and f.0B (L) × m.2B (H) crosses. However, crosses of f.0B (H) × m.2B (H) and f.0B (H) × m.2B (L) on one hand, and f.0B (L) × m.2B (H) and f.0B (L) × m.2B (L) on the other were not significantly different. These results indicate that the genetic control of B-TR is independent of which genotype (H or L B-TR) the 2B male progenitor possesses. On the contrary, the genotype of the 0B female progenitor seems to determine the resulting B-TR.

According to Carlson (1986) the preferential fertiliza-

TABLE 7. Mean B transmission rate ± SE in G3 in f.0B (H) × m.2B (H), f.0B (H) × m.2B (L), f.0B (L) × m.2B (H), and f.0B (L) × m.2B (L) crosses.

	OB	2B	
		Male progenitor H B-TR	Male progenitor L B-TR
Female progenitor H B-TR		0.71 ± 0.04	0.70 ± 0.05
Female progenitor L B-TR		0.48 ± 0.04	0.48 ± 0.04
		1	2
		3	4

tion mechanism is partially understood. This phenomenon is not due to either B migration to a certain pole during the process of nondisjunction at the second pollen grain mitosis or to a determinate position of the sperm nuclei with and without Bs in the pollen tube during its germination (Shi et al., 1996). Carlson (1986) suggests that the Bs confer a certain competitive ability during fertilization to the sperm nucleus that carries them, but the nature of this competitive ability is still unknown. However, a female effect on preferential fertilization was found in a maize line that inhibits preferential fertilization when used as female progenitor (Carlson, 1969). Our results indicate, for the Pisingallo maize population (VAV 6313), that the B-TR genotype of the receptor f.0B plant determines the rate by which the egg is fertilized by the sperm nucleus carrying 2B. In addition, since in our experimental design the female progenitor has no Bs, we conclude that these genes are located on the regular A chromosome set.

Carlson (1978, 1986) considered that there are two possible hypotheses to explain the ability of Bs to undergo preferential fertilization. The first assumes that a specific effect of the proximal region of the B chromosome occurs. The second assumes a nonspecific effect of extra chromatin in the sperm nucleus. Our results suggest that the detection of differences between sperm with and without Bs is controlled by the female genotype. Thus, some genotypes increase the frequency of fertilization by B-carrying sperm, whereas other genotypes do not. The latter result in a random fertilization of the 0B or 2B sperm nucleus results in a Mendelian B-TR. All these results indicate that the presence of B chromosomes determines the sperm phenotype which would be accepted by the egg cell.

On the other hand, Rosato et al. (1996) determined by crosses f.1B \times m.0B that B-TR is also genetically controlled on the female side. They also obtained two groups: a H B-TR group (Mendelian B-TR = 0.5), and a L B-TR (B-TR = 0.4). Considering these results of Rosato et al. (1996) and those of the present paper, it could be concluded that there is an equilibrium that keeps the frequency of individuals with Bs in the population. This equilibrium would be kept by the balance among "anti-B" genes, causing a reduction in female B-TR, and "pro-B" genes causing an increase in male B-TR, but controlled by the female progenitor genotype.

It was recently determined that genes controlling B-TR in rye act on the meiotic behavior of the Bs and that they are located on the B chromosomes (Jiménez et al., 1997; Puertas et al., 1998). The difference between H and L B-TR lines in rye is due to a different ability of 2B individuals to form univalents (L line) or bivalents (H line) at metaphase I. When the Bs form univalents, they are eliminated as micronuclei and most pollen grains have no Bs. On the contrary, in maize, the meiotic behavior of 1B and 2Bs individuals belonging to either the H and L B-TR groups indicates that L B-TR is independent from pairing frequency or meiotic loss of the B chromosome (Chiavarino et al., 1997b). Also, the results here show an effect of the female parent that is not controlled by pairing. The contrasting results in maize and rye show that their B-TR is genetically controlled in a different manner. It is interesting to note that the basic mechanism of B

accumulation in all Poaceae consists of nondisjunction in the pollen, whereas the mechanisms controlling the B-TR to the progeny seem to be species specific.

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