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Cytology of F_1 hybrids and chromosome number of F_2 and BC_1 progeny of the cross *Bromus riparius* × *B. inermis*

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Summary. Hybrids between *B. inermis* Leyss (2n = 8x = 56) and *B. riparius* Rehm. (2n = 10x = 70) were easily made. The F_1 hybrids had a fertility of 20%–50% under open-pollination and backcrossing to *B. inermis*. Chromosome pairing in *B. riparius* was predominantly as bivalents (29.04–33.85 per cell for plant means). Bivalents also predominated in the F_1 hybrid (2n = 9x = 63) and there was a high level of pairing with no reduction in chiasma frequency. It was impossible to estimate the frequency of auto-versus allosyndetic pairing. Chromosome pairing in a hybrid between *B. arvensis* (2n = 2x = 14) and *B. riparius* confirmed that the *B. riparius* complement is capable of complete autosyndetic pairing. Chromosome numbers in the F_2 progeny ranged from 2n = 56 to 72 but they were skewed towards 2n = 63 to 70. Backcrosses ranged from 2n = 56 to 63, as expected, with the distribution skewed towards 2n = 56. Selection towards the 2n = 56 level would be difficult in the F_2. Empirical observation suggested that cytoplasm had a major influence on morphology in the backcrosses. Additional studies are required to determine the best breeding scheme to introgress germ plasm between *B. inermis* and *B. riparius*.

Key words: *Bromus* – F_2 progeny – Backcross – Chromosome pairing – Chromosome numbers

Introduction

Smooth bromegrass (*Bromus inermis* Leyss.) is an important forage species in eastern and western Canada. It has high yields of highly digestible forage and is winter-hardy and widely adapted. It suffers, however, from several shortcomings which have limited its use under some management regimes. Regrowth of smooth brome is limited because regrowth does not come from leaf meristems, as in grasses such as orchard grass (*Dactylis glomerata* L.), but from rhizomes. Smooth bromegrass is strongly rhizomatous and is sometimes considered too aggressive to use in mixtures with species such as alfalfa (*Medicago sativa* L.).

Limited efforts to improve smooth bromegrass via interspecific hybridization were made (Nielsen 1963; Nielsen et al. 1962a; Elliott 1949). More recent efforts gave some encouraging results (R. P. Knowles and V. S. Baron, personal communication). However, these efforts may have been discouraged because of problems with taxonomic identification (Nath and Nielsen 1961), difficult cytology, and complex genetic phenomena associated with high polyploids. Nielsen et al. (1965) noted that backcross progeny quickly reverted to the parental types and suggested some complex phenomena of genomic segregation to explain the observation. Recently it was shown that progeny selected for parental characteristics from smooth bromegrass × Regar bromegrass retained the hybrid chromosome number of 2n = 63 (R. P. Knowles, K. C. Armstrong and V. S. Baron, unpublished results). Thus there is a need to study the cytology of F_1 hybrids to determine if recombination occurs between the parental chromosomes and to determine if there is selection for gametic numbers in advanced generations.

Meadow bromegrass (*B. riparius*, 2n = 70) has recently received attention both as a source of germ plasm to improve smooth bromegrass and as a useful species in its own right. Unlike smooth bromegrass, it does not produce elevated growing points in vegetative shoots (or to a lesser degree) and is, therefore, capable of better aftermath production. Also, it is not aggressively rhizomatous and could be more compatible in mixtures. Vegetative growth is more vigorous in the fall, so it can extend the

grazing season (R. P. Knowles, personal communication). It is a less reliable seed producer than smooth bromegrass and seed requires more processing. The cultivar Regar was released by the Colorado Experiment Station in 1966. There have been considerable problems with the taxonomic identification of this cultivar. It was designated as *B. biebersteinii* Roem et Schult, but recent taxonomic treatments by Tzvelev (1976) and Smith (1980) make this unlikely. It seems more probable that the material belongs to the *B. riparius* Rehm complex (*Bromopsis riparia* (Rehm) (Halub.)).

The purpose of the present study was to: (1) make hybrids between species designated as *B. riparius* and *B. inermis*; (2) study chromosome pairing in *B. riparius* and the F_1 hybrid to determine if there is recombination between the chromosomes of *B. riparius* and *B. inermis*; (3) determine the chromosome number in backcross progeny (in both cytoplasms) and in F_2 progeny to determine the distribution of chromosome numbers and the percentage of parental types; (4) make some preliminary empirical observations on the segregation of traits that define the *B. riparius* and the *B. inermis* genotypes.

Materials and methods

The plant materials used are listed in Table 1. Clones of *B. inermis* were selected from the cultivars Baylor, Tempo, and Saratoga. Clones designated as *B. riparius* were selected from the cultivar Regar and the Russian cultivars Krasnodarski 8 (S71-18), Krasnodar VIR K27534 (S42-10), and an introduction received as *B. biebersteinii* (S70-25) and one received as *B. variegatus* (S71-30). These clones were supplied by Dr. R. P. Knowles, Research Station, Saskatoon, Seeds from the parents and crosses were germinated and planted in peat pots in the greenhouse prior to planting into the field during the spring. Vernalization occurred in the field the following winter. The next spring the plants were dug, repotted, and placed in a cool (15 °C) growth room to even out maturity differences. When stem elongation was observed, the plants were moved into a greenhouse with 16-h days, with a day and night temperature of approximately 20° and 15 °C, respectively.

Table 1. Source of clones used in crossing

Species	2*n*	Source
B. inermis	56	Baylor
	56	Saratoga
	54	Tempo (aneuploid clone)
B. inermis (73-2)	28	B.G. Novosibirsk, USSR
B. erectus (70-89)	28	B.G. Vacratot, Hungary
B. riparius (S71-18)	70	Krasnodarski 8 (via Sweden)
B. riparius (S42-10)	70	Krasnodar VIR K27534
B. biebersteinii	70	Regar (PI 172390 Turkey)
B. biebersteinii (S70-25)	70	Ottawa 1927/8572 (Hungary)
B. variegatus (S71-30)	70	Ottawa 1927/9845 (Grignon, France)
B. arvensis	14	B.G. Bremen, Germany

Table 2. Number of crosses, seed set and plants obtained in crosses of bromegrass

	Florets	Seeds	F_1 plants
B. riparius × *B. inermis*	1,032	51	28
B. inermis × *B. riparius*	425	127	–
B. riparius × 4x *B. inermis*	201	0	0
4x *B. inermis* × *B. riparius*	111	1	0
B. riparius × 4x *B. erectus*	405	12	0
4x *B. erectus* × *B. riparius*	38	0	0
B. arvensis × *B. riparius*	223	51	1

Panicles and spikelets were trimmed to leave only florets of similar maturity. (Immature spikelets were removed with scissors and the upper florets on the remaining spikelet were removed to leave only 2–3 florets per spikelet.) The remaining florets were emasculated with tweezers. After emasculation the panicles were enclosed in dialysis tubing. When the florets on emasculated panicles began to open, a suitable unemasulated panicle was enclosed in the dialysis tubing and closed at the top to exclude other pollen. The stem of the pollen panicle was immersed in a vial of water which was replenished each day. The dialysis tube was agitated every day to aid in pollen release and, when pollination was completed, the tubing was opened and the pollen panicle was removed. This process was normally completed in 3–4 days. *Bromus riparius* was used as the female parent in the original crosses. However, the backcrosses were made to produce populations with both *B. inermis* and *B. riparius* cytoplasms. F_1 plants were planted in the field in a small isolation block and F_2 seed was harvested from these plants.

Crosses to produce F_1 hybrids with tetraploid (2n = 28) *B. inermis*, tetraploid (2n = 28) *B. erectus* Huds., and diploid (2n = 14) *B. arvensis* L. were also made. The genomic constitution of these species are known as well as their meiotic behaviour in interspecific hybrids with octoploid (2n = 56) *B. inermis* (Armstrong 1973, 1977, 1980). Hybrids between decaploid (2n = 70) *B. riparius* and lower ploidy level species would help determine the genomic constitution of *B. riparius*.

Chromosome counts were made using root tips obtained from juvenile seedlings grown in soil or vermiculite. The root tips were pretreated in cold 0.05% colchicine (0°–2 °C) for 24 h and were then fixed in 3:1 (95% ethanol:glacial acetic acid) for a minimum of 1 h. Hydrolysis in 1 *N* HCl at 60 °C for 12 min was followed by staining in leuco-basic fuchsin for 30–60 min. Root tips were then squashed in 45% acetic acid and pressed under a coverslip before microscopic examination.

Panicles for meiotic studies were fixed in 6:3:1 (95% ethanol:chloroform:glacial acetic acid) and stored in a refrigerator until used. Suitable panicles are usually completely extruded from the flag lead sheath (this varies depending on light intensity and quality). The florets were staged and suitable anthers were stained in Snow's alcoholic carmine (Snow 1963) for 3–7 days. Anthers were then squashed in 1% aceto-carmine in 45% acetic acid for microscopic examination.

Results

Seed set: interspecific crosses

Crosses between *B. inermis* and *B. riparius* were made in the greenhouse in May and June. During this time there was cool damp weather which affected anther dehiscence. The results from the crosses (Table 2) did not represent

the maximum seed set which could be obtained, but did indicate that *B. riparius* and octoploid *B. inermis* can be intercrossed very easily. Twenty-eight F_1 hybrids were obtained from the *B. riparius* × *B. inermis* cross and none from the crosses between *B. riparis* and tetraploid *B. inermis* (Table 2). Evidence of fertilization by ovule swelling was not evident in this cross and shrivelled seed was not obtained. Similarly, hybrids were not obtained from intercrossing *B. riparius* and 4 × *B. erectus*. The seed obtained when *B. riparius* was used as the female were from selfing. Crosses to *B. arvensis* resulted in one hybrid plant from 223 florets (Table 2). This annual species can be crossed with many of the perennial species of section *Pnigma*.

A sample of the seed set from the backcrosses and open-pollination progeny are given (Table 3). Seed set from the backcrosses ranged from about 20% to 50%, while those from open-pollination in an unreplicated spaced-plant nursery ranged from about 27% to 45%. Thus, there is no major problem with fertility in these crosses.

Table 3. Seed yield from open-pollination among F_1s and backcrosses of *B. riparius* × *B. inermis* hybrids to *B. inermis*

	Florets	Seeds	Seed set (%)
Backcrosses			
Tempo × 2-49-4	146	73	50.0
× 2-50-7	140	26	18.6
Open-pollination			
2-50-6	284	86	30.3
2-50-9	250	68	27.2
2-50-8	210	93	44.3

Chromosome pairing

Meiosis was studied in several *B. riparius* plants and *B. riparius* × *B. inermis* F_1 hybrids to determine if recombination between the chromosomes of the parents occurred (Table 4). The chromosome of *B. riparius* (2n = 70) essentially paired as 35 bivalents, but a low frequency of multivalents (trivalents to septavalents) was also observed. The bivalents frequently were present as ring bivalents. This pattern approaches that of an alloploid possessing five different genomes.

The chromosomes of the *B. riparius* × *B. inermis* F_1 hybrids (2n = 63) principally formed bivalents which existed primarily as rings. Multivalents ranging from trivalents to hexavalents were also at a low formed frequency. Because the chromosome number of the F_1 hybrids was 2n = 63, it was expected that the univalent frequency would be higher in these plants than in the *B. riparius* parent. These unpaired chromosomes probably represent the fifth genome found in meadow brome, and they also paired occassionally as trivalents in the F_1 hybrids.

Chromosome pairing in the hybrid with *B. arvensis* (2n = 14) × *B. riparius* suggested a different genomic composition. In this hybrid, the seven *B. arvensis* chromo-

Table 4. Meiotic pairing in *B. riparius* parents and F_1 hybrids with *B. inermis* and *B. arvensis*

	2*n*	I	II	0II	III	IV	V	VI	VII	VIII	No. of cells
B. riparius											
Regar S72-6	70	0.23	33.38	16.7	0.08	0.46	0.00	0.15	0.00	0.00	13
S72-6	70	0.57	33.85	20.86	0.00	0.43	0.00	0.00	0.00	0.00	7
S71-16	70	3.41	29.04	22.82	0.77	1.23	0.18	0.09	0.00	0.04	22
S71-18	70	0.68	31.04	19.80	0.00	1.56	0.00	0.24	0.00	0.04	25
S70-25	70	0.00	33.00	–	0.00	1.00	0.00	0.00	0.00	0.00	10
S42-10	70	0.86	30.56	16.57	0.57	0.71	0.00	0.14	0.14	0.00	7
B. riparius × *B. inermis* F_1 hybrids											
S42-10 × Baylor	63	4.88	25.38	23.75	2.25	0.12	0.12				8
Regar × Saratoga	63	5.48	25.23	20.00	1.77	0.29	–	0.06			31
		3–9	22–28	14.26	0–4	0–2	–	0–1			
Regar × Saratoga	63	6.07	26.29	21.07	0.93	0.25	0.14				28
		4–7	22–28	17–25	0–2	0–2	0–1				
S71-16 × Baylor	63	3.74	24.37	21.47	3.16	0.16	0.11				19
		2–6	23–27	19–24	1–5	0–1	0–1				
S71-16 × Baylor	63	5.78	25.78	21.78	1.00	0.67	–	0.11			9
		3–7	23–28	20–24	0–4	0–2	–	0–1			
B. arvensis × *B. riparius*	42	13.30	13.40	4.60	0.50						10
		10–18	10–14	0–10	0–4						

Table 5. Chiasma frequency divided by the somatic chromosome number or the number of pairing units primarily involved in pairing

	2*n*	Chiasmata	Xma/2*n*	Xma per bivalent	Cells
B. riparius					
Regar S72-6	70	52.54	0.75	1.50	13
Krasnodarski 8					
S71-16	70	59.09	0.84	1.69	22
S71-18	70	57.74	0.82	1.65	25
Krasnodarski VIR					
S42-10	70	53.14	0.76	1.52	7
B. riparius × *B. inermis*					
S42-10 × Baylor	63	55.88	0.89	1.94	8
Regar × Saratoga	63	49.55	0.79	1.80	31
	63	50.68	0.80	1.80	28
S71-16 × Baylor	63	54.42	0.86	1.88	18
	63	52.11	0.83	1.84	9
B. arvensis × *B. riparius*	42	19.10	0.54[a]	1.34	10

[a] The chiasma frequency per cell was divided by 35 because the *B. arvensis* chromosomes do not pair with the chromosome of *B. riparius*

somes can be identified by their larger size, and they remained unpaired. Seven smaller *B. riparius* chromosomes also remained unpaired the majority of the time in this hybrid, although they formed trivalents with the other meadow brome chromosomes at a low frequency (0.50 per cell). A maximum of four trivalents were observed in one cell. The other chromosomes paired as bivalents at a frequency of 13.40 per cell. These results suggest that instead of five different genomes, *B. riparius* has two different genomes, each with two copies, and the fifth genome may be partially homologous to one of these two genomes.

The chiasma frequency was calculated for each plant based on the configuration of the bivalents and multivalents (Table 5). The chiasma frequency per chromosome (Xma/2n) was calculated and compared for *B. riparius*, *B. riparius* × *B. inermis*, and the *B. arvensis* × *B. riparius* hybrid. In *B. riparius* this value ranged from 0.75 to 0.84 and in the *B. riparius* × *B. inermis* hybrids from 0.79 to 0.87. The number of cells scored from the *B. arvensis* × *B. riparius* hybrid was low because the meiocytes from this hybrid generally had sticky meiotic chromosomes, which made interpretation difficult. If this sample is an accurate reflection of autosyndetic pairing among the 35 chromosomes of *B. riparius*, then the lower chiasma frequency per chromosome perhaps suggests that the *B. riparius* genomes are somewhat differentiated from one another and pairing in the hybrids is allosyndetic, and that *B. riparius* and *B. inermis* contain homologous genomes.

Chromosome number of F_2 and backcross progenies

In the 123 F_2 progeny, the chromosome number ranged from 2n = 56 to 72. Twenty had a chromosome number of 2n = 63 and 68 had a chromosome number of greater than 2n = 63 (Table 6). Only 35 of the progeny had a chromosome number of less than 2n = 63. Thus, the distribution is skewed towards the higher chromosome numbers.

The backcross progeny were made with both *B. inermis* and the F_1 hybrids as the female, so that one set of backcrosses contained cytoplasm from *B. riparius* while the other set contained cytoplasm from *B. inermis*. The chromosome numbers of both progenies ranged from 2n = 55 to 63. There was a tendency for a higher frequency of progenies with 2n = 56 when *B. inermis* was used as the female, but some of the *B. inermis* clones were partially self-fertile, so the presence of a low number of selfs resulting from incomplete emasculation cannot be ruled out. In both backcrosses, the distribution of chromosome numbers was skewed towards the lower numbers, but the modal class could be different with different cytoplasm.

A few backcrosses were made to the MB parent (2n = 70). There was not a sufficient number to determine the distribution but as expected, the chromosome number ranged from approximately 2n = 63 and higher.

Progeny which contained telocentric or acrocentric chromosomes were common. In the backcross progeny, 40% of the plants had one telocentric or acrocentric, which resulted from a break at the centromere of un-

Table 6. Chromosome numbers in F_2 progeny and backcrosses of the F_1 ($2n=63$) of *B. riparius* × *B. inermis*

Progeny	Chromosome numbers[a] ($2n$)																	
	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	Total
F_2 (*B. riparius* × *B. inermis*)	–	3	–	3	3	5	8	13	20	16	3	11	8	12	3	13		2	123
F_1 × *B. inermis*	1	15	10	10	22	14	3	3	2										
B. inermis × F_1	7	26	8	13	8	10	6	3	3										
F_1 × *B. riparius*								3	3	2	4	7	2						

[a] Plants with $2n=55+1$ telocentric were recorded as $2n=56$ and similarly for the other classes

paired meiotic chromosomes. These results indicate that bromegrass chromosomes are highly subject to centric breakage. For simplicity, the telocentrics were tabulated as complete chromosomes (Table 6).

Discussion

Hybrids can be made between smooth bromegrass (*B. inermis*) and meadow bromegrass (*B. riparius*) with relative ease. These results confirm those of earlier reports which probably involved the same or related species (Elliott 1949; Nielsen 1963; Nielsen et al. 1962a, b; R.P. Knowles and V.S. Baron, personal communication). There is also a possibility that hybrids occur from natural open-pollination if flowering coincides (e.g. Hanna 1961). Therefore, hybrid production represents no obstacle to interspecific gene transfer. Fertility of the F_1 progeny is also adequate. The fertility of the F_2 and BC_1 progeny have not been studied in detail, but the preliminary information is that all plants possess a workable level of fertility. This would be expected based on previous reports (Nielsen et al. 1962b).

In order to introgress germ plasm from one species to another, it is necessary that recombination occur between the chromosomes of the parents. It is known that the chromosomes of *B. inermis* are capable of autosyndesis in hybrid combinations (Armstrong 1973, 1977). Similar evidence is provided for *B. riparius* in this study by the *B. arvensis* × *B. riparius* hybrid and in a previous study involving hybrids with *B. ramosus* (Huds.) (Armstrong 1984). This suggests that pairing in the F_1 of *B. riparius* × *B. inermis* could be all autosyndetic, particularly with respect to bivalent and trivalent formation. Therefore, the only evidence for allosyndetic pairing may exist in multivalent formation of greater than three chromosomes, but these could be accounted for by autosyndetic pairing, since quadrivalents have been reported in tetraploid cytotypes of *B. inermis* (Armstrong 1980). Therefore, there may be little or no recombination between *B. inermis* and *B. riparius*. However, if it is assumed that *B. inermis* and *B. riparius* are autoploids in which diploidization has resulted in bivalent pairing, then the same mechanism could be operating in the F_1 hybrids ($2n=63$). In this interpretation, *B. inermis* and *B. riparius* contain homologous genomes, and a high frequency of recombination occurs between *B. inermis* and *B. riparius* genomes. The additional genome from *B. riparius* could be partially homologous to the *B. inermis* genomes.

The distribution of chromosome numbers in F_2 progeny indicates the difficulty of selecting progeny with the parental chromosome number, since these occur at very low frequency. Selection based on fertility and morphology may not be sufficient, since it is not yet known if fertility is correlated with chromosome number in this material, and selection for plants containing both *B. inermis* and *B. riparius* traits may result in selection for intermediate chromosome numbers. In fact, selections made by R.P. Knowles (Agriculture Canada, Research Station, Saskatoon, Saskatchewan) for such combinations resulted in the selection of many progeny which contained the F_1 hybrid number ($2n=63$) or an intermediate number between $2n=56$ and $2n=63$ (unpublished results).

The frequency of plants approaching the euploid level of $2n=56$ is much higher among the backcross progeny, suggesting that it may be advisable to carry out at least one backcross in order to select such plants. Even if chromosome pairing were completely autosyndetic, these plants should contain 14 chromosomes from *B. riparius* and 42 from *B. inermis*. The analysis of chromosome paring in these progeny should have a direct bearing on determining if recombination is occurring. Additional backcrosses may not be advisable at this point, since the progeny may rapidly revert to the *B. inermis* type. It may be advisable at this point to produce open-pollinated progeny from these plants and attempt to select fertile recombinant types in later generations.

Several explanations are possible to explain the morphological difference between *B. riparius* and *B. inermis*. First, the genetic differences may involve all the genomes in the species. If this is the case, then recombination between any of the genomes could transfer some of the traits. In this case recombination in the BC_1 euploids is

a workable method. Secondly, the differences may all be carried on the extra genome carried by *B. riparius* (2n = 70) versus *B. inermis* (2n = 56). In this case, recombination must occur in the F_1 hybrid (2n = 63) and breeding of progeny at this ploidy level for several generations may be reasonable to maximize recombination. The third possibility is that some of the differences may be cytoplasmic. This question was addressed in this study by creating reciprocal backcross progeny, one containing *B. inermis* cytoplasm and the other *B. riparius* cytoplasm. Detailed studies have not been completed, but the morphology of the two backcross progeny suggest that the progeny with *B. riparius* cytoplasm tend to resemble the *B. riparius* parent more, while the progeny with *B. inermis* cytoplasm tend to resemble the *B. riparius* parent more. This appears to be true even in the near euploid (2n = 56) progeny in both backcrosses. In the *B. inermis* cytoplasm, the *B. riparius* traits are noticeably evident only in those plants carrying extra chromosomes, e.g., 2n = 60, 61, 62, 63. This observation requires further verification. If true, this supports an observation made by Nielsen et al. (1962 b) in reciprocal crosses of *B. inermis* and *B. tyttholepis* (Nevski) Nevski. The mechanism involved also requires verification, since reciprocal differences may involve mechanisms involving cytoplasmic differences or they may involve gamete selection based on compatibility/viability mechanisms. It would also be useful to determine if the transmission of organelles is unidirectional in *Bromus* hybrids.

This study has confirmed that (1) hybrids can be made easily between *B. inermis* and relatives such as *B. riparius*, and the hybrids and their F_2 and BC_1 progeny are sufficiently fertile for breeding experiments; (2) there is no definite proof for recombination between the genomes of *B. riparius* and *B. inermis* in the F_1 hybrids. This could explain the rapid reversion to parental types seen in previous studies and suggested in this work; (3) the F_2 progeny contain very few plants with the parental chromosome number (the majority remaining at 2n = 63) and the distribution is skewed towards the higher chromosome number. The chromosome number of BC_1 progeny reverts to the parental numbers rapidly; (4) preliminary observations indicate that the morphological differences between *B. inermis* and *B. riparius* are caused by chromosomal and cytoplasmic differences. This is because (a) BC_1 plants with *B. inermis* cytoplasm display *B. riparius* traits if they have extra chromosomes, but (b) BC_1 plants with *B. riparius* cytoplasm display *B. riparius* traits more strongly even in the absence of the extra chromosomes (2n = 56+). These observations require further verification. Observation (a) may suggest that the chromosomal genes controlling *B. riparius* traits may reside principally on the extra genome contained in *B. riparius* (2n = 70 versus 2n = 56) and, therefore, rapid backcrossing to *B. inermis* to restore the parental chromosome number would result in loss of the *riparius* traits. Some confirmation of reciprocal differences could be further obtained by backcrossing *B. inermis* into *B. riparius* cytoplasm and *B. riparius* into *B. inermis* cytoplasm. It is theoretically possible to develop 5 populations: (1) *B. inermis* chromosomes (2n = 56) in *B. inermis* cytoplasm (*B. inermis*); (2) *B. inermis* chromosomes (2n = 56) in *B. riparius* cytoplasm; (3) *B. riparius* chromosomes (2n = 70) in *B. riparius* cytoplasm; (4) *B. riparius* chromosomes (2n = 70) in *B. inermis* cytoplasm; and (5) *B. riparius* chromosomes (2n = 56, minus the extra *B. riparius* genome) in *B. inermis* cytoplasm.

An understanding of the control of *B. riparius* traits is extremely important in developing methods to recombine *B. inermis* and *B. riparius* traits. These results may also have implications for other combinations of *Bromus* polyploids.

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