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REVIEW

Are B chromosomes useful for crop improvement?

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Societal Impact Statement

Ensuring the sustainable production of food within the context of an increasing world population is a huge challenge facing humankind. Here we review the existence of additional, non-essential chromosomes, known as B chromosomes, and consider their potential usefulness for crop improvement. These enigmatic chromosomes have long fascinated scientists and although their origin and function in plants is somewhat obscure, new research is beginning to shed light on these mysterious chromosomes. This work suggests that B chromosomes may be useful for crop improvement, particularly in grasses, where they show promise as a mechanism to introduce new genes, which could potentially help us to produce more efficient crops.

Summary

The question of the usefulness of supernumerary B chromosomes (Bs) has long fascinated cytogeneticists. Since their discovery in 1907 thousands of species with Bs have been discovered, but their function in the genetics system remains enigmatic, from their origin, evolution, and adaptive significance, as well as their molecular structure and organization. New research is beginning to answer some of these tantalizing questions. Here, we summarize the known data and conclude that Bs are potentially useful, but only in a few known cases, especially in the grasses, and notably in terms of their engineering as plant artificial chromosomes (mini-chromosomes) to carry whole suites of transgenes outside of, and free from interference with, the normal genome.

KEYWORDS

A/B interchanges, artificial chromosomes, B-chromosomes (Bs), Bs in hybrids, chiasmata, gene mapping, mini-chromosomes, nondisjunction

1 | INTRODUCTION—WHAT ARE B CHROMOSOMES?

The continuity of chromosomes between one division of the nucleus and the next was a major topic of discussion in the early days of the science of cytogenetics. Wilson (1907, 1909) was studying this question in the insect *Metapodius terminalis*, the leaf-footed plant bug, when he made a remarkable discovery: he found B chromosomes,

which he called supernumeraries. In *Metapodius* the standard chromosome complement consists of $2n = 20$ autosomes, plus a pair of sex chromosomes, and in addition to that, certain individuals also carried from 0 to 6 of what we now call supernumerary B chromosomes (Bs). The properties described by Wilson for these supernumeraries were as follows: the number varies between individuals, with some having none; there is no pairing between these supernumeraries and the standard A chromosome set; no obvious phenotypic effects; no

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interaction with the environment and an irregular mode of inheritance. These properties are essentially the way that we define B chromosomes today, with the additional facts that they are usually smaller than the basic A chromosome set (As) and often heterochromatic. They can be detected at mitosis and meiosis (Figure 1), and are now known in close to two thousand species of plants and animals (Jones, 2017; Jones & Rees, 1982). A number of review papers deal with the story of B chromosomes (Table 1), including the most recent discoveries that they may contain transcribed genes. The idea that they are selfish genetic elements is still current, based on the fact that many of them have mechanisms of nondisjunction, or other modes of accumulation, which boosts their number over generations until modulated by their harmful effects and elimination due to pairing failure at meiosis.

There are many questions on the properties of these enigmatic Bs, concerning their origin, their behavior as selfish DNA, their genetic status in terms of any transcribed genes, their function in the genetics systems in natural populations of their hosts and whether they have any useful properties or applications. In some cases, we are tantalizingly near to answering these questions.

2 | ROMAN'S A-B INTERCHANGE DEMONSTRATES NONDISJUNCTION OF THE MAIZE B

Maize (*Zea mays*) is the main species where we can confidently say that Bs have potentially useful applications. The presence of B chromosomes in maize was first reported by Kuwada (1915), working with sweet corn. They were named as B chromosomes (Bs) by Randolph (1928), to distinguish them from chromosomes of the basic complement referred to as A chromosomes (As). The maize B is smaller than any of the As, is rich in heterochromatin and has a near terminal centromere (Figure 2). It is genetically relatively inert, and has no effect on plant morphology or vigor when present in low numbers, and is only detrimental when 10 to 20 are present (Jones & Rees, 1982). The genetic characteristics of the maize Bs have been described in detail by Randolph (1941). In crosses made where only one of the parents carries Bs, such as ♀0B × ♂1B or ♂0B × ♂2B the progeny had more than the number of Bs expected

by Mendelian segregation. This outcome could not be explained by the behavior of the Bs at meiosis, but suggested a mitotic drive (*mitotic nondisjunction*) taking place during the divisions in the pollen grains which gave rise to the male gametes (sperm nuclei). Cytological observations were ruled out for technical reasons and genetic analysis could not be performed since the Bs carried no known genes or obvious effects on the phenotype. Roman (1947) resolved this problem of their transmission using an interchange, generated by X-rays, between A chromosome 4 and the B (A-B interchange, designated as TB-4a, Figure 3). The system works on the basis that the behavior of the B is independent of it remaining intact. The break point, in chromosome 4 is in the short arm, while for the B it is close to the junction of euchromatin heterochromatic regions (Figure 3.) The details of the behavior of the interchanges at meiosis, and their transmission through gametogenesis, are described in detail by Roman (1947) and are given in diagrammatic form by Jones and Rees (1982).

To carry out the analysis a normal female parent carrying the recessive *su* marker gene for sugary endosperm on chromosome four was crossed reciprocally with a male heterozygous for the interchange (Figure 3). The chromosome 4 segment on the B carried the dominant *Su* allele for non-sugary endosperm, and the inheritance of the marker was followed from parents to offspring. From crosses with $B^{4Su} B^{4Su}$ as the female parent all of the kernels had non-sugary endosperm—clearly B^{4Su} was transmitted to the triploid endosperm. When $B^{4Su} B^{4Su}$ was used as the male however, about half the grains were non-sugary and about half were sugary. In this case the endosperm nuclei in the sugary grains were lacking B^{4Su} . How could this be? It seemed to suggest there are two kinds of sperm nuclei, and that nondisjunction had taken place at the second pollen grain mitosis. The sperm nucleus that fertilized the egg carried two B^{4Su} chromatids and the sperm nucleus which fertilized the polar nuclei to produce the endosperm carried none, and this was confirmed.

It was also noticed that the ratio of non-sugary to sugary endosperm varied, and that the sperm nuclei carrying the B chromatids had a preference for fertilizing the egg nucleus. Roman confirmed that the preferential fertilization by the B-carrying sperm worked for normal Bs, as well as for the B/A interchange. Investigations into the mechanism of preferential fertilization, which happens about

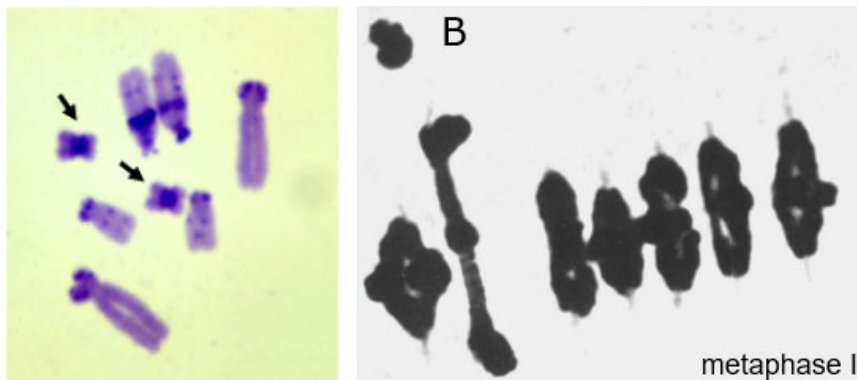


FIGURE 1 Right panel, B chromosomes at c-metaphase in *Crepis capillaris* with 2 Bs; left panel, meiosis in rye, *Secale cereale*, with 1 B

TABLE 1 Selected reviews on B chromosomes

1982	Jones RN, Rees H. <i>B chromosomes</i> . New York: Academic Press.
1995	Jones RN. B-chromosomes in plants. <i>New Phytologist</i> 131(4): 411–434.
2005	Camacho JPM. B chromosomes. In: Gregory TR ed. <i>The evolution of the genome</i> . Amsterdam: Elsevier.
2006	Burt A, Trivers R. B Chromosomes. <i>Genes in Conflict: The Biology of Selfish Genetic Elements</i> . Cambridge: Harvard University Press, 325–380.
2013	Houben A, Banaei-Moghaddam AM, Klemme S. Biology and Evolution of B Chromosomes. In: Greilhuber J, Dolezel J, Wendel JF eds. <i>Plant Genome Diversity Volume 2</i> : Springer Vienna, 149–165.
2014	Houben A, Banaei-Moghaddam AM, Klemme S, Timmis JN. Evolution and biology of supernumerary B chromosomes. <i>Cell Mol Life Sci</i> 71(3): 467–478.
2015	Banaei-Moghaddam AM, Martis MM, Macas J, Gundlach H, Himmelbach A, Altschmied L, Mayer KF, Houben A. Genes on B chromosomes: Old questions revisited with new tools. <i>Biochim Biophys Acta</i> 1849(1): 64–70.
2017	Valente GT, Nakajima RT, Fantinatti BE, Marques DF, Almeida RO, Simoes RP, Martins C. B chromosomes: from cytogenetics to systems biology. <i>Chromosoma</i> 126(1): 73–81.
2017	Houben A. B Chromosomes – A Matter of Chromosome Drive. <i>Frontiers in Plant Science</i> 8(210).
2017	Jones N. New species with B chromosomes discovered since 1980. <i>The Nucleus</i> 60(3): 263–281.
2017	Ruban A, Schmutzer T, Scholz U, Houben A. How Next-Generation Sequencing Has Aided Our Understanding of the Sequence Composition and Origin of B Chromosomes. <i>Genes</i> 8(11): 294.

two thirds of the time, and provides the mitotic drive of the maize B, have so far failed to provide a complete understanding of the process (Carlson, 1986).

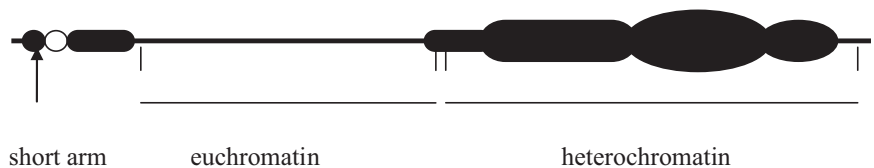
3 | B CHROMOSOMES HAVE APPLICATIONS IN GENE MAPPING IN MAIZE

Roman's system of using X-rays to produce B-A translocations has proved to be useful for gene mapping. A large number of such translocations have been produced, and the list is summarized by Beckett (1978). Nondisjunction of the B^A chromosome at second pollen grain mitosis is the basis of the system. Crosses are made between homozygous recessive females and a set of dominant tester translocation males. The F₁ progeny will have the dominant trait in the endosperm (or the plant) when the dominant allele in the male is carried on the B^A chromosome of the translocation, and the recessive phenotype will be "uncovered" in some of the F₁ through nondisjunction, when the sperm nucleus lacking the B^A chromosome fertilizes the egg. When a recessive gene of unknown locus is crossed as female to each member of the series, it can be uncovered by one of the translocations of the series and mapped to the arm concerned (Beckett, 1978, 1991; Birchler, 1991; Birchler & Alfenito, 1993; Carlson, 1986). More than 100 B-A translocations have now been listed and described, one for each arm (Beckett, 1991). B-A lines can

also be developed with points of breakage in different places to give some information on linkage relationships of genes within an arm. Maize B-A Translocations have also been used for mapping RFLPs (Weber & Helentjaris, 1989).

4 | B CHROMOSOME EFFECTS ON A CHROMOSOME CHIASMATA IN DIPLOIDS

There have been a number of studies of the behavior of Bs at meiosis, not only in terms of the inheritance pattern of the Bs themselves, but also on the effects they may have at meiosis on the A chromosome set (Table 2). The principle question in relation to the As is to what extent, and how, the Bs influence the pattern of chiasma frequency and distribution. The analysis shows that the effect may lead to an increase or decrease in the mean number of chiasmata in meiocytes, and that these changes may or may not be associated with changes in the variation between cells, namely the between cell variance. The *raison d'être* for this analysis being that Bs may influence patterns of genetic recombination which could have significance in modulating the release of new genetic variation, or adaptive features, in natural populations, as well as usefulness in crop improvement. The weakness in terms of this reasoning, however, is that we lack evidence relating variation in patterns of chiasma distribution to outcomes of variation in phenotypes, other than in a theoretical sense.

**FIGURE 2** The maize B chromosome

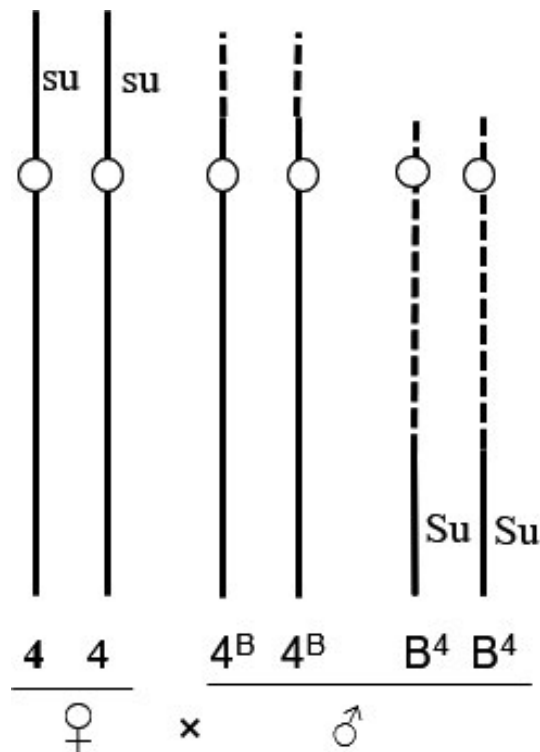


FIGURE 3 The structure of Roman's TB-4a interchange

As far as plants are concerned there are only four species which can be described as crop plants, the principle ones being *Triticum* species, *Lolium perenne*, *Secale cereale*, and *Zea mays*. The maize story is the one where the increase in mean pollen mother cell chiasma frequency is supported by an increased genetic recombination between marker genes on the long arm of chromosome 3 (Hanson, 1969). There is clearly more research needed here to provide the cytogenetic basis for these effects of Bs before we can say that they are useful.

The latest information is that B chromosomes are associated with the redistribution of genetic recombination toward lower-recombination chromosomal regions in perennial ryegrass (Harper et al., 2018). This has potential applications in plant breeding and crop improvement. In this study, the effects of the presence/absence of B chromosomes on genetic recombination was investigated through generating DArT marker genetic maps for 6 perennial ryegrass diploid populations, the pollen parents of which contained either two B or zero B chromosomes. While overall cytological estimates of chiasma frequencies were significantly lower in pollen mother cells with two B chromosomes as compared to zero Bs, the recombination frequencies within some marker intervals were actually increased, particularly for marker intervals in lower recombination regions of chromosomes, i.e., pericentromeric regions. Thus, in perennial ryegrass, the presence of two B chromosomes redistributed patterns of meiotic recombination in pollen mother cells in ways which could increase the range of allelic variation available to plant breeders.

5 | EFFECTS OF B CHROMOSOMES ON CHROMOSOME PAIRING IN HYBRID PLANTS

Mochizuki (1964) was the first to report that the B chromosomes of *Aegilops mutica* could suppress homoeologous pairing in the F1 hybrid with bread wheat (*Triticum aestivum*) × *Ae. mutica*. This work started a flurry of excitement in the wheat cytogenetics community to exploit the potential of this finding for practical applications in both the cereals and the grasses. The reasons for excitement are clear enough, namely that the Pooideae subfamily of the Poaceae contains many of the most agronomically important temperate cereals and grasses, such as wheat, barley, oats and ryegrass. The high status of the cereals and grasses for use as food for human consumption or as forage for farm animals has led to extensive crop improvement programmes, often involving wide crosses and selection of useful hybrids. However, these wide interspecific or intergeneric crosses are often bedevilled by reduced levels of fertility, or failure of recombination or successful segregation at meiosis; Mochizuki's work offered a possible way to ameliorate the frustrations of chromosome engineers. Some intergeneric crosses between wheat and rye have been used successfully for crop improvement, and the effects upon meiotic pairing of the particular rye cultivars used have been evaluated (Fedak & Gupta, 1991). In all of the wheat × rye hybrids involving B chromosomes, the wheat variety "Chinese Spring" has always been the female parent, and the pollen parent has always been either Transbaikal or Japanese JNK strain of rye. The results of these investigations are summarized and referenced in detail in the table found in Jenkins and Jones (2004). The results are contradictory, and there is no consistent pattern for the way in which the Bs of rye interact with the pairing control genes of wheat. The rye Bs do appear to carry genetic elements that interact with the pairing control genes of wheat under some circumstances, depending on the source of the B and which wheat chromosomes are missing in the various nullisomic hybrids used.

The most hopeful approach we have so far for the usefulness of B chromosomes in plants comes from the work of Evans and Macefield (1973, 1974), who made a remarkable discovery on the effect of Bs on chromosome pairing in hybrids between the ryegrasses *L. temulentum* × *L. perenne*. The genome size, and therefore the chromosomes, of *L. temulentum* are 33% larger than those of *L. perenne*, and it comes as some surprise to learn that in the hybrid there is a high degree of pairing and chiasma formation between the homoeologous asymmetrical bivalents (Figure 4).

When 2Bs are present however, contributed by the *L. perenne* parent, there are only half the average number of bivalents, and those that are formed are mainly rods with a single chiasma. At the tetraploid level there is another remarkable event (Figure 4): namely the contrast in chromosome pairing in the hybrids with and without Bs. When Bs are lacking there is pairing and chiasma formation between homoeologous and homologous bivalents, giving rise to multivalents as well as bivalents and univalents, but the presence of Bs diploidises meiosis and only bivalents are formed involving

TABLE 2 Effects of Bs on chiasma frequency and distribution in A chromosomes

Plants	
Chiasma frequency increased	
<i>Acanthophyllum laxiusculum</i> ($2n = 2x = 30 + 0-3Bs$)	Ghaffari and Bidmeshkipoor (2002)
<i>Allium flavum</i> ($2n = 2x = 16 + 0-2Bs$)	Loidl (1982)
<i>Centaurea kandavanensis</i> ($2n = 2s = 20 + 0-3Bs$)	Ghaffari (1998)
<i>Crepis capillaris</i> ($2n = 2x = 6 + 0-3Bs$) Cell variance also increased	Parker, Jones, Edgar, and Whitehouse (1990)
<i>Listera ovata</i> . ($2n = 2x = 34 + 0-8Bs$)	Vosa and Barlow (1972)
<i>Puschkinia libanotica</i> ($2n = 2x = 10 + 0-7Bs$) Between cell variance also reduced	Barlow and Vosa (1970)
<i>Secale cereal</i> wild rye ($2n = 2x = 14 + 0-4Bs$)	Zečević and Paunović (1969)
<i>Silene maritima</i> ($2n = 2x = 24 + 0-15Bs$)	Cobon and Murray (1983)
<i>Zea mays</i> ($2n = 2x = 20 + 0-10Bs$) Bs also increased genetic recombination between marker genes on the long arm of chromosome 3	Ayonoadu and Rees (1968); Hanson (1969)
Chiasma frequency reduced	
<i>Aegilops speltoides</i> , <i>Ae. mutica</i> ($2n = 2x = 14 + 0-3Bs$)	Simchen, Zarchi, and Hillel (1971)
<i>Agropyron mongolicum</i> , <i>A. cristatum</i> ($2n = 2x = 14 + 0-6Bs$)	Chen, Jahier, and Cauderon (1993)
<i>Artemisia frigida</i> ($2n = 2x = 18 + 0-2Bs$)	Bakshi, Kaul, and George (1987)
<i>Briza humilis</i> ($2n = 2x = 14 + 0 = 4Bs$)	Murray (1984)
<i>Lolium perenne</i> ($2n = 2x = 14 + 0-3Bs$)	Cameron and Rees (1967)
<i>Najas marina</i> ($2n = 2x = 12 + 1B$)	Viinikka (1973)
No effect	
<i>Allium sphaerocephalon</i> ($2n = 2x = 16 + 0-2Bs$) but the between cell variance significantly increased	Guillén and Rejón (1984)
<i>Brachycome lineariloba</i> ($2n = 2x = 2 + 0-3Bs$)	Carter and Smith-White (1972)
<i>Secale cereale</i> experimental population ($2n = 2x = 14 + 0-4Bs$) but increase in between cell variance. Effects are chromosome specific	Jones and Rees (1967); White and Rees (1985)
Animals	
Chiasma frequency increased	
<i>Dichroplus pratensis</i> ($2n = 2x = 19\delta/20\phi + 0-4$) Between cell variance also increased	Bidau (1987)
<i>Euthystira brachyptera</i> ($2n = 2x = 17\delta + 0-1B$) and between cell variance also increased	Fletcher and Hewitt (1980)
<i>Myrmeleotettix maculatus</i> ($2n = 2x = 17\delta + 0-3Bs$)	John and Hewitt (1965)
<i>Rattus fuscipes</i> ($2n = 2x = 38 + 0-3Bs$)	Thomson, Westerman, and Murray (1984)
Chiasma frequency reduced	
<i>Trimerotropis pallidipennis</i> ($2n = 2x = 23\delta + 0-1$)	Confalonieri (1992)
No effect	
<i>Dichroplus elongatus</i> ($2n = 2x = 23\delta/24\phi + 0-6Bs$) but change in pattern of chiasmata distribution within bivalents	Remis and Vilardi (1986)
<i>Heteracris littoralis</i> ($2n = 2x = 23\delta/24\phi + 0-3Bs$)	Cano and Santos (1988)
<i>Locusta migratoria</i> ($2n = 2x = 23\delta + 0-5Bs$) and no effect on between cell variance either	Viseras, Salcedo, and Camacho (1988); Cabreró, Viseras, and Camacho (1984)

homologous chromosomes. B chromosomes from *L. rigidum* behave in the same way in hybrids with *L. temulentum* (Evans & Taylor, 1976), but this does not happen in all hybrids. Another potentially useful effect of Bs on chromosome pairing in hybrids was discovered when

X-irradiated inflorescences of *L. perenne* produced a centric B^A fragment that was found to have lost the capacity to undergo nondisjunction at pollen grain mitosis, and was transmitted in the normal mendelian manner (Evans & Macefield, 1977). In diploid hybrids of

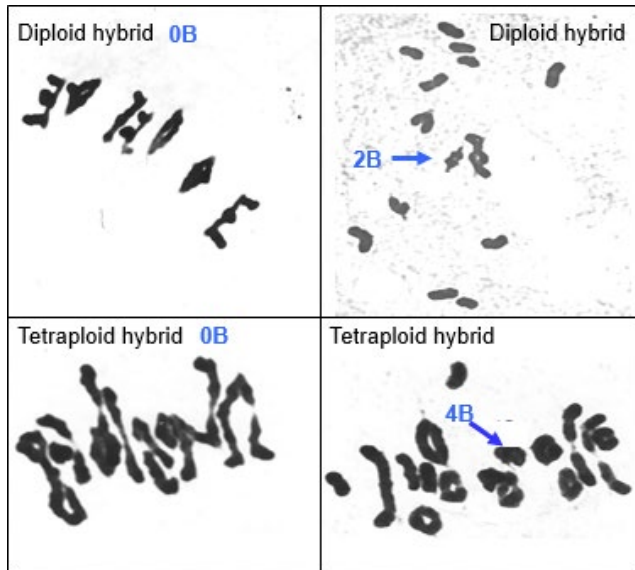


FIGURE 4 Chromosome pairing at metaphase I of meiosis in diploid and tetraploid hybrids of *Lolium temulentum* x *Lolium perenne*

L. temulentum x *L. perenne* it was found that this fragment could, to some extent, partially suppress homoeologous pairing at metaphase I, although this promising line of work has not been taken any further. It is exceptional to create B^A fragments that are regular in their inheritance, since standard B chromosomes cannot normally be made to function in this way, which opens up many practical opportunities.

6 | B CHROMOSOMES CAN BE USED FOR UNDERSTANDING NONDISJUNCTION

Nondisjunction is a phenomenon of failed chromosome segregation either in mitosis or meiosis. In humans mitotic nondisjunction is often connected to tumorigenesis, while the inability of homologs to separate in meiosis leads to the formation of unbalanced gametes. Further combination of normal and unbalanced gametes results in aneuploid zygote formation. These zygotes are either non-viable or give rise to embryos with severe developmental abnormalities such as trisomy (Day & Taylor, 1998).

While nondisjunction of A chromosomes has harmful effects, B chromosomes use it for their own benefit. In many plants, as well as animal species, Bs possess a specific accumulation mechanism, also called B chromosome drive (Jones, 1991). The drive is essential for the successful maintenance of Bs in populations, and for the balancing of their loss due mitotic and/or meiotic elimination. The timing, and the way that the drive works, is different for Bs of different species, but in many cases it plays a key role in both premeiotic and post meiotic drive, as reviewed by Houben (2017).

Despite the fact that chromosome drive involving nondisjunction is widespread among B-carrying species, the understanding of its control is still limited. The parts of Bs responsible for nondisjunction are known only for rye and maize. In rye, a trans-acting control region is located at the end of the long arm and includes

two B-specific repeat families, E3900 and D1100, which are shown to be transcriptionally active in anthers where the nondisjunction process occurs (Banaei-Moghaddam et al., 2012; Carchilan et al., 2007). In addition, cis-acting pericentromeric sticking sites are required to ensure B-nondisjunction (Endo et al., 2008). The absence of one of these elements makes Bs behave in the same way as As and segregate regularly. The maize Bs are characterized by the presence of two factors on the long arm which act in trans, and which are responsible for the nondisjunction process (Birchler & Han, 2013). The centric heterochromatin of maize Bs was also shown to be involved into nondisjunction control (Carlson, 2006). For both rye and maize it seems that nondisjunction does not depend on centromere function, but rather on sequences located in centromeric and pericentromeric region (Banaei-Moghaddam et al., 2012; Han, Lamb, Yu, Gao, & Birchler, 2007). Now new technologies have opened up new possibilities for the detailed analysis of B-derived transcripts and for deciphering the exact way of nondisjunction control. Assuming that basic aspects of chromosome biology may be conserved among all eukaryotes, the data obtained from Bs may be useful in understanding mechanisms of chromosomal nondisjunction in human cells.

7 | B CHROMOSOMES AS MINI-CHROMOSOMES

Artificial or engineered chromosomes (mini-chromosomes) do not require many components to function properly; essential components are centromere, telomeres, origin of replication and genes of interest. Engineered chromosomes are used as nonintegrating vectors. Since they were first successfully constructed in yeast in 1983 (Murray & Szostak, 1983) and in bacteria in 1989 (O'Connor, Peifer, & Bender, 1989), engineered chromosomes have proven to be useful in several situations. Bacterial and yeast artificial chromosomes have been used to clone large DNA inserts, which are still in high demand for sequencing and mapping. Currently, the use of mini-chromosomes in higher organisms appears to be most attractive to those studying in plants. It offers the next generation of crop genetic engineering, with the possibility to introduce multiple genes, or even whole metabolic pathways, in a single step without interfering in the functions of existing genes in the normal genome (Yu, Yau, & Birchler, 2016).

The construction of mini chromosomes may be based on “top-down” or “bottom-up” approaches. The first involves endogenous chromosomes as basis for further modifications, including the truncation of end parts and the insertion of sequences of interest. The second approach involves the construction of entire artificial chromosome by assembling all the necessary parts of it *de novo*. The only success of the “bottom-up” approach in plants was the generation of a maize mini-chromosome, which was shown to be stable and to segregate in meiosis with a ratio close to Mendelian inheritance (Carlson et al., 2007). However, certain aspects of this work were subject to criticism (Houben, Dawe, Jiang, & Schubert, 2008) and require further experimental evidence. At the present time the most successful

methodology was developed for mini-chromosome construction in maize (Yu, Han, Gao, Vega, & Birchler, 2007). Both, maize A- and B chromosomes were used as a basis for the “top-down” generation of engineered chromosomes. To reduce the size and complexity of maize Bs during mini-chromosome construction, telomere mediated chromosomal truncation was adopted (Yu, Lamb, Han, & Birchler, 2006). However, the recovery of truncated chromosomes derived from A chromosomes is not possible in diploid backgrounds due to the lack of compensation for the loss of key genes, meaning that tetraploids are required at the primary stage of mini-chromosome generation (Gaeta, Masonbrink, Krishnaswamy, Zhao, & Birchler, 2012). Bs can tolerate truncation due to their dispensable nature, and can be recovered with higher frequency (Yu et al., 2007).

The main properties required for functional mini-chromosomes were defined in Yu et al. (2016) as follows: synthetic chromosomes should have minimal interference with host growth and development and possess no genes of their own; they should be stable in mitosis and meiosis and transmit from cell to cell and generation to generation; they should allow modification, addition, and deletion of genes on them. By definition, Bs do not interfere with the host phenotype if present in low numbers, and until recently Bs were supposed to have no genes of their own. Even so, the latest findings demonstrate that some Bs may not only possess gene sequences, but those sequences may even be functional (Akbari, Antoshechkin, Hay, & Ferree, 2013; Banaei-Moghaddam, Meier, Karimi-Ashtiyani, & Houben, 2013; Ma et al., 2016), nonetheless Bs may be the perfect system for integrating and expressing genes of interest without significant disturbance to the core genome. It was shown using a GUS gene expression cassette integrated on B- or mini B chromosomes of maize that Bs can accept and express foreign genes (Yu et al., 2007), but the most challenging part is the transmission and stability of the Bs. The transmission success of mini Bs can vary according to host genotype, and an understanding of B transmission control is thus important for the successful use of B-based mini-chromosomes (Houben & Schubert, 2007).

Once constructed for one species, mini-chromosomes will not necessarily be functional in other species, especially due to centromere identity. As discussed in Jin et al. (2004), centromeres of one parental genome in wide crosses are often weaker, causing chromosome elimination. Most likely, *de novo* generation of artificial chromosomes will be required for almost every plant species with the exception of closely related taxa.

8 | CONCLUDING REMARKS

B chromosomes are known in well over a thousand species (Jones, 2017), and are especially common in grasses and cereals. It comes as no surprise therefore that many researchers have looked for ways to find their usefulness, and practical applications, particularly in crop plants, and also to justify their widespread occurrence in nature. Thus far the story is not one of much success, and what has shown most promise is mainly confined to maize. The applications of maize Bs for

chromosome mapping are well established, and their potential as mini chromosomes also holds promise. The maize Bs are dispensable, and can be present in low numbers without any noticeable effects on the host phenotype. They are ideal candidates for plant artificial chromosomes, and can carry enough genes to code for a whole biochemical pathway without any conflict with the host genome. B chromosomes are useful, albeit to a limited extent and mainly for one species, yet they continue to engage researchers and we look forward to further developments in the field.

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