

# B Chromosomes in Wheat: Evolution, Functions and Breeding Potential

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**Abstract:** Supernumerary B chromosomes (Bs) have been documented in over 2000 species across the plant, animal, and fungal kingdoms, representing one of the most intriguing components of the genome that have consistently garnered significant attention in the past. These Bs form a distinct category of chromosomes that are not deemed essential. While coexisting with the standard set of chromosomes in an organism, the copy numbers of Bs can vary among individuals within a population or even among cells within a single organism. Multiple processes, including chromosomal rearrangement, uneven segregation, chromatid non-disjunction, and deletion in specific regions, lead to the formation of the Bs from the A chromosome. These dispensable Bs possess their own genetic content and do not undergo recombination with A chromosomes. Although various roles of Bs in breeding have been explored in the literature, their specific role in wheat improvement remains unclear. The understanding of their origins, composition, and evolutionary history in wheat is still incomplete. Therefore, this review discusses the current knowledge of the genetic makeup of Bs, their functions, their relationship with A chromosomes, and the morphogenetic consequences in the context of wheat.

**Keywords:** B chromosome; wheat; evolution; breeding



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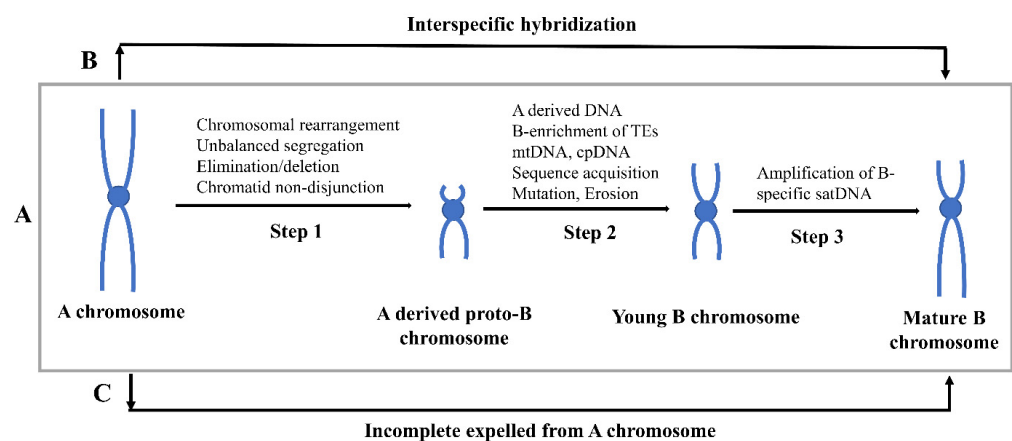
## 1. Genetic Evolution of Bs in Wheat

B chromosomes (Bs) are supernumerary or accessory chromosomes frequently inherited preferentially, deviating from Mendelian segregation, found among plants, animals and fungi [1–3]. When chromosome transmission rates exceed 0.5 and do not follow the Mendelian law of equal segregation, the ensuing transmission advantage is referred to as ‘drive’. Although Bs may exhibit the most common form of drive known for genetic components [4], little is known about the cellular and molecular mechanisms behind their drive. Bs are not required for organism growth or development, yet they are abundant in all eukaryotic phyla and are assumed to represent a sort of selfish DNA [3–6]. The drive

of Bs occurs in a species-specific manner at pre-meiotic, meiotic, or post-meiotic divisions. In addition to drive, non-Mendelian inheritance of Bs could be influenced by mitotic and meiotic instability. The maximum number of Bs tolerated by the host varies by species (for example, maize, wheat, chives, and rye can carry up to 34, 20, 6, and 2 Bs, respectively [7]).

## 2. Relationship Between Bs and A Chromosome Genome

The origin of B chromosomes remains one of the most intriguing questions since their discovery, giving rise to numerous hypotheses and interpretations [8]. The dominant opinions and explanations imply that the B chromosome originated from the A chromosome. Chromosomal rearrangement or unbalanced segregation results in an extra copy of A chromosomes that acquire additional genetic materials and ultimately forms the Bs [8–15]. During their evolution, Bs incorporate various mobile elements and unique coding and non-coding sequences, sometimes amplifying and sometimes degenerating due to very small selection pressure [16]. This interpretation has been strengthened by the recent next-generation sequencing of some plant species, including rye (*Secale cereale*), goat grass (*Aegilops speltoides*), maize (*Zea mays*), barley (*Hordeum vulgare*) and sorghum (*Sorghum bicolor*) [15,17–20]. The other interpretation encompasses the idea that the B chromosome has developed from the sex chromosome and through interspecific hybridization [21,22]; however, some others have argued that the B chromosome can be incompletely expelled from the A chromosome [23] (Figure 1).



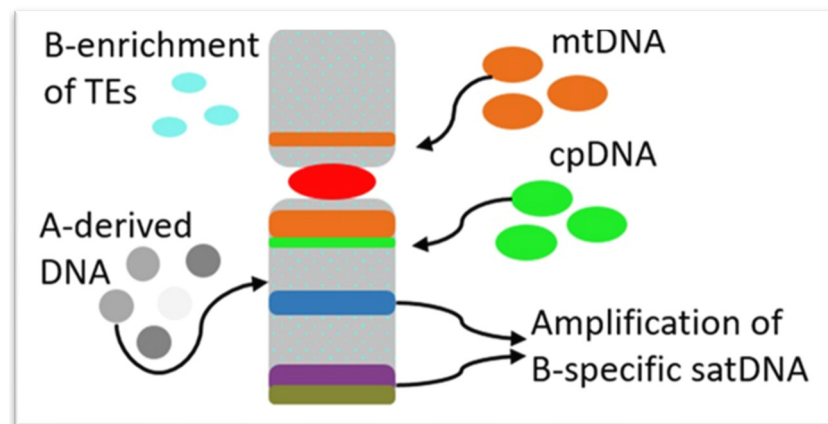
**Figure 1.** Schematic diagram showing models regarding the origin of Bs from A chromosomes. Bs originated from the A chromosome through (A) stepwise modifications, (B) interspecific hybridization and/or (C) incomplete expelled from A chromosomes. Derived proto-B were developed due to chromosomal rearrangement, unbalanced segregation, chromatid non-disjunction, and deletion of specific segments. Transposable elements, mtDNA, and cpDNA are attached with proto-Bs, which undergo amplification, resulting in mature B chromosomes.

There are several models on the evolutionary dynamics of Bs. The first one is related to the selfish drive mechanisms that help Bs to spread among the population [24,25]. The second one is that Bs can be maintained without drive mechanisms if they have beneficial effects [26]. However, some plants show that models can work together to maintain the B chromosome in the population. As an example, in rye, Bs have beneficial effects, and there is still driving effect [27], suggesting the cooccurrence of drive and beneficial functions, making it more complex. Some reports suggest that Bs can accommodate into the genome by being translocated to autosomes or sex chromosomes or could acquire regular behavior during meiosis if two Bs pair with each other, in the cases of grasshoppers and maize [28].

## 3. Role of B Chromosomes

Considering that many Bs have originated from the A genome, this raises valid questions about the consequences of partial genome duplication and subsequent transcription when Bs are present in an organism. On occasion, the presence of Bs has been demonstrated

to impact the transcription of loci within the A genome, particularly when small RNAs produced by duplicated sequences on the Bs target similar loci within the A genome (Figure 2).



**Figure 2.** Internal structure of the B chromosome in a wheat plant. B-specific repeat accumulation is caused by gene erosion/silencing and meiotic recombination limitation. High levels of B-specific repetitions, an effective drive mechanism, and a manageable effect on the host organism's fitness were all possible for Bs to attain. Satellite DNA is satDNA; mitochondrial DNA is mtDNA; and chloroplast DNA is cpDNA.

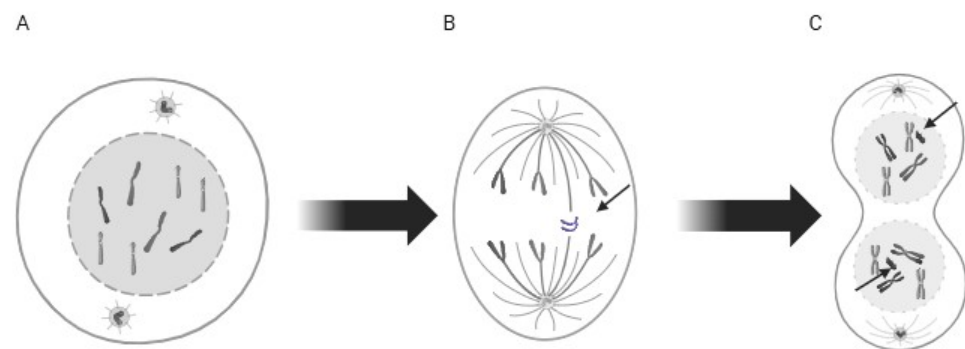
Bs have applications in gene mapping, effects on A chromosome chiasma in diploids, and have an effect on chromosome pairing in hybrid plants. Bs assist cytogenetics analysis and provide ideal candidates for fluorescence within in situ hybridization (FISH), as well as in genomic in situ hybridization (GISH) studies on various aspects of nuclear organization and activity. Considering Bs as being the 'painting', comparisons can be made between individuals with and without them, as well as having a range of numbers when they are present [29]. In the case of rye Bs, it is also possible to make alien addition lines in wheat and then to use probes for B-specific sequences, together with those for total genomic DNA, to visualize the arrangement of whole Bs at the interphase [30]. Additionally, considering the background of this line of work, the interphase behavior of rye Bs in hexaploid *Lindstrom* wheat has previously been documented in terms of nuclear distribution and patterns of association [30]. Bs were discovered to exhibit a high amount of co-orientations, with similar ends facing in the same direction, with a preference of being associated in pairs over occupying separate nuclear domains. Bs can also be used for understanding non-disjunction. However, in low numbers, Bs are neutral in their phenotypic consequences and damaging in excessive numbers, influencing a wide variety of nuclear and exophenotypic features. They are especially harmful to fertility and have the puzzling effect of changing their phenotype in some situations based on their presence in odd- or even-numbered combinations [30].

#### 4. Phenotypic and Cytogenetic Consequences of Bs in Wheat

The role of Bs in wheat growth and development remains unclear. While Bs are not considered essential, phenotypic effects associated with them have been documented. These effects typically accumulate based on the quantity of Bs present, rather than their mere presence or absence. When present in low numbers, Bs tend to have a minimal or negligible impact on an organism's phenotype. However, when their numbers increase significantly, they often exert a negative influence on the overall fitness and fertility of an organism. This phenomenon has been extensively reviewed and discussed in prior studies [4,5,7]. However, given that Bs are a significant source of intraspecific variation in nuclear DNA content [3], we anticipate that they may play an important role in the seed set, growth, and development of wheat, depending on their number. They have a significant impact on seed germination and pollen fertility in wheat. According to earlier

research, there are differences in fertility between 2B and 0B plants [4]. Additionally, Bs were shown to increase the pollen grain germination potential in rye [31] and pearl millet [32] under in vitro conditions. *Allium*, however, showed both beneficial and harmful effects [33,34]. Additionally, we are convinced that Bs may play a beneficial function in adaptations because Plowman and Bougourd [35] found that Bs had a positive impact when under drought stress.

Bs are kind of supplementary chromosomes over the standard diploid or polyploid (As) chromosomes. The exact stage of their origin is unknown; however, during meiosis, Bs pair and form chiasmata among themselves with some exceptions due to being heterologous [36] or too short to pair and do not pair or recombine with A chromosome so far. Therefore, they follow their own species-specific evolutionary pathway. In Bs carrying wheat, the mitotic transmission of Bs is dis-junctional during growth and development (Figure 3). Therefore, the number of Bs remains the same in mitotic cells, with some exceptions in *Aegilops speltoides* [6] and *Crepis capillaris* [12]. However, the variation in the number of Bs in mitotic cells (exception) is due to the non-disjunction of Bs' sister chromatids during the anaphase, resulting in an absence of Bs in one daughter cell but accumulation in other cells [12]. Univalent Bs are mostly formed. However, bi- or multivalent results in metaphase I vary due to their number in different species. Mostly, they are lost either during the first meiosis stage or in the second anaphase, as they carry dissimilar genetic information that might be used in the future to manipulate A chromosomes' behavior during meiosis in wheat [36].

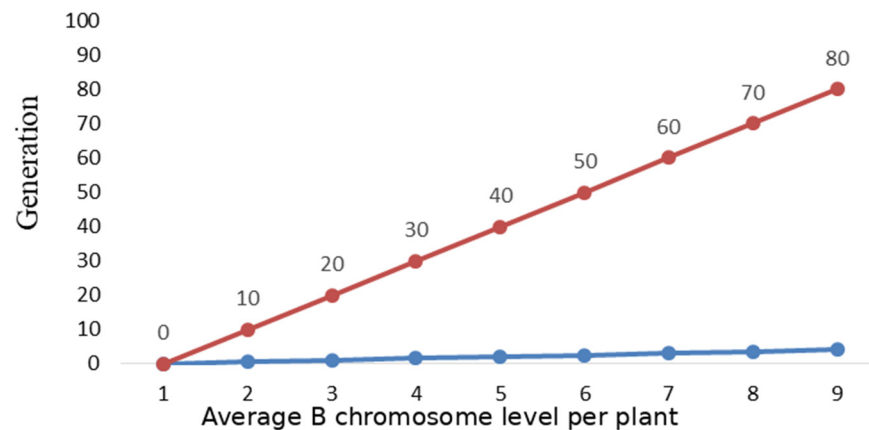


**Figure 3.** The drawing figure shows the mitotic transmission of B chromosome at the first pollen mitosis stage. (A) Metaphase, (B) sister chromatids of the B chromosome travelling to opposite poles via non-disjunction of the B chromosome, and (C) daughter cells having a B chromosome.

### 5. Factors Affecting Bs: Soil Moisture and Temperature

To explore the relationship between environmental factors, such as soil moisture and temperature, and the presence or absence of B chromosomes (Bs), we have discussed chromosomal instability, stress responses, and the behavior of Bs under different conditions. Temperature fluctuations have been widely studied in relation to their effect on the stability of chromosomes during cell division. It has been shown that extreme temperatures (either hot or cold) can affect spindle formation, chromosome alignment, and segregation, leading to increased rates of aneuploidy and chromosomal instability [37]. For organisms with Bs, temperature stress might provide an opportunity for B chromosomes to either persist or be lost more readily during division [38]. Soil moisture stress (such as drought or excessive water) can influence plant growth and, by extension, chromosomal stability [39]. Studies have found that moisture stress can lead to disturbances in cell division, which may promote the occurrence of chromosomal errors, including the formation of Bs. In plants, moisture stress can affect the regulation of the cell cycle, making them more prone to errors during mitosis and meiosis [40]. Temperature and moisture stress can have a synergistic effect on chromosomal segregation, leading to changes in the number and stability of Bs (Figure 4). Temperature stress, for instance, can reduce the efficiency of cell cycle checkpoints, while moisture stress can cause osmotic imbalances, both of which

may promote errors in chromosomal division [41]. B chromosomes are often considered to be an evolutionary curiosity, as they can provide certain adaptive advantages under stressful conditions. In some cases, Bs may carry genes that help organisms cope with environmental stresses.



**Figure 4.** Computer-generated graph illustrating an average level of Bs in response to different temperature and soil moisture conditions. Here, blue line represents the average level of Bs, while red line indicates the generation level in response to different temperatures and soil moisture conditions.

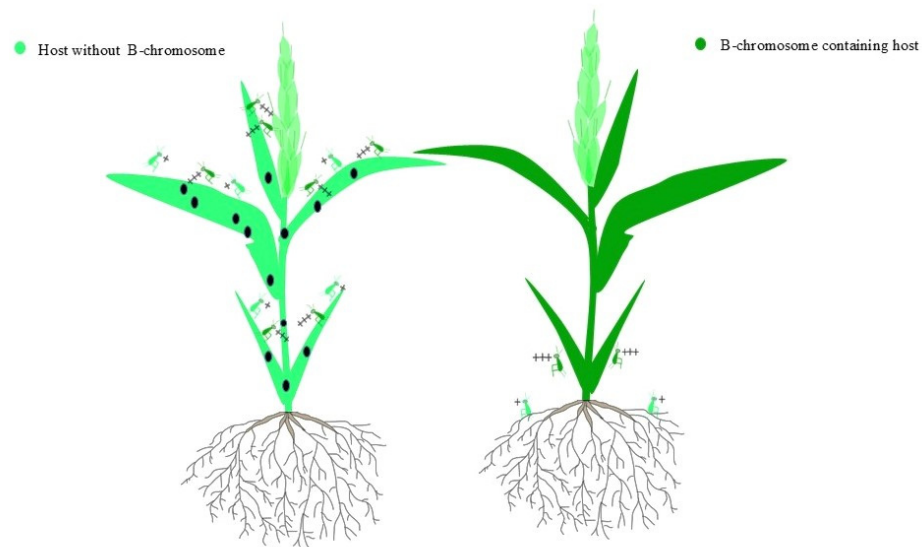
Understanding how environmental factors like temperature and moisture influence the behavior of B chromosomes could reveal whether these chromosomes have any adaptive significance [42]. To study the effects of temperature and moisture on B chromosomes specifically, several experimental techniques can be used to track chromosome behavior during mitosis and meiosis, such as fluorescence in situ hybridization (FISH) or chromosome counting using microscopy [43]. These environmental factors are known to impact mitosis and meiosis, which are processes that are crucial to the behavior and segregation of Bs. Understanding how these factors influence the presence or stability of Bs can provide insights into their roles in adaptation, evolution, and stress resilience in certain species.

B chromosomes have been a subject of interest due to their unusual inheritance and potential involvement in stress adaptations. Soil moisture and temperature are key environmental factors that influence plant and animal survival and reproductive success [44]. Since these environmental factors can lead to fluctuating stresses, it is plausible that they could play a role in promoting the appearance or disappearance of Bs in a population [45]. Understanding this relationship could reveal how these extra chromosomes contribute to an organism's ability to adapt to changing conditions, potentially by providing genetic diversity or aiding stress tolerance mechanisms. Such research could also have implications for understanding the evolutionary significance of non-mendelian inheritance mechanisms and their roles in species survival [46].

## 6. Role of Bs in Wheat Resistance to Disease

The role of Bs in plant defense systems is not fully understood. To develop disease-resistance crop varieties by manipulating Bs, the knowledge about their role in pathogen and crops is necessary. The role of Bs in pathogen and crops is shown in Figure 5, based on a few studies. Bs have been observed in several fungal species, including *Nectria haematococca*, *Magnaporthe oryzae*, *Fusarium oxysporum*, f. sp. *radicis-cucumerinum*, *Alternaria alternata*, *Cochliobolus heterostrophus* and *Leptoshaeria maculans* [8]. It has been found that Bs cause an increase in the pathogenicity of respective pathogens [47–50]. On the other hand, Bs were found to increase the resistance of their crops' hosts to pathogens, as seen in the oat plant *Avena sativa*, where they increased resistance to rust caused by the fungus *Puccinia coronata* f. sp. *Avenae* [51].





**Figure 5.** Interaction between plants and pathogens with Bs and without them. The number of plus signs on the pathogen represents the degree of virulence in it.

In rye, Bs have been associated with increased tolerance to heat stress. Rye plants with Bs exhibit an enhanced expression of the heat shock protein gene *Hsp101*, as well as significant upregulation of the truncated gene variant tE3900 under heat stress. This upregulation supports plant survival in warmer conditions, indirectly strengthening overall plant health and reducing susceptibility to pathogens that may exploit weakened or stressed plants [9]. Studies on chive (*Allium schoenoprasum*) and ryegrass in natural habitats have found that individuals with Bs tend to exhibit better survival rates than those without them. This pattern suggests that Bs may influence immune response pathways or stress resistance genes, thereby helping the plants to thrive in pathogen-rich environments [9]. Disease-resistant wheat can be developed by implementing the following breeding programs: (a) Crossing wheat cultivar and Bs containing wheat races that provide resistance to diseases such as wheat streak mosaic virus and barley yellow dwarf virus. (b) Genetically engineering disease-resistant gene from other crops to Bs containing wheat. Until now, there is no trustworthy evidence about Bs in wheat that contain disease-resistant genes. Therefore, rigorous research needs to be conducted to discover disease-resistant genes containing Bs in wheat. However, Bs can also have negative effects on plant growth and development. Therefore, the study of Bs in wheat and their potential use in breeding programs requires careful consideration and further research.

## 7. Potential Application of Bs in Wheat Breeding

The potential of Bs in wheat for future improvement lies in the possibility that they may contain genes or other genetic elements that could contribute to desirable traits, such as stress tolerance, disease resistance, and improved yield [1]. Bs are known to contain various types of repetitive DNA sequences, which can sometimes have functional roles in gene regulation and expression [52]. Higher variability in crop species leads to enhanced tolerance to diverse climatic conditions. Bs may carry transposable elements, which can promote genetic variability and adaptations to changing environments. While the functional significance of these genetic elements in Bs is not well understood, they represent a potentially rich source of genetic diversity that could be harnessed for wheat improvement through genetic engineering or breeding. Identification of functions regulated by Bs may enhance their application in developing climate-resilient wheat cultivars to ensure sustainable wheat crop production.

So far, Bs have been utilized in various research applications, including mapping the A genome, influencing recombination, and investigating centromere structure and non-disjunction processes, as described by Jones et al., 2008 [3]. To this end, Bs can play a

significant role in developing chromosome-based vectors for gene transfers. For instance, recent works have adapted telomere-mediated chromosome truncation for both As and Bs in maize [53–56]. Regarding the potential use of Bs as vectors for transgenes, it is important to note that Bs typically have a minimal or null impact on an individual's phenotype. Concerns about reduced vigor due to a high number of Bs only arise in specific cases [57].

For example, in maize, Bs have been utilized as platforms for the development of engineered mini chromosomes. These mini chromosomes offer the potential to simplify the process of stacking multiple transgenes at a single locus, as discussed in the review by Birchler in 2015 [58]. Overall, a construct containing telomere repeats is introduced into the tissue through bombardment. Successful integration of this construction results in the cleavage of the chromosome at the insertion point. Truncated Bs are more readily obtained than truncated A chromosomes, primarily because Bs are non-essential. Cells containing truncated Bs do not experience aneuploidy, a condition that can occur when A chromosomes are truncated.

Moreover, Bs have been reported in several wheat varieties, indicating that they are a naturally occurring component of the wheat genome [59]. This means that they may be more readily integrated into existing wheat breeding programs, as opposed to the introduction of entirely new genes from other species. However, it is important to note that the potential benefits of Bs in wheat improvement are still largely speculative, and further research is needed to better understand their functional roles and to evaluate their practical applications in wheat breeding and production.

## 8. Outlook

Bs contribute to genetic diversity by harboring non-essential genetic material. Their potential role in speciation and their influence on the genetic structure of populations over time are noteworthy. The presence of Bs can indirectly impact the fitness of an organism, exerting an influence on adaptations and survival, particularly in response to specific environmental conditions. Bs have the potential to influence plants in various ways, contributing to the genetic diversity within populations and shaping reproductive strategies. The non-essential genetic material in Bs has the capability to modify gene expression and regulation, thereby impacting the phenotype of plants. Considering the significant aspects of Bs in wheat, we further propose exploring the following key areas.

Expanding genomic and epigenomic studies on Bs: The unique genetic content of Bs and their non-recombining nature make them valuable for examining chromosomal drive and selfish genetic elements. Future studies could utilize high-throughput sequencing and epigenomic mapping to uncover functional and regulatory elements in Bs that may impact gene expression in wheat. Understanding these elements could reveal mechanisms that Bs use to maintain their population within host genomes, potentially unlocking tools for targeted gene insertion and genetic manipulation.

Investigating the influence of environmental factors on Bs' behavior: Bs appear to be responsive to environmental stressors, such as soil moisture and temperature. Research into how environmental conditions modulate Bs' behavior could provide insights into plant adaptation mechanisms. Identifying specific environmental triggers that influence Bs' stability, transmission rates, or drive could allow breeders to harness Bs for developing wheat varieties better adapted to climate change.

Enhancing disease resistance through Bs: Bs have shown promise in augmenting pathogen resistance in several plant species, suggesting that they may have potential applications in disease-resistant wheat cultivars. Further research could focus on the role of Bs in the immune responses of wheat to specific pathogens, leading to new, more resilient varieties. Characterizing pathogen-resistant genes or non-coding RNAs in Bs could contribute to breeding programs focused on sustainable crop protection.

Bs for increased genetic diversity in breeding: Bs offer a unique source of genetic variability. Research into the role of Bs in creating genetic diversity can help breed wheat cultivars with improved tolerance to abiotic stresses. This could be achieved by selectively

amplifying or silencing specific Bs genes linked to desirable traits. Moreover, with advances in CRISPR and gene-editing technologies, Bs could be strategically manipulated as vectors for introducing beneficial traits into wheat genomes.

B-based chromosomal vectors for trait stacking: Bs have been used to develop mini chromosomes in other crops, such as maize, for stacking multiple transgenes at a single locus. In wheat, Bs could be engineered to function as stable carriers of multiple transgenes, facilitating complex trait stacking that enhances productivity, quality, and resilience. This approach could reduce the genetic load and avoid issues related to aneuploidy in A chromosomes, making trait integration more efficient.

**Author Contributions:** M.M.I. designed and arranged this study; D.M.D., S.O.N., A.B.S. (Abu Bakar Siddique 1), M.Z., A.B.S. (Abu Bakar Siddique 2) and O.H. collaborated on the data collection, analysis, and interpretation; M.A.A. reviewed, edited, and rewrote this paper, as needed. All authors have read and agreed to the published version of the manuscript.

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