Triticeae Genomics and Genetics, 2025, Vol.16, No.6, 237-244
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Research Insight Open Access

Chromosome Rearrangements and Genome Evolution in Hexaploid Wheat

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Triticeae Genomics and Genetics, 2025, Vol.16, No.6 doi: 10.5376/tgg.2025.16.0026
Received: 06 Sep., 2025
Accepted: 23 Oct., 2025
Published: 06 Nov., 2025

Preferred citation for this article:
Wang Y.L., and Ma C.X., 2025, Chromosome rearrangements and genome evolution in hexaploid wheat, Triticeae Genomics and Genetics, 16(6): 237-244 (doi: 10.5376/tgg.2025.16.0026)

Abstract *Triticum aestivum* (AABBDD) is an important staple food crop worldwide. Its evolutionary history is complex, having undergone multiple polyploidy events and extensive chromosomal rearrangements. This study provides an overview of the structural characteristics of the hexaploid wheat genome and the functional differentiation among the A, B, and D subgenomes. It conducts a detailed analysis of the types of chromosomal rearrangements and their driving mechanisms, with a focus on the roles of homologous recombination and transposition elements. Meanwhile, this study also emphasizes the impact of chromosomal structural variations on gene expression regulation, adaptive evolution, and trait diversification, especially the significance driven by both natural selection and artificial breeding. Through case analysis, it demonstrates the practical application value of chromosomal rearrangement, such as the fusion process of the A, B, and D genomes. And the wide application of wheat-rye translocation lines such as 1BL/1RS in disease-resistant breeding. By revealing the relationship between chromosomal structure and functional genomes, this study is expected to promote molecular design breeding of high-yield and stress-resistant wheat varieties.

Keywords Hexaploid wheat; Chromosomal rearrangement; Genomic evolution; Structural variation; Polyploidization

1 Introduction

Hexaploid wheat (*Triticum aestivum* L.) did not emerge suddenly from A single mutation. Instead, it underwent a series of complex natural hybridization and polyploidization processes before finally developing the current AABBDD structure containing three subgenomes A, B, and D (Zhang et al., 2021). During this process, A and B originated from tetraploid wheat (*Triticum turgidum*, AABB), while the D genome was later introduced through hybridization with *Aegilops tauschii* (DD). This long and repetitive evolutionary path has enabled hexaploid wheat to accumulate a rich genetic background and has also made it occupy an extremely important position among the major crops worldwide (Liu et al., 2025).

However, the genomic structure of wheat is not static. In addition to polyploidy, chromosomal translocations, inversions, centromeric relocations and other seemingly "chaotic" changes have also been pushing it forward (Zhao et al., 2023). Sometimes, these structural changes can cause fluctuations in gene expression; Sometimes, they may affect the recombination frequency and even agronomic traits, such as disease resistance or adaptability (Huo et al., 2018; Lv et al., 2023). Of course, not all variations bring benefits, but it is precisely these constantly adjusting processes that have shaped the form of wheat that we see today. To truly understand the significance of these structural changes, especially those that "subtly" influence the direction of breeding, delving into the mechanisms behind chromosomal rearrangements is an indispensable and crucial step.

This study will systematically explore the types, mechanisms and evolutionary consequences of chromosomal rearrangements in hexaploid wheat, integrate the latest progress in fields such as genome assembly, comparative genomics and multi-omics analysis, summarize the polyploid origin of wheat, and describe in detail the changes in chromosomal structure and their impact on genomic function and breeding potential. By clarifying the role of chromosomal rearrangement in the evolution of wheat genomes, this study provides strong support for the genetic improvement and sustainable production of wheat in the future.

2 Structural Characteristics of the Hexaploid Wheat Genome

2.1 Composition and functional divergence of the A, B, and D genomes

The three subgenomes - A, B, and D - each undertake different "tasks" in hexaploid wheat. They come from different ancestors, and this background itself determines that they will not be exactly the same. Not all gene families can find "common points" with each other in wheat germplasm. In fact, the truly universally shared part accounts for only about 23% (Cheng et al., 2025). The D genome is particularly special. It shows more genetic variations during the formation of hexaploids, which is quite crucial in breeding. Furthermore, the distribution of transposition elements and the phenomenon of gene duplication were not evenly distributed among the three subgenomes A, B, and D. These differences ultimately contributed to the functional complexity and plasticity of the wheat genome (Liu et al., 2025).

2.2 Relationships and regulatory mechanisms of homologous chromosomes and genes

In hexaploid wheat, homologous chromosomes from different subgenomes do not live independently of each other. There are indeed interactions among them, but the ways are rather complex. The interactions between these chromosomes largely depend on sequence similarity and some transposable elements specific to subgenomes. In other words, although homologous genes may seem similar, their expression level is often limited by the chromatin environment of the subgenome where they are located (Wang et al., 2025). For instance, if the genes are from wild relatives, the situation is even more different: the introduced genes may have reduced expression due to regulatory disorders, and the original homologous copies may not be able to "fill in" (Coombes et al., 2021; Jia et al., 2021). In addition, three-dimensional structures like topological associative domains (Tads) also play a regulatory and stabilizing role behind the scenes.

2.3 Features of large-scale genome duplication, deletion, and expansion

The hexaploid wheat genome itself is not "calm". It has experienced many fluctuations after multiplexing, including large-scale repetition, fragment deletion and amplification. This state of "constant change" has actually shaped its complexity today. The insertion of transposition elements and the repetition of fragments not only bring about new genes but also rewrite functions. Structural variations such as presence/absence variations and copy number variations have now been found in the wheat genome with more than 1.9 million non-redundant events, especially concentrated around the centromere (De Oliveira et al., 2020; Cheng et al., 2025). Sometimes, large fragment deletions may also be the result of human manipulation, such as gamma-ray induction or gene infiltration breeding. Such variations sometimes directly affect agronomic traits (Komura et al., 2022). So, to some extent, the "turmoil" of structure is also one of the sources of the diversity and adaptability of wheat.

3 Major Types and Mechanisms of Chromosome Rearrangements

3.1 Structural variations such as inversions, translocations, duplications, and deletions

It is actually not a rare thing for the structure of chromosomes to change. Once a double-strand break occurs in DNA, if the subsequent repair is not handled properly, problems are very likely to arise. Either an extra section was inserted or the position was connected wrongly. Thus, the common types of rearrangement such as inversion, transposition, repetition and absence were thus formed. At certain times, rearrangement occurs very intensely, such as large-scale chromosome breakage and recombination. Within just one cell cycle, the structural appearance may change significantly (Pellestor, 2019; Pellestor et al., 2021; Krupina et al., 2023). Inversion duplication is sometimes not complicated. It is that the DNA at the breakpoint turns back and "self-initiates" synthesis, resulting in a wrong connection again. This pattern is also common (al-Zain et al., 2023). To figure out where these rearrangements come from, high-resolution breakpoint analysis is needed; otherwise, the ins and outs won't be clear.

3.2 Roles of homologous and non-homologous recombination in chromosomal rearrangements

When it comes to the "behind-the-scenes drivers" of rearrangement, homologous recombination (HR) and non-homologous end join (NHEJ) are basically the "main forces". HR is supposed to be a fine-tuning tool that precisely repairs by similar sequences. However, unfortunately, it sometimes "makes mistakes", and multiple intrusions may cause structural troubles such as translocation (Kot et al., 2021). NHEJ is more straightforward.

Even without sequence control, it can still force both ends together, but problems such as messy insertion points and base loss are hard to avoid. In addition, copy-related mechanisms such as FoSTeS or MMBIR often get involved. When the copy fork stalls or templates switch, inversions or complex concatenation follow (Burssed et al., 2022). There are many types of rearrangements, and to a large extent, it depends on which repair mechanism takes the lead.

3.3 Transposons and repetitive sequences driving genome structural dynamics

Sometimes, chromosomal rearrangement is not even caused by "correction errors", but rather that certain sequences themselves are "too noisy". Transposons and repetitive DNA fragments are like this. They not only keep jumping in the genome but also tend to cluster together. This kind of accumulation often provides ready-made "anchor points" for rearrangement. Especially for repetitive units like LINE and satellite sequences, if non-allelic recombination (NAHR) occurs, large fragment structural changes are almost inevitable (Luo, 2025). For instance, retrotransposons particularly tend to aggregate around centromeres. This behavior intensifies regional duplication and instability, providing a "testing ground" for the structural evolution of the genome (Gozashti et al., 2025). In other words, they not only participate in structural changes but may also profoundly influence gene functions and even species adaptation.

4 Roles of Chromosome Rearrangements in Hexaploid Wheat Evolution

4.1 Genome conflicts and structural stabilization after polyploidization

The step of doubling did not immediately stabilize the hexaploid wheat. At the very beginning, there were many contradictions among the genomes and their structures were also very unstable. Especially among the three subgenomes A, B and D, integration is not an easy task. Chromosomal translocations such as 4A, 5A, and 7B, as well as the rearrangement of centromeric positions, are actually gradually explored during the process of genomic "self-repair" (Zhao et al., 2023; Liu et al., 2025). And the accumulation of those specific centromere repeat sequences is not a useless decoration. It plays a significant role in cell division, especially in the later stage of hybridization. With them present, chromosomes are more likely to separate correctly and the genome is more complete.

4.2 Effects of chromosome rearrangements on gene expression and trait variation

Sometimes, gene expression can be "dragged down" by structures. Once chromosomal rearrangement alters the position of regulatory elements or the openness of chromatin, the expression of genes also fluctuates accordingly. Especially for those genes involved in translocation, they evolve at a faster rate and the recombination frequency may also change, making it easy for new phenotypes to "emerge". However, it doesn't always bring good things. In some cases, structural changes may instead disrupt the original balance. However, in breeding, this kind of interference sometimes becomes a means instead. For example, by using the infiltration of rye chromosome fragments, disease resistance was successfully introduced (Figure 1) (Wang et al., 2023). In addition, the activity of transposers and fragment duplication are often involved, which alter the regulatory logic of the genome and make wheat more flexible at the expression level.

4.3 Contributions of rearrangements to adaptive evolution and environmental stress responses

Not every adaptation to the environment relies on sudden changes. In fact, changes in the structure of chromosomes themselves can also help species adapt. For hexaploid wheat, chromosomal rearrangement is like a "quick adjustment" tool. When the external environment undergoes drastic changes or the pressure of breeding selection increases, it can rapidly bring about genetic variations. For instance, genetic segments from wild species, combined with some complex rearrangements, not only enhance disease resistance but also affect yield and quality. These seemingly chaotic changes actually have certain directionality behind them (Zhao et al., 2023; Liu et al., 2025). Moreover, the transposon in the wheat genome is also very active. Coupled with the fact that the centromeric region itself is prone to "movement", the flexibility of the overall structure is also enhanced accordingly. It can be said that throughout the evolution of wheat, these "constantly adjusting" mechanisms have never ceased.

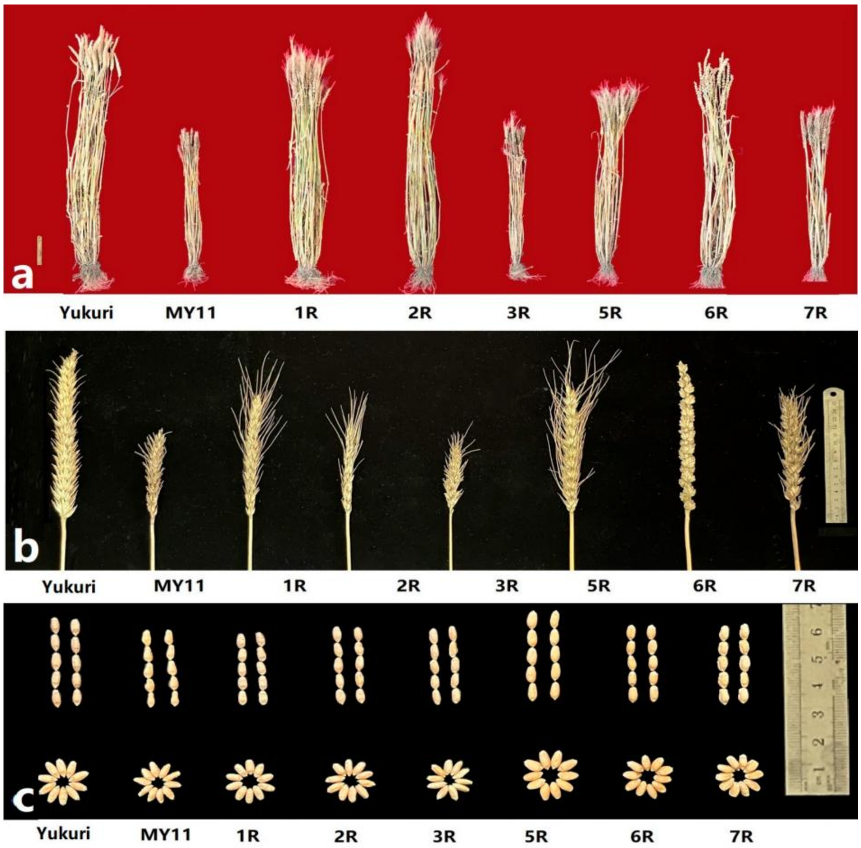

Figure 1 Plants (a), spikes (b), and seeds (c) images of Yukuri, MY11and six wheat-rye addition lines (Adopted from Wang et al., 2023)

5 Detection Technologies and Analytical Methods for Chromosome Rearrangements

5.1 Application of optical mapping, Hi-C, and long-read sequencing in structural variation detection

How to detect structural variations has always been an unavoidable problem in the study of genomic rearrangement. Especially for crops like wheat, which have a large and complex genome, relying solely on a single technology often leads to neglecting one aspect for another. For instance, optical spectra can reveal which regions are broken, how they are rearranged, and also indicate the direction, distinguishing between equilibrium and non-equilibrium rearrangements. However, this needs to be combined with other methods, and there are blind spots when used alone (Qu et al., 2023). Hic is not only capable of creating three-dimensional structure diagrams. It can also identify rearrangement types such as translocation and inversion, even see the breakpoints, and extract copy number information from the same dataset (Burden et al., 2025;) Galbraith et al., 2025. Long-read sequencing, such as PacBio and Oxford Nanopore, has more advantages when dealing with repetitive and disordered fragments. It can accurately locate breakpoints and has become a standard feature in many high-standard national-level testing processes.

5.2 Visualization value of cytogenetic techniques such as FISH and GISH

When it comes to which method is the most intuitive, the visualization technology at the cellular level is still irreplaceable. Methods like FISH and GISH, although "old-fashioned", can really directly identify where the problem lies on the chromosome. The resolution of FISH can reach the level of thousands of bases, and it is effortless to locate structural problems such as translocation and inversion (Qu et al., 2023; Xia, 2025). GISH is particularly useful for polyploid species. In a subgenomic mixed crop like wheat, the components of each genome can be clearly distinguished, and even which fragments are introduced from exogenous sources, such as wild species transplanting fragments (Hu et al., 2020). Although they are not as information-rich as high-throughput technologies, they have irreplaceable intuitive value in the judgment of spatial position and chromosomal background.

5.3 SV, CNV, and translocation identification based on reference genome analysis pipelines

The rearrangement recognition processes that rely on algorithms are also indispensable to the reference genome. High-throughput sequencing data, such as double-end sequencing or long-read assembly, can quickly identify large fragment variations, but only if there is a control reference to facilitate the comparison of which variations are specific and which may be common but harmless (Mitsuhashi et al., 2020; Jilani & Haspel, 2021; Eisfeldt et al., 2024. These processes can not only locate the breakpoints but also restore the direction and connection sequence of the variant fragments, which is particularly important when it is necessary to distinguish between pathogenicity and natural diversity. Of course, it is difficult to cover all aspects by relying solely on such processes. Only by integrating them with optical, Hi-C, FISH and other data can the accuracy of detection and the analytical ability for complex rearrangements be improved, especially in genomes with intense structural dynamics like those of hexaploid wheat.

6 Case Studies: Chromosome Rearrangements in Wheat Origin and Breeding

6.1 Evidence of chromosomal rearrangements during A, B, and D genome fusion in *Triticum aestivum* origin

The evolutionary process of wheat is not as simple as just putting together three sets of genes. Before the fusion of the A, B and D genomes, each had distinct chromosomal structures. However, after the fusion, these differences triggered a series of rearrangements. Translocation and inversion among 4A, 5A, and 7B are not isolated phenomena but structural features that are widely present in hexaploid wheat and its wild relatives (Shi et al., 2022). Evidence from techniques such as FISH and chromosome staining also indicates that these rearrangements do not only occur in modern wheat; they began as early as the stage when subgenomic D was introduced (Figure 2). These changes not only helped stabilize the newly formed wheat genome but also accelerated the integration among the three subgenomes.

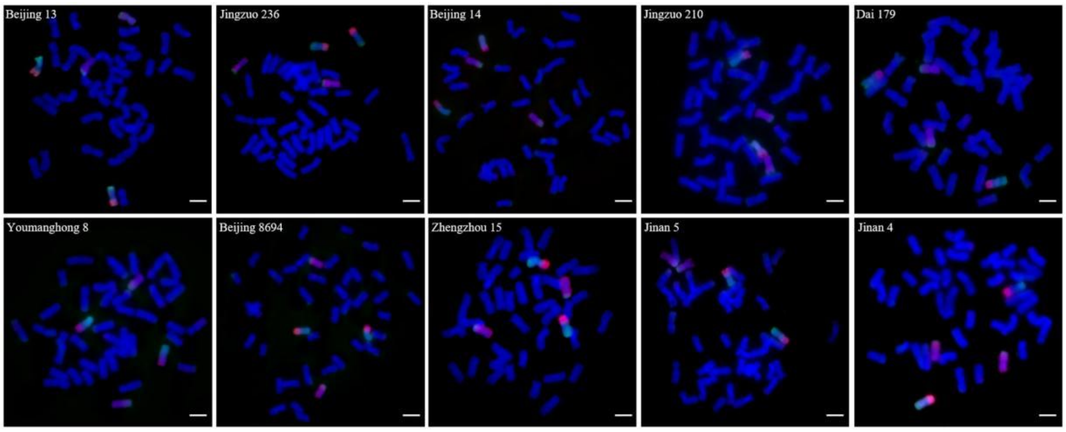

Figure 2 Characterization of chromosomal translocations 4AS·4AL-1DS and 1DL·1DS-4AL derived from wheat cultivar Bima 4 (Adopted from Shi et al., 2022)

6.2 Application of wheat–rye translocations in disease resistance breeding

Not all chromosomal rearrangements occur naturally; they can also be "artificially" created in breeding work. For instance, chromosomal translocations like 1BL/1RS in rye and wheat have long been widely used for disease resistance improvement. This translocation brought the resistance gene from rye into wheat and incidentally improved some yield-related traits (Jiao et al., 2024). What's more interesting is that the repetitive sequence of chromosome 1RS is particularly active, with many deletions and variations, indicating that it is not a static structure but is constantly evolving. However, these changes did not affect its status as a "darling" in breeding; instead, due to its significant effects, it was retained for a long time.

6.3 Structural variations associated with yield and stress tolerance in modern cultivated wheat

Structural variations are almost everywhere in the wheat varieties grown today. Not only the inversions or translocations that are very "conspicuous" at first glance, but even the increase or decrease in copy number is often found to be linked to yield and stress resistance. Through pan-genome comparison, many variations have been traced back to the breeding starting materials, and some are directly related to adaptation to specific environments (Salina et al., 2022). Sometimes, the presence of these variations can also inhibit unnecessary recombination, thereby stably maintaining the combination of superior traits. Whether naturally formed or preserved during the breeding process, these chromosomal rearrangements are constantly shaping the expressiveness and adaptability of modern wheat.

7 Conclusion and Future Perspectives

The chromosomal structure of hexaploid wheat (*Triticum aestivum*) is not always stable as before. From the moment it was formed by the combination of the A, B and D genomes, various structural changes have never ceased. Over the past two decades, researchers' attention to this type of chromosomal rearrangement phenomenon has continued to rise, not only because it leaves traces in genomic evolution, but also because it can actually affect the formation of agronomic traits. Transposition, inversion, repetition, absence... These seemingly "chaotic" changes have actually played a considerable role in regulating gene expression, mitigating the interference of redundant genes, and enhancing adaptability to adverse circumstances. Isn't a classic case like the 1BL/1RS translocation the best proof that structural variations can be transformed into high-yield and disease-resistant advantages? Sometimes, it is precisely these "reassembled pieces" on the genome that endow wheat with stronger environmental adaptability and breeding potential.

However, it is not that easy to figure out these structural variations. How large is the genome of wheat? 17Gb. And repetitive sequences are everywhere, like a maze. This places extremely high demands on the identification and splicing of structural variations. Although we already have some new technologies at hand, such as long-read sequencing and Hi-C, which theoretically can figure out these complex structures, in practice, the resource investment is not small. In addition, to precisely distinguish homologous sequences from the A, B, and D subgenomes, sometimes the conclusions drawn by different tools are not exactly the same, and there are always some ambiguous areas in the results. Not only that, balanced structural variations, such as inversions, remain one of the most challenging aspects to overcome in current bioinformatics detection. To clarify the specific impact of these variations on traits, it is necessary to analyze them in combination with other data such as the transcriptome and epigenome, which adds a lot of difficulty to the research.

The future direction seems to be quite clear: we should not only apply these research achievements to breeding, but also prevent them from remaining just "visible but intangible". The first step is to make the detection of structural variations faster, more accurate and more stable. At the same time, the detection scope should be expanded to cover more wheat germplasm backgrounds and establish a clear "structural variation map". Next, it is not only about identification but also about verifying the function. For instance, through CRISPR/Cas splicing experiments, RNA sequencing or ATAC-seq and other means, it is further clarified which variations can truly affect the phenotype. Take it a step further and incorporate these structural variation information into the genomic selection model to truly integrate them into the breeding process. In addition, do not overlook their interaction with the environment - certain variations may only show their effects in specific climates or adverse conditions. Structural variation is not a solo battle. There are still many unsolved links in its relationship with the environment, gene expression, and phenotypic changes. In conclusion, to turn chromosomal rearrangement into a "powerful tool" in breeding, the collaboration of genomics, bioinformatics technology and breeding strategies is indispensable.

Acknowledgments
We appreciate Dr Wu from the Hainan Institution of Biotechnology for his assistance in references collection and discussion for this work completion.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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