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Pangenome Construction of *Triticum aestivum* and Its Implications for Genetic Diversity

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Abstract Common wheat (*Triticum aestivum*) is a globally important staple food crop. However, the use of a single reference genome limits our understanding of its extensive genomic diversity. This study explores the construction of a wheat pan-genome, utilizing advanced sequencing technology, map-based genomic characterization, and integrated bioinformatics processes to capture core genes and non-essential gene content. We analyzed structural variations, gene presence and deletion variations (PAV), and copy number variations (CNV), revealing significant genetic diversity in common wheat (*T. aestivum*). These findings have profound significance for wheat breeding, enhancing trait association research, genomic selection, and adaptability to climate change. We further discussed the evolutionary insights gained from pan-genome data, including domestication events, population structure and gene family expansion, and highlighted the key contributions of the "10+ Wheat Genome Project". A comprehensive understanding of the wheat genome highlights the necessity of continuously developing inclusive and scalable pan-genomes, integrating multi-omics data, and conducting international cooperation, ultimately aiming to support sustainable agriculture and crop improvement.

Keywords Triticum aestivum; Pangenome; Genetic diversity; Wheat breeding; Structural variation

1 Introduction

The name "wheat" (*Triticum aestivum*) might sound somewhat academic, but it is actually the bread wheat that people eat in their daily lives. Its status needs no exaggeration. A large part of the daily calories and proteins of billions of people are supplied by it (Cavalet-Giorsa et al., 2023). For many places, the stability of wheat production determines the stability of food security.

The problem is that the population is still growing and the climate is becoming increasingly difficult to predict. The requirements for wheat have naturally increased-not only high yield, but also disease resistance, drought resistance, and preferably better nutrition (Bayer et al., 2022). These demands may sound self-evident, but the scientific research foundation behind them was actually not as solid as imagined before (Huang et al., 2024).

Over the past few decades, most research on wheat genomes has revolved around a reference genome. In other words, we use a "standard sample" to represent all wheat (Zanini et al., 2021). It sounds convenient, but the problem is obvious-there are significant genetic differences among different varieties, and even among some of its wild relatives. Using one sample to infer the situation of an entire species is like using one person's height to represent the height distribution of all mankind. This approach misses a lot of things, such as whether certain genes exist or not, changes in gene structure, or new genes closely related to agronomic traits (Przewieslik-Allen et al., 2021).

In this case, the idea of "pan-genome" was proposed. It does not focus on a single genome but rather assembles multiple gene groups from different sources to view the complete genetic picture within a species. Genes that are present in all varieties are core genes, while those that are only found in some varieties are auxiliary genes. Regulatory elements and structural variations can also be captured in the pan-genome. Nowadays, the pan-genome data and map databases of wheat can be presented in a visual way. Researchers can use them to compare the genetic differences of different varieties, and breeders can also select more suitable materials based on this (Barabaschi et al., 2025).



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The starting point of this study is very straightforward-by constructing the wheat pan-genome, to clarify which gene differences are related to important traits. Not only modern wheat, but also ancient subspecies are included. After comparison, some new gene loci and structural variations that were not noticed in the past can be found, and useful alleles can also be unearthed, enriching the genetic chassis of wheat. Nowadays, sequencing and analysis technologies are much more mature than before, and the assembly of the pan-genome will become increasingly precise, which is precisely an important step in promoting sustainable wheat production.

2 Advances in Pangenome Construction Technologies

2.1 Sequencing platforms and assembly methods

If it were ten years ago, to say that all the genetic diversity of wheat should be fully understood, more people would have thought it was a fairy tale. The genome of wheat is large and complex, with triploids and hexaploids mixed together. However, in recent years, the situation has changed. Sequencing technology has been updated rapidly and the cost is not as terrifying as before. The conditions for conducting such research have become much more lenient. The three commonly used assembly methods did not exist from the very beginning but gradually evolved through research and practice. For instance, de novo assembly-completely independent of existing reference genomes, directly piecing together a version that belongs to a certain variety itself; Reference-based iterative assembly-first use the existing version as the foundation, and then add new segments of other varieties. There is also the increasingly popular atlas pan-genome in recent years, which can directly "draw" the differences among different varieties (Hu et al., 2024). But don't think that having a method will solve the problem once and for all. The genome of wheat is full of repetitive sequences, interspersed with deletions and diversity changes, and it is particularly difficult to assemble these things. Often, it is still necessary to rely on high-throughput and high-precision platforms to support the entire process.

2.2 Data integration and graph-based pangenomes

To assemble the genes of multiple varieties into a large map sounds like building with blocks, but in fact, it is not at all easy. However, the amount of information brought by this method is indeed astonishing, especially in terms of gene deletions (PAVs) and structural variations, where the differences can be seen at a glance (Zanini et al., 2021). Nowadays, some platforms have turned this idea into tools, such as Wheat Panache, and many researchers are already using it. Its advantage is that the operation is intuitive-it can directly compare the genetic regions of different varieties, and even complex variations can be detected (Figure 1) (Bayer et al., 2022). Moreover, this kind of map is not just for "watching the spectacle". It can mark which regions are encoded and which are regulated, and can also integrate transcriptome and epigenome data together. To put it bluntly, this is no longer a simple jigsaw puzzle; it's more like opening a door for in-depth research.

2.3 Challenges in constructing a wheat pangenome

The problem, of course, has always existed. The genome of wheat is inherently large, and with its high repetition rate and polyploid structure, the difficulty of analysis can be imagined. Some people might say, "Isn't technology getting more and more advanced?" Yes, but the volume of data is also expanding at a rapid pace. Just for storage and management, very strong computing resources are required. The real challenge lies in how to precisely identify variations from piles of sequences, complete integration, and then produce clear and usable visual results. Moreover, not every researcher is proficient in operating those complex data tools, which leads to a lot of data being "useful but not applicable". It is precisely for this reason that many teams nowadays emphasize the need to build "user-friendly" analysis platforms. Only when more people can make it accessible and smooth for them to use can pan-genome research be truly implemented.

3 Genetic Diversity Uncovered by the Wheat Pangenome

3.1 Core and dispensable gene content

Wheat's genes are more than just present or absent. Pan-genome studies reveal that they actually consist of two components: core genes common to all wheat varieties, and a subset of genes found only in certain varieties, often referred to as nonessential genes or, more bluntly, "variable genes." To give specific numbers, the pan-genome of hexaploid bread wheat contains approximately 140 500 genes, of which approximately 81 070 are in the core



portion. On average, each variety contains around 128 656 genes (Montenegro et al., 2017). While this may sound like a large number of genes, what's even more interesting is that these "nonessential" genes are actually a treasure trove of genes associated with traits. Abilities such as drought resistance, disease resistance, and adaptability to diverse environments are often found in these genes with greater variability.



Figure 1 Wheat Panache screenshot showing an *Aegilops ventricosa* introgression at the beginning of chromosome 2 in cultivars Stanley, Jagger, Mace, and SY Mattis. Black boxes were added to show the region missing in cultivars where the introgression replaced parts of chromosome 2A. The graph assembly started with the IWGSC v1 assembly leading to linearized regions following the same naming scheme as the IWGSC v1.0 assembly (chr1A_part1, chr1A_part2, chr2A_part1, ...). CS, 'Chinese Spring'. Shown here is the beginning of the first part of chr2A. Black blocks are gene models. White regions correspond to regions that are present in the graph but contain no genes (Adopted from Bayer et al., 2022)

3.2 Structural variants (SVs) and their distribution

The differences between genomes are sometimes not minor repairs but radical alterations. Pan-genome research shows that the number of structural variations among wheat varieties is astonishing. Chromosomal rearrangement is one type, and the other type is the mixture of genetic fragments from wild relatives (Przewieslik-Allen et al., 2021). In other words, some varieties may carry a portion of "wild" genes. The relationship between these structural variations and phenotypes is not loose. Traits such as stress resistance and yield can often find clues in SV. However, their distribution in the genome is not uniform. In some areas, there is almost no movement, while in others, the frequency of variation is so high that it seems like a "hotspot". Often, these highly variable regions are precisely linked to the adaptability and breeding history of wheat (Zanini et al., 2021). This makes one can't help but suspect that our previous research might have missed quite a few important positions.

3.3 Gene presence-absence variation (PAV) and copy number variation (CNV)

Not every wheat variety has the same genes. Some genes are completely absent in certain varieties but actively present in others. This is known as PAV (Bayer et al., 2022). This difference is one of the important sources of genetic diversity in wheat. Especially among the genes related to disease resistance and environmental stress response, the proportion of PAV is even higher. In other words, it is precisely these differences that enable wheat to display its unique abilities in various environments. As for CNV-the variation in gene copy number-although it seems like a technical detail, its impact is not small at all. The same gene may have only one copy in one variety, but several copies may be replicated in another. This "more" or "less" will change the intensity of gene expression and thereby affect the manifestation of traits. Of course, these differences only count if they can be seen.



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Pan-genome databases like Wheat Panache can now visually display and compare PAV with CNV. Researchers and breeders can directly query and quickly compare, which makes the study of genetic diversity and the targeted breeding of new varieties more confident (Bayer and Edwards, 2023).

4 Implications for Wheat Breeding and Crop Improvement

4.1 Enhanced trait association and marker development

Some traits, such as drought resistance, salt tolerance, or the taste of the grains, are visible and tangible to everyone, but they are often the result of complex genes at work. The traditional reference genome is not omnipotent-some key variations cannot be found at all because they only occur in a few species (Tiwari et al., 2024). This is precisely where the pan-genome comes into play. It can make up for the missing part in the past, such as the presence of a deletion variation (PAV) or a newly emerged allele. Many new genetic markers have been unearthed from these differences. Tools like genome-wide association analysis (GWAS), with these markers, make it as easy to locate traits as "matching them" (Montenegro et al., 2017). The current k-mer analysis method can even directly identify the key genes that affect the protein content of grains. With these targets in place, quality improvement is no longer just a matter of luck but has a clear direction.

4.2 Improving genomic selection and prediction accuracy

If one could know the destination of breeding earlier, a lot of time and resources could be saved. The introduction of the pan-genome is actually helping us look at the map in advance. The common genomic selection model has a drawback-it cannot cover all genes, especially those "non-mainstream" genes that are absent from the reference genome. The pan-genome can precisely fill this gap and make the prediction results closer to reality (Zhang et al., 2024). Machine learning is not omnipotent, but when combined with the pan-genome, it does have more advantages in dealing with complex traits (Bayer et al., 2021). This combination can help us avoid detours and screen out potential materials in advance. The breeding cycle has been shortened and the accuracy of seed selection has also improved. More importantly, these more abundant genetic information enable us to select materials that are both disease-resistant and of high quality with decent yields, no longer relying solely on experience for judgment, but rather backed by data.

4.3 Facilitating adaptation to climate change and emerging threats

The climate is becoming increasingly unpredictable, and the changes in pests and diseases are also rapid. New problems in agriculture are increasing year by year. Wheat, as the staple food, is naturally the first to face the challenge. The pan-genome enables us to extract valuable genetic information from modern cultivated varieties and wild relatives. Many genes that are drought-tolerant, disease-resistant and adaptable to extreme climates have actually been hidden in those unnoticed varieties long ago (Mangal et al., 2024). In the past, it might have taken several years to find these genes. Now, with the "accelerator" of the pan-genome, the speed is much faster and the application is more precise. In the context of unstable climate and increasing threats, this ability is almost a necessity (Fernandez et al., 2021). Only by identifying and making good use of these "hidden" useful alleles can we possibly ensure the stability of future wheat yields and quality.

5 Evolutionary and Ecological Insights from the Wheat Pangenome

5.1 Understanding domestication and divergence

The more refined the breeding, the more simple the inheritance-this is a common saying in the industry. The data from the pan-genome basically also confirm this statement. Those superior varieties that have undergone long-term domestication and strict screening have indeed "tightened" their genetic diversity significantly (Montenegro et al., 2017). However, this is not the whole truth. There are still many variations in the so-called "non-essential" gene regions. Although not every breed has these genes, they are often closely related to adaptability or specific traits. If we only look at modern varieties, this story actually cannot be told completely. If we compare wild relatives and local species together, we can see more details: some genes have been retained all the way, while others have quietly disappeared during the process of evolution. Behind every retention or loss, the shadow of human breeding selection can almost always be found.

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5.2 Population structure and geographic differentiation

The differences in the appearance and performance of wheat in different places are not only caused by the environment, but also the involvement of genes is obvious. The pan-genome can help us track these differences and see if certain genes are only present in varieties of specific regions and cannot be found anywhere else (Schreiber et al., 2024). PAV and SNP data record this "presence" and "absence", "similarity" and "difference". When put together, they can depict the relationships among wheat populations and how they gradually adapt to local conditions. However, this is not a simple issue of geographical grouping. Core genes and helper genes each have their own roles in regional adaptability. The absence of either type would be incomplete. More importantly, the pan-genome not only helps us review history, but also monitors the present, enabling us to identify in advance those variations that may be particularly crucial for future breeding.

5.3 Gene family expansion and functional innovation

If genetic diversity is regarded as a warehouse, then the expansion of gene families is like adding new goods to the warehouse. Pan-genome research has found that many gene families in wheat have become more "fancy" in function, especially those related to stress coping. The changes are not only reflected in quantity but also in the situation of "changing jobs". Some genes that originally operated in organelles have entered the cell nucleus through polyploidy or gene transfer (Chen et al., 2023). These members, known as nuclear organelle genes (NOGs), have taken on new tasks, giving wheat more leeway in performing under adverse conditions. These changes may not seem obvious on the surface, but for breeding, they mean more functional reserves that can be utilized. The environment changes and genes adjust accordingly. The pan-genome can precisely bring out such details, making improvement more operational.

6 Case Study

6.1 Significance of the project for pangenome construction

Everyone knew from the beginning that wheat was too complex and that a single reference genome was definitely not enough. But to really break through this limitation, it still had to be driven by specific projects. The "Ten+Wheat Genome Project" was launched in this context. It tested more than ten varieties, both common and highly representative. To be honest, previous data were often "out of focus", especially when faced with global wheat variations. This project, through sequencing and assembly, has revealed the true appearance of each variety, from structural rearrangements to differences in the number of genes. It involves everything. It cannot be said that all problems have been solved, but at least the foundation of the pan-genome has been laid more firmly, allowing researchers to understand the overall genetic structure of wheat more systematically.

6.2 Key discoveries and interpretations

As soon as the data came out, several details quickly caught the attention of the research team. For instance, some structural variations are not merely conventional genetic alterations. Some are chromosomal rearrangements, and others directly result from gene infiltration of wild relatives (Figure 2) (Walkowiak et al., 2020). This makes people realize that the evolutionary path of wheat is far more tortuous and complex than imagined. There were also some discoveries that, at first hearing, were quite unexpected. The reference genome of spring wheat in China is actually lacking quite a few genes. However, in some varieties, completely "exclusive" genes can still be found (White et al., 2024). These results not only helped clarify the boundary between core genes and variable genes, but also filled the gap in the previous map. The team also specifically analyzed genes related to disease and pest resistance. Genes like Sm1 have been detailedly characterized, and the results proved that its existence does indeed bring about real functional differences. As for the expression level, the activity levels of different subgenomes are not consistent, and the expression patterns among different tissues and varieties also vary significantly. The results of the transcriptome almost remind us that wheat is a naturally "restless" crop.

6.3 Broader implications for research and breeding

These achievements are not simply a few more records in the database. They have left more room for maneuver in the search for trait markers, the development of new markers, and the exploration of superior alleles. Breeders can select the appropriate ones from a wider range of options and also improve varieties in a more targeted manner,



enabling them to have higher yields and better resistance in different environments (Long et al., 2024). However, this can also be regarded as a reminder-one should not always focus on pondering over a few main varieties. The true value of the pan-genome lies in the global diversity of wheat. The outcome of this project is actually telling us: We need to broaden our horizons. Ultimately, this method is not only feasible but also can indeed accelerate the pace of breeding. This step is indispensable if we want to discover more functional genes and promote molecular breeding.

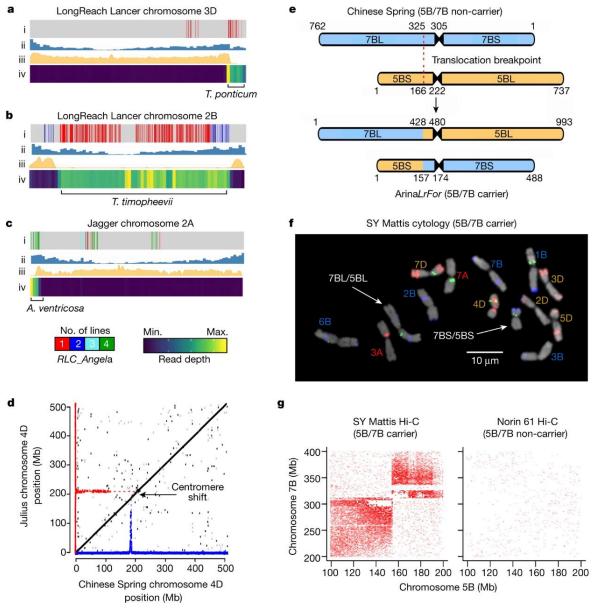


Figure 2 Introgressions and large-scale structural variation in wheat (Adopted from Walkowiak et al., 2020)

Image caption: a-c, *T. ponticum* introgression on chromosome 3D in LongReach Lancer (a), *T. timopheevi* introgression on chromosome 2B in LongReach Lancer (b) and *A. ventricosa* introgression on chromosome 3D in Jagger (c). Track i, map of polymorphic RLC-*Angela* retrotransposon insertions (legend at bottom); track ii, density of projected gene annotations from Chinese Spring (blue bars, scaled to maximum value); track iii, per cent identity to Chinese Spring based on chromosome alignment (yellow; scale is 0%-100%); track iv, read depth of wheat wild relatives (blue-yellow heat map; legend at bottom). d, Dot plot alignment showing chromosome-level collinearity (black) with relative density of CENH3 ChIP-seq mapped to 100-kb bins for Chinese Spring (blue) and Julius (red); the arrow indicates a centromere shift. e, Robertsonian translocation between chromosomes 5B and 7B in Arina*LrFor*. f, g, Cytology (f) and Hi-C (g) confirm the 5B/7B translocation in SY Mattis (left) compared with the non-carrier Norin 61 (right). In f, five independent cells were observed; the translocation was confirmed independently ten times. Scale bar, 10 μm (Adopted from Walkowiak et al., 2020)



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7 Future Perspectives and Research Directions

7.1 Toward a more inclusive and scalable wheat pangenome

A considerable number of wheat genomes have been identified so far, but compared with the overall picture, they are still just the tip of the iceberg. It is unrealistic to rely solely on a few major cultivated varieties to represent all genetic diversity. The future pan-genome must be "expanded"-cultivated species should be included, local varieties should be added, and wild relatives should not be left out. Anything that can supplement information should be included. However, this matter is not easy. The amount of data gradually accumulated and eventually turned into a huge and structurally complex problem. The management of a single genome is easy to solve, but when dozens of them are put together, it is easy to get out of control. To support subsequent analysis, it is necessary to have an extensible data architecture and a graph-based expression method (Petereit et al., 2022). There is another often overlooked aspect-some teams only focus on the current data and fail to incorporate the new assembly results in a timely manner. Over time, resources become "outdated". For the pan-genome to remain usable and worthwhile, the update mechanism must keep up with the pace.

7.2 Integrating multi-omics for functional insights

Having a gene sequence does not mean understanding the story of genes. Whether it expresses itself, when it expresses it, and in which organization it expresses it, all these will be revealed by other "omics" information. Transcriptome, epigenome and proteome data are best viewed together. Some traits may look similar, but their regulatory mechanisms may be completely different. Multi-omics integration can bring out such differences and also identify the key regulatory loci that control traits (Badet et al., 2019). Especially when it comes to complex traits or the interplay of genes and the environment, it is much more reliable than a single omics. Moreover, its value lies not only in explaining existing traits but also in accelerating the discovery and verification of new traits. No matter how perfect the pan-genome is, if it is disconnected from functional information, its help to breeding will also be discounted.

7.3 Ethical, technical, and policy considerations

However, no matter how much data there is, the question of who can use it and how can it be used cannot be ignored. With the expansion of wheat pan-genome resources, ethical and policy discussions have also been put on the agenda (Hossain et al., 2021). Not all countries have equal access to resources, and not all places that provide germplasm can truly benefit. Furthermore, technical issues cannot be relaxed. Confusion in formats, incompatible tools, and complex platform operations-once these issues accumulate, data can become a burden that is "visible but unusable." The biggest fear for researchers and breeders is having too much data and not knowing where to start. Therefore, relying solely on a database is not enough; clear regulations and collaborative mechanisms are also necessary. Whether for global sharing or local application, the rules must be clear. Otherwise, no matter how much data there is, it will be difficult to truly serve the goals of food security and sustainable agricultural development.

8 Concluding Remarks

There are significant differences among wheat varieties, a point that has actually been mentioned long ago. But for many years, research has always relied on that one reference genome, and many details have thus been "covered up". It was not until the pan-genome was truly established that it was as if the veil covering the picture had been lifted, revealing its complete genetic appearance.

These differences are not merely the variations of a few genes. Some people may find that certain genes have simply disappeared in some varieties, while others have undergone structural changes. Among such variations, those related to disease resistance, stress tolerance or quality are not uncommon. The value of the pan-genome lies in its ability to bring out such deeply hidden differences, rather than merely focusing on a "standard answer" as in the traditional approach.

Of course, it's one thing for science to look good, but it's another for breeding to be practical. Those genes from local varieties or wild materials are often the key to breaking through the bottleneck. Using them for breeding can make wheat more resilient in the face of drought, high temperatures and pests and diseases. Especially when the



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climate is becoming increasingly unstable and the pressure on agriculture is constantly increasing, this kind of genetic resource becomes particularly valuable.

More realistically, the pan-genome has significantly shortened the time from gene discovery to field application. In the past, it might take several years to improve a trait, but now the breeding cycle is being continuously compressed. The goal is straightforward: high output, stable quality, and environmental friendliness.

However, in the final analysis, this is not something that a certain research group can accomplish behind closed doors. The data needs to be continuously supplemented by someone, the omics information should be in line with the standards, and the analytical tools should not be made too "aloof". Researchers, breeding institutions and policymakers need to reach a consensus in terms of both concepts and actions. The data structure must also keep up with the demands, and the acquisition method should not become "whoever grabs it uses it". Only by achieving these can the role of the pan-genome not remain just on paper-it will truly drive wheat breeding and sustainable agriculture forward.

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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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