Rice Genomics and Genetics 2025, Vol.16, No.5, 245-253
http://cropscipublisher.com/index.php/rgg

Review Article **Open Access**

The Role of Structural Variants in Rice Domestication and Environmental Adaptation

Weijie Sun, Jiawei Li
Modern Agricultural Research Center, Cuixi Academy of Biotechnology, Zhuji, 311800, Zhejiang, China
Corresponding email: jiawei.li@cuixi.org

Rice Genomics and Genetics, 2025, Vol.16, No.5 doi: 10.5376/rgg.2025.16.0021
Received: 12 Jul., 2025
Accepted: 28 Aug., 2025
Published: 09 Sep., 2025

Preferred citation for this article:
Sun W.J., and Li J.W., 2025, The role of structural variants in rice domestication and environmental adaptation, Rice Genomics and Genetics, 16(5): 245-253 (doi: 10.5376/rgg.2025.16.0021)

Abstract Structural variants (SVs), as an important form of genomic genetic variation, play a key role in the domestication of rice and its adaptation to complex environments. With the development of third-generation sequencing technology and pan-genomics, an increasing number of studies have revealed the extensive functions of SV in regulating agronomic traits, environmental stress responses, and germplasm diversity. This study systematically reviewed the genetic evidence of SV during the domestication of rice, covering key structural variation events in domestication-related traits such as plant type, flowering period, and grain shedding. At the same time, it explored the functional mechanisms of SV in adaptation to adverse conditions such as drought, salt stress, and cold damage, including regulatory region reconstruction, cis-element changes, and gene replication and deletion processes. This paper further introduces the current mainstream SV detection techniques and their applications in pan-genome construction and functional annotation, with a focus on analyzing how SV regulates gene expression through chromatin accessibility changes, quantitative trait loci (eQTL) reconfiguration, and non-coding RNA networks. Through the analysis of typical cases (such as OsSPL14, OsHKT1;5), this study clarifies the application value of SV in the improvement of rice traits. This study aims to provide theoretical support for a deeper understanding of the functions of structural variations and offer new ideas and strategies for molecular design breeding and precise improvement of rice.

Keywords Rice; Structural variation; Domestication; Environmental adaptation; Pan-genome

1 Introduction

Rice (*Oryza sativa*) is almost the daily food supply for more than half of the world's population. It is not an exaggeration to say that it is related to food security (Fornasiero et al., 2022; Li et al., 2025). However, apart from the act of "eating", it is also widely used as a classic model for studying domestication and crop improvement. Ultimately, rice was not a crop that was obedient from the very beginning. Many of the superior traits we see today have actually been gradually domesticated through long-term artificial selection, such as those selected step by step from ancestral materials like common wild rice (Li et al., 2021; Zheng et al., 2021). Behind this, many key genes related to output, stress resistance, and even climate change response have been identified.

When it comes to genetic variation, the SNP might be the most familiar to everyone. However, when studying the traits of rice, structural variation (SV) often causes more waves. SV refers to those relatively large genomic variations - some are inserted in a large segment, some are simply missing, duplicated, or even the sequence is changed, such as inversions and translocations (Kou et al., 2020; Zheng et al., 2023). Although they are not the most abundant in the genome, each one may have a domino effect. Studies have found that SV, compared with SNP, often involves larger segments of genetic material. Therefore, they play a more significant role in influencing gene expression, crop trait diversity, and even environmental adaptation (Fuentes et al., 2019; Shang et al., 2022). If it weren't for the rapid upgrading of sequencing technology in recent years, especially the development of pan-genome analysis, many of these structural variations hidden in different species or subpopulations might not have been easily discovered. Nowadays, researchers have identified tens of thousands of SVS in cultivated rice and wild rice, and many of them are linea-specific (Wang et al., 2022). These findings precisely provide a new breakthrough for us to understand the genetic structure of rice and even further guide molecular breeding.

This study will clarify its role in rice domestication, environmental adaptation, and agronomic trait diversity. By integrating high-quality genome assembly, population scale resequencing, and functional genomics, it aims to map the evolutionary patterns of SVs, identify their associations with key traits such as grain size, stress resistance, and plant type, and reveal the genetic mechanisms by which they adapt to different environments. This research not only enables an in-depth understanding of the evolutionary history of rice but also provides valuable resources for breeding programs, allowing for targeted improvement of rice varieties to address future food security challenges.

2 Genetic Evidence of Structural Variants During Rice Domestication

2.1 Key SV events revealed by genome comparisons between wild and cultivated rice

The genomic differences between wild rice (*Oryza rufipogon*) and cultivated rice (*Oryza sativa*) are far more complex than initially imagined. Especially after using long-read sequencing and whole-genome comparative analysis, researchers found that there were a large number of structural variant (SV) events between the two, and many variant types were concentrated in the regions where transposition factors were active (Shang et al., 2022; Zheng et al., 2023). Especially in wild rice, approximately nearly half (49%) of the SV is unique to it. However, many such variations have been lost during domestication, resulting in the disappearance of approximately 1.76% of the genes in cultivated rice (Kou et al., 2020). Moreover, not only insertions and deletions, but also SVS like inversions and duplications frequently occur. Some of these specific variations, such as the 824 bp deletion in japonica rice related to grain length, were directly linked to important agronomic traits by GWAS analysis.

2.2 Regulatory roles of SVs in domestication-related traits (plant architecture, flowering time, grain shattering, etc.)

Domestication has changed many traits of rice, but not every trait change comes from simple mutations. In fact, many regulations that affect plant type, flowering period, grain drop and grain shape are all orchestrated by SV. Especially those SVS that appear in promoters or within genes often directly affect the expression level of genes (Fuentes et al., 2019). For instance, a 17.1 kb tandem repeat at the GL7 locus can make the grains longer. The 1.2kb missing section of qSW5 will affect the width of the grains. In addition, some SVS can cause the plants to become shorter or the shape of the grains to change. The "extent of change" of these structural variations is often much greater than that of ordinary SNPS because they can not only regulate expression but also may reconstruct the regulatory network. Incidentally, some SVS are also associated with traits such as grains being less prone to dropping and tolerance to waterlogging, which also indicates that they were not "supporting roles" in the domestication process.

2.3 Differentiation of major SV loci between the two major Asian rice subspecies (*indica* and *japonica*)

Although *indica* rice and *japonica* rice, these two subspecies seem to belong to the same genus of rice, when comparing their SV differences, it becomes clear why their ecological adaptations and trait manifestations are so distinct. Many studies have found that there are large inversions, copy number variations and differences in the presence or absence of a certain sequence in their genomes. An inversion of 4.3 Mb in size can almost directly distinguish *indica* rice from *japonica* rice (Kou et al., 2020). What's more interesting is that these SVS are often concentrated in regions related to domestication, that is, near the genes that regulate yield, quality and stress resistance. Some variations almost only occur in a certain subspecies or are more common in that subspecies, and it is precisely these differences that define the adaptability of *indica* and *japonica* to different environments and typical agronomic manifestations.

3 Mechanisms Linking Structural Variants and Environmental Adaptation

3.1 Functional roles of SVs in rice responses to drought, salinity, and cold stresses

Often, whether rice can survive drought, saline-alkali conditions or cold is not only determined by the strength of a certain gene, but also by whether there is a structural variation (SV) "working in the dark" behind this gene. In the analysis of a large number of rice genomes, SV often appears in those regions related to adverse conditions, and the density is not low. Sometimes, these SVS can cause regulatory sites to "shift", and sometimes they simply affect the dose of genes or disrupt the coding sequence. Transcription factors such as OsNAC6 and OsMYB6, which are involved in regulating root development and antioxidant defense, are related to these variations. Studies have shown that they can actually enhance drought and salt resistance (Lee et al., 2017). However, not all SVS are positive. Some allelic variations, such as those found on OsWRKY45 or OsDIRP1, may also play a negative role in certain contexts (Tao et al., 2011; Cui et al., 2018). The "adaptability" of different SVS to environmental stresses is likely to depend on the context and the timing of expression.

3.2 Cis-regulatory SVs and their impact on gene expression via regulatory element remodeling

The expression level of a gene sometimes does not depend on the gene itself, but rather on whether the cis-type element at its "front gate" has changed. SVS in the promoter region are particularly fond of "tamping", as they reconstruct the original regulatory map. As a result, the expression volume changes, and so do the spatiotemporal patterns (Ding et al., 2021). For instance, a single nucleotide variation in the promoter of the Ghd8 gene can enhance its expression, thereby improving the cold resistance of japonica rice (Figure 1) (Wang et al., 2019).

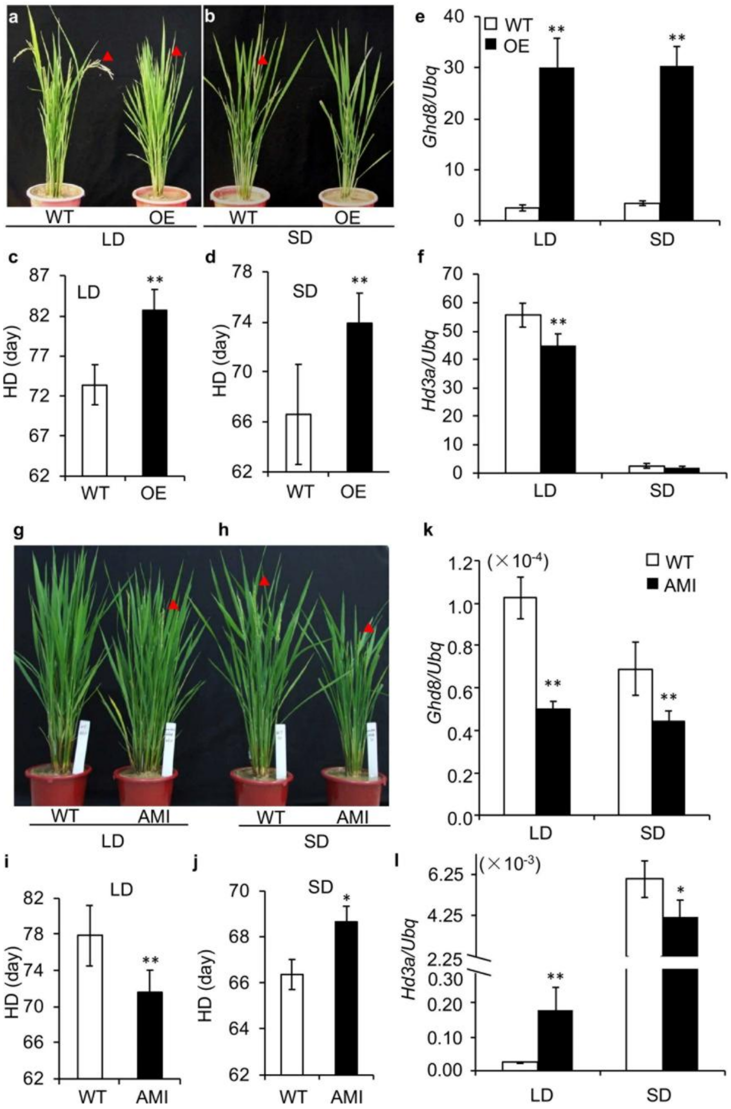

Figure 1 Altered expression of *Ghd8* affects rice heading date (Adopted from Wang et al., 2019)

Image caption: (a–d) Phenotype performances of wild type (WT) and *Ghd8* overexpression line (OE) under LD conditions (14.5 h light: 9.5 h dark) (a) and SD conditions (9 h light: 15 h dark) (b). Arrows indicate the first emerging panicle. Heading date of WT and OE in LD (c) and SD (d) conditions. (e,f) The expression of *Ghd8* (e) and *Hd3a* (f). (g–j) Performances of WT and artificial microRNA line (AMI) of *Ghd8* in LD (g) and SD (h) conditions. Heading date of WT and AMI plants under LD (i) and SD (j) conditions. (k,1) The expression of *Ghd8* (k) and *Hd3a* (l) in WT and AMI plants. Asterisks ** and * represent significant difference compared to WT by t-test at $p < 0.01$ and $p < 0.05$ levels, respectively. Error bars indicate the mean ± SD, with three to five replicates (Adopted from Wang et al., 2019)

For genes like OsSTOMAGEN that control stomatal density, once the cis-element is rewritten, not only will drought tolerance be affected, but water use efficiency will also change accordingly (Karavolias et al., 2024). These variations are often targeted by natural selection, which is why they are always given priority in breeding.

3.3 SV-driven gene loss and duplication in ecological adaptation processes

Some SVS do not immediately change the function of a gene, but they quietly "replicate" a few copies or simply "delete" the original, which can also have a considerable impact on environmental adaptation. Gene duplication can double the expression levels of some stress response genes, while the loss of certain negative regulatory factors is sometimes beneficial to plants (Fuentes et al., 2019). In the high-frequency SV region, such "variant burdens" not only failed to become a burden but also gave rise to many new alleles, some of which were even used for agronomic improvement. What is more complex is that behind many SVS, transpositional factors are also involved, and even serial repetitions occur. This dynamic change in structure enables the regulatory network of rice to evolve particularly rapidly and be more adaptable to various extreme climates (Lou et al., 2017; Li, 2024).

4 Technologies and Analytical Methods for SV Detection

4.1 Advantages of long-read sequencing technologies (PacBio, ONT) in SV identification

Some structural variations (SVS) are hidden in large areas of repetition, and conventional short-read techniques can easily "overlook" them. This problem has been precisely solved by long-read sequencing platforms such as PacBio and ONT. PacBio HiFi read length not only has a wide coverage but also high base accuracy, capable of identifying insertions and deletions as small as a few dozen bases. Although ONT has a slightly lower single-base accuracy rate, it can pull out continuous read lengths of 2 Mb or even longer, and shows more advantages when dealing with large areas of repetition or complex regions (Lang et al., 2020; Harvey et al., 2023). Of course, both platforms have their own shortcomings. However, when used in combination, they are highly complementary, not only enhancing the completeness of genome assembly but also making SV annotations more accurate.

4.2 Genome-wide SV reconstruction and pan-genome construction in diverse populations

The construction of a pan-genome is no longer as simple as "piecing together a set of reference genomes". Especially in crops with extremely strong germplasm diversity such as rice, conducting long-read sequencing based on different populations can more comprehensively explore different types of SVS such as insertions, deletions, duplications, and PAVs (presence/deletion variations). The emergence of map-based pan-genomes and super pan-genomes gives us the opportunity to concatenate linaly-specific SVS and construct a dynamically changing whole-genome structure map, which is not only convenient for GWAS localization (Shang et al., 2022), It also provides a new perspective for studying the evolutionary paths and trait effects of these variations in the population. To truly understand the relationship between SV and phenotypes, this step is inevitable.

4.3 Advances in bioinformatics tools for SV annotation, visualization, and functional prediction

There are more and more tools and their functions are becoming increasingly detailed. Nowadays, in order to accurately detect SV, many research teams have begun to use software specifically optimized for long reads such as SVIM-asm, Sniffles, cuteSV, pbsv or DeBreak to handle complex or multiallelic events (Chen et al., 2023). If it is a group-level analysis, a tool like PanPop can significantly enhance the integration efficiency of SV data. As for subsequent annotations and visualization, some databases and platforms are also being continuously updated. For example, the Rice Super Pan-Genome resource integrates rich SV annotation information and browsing interfaces (Shang et al., 2022). It is worth noting that the latest functional prediction methods are no longer confined to coding regions but have also begun to attempt to analyze non-coding regulatory regions, which is crucial for understanding how SV affects gene expression and even phenotypic traits.

5 Epigenetic and Transcriptomic Regulation Mediated by SVs

5.1 Impact of SVs on chromatin accessibility and histone modifications

In rice, the active state of chromatin is not always static, and changes in histone modifications are often accompanied by the emergence of structural variations (SV). Histone markers like H3K4me3 and H3K27me3 have long been regarded as key markers for regulating transcription. Studies have found that the distribution and function of these markers can be interfered with or remodeled by SV, thereby affecting gene accessibility and expression activity (Osakabe et al., 2018; Probst, 2022; Sokolova et al., 2022). It is worth noting that regions rich in active markers, such as sequences carrying H3K4me3, tend to be less "tolerant" of structural disturbances. However, SV is more common in heterochromatin (Lyu, 2024). In other words, not all regions are equally "welcoming" to variations. Some places change frequently, while others tend to be more conservative. The way this variation affects chromatin accessibility, nucleosome stability and even participates in the regulation of stress responses cannot be ignored.

5.2 SV-mediated reconstruction of expression quantitative trait loci (eQTLs)

Expressing quantitative trait loci (eQTL) has always been an important entry point in the study of expression regulation. But when SV gets involved, things will become a little more complicated. An SV may directly interrupt a control element or make it function again in a different position. This leads to the emergence of new EQtls or the reconfiguration of the original EQtls. In the transcriptome studies of rice, this situation is not uncommon - some genes are jointly regulated by multiple local and remote EQtls, and the complexity of the network far exceeds expectations (Liu et al., 2022). The influence of SV on gene expression is sometimes more intense than that of SNP, especially more obvious in non-coding regions (Chiang et al., 2016). Analyzing eQTL together with phenotypic QTL often enables the identification of those genes that truly "cut" in the regulation of agronomic traits.

5.3 Interactions between SVs and non-coding RNAs (lncRNAs, miRNAs)

Non-coding Rnas, such as lncrnas and mirnas, are not simply "non-coding" entities; they are highly active in regulatory networks. However, the expression of these RNA molecules themselves may also be affected by SV. Although direct research in this regard in rice is still advancing, existing evidence suggests that SV may indirectly affect the expression and function of these non-coding Rnas by rewriting chromatin structure or altering regulatory regions (Nunez-Vazquez et al., 2022; Jiang & Berger, 2023). The presence of SV in a gene segment may lead to an earlier or delayed transcriptional initiation of adjacent lncrnas, and may also interfere with miRNA binding sites. This "chain reaction" forms a dynamic regulatory relationship among SV, apparent state and non-coding RNA. It is not merely a one-way regulatory channel but more like a feedback network. Especially in the process of crop adaptation and domestication, this network relationship becomes increasingly important.

6 Case Studies: Representative Applications of SVs in Trait Improvement and Environmental Adaptation

6.1 Structural variation in the OsSPL14 gene and its role in plant architecture improvement

The *OsSPL14* (also known as IPA1) gene is often mentioned in the regulation of rice plant type. Not every mutation attracts widespread attention, but the point mutation in it unexpectedly disrupted the regulation of OsmiR156, leading to the amplification of *OsSPL14* expression. The result is: fewer tillers, thicker stems, larger ears, not only increased yield but also enhanced lodging resistance (Jiao et al., 2010; Wang et al., 2017; Yan et al., 2021). Of course, this kind of variation is essentially a structural variation (SV), but its impact goes far beyond the structural level. Later, researchers attempted to overexpress this favorable allele or introduce it into different background materials through targeted introduction. The results all indicated that this type of SV could directly affect plant type, hormone levels, and even rice quality (Lian et al., 2020). The role of SV in breeding is very directly demonstrated in this case.

6.2 Copy number variation of OsHKT1;5 and its contribution to salt stress tolerance

Not all salt tolerance comes from a certain "magic gene", but OsHKT1; 5 is undoubtedly one of the sodium transporters that have been studied more thoroughly at present. Natural variations of this gene, especially changes in copy number, have been found to help plants excrete sodium more effectively, particularly in the aboveground parts (Negrao et al., 2013; Liu et al., 2021). In salt-tolerant varieties like "Nona Bokra", amino acid substitutions at some key sites, along with an increase in gene dosage, ultimately improved the transport capacity of sodium ions. These SVS were not locked at the very beginning but gradually emerged during the actual screening process. For this very reason, they have become important targets in salt-tolerant breeding (Kobayashi et al., 2017).

6.3 Transcriptomic regulation by SVs in cold tolerance of japonica rice at high latitudes

Whether japonica rice can withstand the cold and achieve stable production in the north is actually influenced by multiple factors, but the variations in the regulated areas are particularly worth mentioning. For example, structural variations in the promoter and coding region of the *CTB5* gene have been found to enhance its expression activity under cold stress, thereby improving the cold tolerance level during the seedling stage and reproductive stage (Figure 2) (Guo et al., 2025). This is not an isolated case. In the joint study of pan-transcriptome and eQTL, cold response genes such as *OsMAPK3*, *OsLEA9*, and *OsWRKY61* also showed significant SV-driven expression differences, including splicing variations and changes at the regulatory level (Lou et al., 2022). These genes seem to have been selectively strengthened during the domestication process of high-latitude japonica rice varieties, which also indicates that the "behind-the-scenes role" of SV in adaptive evolution should not be underestimated.

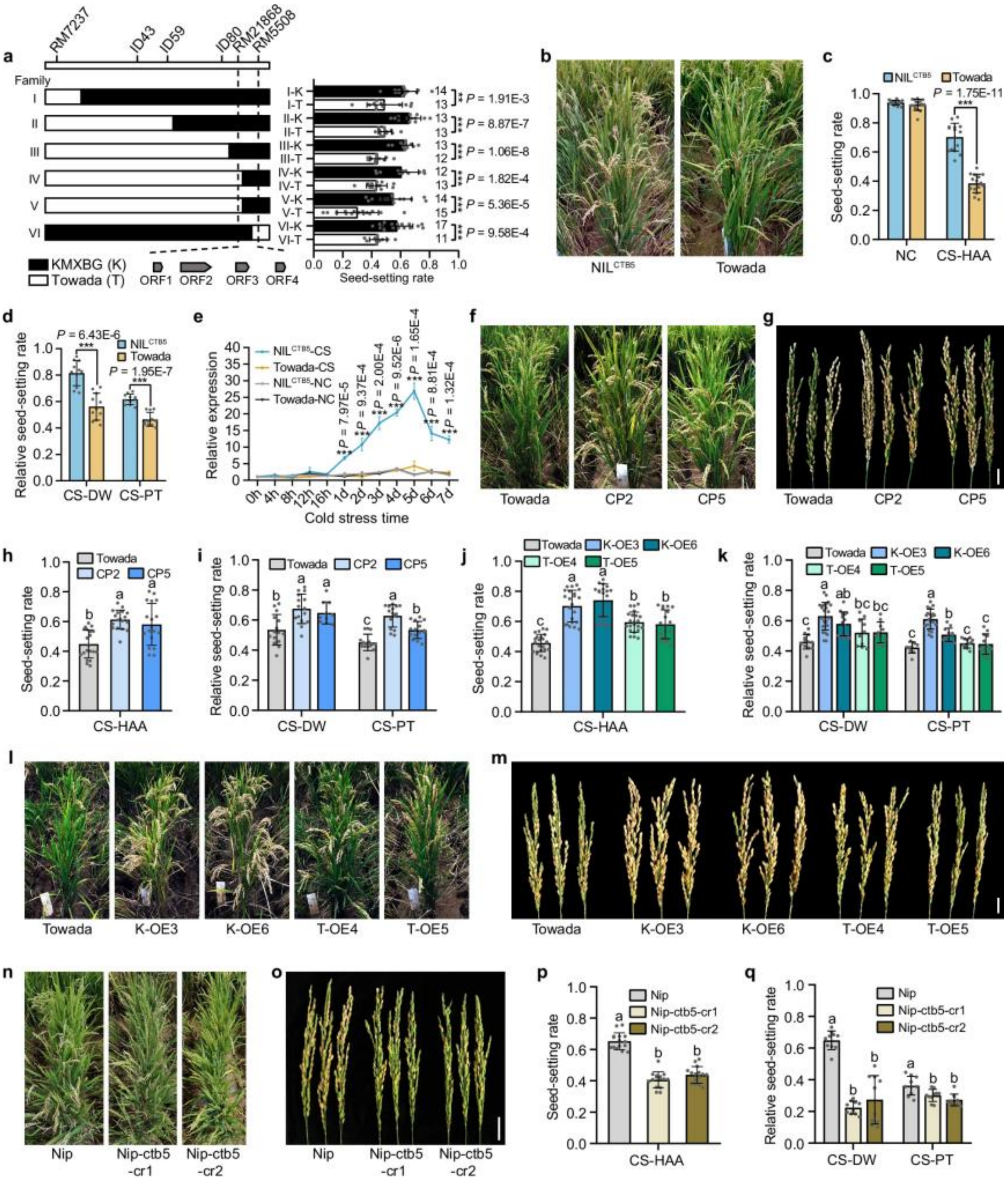

Figure 2 *CTB5* is essential for cold tolerance at the booting stage (Adopted from Guo et al., 2025)

7 Conclusions and Future Perspectives

In recent years, a number of large-scale rice genome studies have been carried out one after another under the impetus of technology, uncovering an astonishing amount of variant information - often in the millions. These variations, especially their enrichment in regulatory regions and stress-resistant related genes, have attracted the attention of researchers. But strangely enough, those effects that have a significant impact on traits are often hard to detect in traditional SNP analysis. For instance, behind key agronomic traits such as grain shape, plant height and drought tolerance, there may be some structural variations (SVS) rather than single-point mutations. The causes behind these structural variations are actually not simple. Some are caused by recombination between non-allelic genes, while others result from the insertion of transposable factors. In other words, they are not merely "abnormal events" in the genome, but may also be involved in the process of species evolution and adaptation (especially changes in population structure). So, from a theoretical perspective, studying SV is not merely for breeding, but more importantly, to figure out how plants "adapt" and "shape" themselves.

But from another perspective, SV is not only a scientific research material but is also increasingly becoming a "tool". They reveal some previously overlooked new alleles with breeding potential, and it is not difficult to directly apply them to molecular design breeding. Methods like GWAS and genomic prediction, when SV is taken into account, have significantly enhanced explanatory power for complex traits. This also enables some truly "useful" variations to surface, thereby serving tag selection and precise editing. Now, resources including the pan-genome and SV maps have begun to play a role in rice breeding, with the goal of achieving high yields, stable yields, stress resistance and high quality.

Looking ahead, multi-omics integration is likely to be the next key direction in SV research. Not only the genome, but also the transcriptome, epigenome and even phenome must be combined to clearly understand what a certain SV is doing, how it regulates and what traits it affects. And how should these priorities be ranked? It all depends on the data. Fortunately, deep learning and bioinformatics tools are also developing rapidly nowadays. Not only has the annotation efficiency improved, but the functional prediction of rare SVS has also become reliable. When big data is combined with these tools, it is really worth looking forward to whether the SV mechanism behind complex traits can be clarified in the future. This might be a brand-new breakthrough for rice breeding.

Acknowledgments

We would like to express our gratitude to the reviewers for their valuable feedback, which helped improve the manuscript.

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.

References

Chen Y., Wang A., Barkley C., Zhang Y., Zhao X., Gao M., Edmonds M., and Chong Z., 2023, Deciphering the exact breakpoints of structural variations using long sequencing reads with DeBreak, Nature Communications, 14: 283.
https://doi.org/10.1038/s41467-023-35996-1

Chiang C., Scott A., Davis J., Tsang E., Li X., Kim Y., Hadzic T., Damani F., Ganel L., Montgomery S., Battle A., Conrad D., and Hall I., 2016, The impact of structural variation on human gene expression, Nature genetics, 49: 692-699.
https://doi.org/10.1038/ng.3834

Cui L., Min H., Byun M., Oh H., and Kim W., 2018, OsDIRP1, a putative RING E3 ligase, plays an opposite role in drought and cold stress responses as a negative and positive factor, respectively, in rice (*Oryza sativa* L.), Frontiers in Plant Science, 9: 1797.
https://doi.org/10.3389/fpls.2018.01797

Ding Y., Zhu J., Zhao D., Liu Q., Yang Q., and Zhang T., 2021, Targeting cis-regulatory elements for rice grain quality improvement, Frontiers in Plant Science, 12: 705834.
https://doi.org/10.3389/fpls.2021.705834

Fornasiero A., Wing R., and Ronald P., 2022, Rice domestication, Current Biology, 32: R20-R24.
https://doi.org/10.1016/j.cub.2021.11.025

Fuentes R., Chebotarov D., Duitama J., Smith S., De La Hoz J., Mohiyuddin M., Wing R., McNally K., Tatarinova T., Grigoriev A., Mauleon R., and Alexandrov N., 2019, Structural variants in 3000 rice genomes, Genome Research, 29: 870-880.
https://doi.org/10.1101/gr.241240.118

Guo H., Gao S., Li H., Yang J., Li J., Gu Y., Lou Q., Su R., Ye W., Zou A., Wang Y., Sun X., Zhang Z., Zhang H., Zeng Y., Yuan P., Peng Y., Li Z., and Li J., 2025, Natural variation of *CTB5* confers cold adaptation in plateau *japonica* rice, Nature Communications, 16: 1032.
https://doi.org/10.1038/s41467-025-56174-5

Harvey, W., Ebert P., Ebler J., Audano P., Munson K., Hoekzema K., Porubsky D., Beck C., Marschall T., Garimella K., and Eichler E., 2023, Whole-genome long-read sequencing downsampling and its effect on variant-calling precision and recall, Genome Research, 33: 2029-2040.
https://doi.org/10.1101/gr.278070.123

Jiang D., and Berger F., 2023, Variation is important: warranting chromatin function and dynamics by histone variants, Current Opinion in Plant Biology, 75: 102408.
https://doi.org/10.1016/j.pbi.2023.102408

Jiao Y., Wang Y., Xue D., Wang J., Yan M., Liu G., Dong G., Zeng D., Lu Z., Zhu X., Qian Q., and Li J., 2010, Regulation of *OsSPL14* by OsmiR156 defines ideal plant architecture in rice, Nature Genetics, 42: 541-544.
https://doi.org/10.1038/ng.591

Karavolias N., Patel-Tupper D., Cruz A., Litvak L., Lieberman S., Tjahjadi M., Niyogi K., Cho M., and Staskawicz B., 2024, Engineering quantitative stomatal trait variation and local adaptation potential by cis - regulatory editing, Plant Biotechnology Journal, 22: 3442-3452.
https://doi.org/10.1111/pbi.14464

Kobayashi N., Yamaji N., Yamamoto H., Ôkubo K., Ueno H., Costa A., Tanoi K., Matsumura H., Fujii-Kashino M., Horiuchi T., Nayef M., Shabala S., An G., Ma J., and Horie T., 2017, OsHKT1;5 mediates Na^+ exclusion in the vasculature to protect leaf blades and reproductive tissues from salt toxicity in rice, The Plant Journal, 91(4): 657-670.
https://doi.org/10.1111/tpj.13595

Kou Y., Liao Y., Toivainen T., Lv Y., Tian X., Emerson J., Gaut B., Zhou Y., and Purugganan M., 2020, Evolutionary genomics of structural variation in Asian rice (*Oryza sativa*) domestication, Molecular Biology and Evolution, 37: 3507-3524.
https://doi.org/10.1093/molbev/msaa185

Lang D., Zhang S., Ren P., Liang F., Sun Z., Meng G., Tan Y., Li X., Lai Q., Han L., Wang D., Hu F., Wang W., and Liu S., 2020, Comparison of the two up-to-date sequencing technologies for genome assembly: HiFi reads of Pacific Biosciences Sequel II system and ultralong reads of Oxford Nanopore, GigaScience, 9(12): giaa123.
https://doi.org/10.1093/gigascience/giaa123

Lee D., Chung P., Jeong J., Jang G., Bang S., Jung H., Kim Y., Ha S., Choi Y., and Kim J., 2017, The rice OsNAC6 transcription factor orchestrates multiple molecular mechanisms involving root structural adaptions and nicotianamine biosynthesis for drought tolerance, Plant Biotechnology Journal, 15: 754-764.
https://doi.org/10.1111/pbi.12673

Li J.Q., 2024, Harnessing entomopathogenic fungi for pest control in rice: case studies and efficacy, Molecular Microbiology Research, 14(1): 92-98.
https://doi.org/10.5376/mmr.2024.14.0010

Li J., Zeng Y., Pan Y., Zhou L., Zhang Z., Guo H., Lou Q., Shui G., Huang H., Tian H., Guo Y., Yuan P., Yang H., Pan G., Wang R., Zhang H., Yang S., Guo Y., Ge S., Li J., and Li Z., 2021, Stepwise selection of natural variations at *CTB2* and *CTB4a* improves cold adaptation during domestication of *japonica* rice, The New Phytologist, 231(3): 1056-1072.
https://doi.org/10.1111/nph.17407

Li X., Dai X., He H., Chen W., Qian Q., Shang L., Guo L., and He W., 2025, Uncovering the breeding contribution of transposable elements from landraces to improved varieties through pan-genome-wide analysis in rice, Frontiers in Plant Science, 16: 1573546.
https://doi.org/10.3389/fpls.2025.1573546

Lian L., Xu H., Zhang H., He W., Cai Q., Lin Y., Wei L., Pan, L., Xie X., Zheng Y., Wei Y., Zhu Y., Xie H., and Zhang J., 2020, Overexpression of *OsSPL14* results in transcriptome and physiology changes in *indica* rice ‘MH86’, Plant Growth Regulation, 90: 265-278.
https://doi.org/10.1007/s10725-019-00569-0

Liu C., Zhu X., Zhang J., Shen M., Chen K., Fu X., Ma L., Liu X., Zhou C., Zhou D., and Wang G., 2022, eQTLs play critical roles in regulating gene expression and identifying key regulators in rice, Plant Biotechnology Journal, 20(12): 2357-2371.
https://doi.org/10.1111/pbi.13912

Liu, Y., Chen, X., Xue, S., Quan, T., Cui, D., Han, L., Cong, W., Li, M., Yun, D., Liu, B., and Xu Z., 2021, SET DOMAIN GROUP 721 protein functions in saline–alkaline stress tolerance in the model rice variety Kitaake, Plant Biotechnology Journal, 19: 2576-2588.
https://doi.org/10.1111/pbi.13683

Lou D., Wang H., Liang G., and Yu D., 2017, OsSAPK2 confers abscisic acid sensitivity and tolerance to drought stress in rice, Frontiers in Plant Science, 8: 993.
https://doi.org/10.3389/fpls.2017.00993

Lou Q., Guo H., Li J., Han S., Khan N., Gu Y., Zhao W., Zhang Z., Zhang H., Li Z., and Li J., 2022, Cold-adaptive evolution at the reproductive stage in *geng*/*japonica* subspecies reveals the role of *OsMAPK3* and *OsLEA9*, The Plant Journal, 111(4): 1032-1051.
https://doi.org/10.1111/tpj.15870

Lyu J., 2024, Meta-analysis of genetic resistance to major rice pests and pathogens, Molecular Pathogens, 15(6): 273-281.
https://doi.org/10.5376/mp.2024.15.0027

Negrão S., Almadanim M., Pires I., Abreu I., Marôco J., Courtois B., Gregorio G., McNally K., and Oliveira M., 2013, New allelic variants found in key rice salt-tolerance genes: an association study, Plant Biotechnology Journal, 11(1): 87-100.
https://doi.org/10.1111/pbi.12010

Nunez-Vazquez R., Desvoyes B., and Gutiérrez C., 2022, Histone variants and modifications during abiotic stress response, Frontiers in Plant Science, 13: 984702.
https://doi.org/10.3389/fpls.2022.984702

Osakabe A., Lorković Z., Kobayashi W., Tachiwana H., Yelagandula R., Kurumizaka H., and Berger F., 2018, Histone H2A variants confer specific properties to nucleosomes and impact on chromatin accessibility, Nucleic Acids Research, 46: 7675-7685.
https://doi.org/10.1093/nar/gky540

Probst A., 2022, Deposition and eviction of histone variants define functional chromatin states in plants, Current Opinion in Plant Biology, 69: 102266.
https://doi.org/10.1016/j.pbi.2022.102266

Shang L., Li X., He H., Yuan Q., Song Y., Wei Z., Lin H., Hu M., Zhao F., Zhang C., Li Y., Gao H., Wang T., Liu X., Zhang H., Zhang Y., Cao S., Yu X., Zhang B., Zhang Y., Tan Y., Qin M., Ai C., Yang Y., Zhang B., Hu Z., Wang H., Lv Y., Wang Y., Ma J., Wang Q., Lu H., Wu Z., Liu S., Sun Z., Zhang H., Guo L., Li Z., Zhou Y., Li J., Zhu Z., Xiong G., Ruan J., and Qian Q., 2022, A super pan-genomic landscape of rice, Cell Research, 32: 878-896.
https://doi.org/10.1038/s41422-022-00685-z

Sokolova V., Sarkar S., and Tan D., 2022, Histone variants and chromatin structure, update of advances, Computational and Structural Biotechnology Journal, 21: 299-311.
https://doi.org/10.1016/j.csbj.2022.12.002

Tao Z., Kou Y., Liu H., Li X., Xiao J., and Wang S., 2011, *OsWRKY45* alleles play different roles in abscisic acid signalling and salt stress tolerance but similar roles in drought and cold tolerance in rice, Journal of Experimental Botany, 62(14): 4863-4874.
https://doi.org/10.1093/jxb/err144

Wang P., Xiong Y., Gong R., Yang Y., Fan K., and Yu S., 2019, A key variant in the cis-regulatory element of flowering gene *Ghd8* associated with cold tolerance in rice, Scientific Reports, 9: 9603.
https://doi.org/10.1038/s41598-019-45794-9

Wang S., Wu K., Qian Q., Liu Q., Li Q., Pan Y., Ye Y., Liu X., Wang J., Zhang J., Li S., Wu Y., and Fu X., 2017, Non-canonical regulation of SPL transcription factors by a human OTUB1-like deubiquitinase defines a new plant type rice associated with higher grain yield, Cell Research, 27: 1142-1156.
https://doi.org/10.1038/cr.2017.98

Wang Y., Li F., Zhang F., Wu L., Xu N., Sun Q., Chen H., Yu Z., Lu J., Jiang K., Wang X., Wen S., Zhou Y., Zhao H., Jiang Q., Wang J., Jia R., Sun J., Tang L., Xu H., Hu W., Xu Z., Chen W., Guo A., and Xu Q., 2022, Time‐ordering japonica/geng genomes analysis indicates the importance of large structural variants in rice breeding, Plant Biotechnology Journal, 21: 202-218.
https://doi.org/10.1111/pbi.13938

Yan Y., Wei M., Li Y., Tao H., Wu H., Chen Z., Li C., and Xu J., 2021, MiR529a controls plant height, tiller number, panicle architecture and grain size by regulating *SPL* target genes in rice (*Oryza sativa* L.), Plant Science, 302: 110728.
https://doi.org/10.1016/j.plantsci.2020.110728

Zheng X., Pang H., Wang J., Yao X., Song Y., Li F., Lou D., Ge J., Zhao Z., Qiao W., Kim S., Ye G., Olsen K., Liu C., and Yang Q., 2021, Genomic signatures of domestication and adaptation during geographical expansions of rice cultivation, Plant Biotechnology Journal, 20: 16-18.
https://doi.org/10.1111/pbi.13730

Zheng X., Zhong L., Pang H., Wen S., Li F., Lou D., Ge J., Fan W., Wang T., Han Z., Qiao W., Pan X., Zhu Y., Wang J., Tang C., Wang X., Zhang J., Xu Z., Kim S., Kohli A., Ye G., Olsen K., Fang W., and Yang Q., 2023, Lost genome segments associate with trait diversity during rice domestication, BMC Biology, 21: 20.
https://doi.org/10.1186/s12915-023-01512-6