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Research Insight

Marker-Assisted Selection for Lodging Resistance in Rye Breeding Programs

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Abstract Lodging is an important limiting factor in the production of rye (Secale cereale L.), especially in high-input planting systems, which seriously affects yield stability and grain quality. Improving lodging resistance has become an important goal in the genetic improvement of rye. This study systematically analyzed common molecular marker types, such as SSR, SNP and AFLP, as well as their applications in the mapping of anti-lodging related QTLS and candidate genes. The combination of MAS with QTL mapping and genome-wide association analysis (GWAS) provides strong support for analyzing the key genetic loci that affect stem structure and lignin synthesis. It also explores the feasibility of integrating MAS with early generation selection, multi-trait joint breeding and other strategies. Through breeding cases in Germany, Poland and northern China, It demonstrated the successful application of MAS technology in the improvement of rye varieties resistant to lodging. Although it still faces challenges such as group background dependence and environmental interaction at present, MAS remains an important direction for precision breeding. This study aims to enhance the integrated application of genomic selection (GS), high-throughput phenotypic analysis and molecular design breeding to improve breeding efficiency and the accuracy of resistance expression.

Keywords Rye Anti-lodging; Marker-assisted selection; Quantitative trait loci Molecular breeding

1 Introduction

Crops like rye (*Secale cereale* L.) are actually not picky about the environment. They can tolerate poor soil and withstand cold. In many temperate regions, they are an important source of food and feed, and sometimes they are also used as biomass energy. Its genetic diversity not only benefits its own breeding but also provides many useful genetic resources for related crops such as wheat, for instance, introducing disease-resistant or stress-tolerant traits. Techniques such as molecular marker-assisted selection (MAS) have been used in rye breeding to accelerate the introduction efficiency of these superior traits (Han et al., 2020; Zhu et al., 2022).

However, there are still problems. Lodging is a major problem in rye cultivation - once the stems bend or break, not only will the yield drop, but harvesting will also become more difficult. There are many factors influencing lodging, and plant height is one of the more crucial ones. Some studies have found that introducing some dwarfing genes (such as Ddw1) can improve anti-lodging performance. But it's not that simple. The environment varies greatly, and since these genes are dominant, screening for these traits with the naked eye often yields unstable results. Therefore, to truly control the problem of lodging, more precise molecular methods still need to be relied on (Wang et al., 2014; Litvinov et al., 2020).

This study will review and develop molecular marker-assisted selection strategies for the lodging resistance of rye, with a focus on the identification and application of molecular markers related to plant height control and lodging resistance genes. It will integrate genetic, physiological and molecular biological methods to improve selection accuracy and breeding efficiency. This study aims to enhance the yield stability and grain quality of rye under different environmental conditions, thereby supporting temperate sustainable agriculture and crop improvement efforts.



2 Biological Basis of Lodging Resistance in Rye

2.1 Types of lodging and influencing factors (stem strength, root development, plant height)

The most common types of rye lodging in the field can actually be divided into two categories: some have broken stems, and some have loose root systems that cause the entire plant to lean over. Both situations will affect the output, but the factors causing lodging are not exactly the same. For instance, whether the stem can hold up mainly depends on the anatomical structure - whether the number of vascular bundles is sufficient, whether the thick-walled tissue is well-developed, and whether the cell wall is thick enough. The root lodging is more related to whether the root system is deeply rooted and how strong its ability to grip the ground is. Plant height is often regarded as a risk indicator. Tall plants are indeed prone to toppling, but this is not absolute. Some rye varieties, although not short, have a higher content of lignin, cellulose, and hemicellulose in their stems and a harder structure, and thus are less likely to toppling (Niu et al., 2022).

2.2 Morphological and physiological indicators related to lodging resistance

Morphologically speaking, the length of the stem, the weight of the internodes and the wall thickness are often closely related to lodging, but the three do not change in the same direction. If the internodes are too heavy or the stems are too long, the risk of lodging will increase instead. A thicker stem wall can significantly enhance stability. Physiologically, wheat with a high density of vascular bundles and sufficient overall biomass is generally more robust. In addition to the deposition of lignin or silicon, after the hardness of the stem is increased, even if the plant height remains unchanged, the lodging resistance can be significantly improved (Muszynska et al., 2021; Li et al., 2022; Nabatova et al., 2022).

2.3 Genetic variation and heritability analysis of lodging traits

There are already many genetic differences related to lodging resistance in rye materials, and these abnormalities are associated with the tissue structure or chemical composition of the stem. Dwarfing genes like Ddw1, Ddw3 and the more recently reported Ddw4 are typical favorable alleles that can reduce plant height without affecting yield. Heritability analysis also shows that the effects of these genes are stable enough to be selected in breeding programs by relying on the markers associated with them. It is precisely because of such genetic diversity in germplasm resources that molecular marker-assisted selection is feasible in rye lodging resistance breeding (Kantarek et al., 2018; Jarosh and Relina, 2022).

3 Overview of Marker-Assisted Selection (MAS) in Resistance Breeding

3.1 Basic principles and breeding workflow of MAS

In actual breeding, waiting until the crops grow up to see if they have resistance is too costly and too slow. Thus, the approach of MAS becomes attractive. It doesn't start from scratch but combines molecular markers with traditional breeding - it can identify which plants carry "good genes" at an early seedling stage. In this process, the first step is to identify the QTL or gene related to the target trait, and then develop closely linked DNA markers accordingly. The subsequent stages of genotyping, hybridization, backcrossing or pedigree selection are like "precise navigation", helping breeders more efficiently screen out the desired combination of traits. Especially when integrating multiple complex traits, this approach can save a lot of effort in phenotypic identification in the field (Misra & Singh, 2025; Boopathi, 2020).

3.2 Types of molecular markers (SSR, SNP, AFLP) and their characteristics

Not all molecular markers are the same. Codominant types like SSR, although they have strong polymorphism and are suitable for analyzing genetic diversity or making linkage maps, have a slightly more complex operation process and are also relatively time-consuming. SNPS are different. They have many points, are stable, and are suitable for high throughput. They are especially suitable for large-scale projects and are currently the most widely used type of marker. Although AFLP can achieve whole-genome scanning without genomic information, it is a dominant marker with slightly weaker repeatability. It is suitable for initial screening but not very suitable for later detailed analysis. As for which marker to choose, it is not set in stone. It depends on the project goals, financial situation, and whether high throughput or higher resolution is required (Henkrar, 2020; Misra and Singh, 2025).



3.3 Advantages and limitations of MAS compared with conventional breeding methods

Slow breeding selection is an old problem. The emergence of MAS was originally intended to improve this aspect. It can pick out promising plants before the crops grow up, saving a lot of time and field work, especially showing advantages in those traits with low heritability and significant environmental impact. By combining multiple resistance genes, persistence and broad-spectrum properties can also be enhanced. But then again, it's not omnipotent either. For instance, a large amount of resources need to be invested in the early development of markup. Moreover, if there are no markers closely linked to the target gene, subsequent screening will also be difficult to be precise (Zhang et al., 2025). Not to mention that the identification of polygenic traits is inherently complex and prone to environmental interference. Therefore, although MAS has significant advantages in certain scenarios, in practical applications, traditional phenotypic selection remains indispensable. In recent years, the continuous development of high-throughput typing and genomic selection has also brought new possibilities to MAS, especially in terms of improving efficiency and application scope (Mapari and Mehandi, 2024).

4 Gene Identification and QTL Mapping Related to Lodging Resistance

4.1 Progress in QTL mapping for lodging resistance

Not all improvements to lodging resistance rely on changing plant height. Some studies have found in wheat that certain QTLS can enhance stem strength without reducing plant height, which provides a new approach to improving lodging resistance. In fact, for crops like barley, rice and wheat, researchers have already identified many QTLS related to lodging traits on their chromosomes. For instance, 15 QTLS in wheat have been confirmed to be related to stem strength, and 27 stable QTLS associated with stem morphology and lodging index have been identified in barley. These loci remain stable in various environments. This indicates that lodging is not a simple trait controlled by a single gene; it is a composite result controlled by multiple genes. Therefore, it is feasible to use marker-assisted selection to track these key loci (Figure 1) (Long et al., 2020; Niu et al., 2022; Zhang et al., 2022; Rabieyan et al., 2024).

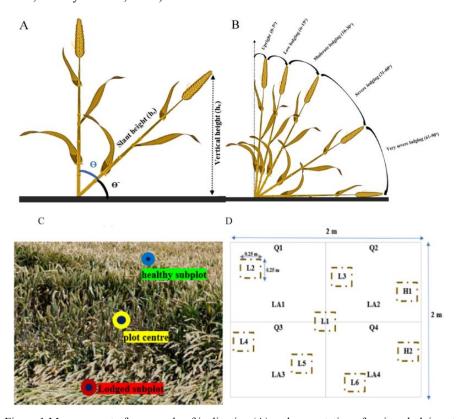


Figure 1 Measurement of crop angle of inclination (A) and presentation of various lodging stages (B). Presentation of the plot center and the healthy/lodged subplots in the field (C). Division of the plot into four quadrants Q1, Q2, Q3, and Q4 (D). LA1, LA2, LA3, and LA4 are corresponding to the lodged area in each quadrant. In this scenario, H1 and H2 present the healthy subplots while L1 to L6 are the lodged subplots (Adopted from Rabieyan et al., 2024)



4.2 Candidate genes associated with stem strength and lignin biosynthesis

Anti-lodging does not necessarily rely on external support. In crops, especially the components of the cell wall, actually play a very important role. For instance, in rice, a gene involved in lignin synthesis, OsPSLSq6, is located in an anti-lodging QTL region. It encodes cinnamoyl-coA reductase - an important member of the lignin synthesis pathway. In rapeseed, researchers, through cross-validation of GWAS and transcriptome data, also identified several genes related to lignin content and stem strength, some of which are transcription factors or glycoside hydrolases. They may indirectly enhance the mechanical properties of the stem by regulating the structure of the secondary cell wall, thereby achieving the effect of "anti-lodging" (Wei et al., 2017; Zhao et al., 2021; Yang et al., 2023).

4.3 Discovery of lodging-associated genetic loci through GWAS

Sometimes, the resolution of traditional QTL localization is not fine enough, which requires GWAS to fill the gap. By analyzing the natural variations among different varieties, GWAS has identified over 120 QTL regions related to lodging in wheat. Many of the genes involved in these regions are involved in the construction of cell walls, hormone regulation, and even root growth. Not only wheat, but also crops such as soybeans have found similar results in related research, especially in terms of the chemical composition and structural stability of the stems. Although these traits themselves are very complex, GWAS has brought about a clearer genetic map. In the future, if the data obtained from GWAS is combined with genomic prediction models, perhaps those genotypes that truly "stand firm" can be selected more accurately (Zhao et al., 2021; Rabieyan et al., 2024; Zhao et al., 2024).

5 Integrated MAS Strategies for Lodging Resistance in Rye Breeding

5.1 Development and screening of molecular markers for lodging resistance

Not all molecular markers can play a role in breeding practice, especially for crops like rye with a complex genetic background. In recent years, with the popularization of technologies such as genotyping sequencing (GBS) and KASP, there has finally been a breakthrough in the specific molecular markers for rye's lodging resistance. Dwarfting alleles like Ddw1 have been successfully located and linked to multiple stable markers, which can directly affect plant height and lodging resistance. Some rham-specific markers developed on PCR and KASP platforms can also distinguish chromosome arms, providing more precise tools for breeding. Compared with phenotypic screening that relies on environmental performance, these genetic markers can indeed target the material at an early stage, significantly improving the efficiency of MAS (Litvinov et al., 2020).

5.2 Multi-trait selection strategies: balancing lodging resistance and high yield

The two goals of high yield and lodging resistance do not always coexist harmoniously in rye breeding. Sometimes, if you want the plants to stand firm, you have to sacrifice a little yield. However, in actual breeding, the two cannot be completely separated. Therefore, some teams have attempted a multi-trait combined selection strategy to simultaneously track multiple QTLS through molecular means, especially those loci related to both stem strength and grain yield (Huang and Wang, 2025). Integrating genotype data and actual phenotypic results in early generations can reduce the waste of resources in later selection and breeding. Even in different genetic contexts, this combined approach has demonstrated flexibility and stability in trait trade-offs (Kumar et al., 2018).

5.3 Combining MAS with early-generation selection and accelerated breeding

Some traits slow down the breeding pace, and lodging resistance is one of them. However, if MAS is combined with early-generation screening or even advanced-generation propulsion technology, both the speed and accuracy can be improved. For instance, in previous generations, genotyping was accomplished with the aid of KASP or GBS technology, which could significantly reduce the time spent waiting for the manifestation of field traits. Subsequent phenotypic verification serves as a supplement to confirm whether the actual expression of these ideal alleles is in line with expectations. Some breeding projects have further introduced genomic selection models, turning MAS into a dynamically updated toolchain and no longer an isolated means. This combination of measures can significantly enhance the overall breeding efficiency, and it will no longer be far away to cultivate stable lodging resistant varieties in different ecological zones (He et al., 2014; Han et al., 2020; Anilkumar et al., 2022).



6 Case Studies: MAS Applications in Lodging-Resistant Rye Breeding

6.1 German hybrid rye programs for lodging resistance improvement

In Germany, breeders are not only confronted with how to increase the production of rye, but also with how to make it "stand firm". Lodging resistance has always been an old problem. The conventional selection methods in the past always struggled to achieve both high yield and resistance to lodging. However, in recent years, some breeding teams have integrated molecular markers into the breeding process, especially in hybrid rye, attempting to solve this long-standing problem through genetic means. They attempted to develop semi-dwarf varieties sensitive to gibberellin, with the aim of reducing plant height without losing yield, while making the stems harder and more wind-resistant. This type of breeding program utilizes the latest SMART strategy and genomic information, which not only makes it more flexible in controlling chain negative effects but also strikes a balance between stability and lodging resistance (Figure 2). Dwarfing genes such as Ddw1 have become key, and the related molecular markers have also accelerated the screening process (Litvinov et al., 2020; Hackauf et al., 2022).



Figure 2 (A) C. purpurea infects the ovary and replaces the rye grain with a dark fungal body, the ergot sclerotium. (B) The gene Rfp1 results in restoration of male fertility in P-type CMS rye hybrids and increases ergot defense. (C) Male sterile plants in P-type CMS rye hybrids with a restorer index of \sim 50% increase yield potential due to a female advantage but weaken the ergot defense (Adopted from Hackauf et al., 2022)

6.2 QTL-based breeding for early-maturing lodging-resistant cultivars in Poland

The situation in Poland is slightly different. The climate is short and the planting window is tight, so early maturity of the variety is the top priority. However, it is often difficult to balance early maturity and anti-lodging, which requires more refined strategies. There, breeders attempted to identify gene regions that could simultaneously control plant height and stem strength through a combination of QTL mapping and marker selection. Long-term field data have also verified the effect: hybrid varieties perform better than population varieties in terms of lodging resistance and have more stable yields. Some achievements are attributed to the combination of molecular means in breeding to control the genetic factors of the risk of tillage from the source, and then continuously iterated through agronomic practice. This approach is considered to be relatively suitable for the farming conditions in Poland (Kostrzewska and Jastrz wob ska, 2025).

6.3 Preliminary MAS-based breeding efforts for winter rye in Northern China

Domestically, especially in the breeding of winter rye in the north, the field of molecular markers has only just begun. However, it's not that they haven't taken action. Some units have already begun to try using high-throughput PCR and KASP markers specifically designed for rye to locate and screen key anti-lodging sites.



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What's more interesting is that researchers have also developed universal markers on the chromosome arms, with the aim of precisely tracking the chromatin segments related to important traits, helping to introduce superior genes into locally adapted varieties. Although it is still in the exploratory stage at present, this set of tools has indeed played an accelerating role in early selection and gene aggregation. From a trend perspective, the combination of molecular technology and phenotypic methods should gradually enhance the breeding efficiency of winter rye in terms of lodging resistance in China (Han et al., 2020; Zhu et al., 2022).

7 Conclusions and Future Perspectives

In rye lodging resistance breeding, researchers usually focus on several prominent phenotypic characteristics, such as the plant being less tall, the stem being thicker, and the possibility of toppling down being smaller. These characteristics do not occur randomly and have a certain genetic basis behind them, such as the well-known Ddw1 dwarfted allele. However, not all anti-lodging rye varieties look the same. Some may have more vascular bundles in their stems, some have thicker cell walls, or have higher lignin and mineral content than other varieties (all of which help to support the plants). As for breeding, molecular marker-assisted selection (MAS) is still quite commonly used at present. At least it can help screen out those unsuitable materials early and save some time. However, it also has limitations, especially the prediction effect is not very stable among different germplasms.

For instance, one of the biggest challenges in MAS is the interaction between the environment and genotypes. Some alleles, such as Ddw1, sometimes behave in a heterozygous state that is somewhat confusing. Moreover, environmental changes can easily mask the traits themselves, making it a bit difficult to achieve "stable selection". Not to mention that once it is used in distant germplasm, the accuracy is even less guaranteed. These circumstances indicate that relying solely on MAS may not be sufficient. It is also necessary to consider integrating it with more comprehensive genomic methods, along with verification in multiple environments, to make it more reliable.

Looking ahead, genomic selection (GS) is clearly a more promising direction. It is no longer confined to a few marker sites but uses the marker data of the entire genome to predict breeding values. Especially after conducting field trials at multiple locations and for many consecutive years, the accuracy of this method is generally higher than that of MAS. Meanwhile, the new generation of high-throughput phenotypic technology has also begun to play a role. It enables us to conduct larger-scale and more accurate measurements of lodging traits, which is most suitable for supplementing genomic data. A further approach is to combine genomic selection, MAS and phenotypic platforms into a more systematic "design breeding" strategy - bringing together multiple favorable genes while taking into account the mutual influence among traits and the interference of environmental changes. This integration approach might be able to solve the past bottlenecks and eventually breed rye varieties that can stand firm under various climatic and cultivation conditions.

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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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