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Case Study **Open Access**

Genome-Wide Association Mapping of Salt Tolerance in Barley Germplasm

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Abstract Salt stress is the main abiotic factor that limits the productivity of barley (*Hordeum vulgare* L.) in global saline-alkali regions. This study employed genome-wide association analysis (GWAS) methods to reveal the genetic basis of salt tolerance in different barley germplasm resources. We evaluated a group of core germplasm resources under controlled salinity conditions and conducted high-resolution GWAS analysis using single nucleotide polymorphism (SNP) markers. Our analysis identified several loci and candidate genes significantly associated with salt stress traits, including those involved in ion homeostasis, osmotic regulation, and stress signaling pathways. A case study focusing on North African germplasm resources highlighted key salt-tolerant genes, such as *HvHKT1;5* and *HvNHX1*, which further emphasizes their significance in breeding projects. Despite the challenges related to population structure and environmental variations, our research results demonstrate the practicality of GWAS in analyzing complex traits and guiding marker-assisted selection (MAS). This study laid the foundation for breeding salt-tolerant barley varieties and emphasized the value of integrating genomic tools into climate-adaptive agricultural breeding strategies.

Keywords Barley germplasm; Salt tolerance; GWAS; Candidate genes; Marker-assisted selection

1 Introduction

In some areas with high soil salinity, barley is often regarded as a "safe grain" for food security. It's not because its yield is necessarily the highest, but because it can tolerate salt more than many crops. Salinization is now spreading worldwide, and the area of affected cultivated land is still expanding. However, a salt environment does not mean that crops will be safe and sound - salt stress can disrupt the ionic balance of plants, reduce biomass, and also impact germination, chlorophyll levels, and antioxidant defense processes. As a result, the growth of the plants is often weakened, and the yield declines accordingly. Sometimes, even quite serious losses occur (Sonia et al., 2023; Thabet and Alqudah, 2023).

It is not an easy task to enhance salt tolerance through traditional breeding. Not only is the genetic structure complex, but it also involves multiple physiological and molecular pathways. In contrast, genome-wide association studies (GWAS) have been proven useful in understanding the genetic basis of salt tolerance. It can identify quantitative trait loci (QTLS), single nucleotide polymorphisms (SNPS), and candidate genes related to key traits, including ion transport, antioxidant capacity, and stress response gene expression, etc. (Việt et al., 2013; Mwando et al., 2020). Previous studies have mapped important QTLs on chromosomes 2H, 4H, 6H, and 7H, and have also identified genes such as *HKT1;5* that regulate sodium ion transport, as well as other genes involved in ion homeostasis and antioxidant defense. (Huang et al., 2008; Mwando et al., 2021).

This study intends to use GWAS to screen out salt-tolerant gene loci and candidate genes in different barley germplasms, and combine genomic, physiological and transcriptomic information to provide genetic markers and resources that can be used for breeding. In this way, the efficiency of mark-assisted selection can be enhanced, and the breeding of salt-tolerant varieties will also be accelerated. Not only that, these achievements are helpful for the sustainable development of saline-alkali land agriculture and can also provide a reference framework for similar research on other crops.

2 Overview of Salt Stress in Barley

2.1 Physiological and biochemical effects of salinity on barley growth

Under salt stress, the response of barley plants is quite intuitive - the biomass of both above-ground and underground parts decreases, the water content of leaves drops, and the level of photosynthetic pigments also decreases (Figure 1) (Eldakkak and El-Shourbagy, 2023). Meanwhile, sodium ions (Na^+) often accumulate excessively, while the absorption of potassium ions (K^+) is inhibited. The Na^+/K^+ ratio is disrupted, making it more difficult to maintain cellular homeostasis and metabolism (Sadiq et al., 2024). However, not all varieties are the same. Some salt-tolerant barley can still maintain a relatively high K^+/Na^+ ratio and relatively good moisture conditions. From a biochemical perspective, salt stress can promote the increase of osmotic regulatory substances such as proline and soluble sugar, and also enhance the activity of antioxidant enzymes such as catalase, ascorbic acid peroxidase, and peroxidase. These reactions can to some extent alleviate oxidative damage. In the salt-sensitive type, the contents of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) tend to increase, indicating aggravated lipid peroxidation and oxidative stress (Yildiz and Acar, 2022).

Figure 1 Illustrated the variation among barley genotypes under control condition and with 100 mM and 200 mM NaCl treatments (Adopted from Sadiq et al., 2024)

2.2 Genetic complexity and heritability of salt tolerance traits

Salt tolerance is not a trait that can be explained by a single gene. It involves multiple physiological and molecular mechanisms (Ouertani et al., 2021). Among barley of different genotypes, the differences in these traits are quite obvious, such as ion homeostasis, antioxidant capacity, and accumulation of osmotic protectants, which usually have high heritability and are regulated by specific genotypes. Recent studies have identified some genomic loci and candidate genes highly correlated with salt tolerance, especially those key genes directly involved in ion transport and antioxidant defense. However, the situation behind this is not simple - the interaction between genotypes and the environment, the superposition of additive and non-additive effects, all make the genetic basis of salt tolerance more difficult to fully clarify (Abdelrady et al., 2024).

2.3 Conventional breeding limitations in improving salt stress resilience

It is not easy for traditional breeding to make breakthroughs in salt tolerance. Polygenic control, significant environmental influence, and complex phenotypic traits all make the screening work slow and cumbersome (Boussora et al., 2024). Coupled with insufficient molecular markers and long breeding cycles, the launch speed of salt-tolerant varieties is naturally limited (Alqudah et al., 2024). These realities also explain why more advanced genomic approaches, such as genome-wide association studies (GWAS), are particularly necessary in analyzing the genetic structure of salt tolerance and promoting the breeding process.

3 GWAS as a Tool for Dissecting Salt Tolerance

3.1 Advantages of GWAS over traditional QTL mapping

Traditional QTL mapping is usually based on specific parent groups, and the range that can be located is often large, but the accuracy is limited (Li, 2020). The approach of GWAS is somewhat different. It directly utilizes the natural genetic diversity from vast germplasm resource banks, making it more detailed in the detection of the association between markers and traits (Huang and Lin, 2024). In this way, not only can single nucleotide polymorphisms (SNPS) significantly associated with salt tolerance traits be identified across the entire genome, but also candidate genes or alleles that are easily overlooked by traditional methods may be discovered.

3.2 Marker-trait association and identification of significant SNPs

In recent barley studies, GWAS has identified many SNPS related to key traits of salt tolerance, such as Na^+ and K^+ contents, Na^+/K^+ ratio, and root and stem biomass under salt stress (Xu et al., 2023). These loci are distributed on chromosomes 2, 4, 5, 6 and 7, and some of these "hotspot" regions are concentrated with candidate genes related to ion transport, protein kinases and stress signal transduction. *HKT1;5* is a typical example. It plays an important role in the transport and distribution of sodium and has a direct impact on the salt tolerance mechanism of barley (Hazzouri et al., 2018). The discovery of these marker-traits provides quite valuable genetic basis for subsequent marker-assisted selection in breeding.

3.3 Integration of GWAS with other omics approaches

Although GWAS alone can identify the associated loci, the effect of screening and verifying candidate genes will be better when combined with transcriptomics and metabolomics (Gharaghanipor et al., 2022). For instance, through integrative analysis, some studies have found that in salt-tolerant and salt-sensitive barley genotypes, some differentially expressed genes (DEGs) are concentrated in pathways such as ion homeostasis, antioxidant defense, and metabolic regulation (Tu et al., 2021). Genes such as *PGK2*, *BASS3*, *SINAT2*, *AQP* and *SYT3* were thus identified and further verified by qRT-PCR. The combination of such multi-omics not only enables people to have a more comprehensive understanding of the molecular mechanism of salt tolerance, but also accelerates the speed of breeding stress-resistant varieties.

4 Germplasm Resources for GWAS in Barley

4.1 Diversity of global barley collections and gene banks

In national or international gene banks around the world, a large number of barley germplasms are preserved - including local varieties, wild relatives, and excellent cultivated varieties. Together, they constitute an extremely rich genetic diversity, which precisely serves as an important basis for identifying new alleles and loci related to salt tolerance during GWAS. In previous studies, some teams directly utilized hundreds or even thousands of germplasms from around the world, covering different geographical and genetic backgrounds, in order to capture as many association signals between markers and traits as possible.

4.2 Importance of landraces, wild relatives, and elite lines in salt tolerance research

In terms of salt tolerance research, local varieties and wild barley (*Hordeum spontaneum*) have their unique value. They often adapt to regions with harsher environmental conditions and carry some alleles that are not present in modern cultivated varieties (Wu et al., 2013). Especially wild barley often outperforms cultivated varieties in terms of osmotic regulation ability and the content of compatible solutes. As for superior strains and modern cultivated varieties, although their diversity is relatively limited, they have a good agronomic background and can serve as reliable controls or references when evaluating new salt-tolerant sources.

4.3 Strategies for core set development and phenotypic screening under salinity

Faced with a vast amount of germplasm resources, researchers often first establish a micro-core set or core set to cover the largest genetic and phenotypic differences with fewer samples. Then, these core sets were placed in the field or controlled environment for salt stress treatment to determine ion content, biomass, yield and some key physiological indicators (Xu et al., 2025). At the same time, by combining advanced phenotypic techniques such as ion flux measurement and transcriptome analysis, salt-tolerant genotypes and their underlying mechanisms can be identified more effectively. This approach makes GWAS more efficient and also provides a shortcut for discovering salt-tolerant candidate genes and breeding related varieties.

5 Major Findings from GWAS on Salt Tolerance

5.1 Identified loci and candidate genes associated with salt-responsive traits

In GWAS analysis, researchers have identified many SNPS and candidate genes related to salt tolerance. These traits include Na^+, K^+ content, Na^+/K^+ ratio, and biomass changes under salt stress. Among them, the *HKT1;5* gene located on chromosome 4 has attracted much attention - it is directly involved in the transport of sodium, can reduce the accumulation of Na^+ in leaves, and thus improve the salt tolerance of plants (Hazzouri et al., 2018). In addition, 54 significant SNPS distributed on chromosomes 2, 4, 5, 6 and 7, as well as 616 candidate genes involved in transport, signal transduction and stress response, were recorded. Genes such as *PGK2*, *BASS3*, *SINAT2*, *AQP* and *SYT3*, which have been verified in combination with transcriptome data, are also closely related to maintaining ion balance and adapting to stress.

5.2 Chromosomal hotspots and pleiotropic regions relevant to salinity stress

On multiple chromosomes, especially on chromosomes 4, 6 and 7, research has identified regions where SNPS are highly concentrated and overlap with the positions of key candidate genes. These places are often referred to as "hotspots", which not only control ion homeostasis but may also simultaneously affect properties such as antioxidant activity and yield (Alqudah et al., 2024). Take chromosome 7H as an example. Some loci on it are related not only to the activity of antioxidant enzymes under salt stress but also to morphological traits, indicating that these loci have a wide range of roles in stress adaptation.

5.3 Functional annotations of genes involved in ion homeostasis, osmoprotection, and signaling

When performing functional annotations on the genes identified by GWAS, some results are quite intuitive - many genes precisely fall into the crucial aspects of salt tolerance. For example, *HKT1;5* and *NHX1* are mainly responsible for expelling Na^+ or isolating it to specific positions within the cell, thereby maintaining ionic balance (Soud et al., 2024). Aquaporin (AQP) acts like a "waterway", helping water flow rapidly. There is another type of gene that encodes antioxidant enzymes - peroxidase, catalase, and ascorbic acid peroxidase - whose task is to eliminate reactive oxygen species and reduce the oxidative stress of cells. On the other side, genes related to signal transduction, such as *LRR-KISS*, *CML*, and *SINAT2*, enable plants to respond rapidly and coordinate various defense mechanisms when exposed to high salt levels (Chang et al., 2024). This information does not merely remain at the research level; it also provides a readily available genetic basis for breeding salt-tolerant barley varieties.

6 Case Study

6.1 Selection of diverse accessions from Tunisia and Algeria for association mapping

In North Africa, the local varieties and genotypes of barley in Tunisia and Algeria have long been systematically collected and evaluated under salt stress conditions. The genetic background of these materials is very broad, and the differences in traits are also considerable - whether it is agronomic traits, morphological characteristics or yield-related indicators, they all show obvious differentiation in the high-salt environment (Allel et al., 2016). Among them, some strains have demonstrated outstanding salt tolerance, such as Tozeur2, Tichedrett, Kerkena and Kebelli2, which can maintain high yields even under high-salt conditions. This makes them particularly valuable in association mapping and breeding.

6.2 Key SNPs and genes (e.g., *HvHKT1;5*, *HvNHX1*) discovered under controlled salinity trials

In the study of barley in North Africa, GWAS and physiological experiments together revealed many loci and genes closely related to salt tolerance. *HvHKT1;5* on chromosome 4 is the key point among them. It plays a core role in the transport and excretion of sodium ions and can significantly reduce the accumulation of Na^+ in leaves, thereby enhancing the salt tolerance of the plant (Figure 2). *HvNHX1* is also worth mentioning. Such genes are responsible for the regionalization of Na^+ and the maintenance of ion balance, and are closely related to the adaptability of plants under salt stress (Xu et al., 2025). In addition, there are some loci related to antioxidant defense and accumulation of osmotic regulatory substances, which provide more clues for understanding the genetic basis of salt tolerance in these germplasms (Alqudah et al., 2024).

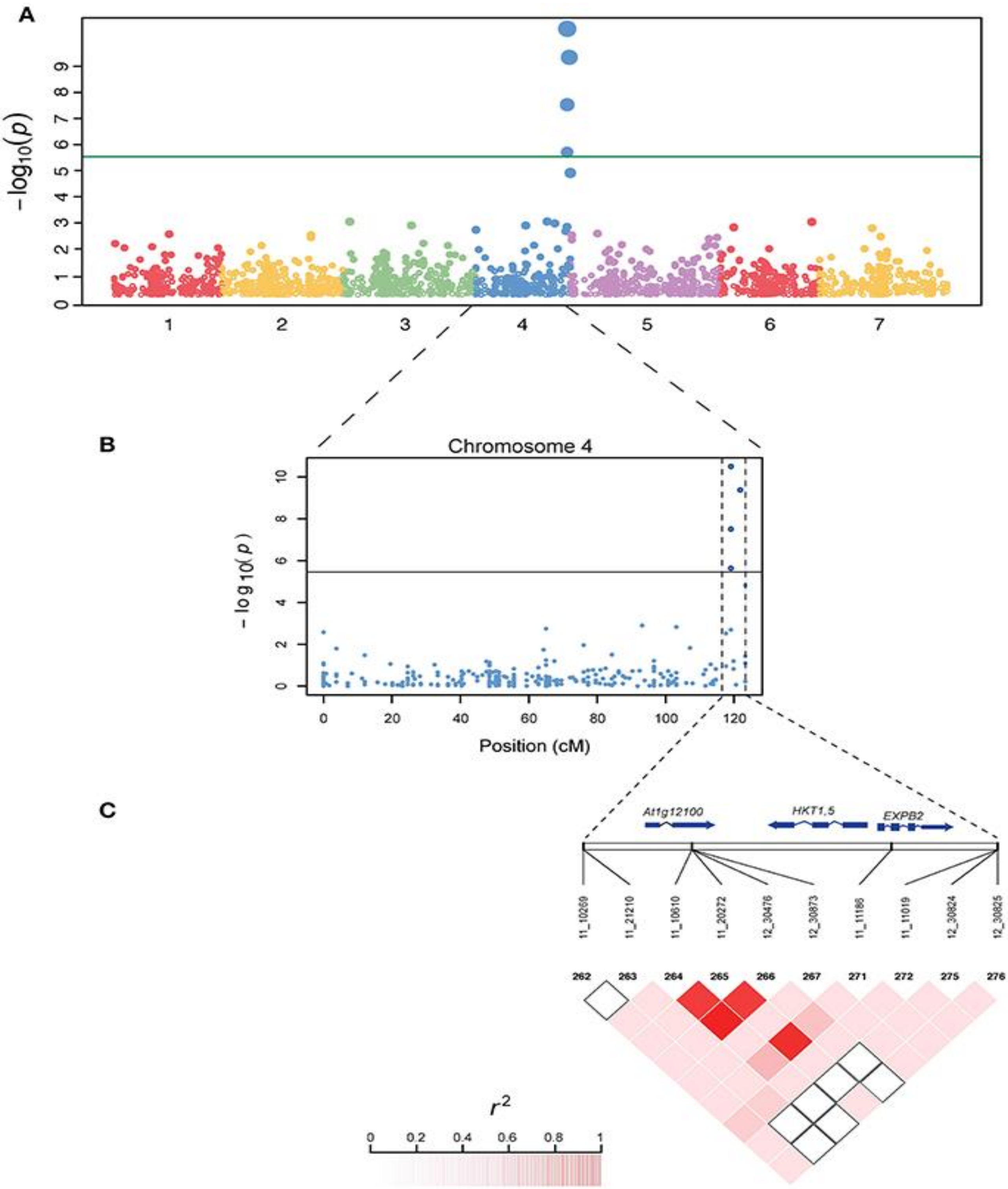

Figure 2 Genome wide association (GWAS) study in barley. (A) A Manhattan plot generated showing the seven barley chromosomes and the significant SNPs on the chromosome 4. The y-axis is the negative log10 transformed *p*-values of SNP from a genome-wide association analysis for Na^+ plotted against the genetic distance in cM. (B) A zoom view of chromosome 4 with the bottom showing the candidate range for the gene *HKT1;5* associated with low Na^+ accumulation in barley using the Morex annotation genome. (C) A panel depicting the extent of linkage disequilibrium in this region based on r^2. The r^2 values are indicated using color intensity at the left bottom. A region of 1.5 Mb associated with *HKT1;5* including other genes are indicated using two vertical dashed lines. Genes are represented in the middle panel (Adopted from Hazzouri et al., 2018)

6.3 Practical applications of findings in regional breeding programs

For regional breeding, these salt-tolerant genotypes and the corresponding genetic markers are not "paper achievements", but tools that can be directly applied. Through marker-assisted selection, favorable alleles in genes such as *HvHKT1;5* and *HvNHX1* can be introduced into superior varieties that adapt to saline-alkali environments. Meanwhile, some phenotypic characteristics - such as the biomass in the upper highlands, higher grain yield, and maintaining strong antioxidant enzyme activity under saline-alkali conditions - can also serve as reliable selection criteria (Allel et al., 2019). This approach not only benefits local breeding but also provides reference and support for other regions with increasingly severe salinization, helping to achieve sustainable agriculture and food security.

7 Challenges and Limitations in GWAS for Salt Tolerance

7.1 Population structure and false-positive associations

A common problem when conducting GWAS is the confounding effect brought about by the population structure. When genetic relationships are too close or there are significant differences among different subgroups, and these have not been fully incorporated into the analysis, it is very easy to have some "seemingly related" markers and trait associations that are actually false (Li, 2020). Hybrid linear models and more refined statistical methods can alleviate this situation, but it is almost impossible to completely eliminate it.

7.2 Limited resolution in complex trait mapping under environmental interaction

Salt tolerance itself is a complex quantitative trait, involving not only multiple genes but also having a strong interaction with the environment (Thabet et al., 2025). When the environment fluctuates greatly or the effect of a single site is small, it is very difficult for GWAS to precisely analyze the genetic structure of this trait (Kumar et al., 2015). In this case, the result might merely be the delineation of a larger genomic region rather than directly locking onto a specific pathogenic gene. Even some loci that are crucial to overall tolerance but have a relatively small effect may be overlooked.

7.3 Need for high-quality phenotyping and environmental standardization

The salt tolerance phenotype is highly sensitive to external conditions. A slight difference in the growth environment or a slight change in the measurement method may lead to different results (Hu and Schmidhalter, 2023). Differences in salinity levels, planting conditions, and measurement methods will all increase noise, making true associated signals more difficult to identify. New phenotypic analysis techniques such as high-throughput imaging and sensor-based automatic measurement seem promising, but they are costly and not easy to popularize, especially in the early breeding stage or in areas with limited conditions. To enhance the reliability of GWAS in salt tolerance studies, the standardization of environmental conditions and phenotypic analysis methods remains a problem that must be addressed.

8 Integration of GWAS with Genomic Selection and Molecular Breeding

8.1 Use of significant GWAS markers for marker-assisted selection (MAS)

Significant SNPS or loci identified in GWAS can often be put to use directly - they can serve as molecular markers to help breeders more quickly identify materials with superior salt-tolerant alleles (Liu et al., 2024). Especially those markers closely linked to key genes can be easily embedded into the breeding process to track and combine beneficial traits (He et al., 2014). In this way, the screening becomes more targeted and the steps for cultivating high-quality seeds can also be simplified.

8.2 Potential of genomic prediction models to improve breeding efficiency

The greatest advantage of genomic selection (GS) is that there is no need to wait until the traits are fully manifested before drawing a conclusion. It relies on genome-wide marker data to predict an individual's breeding value in advance (Spindel et al., 2015; 2016; Li et al., 2017). If the results of GWAS are incorporated into the GS model, such as weighting significant markers or directly setting them as fixed effects, the prediction accuracy tends to be higher (Wang et al., 2024; Pang et al., 2025). Traits such as salt tolerance, which are jointly controlled by multiple genes, are particularly suitable by this method - it can not only increase the genetic gain in each breeding cycle, but also facilitate the faster screening of dominant genotypes from large populations (Zhang et al., 2023; Meuwissen et al., 2024).

8.3 Role of CRISPR and gene editing in validating candidate genes

CRISPR/Cas9 and other gene editing techniques provide very direct tools for verifying the candidate genes identified by GWAS (Kumar et al., 2024). By site-specific modification or even knockout of a certain gene, researchers can clarify its role in salt tolerance and thereby create new allelic variations, preparing for breeding applications. In this way, the achievements of GWAS do not have to remain at the theoretical stage but can enter the actual genetic improvement process more quickly, and also open up a direct path for breeding barley strains with stronger salt tolerance.

9 Concluding Remarks

In salt tolerance studies, GWAS has identified many important SNPS and candidate genes related to Na^+/K^+ balance, ionic homeostasis and antioxidant activity. Key loci like *HKT1;5*, as well as genes involved in ion transport, signaling, and stress response, are located on different chromosomes, and these regions are also considered "hotspots" for salt tolerance. When GWAS WAS combined with transcriptome analysis, the roles of these candidate genes were further verified, and their physiological functions in response to salt stress in plants also became clearer.

These genetic markers are not only research achievements in the laboratory but can also directly enter the breeding process. They provide available tools for marker-assisted selection and genomic prediction, enabling breeders to more specifically introduce favorable alleles into favorable backgrounds, thereby enhancing yield stability and stress resistance under salt stress. Meanwhile, the stress memory of intergenerational and even cross-generational ones also provides new ideas for long-term adaptive breeding.

For future salt-tolerant barley breeding to truly achieve breakthroughs, it is likely to rely on the coordination of several methods - GWAS, high-throughput phenotypic analysis, transcriptomics, and more advanced genomic selection models. Gene editing technologies like CRISPR will also come into play. They can not only verify the functions of key genes but also precisely modify them. When data-driven methods become more mature, the breeding speed of salt-tolerant varieties is expected to accelerate significantly. By then, these varieties will not only be able to maintain stable yields under conditions of increasing salinization and frequent climate change, but also provide solid support for global food security.

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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.

References

Abdelrady W., Ma Z., Elshawy E., Wang L., Askri S., Ibrahim Z., Dennis E., Kanwal F., Zeng F., and Shamsi I., 2024, Physiological and biochemical mechanisms of salt tolerance in barley under salinity stress, Plant Stress, 11: 100403.
https://doi.org/10.1016/j.stress.2024.100403

Allel D., Ben-Amar A., Badri M., and Abdelly C., 2016, Salt tolerance in barley originating from harsh environment of North Africa, Australian Journal of Crop Science, 10: 438-451.
https://doi.org/10.21475/AJCS.2016.10.04.P6663X

Allel D., Ben-Amar A., Badri M., and Abdelly C., 2019, Evaluation of salinity tolerance indices in North African barley accessions at reproductive stage, Czech Journal of Genetics and Plant Breeding, 55(2): 61-69.
https://doi.org/10.17221/50/2017-CJGPB

Alqudah A., Elkelish A., Alammari B., Alsubeie M., Hamed S., and Thabet S., 2024, Genetic mapping determining the key genomic Loci/QTNs for stress resilience via controlling antioxidant defenses in barley under salt stress, Plant Molecular Biology Reporter, 43: 324-335.
https://doi.org/10.1007/s11105-024-01488-9

Boussora F., Triki T., Bennani L., Bagues M., Ali S., Ferchichi A., Ngaz K., and Guasmi F., 2024, Mineral accumulation, relative water content and gas exchange are the main physiological regulating mechanisms to cope with salt stress in barley, Scientific Reports, 14: 14931.
https://doi.org/10.1038/s41598-024-65967-5

Chang H., Wu T., Shalmani A., Xu L., Li C., Zhang W., and Pan R., 2024, Heat shock protein HvHSP16.9 from wild barley enhances tolerance to salt stress, Physiology and Molecular Biology of Plants, 30(5): 687-704.
https://doi.org/10.1007/s12298-024-01455-4

Eldakkak E., and El-Shourbagy M., 2023, Effect of polyamine precursors and antioxidants on growth and metabolism of salt-stressed barley, F1000Research, 12: 262.
https://doi.org/10.12688/f1000research.130979.2

Gharaghanipor N., Arzani A., Rahimmalek M., and Ravash R., 2022, Physiological and transcriptome indicators of salt tolerance in wild and cultivated barley, Frontiers in Plant Science, 13: 819282.
https://doi.org/10.3389/fpls.2022.819282

Hazzouri K., Khraiwesh B., Amiri K., Pauli D., Blake T., Shahid M., Mullath S., Nelson D., Mansour A., Salehi-Ashtiani K., Purugganan M., and Masmoudi K., 2018, Mapping of *HKT1;5* gene in barley using gwas approach and its implication in salt tolerance mechanism, Frontiers in Plant Science, 9: 156.
https://doi.org/10.3389/fpls.2018.00156

He J., Zhao X., Laroche A., Lu Z., Liu H., and Li Z., 2014, Genotyping-by-sequencing (GBS), an ultimate marker-assisted selection (MAS) tool to accelerate plant breeding, Frontiers in Plant Science, 5: 484.
https://doi.org/10.3389/fpls.2014.00484

Hu Y., and Schmidhalter U., 2023, Opportunity and challenges of phenotyping plant salt tolerance, Trends in plant science, 28(5): 552-566.
https://doi.org/10.1016/j.tplants.2022.12.010

Huang J., and Lin X.F., 2024, Advances in animal disease resistance research: discoveries of genetic markers for disease resistance in cattle through GWAS, Bioscience Evidence, 14(1): 24-31.
https://doi.org/10.5376/be.2024.14.0004

Huang S., Spielmeyer W., Lagudah E., and Munns R., 2008, Comparative mapping of HKT genes in wheat, barley, and rice, key determinants of Na^+ transport, and salt tolerance, Journal of Experimental Botany, 59(4): 927-937.
https://doi.org/10.1093/jxb/ern033

Kumar R., Das S., Choudhury B., Kumar A., Prakash N., Verma R., Chakraborti M., Devi A., Bhattacharjee B., Das R., Das B., Devi H., Das B., Rawat S., and Mishra V., 2024, Advances in genomic tools for plant breeding: harnessing DNA molecular markers, genomic selection, and genome editing, Biological Research, 57: 80.
https://doi.org/10.1186/s40659-024-00562-6

Kumar V., Singh A., Mithra S., Krishnamurthy S., Parida S., Jain S., Tiwari K., Kumar P., Rao A., Sharma S., Khurana J., Singh N., and Mohapatra T., 2015, Genome-wide association mapping of salinity tolerance in rice (*Oryza sativa*), DNA Research, 22(2): 133-145.
https://doi.org/10.1093/dnares/dsu046

Li B., 2020, Identification of genes conferring plant salt tolerance using GWAS: current success and perspectives, Plant & Cell Physiology, 61(8): 1419-1426.
https://doi.org/10.1093/pcp/pcaa073

Li H., Su G., Jiang L., and Bao Z., 2017, An efficient unified model for genome-wide association studies and genomic selection, Genetics, Selection, Evolution, 49: 64.
https://doi.org/10.1186/s12711-017-0338-x

Liu N., Guan M., B., Chu H., Tian G., Zhang Y., Li C., Zheng W., and Wang X., 2024, Unraveling genetic mysteries: a comprehensive review of GWAS and DNA insights in animal and plant pathosystems, International Journal of Biological Macromolecules, 285: 138216.
https://doi.org/10.1016/j.ijbiomac.2024.138216

Meuwissen T., Eikje L., and Gjuvsland A., 2024, GWABLUP: genome-wide association assisted best linear unbiased prediction of genetic values, Genetics, Selection, Evolution, 56: 17.
https://doi.org/10.1186/s12711-024-00881-y

Mwando E., Han Y., Angessa T., Zhang X., and Li C., 2021, Fine-mapping and characterisation of genes on barley (*Hordeum vulgare*) chromosome 2H for salinity stress tolerance during germination, The Crop Journal, 10(3): 754-766.
https://doi.org/10.1016/j.cj.2021.10.008

Mwando E., Han Y., Angessa T., Zhou G., Hill C., Zhang X., and Li C., 2020, Genome-wide association study of salinity tolerance during germination in barley (*Hordeum vulgare* L.), Frontiers in Plant Science, 11: 118.
https://doi.org/10.3389/fpls.2020.00118

Ouertani R., Abid G., Karmous C., Chikha M., Boudaya O., Mahmoudi H., Mejri S., Jansen R., and Ghorbel A., 2021, Evaluating the contribution of osmotic and oxidative stress components on barley growth under salt stress, AoB Plants, 13(4): plab034.
https://doi.org/10.1093/AOBPLA/PLAB034

Pang Z., Wang W., Huang P., Zhang H., Zhang S., Yang P., Qiao L., Liu J., Pan Y., Yang K., and Liu W., 2025, Enhancing genomic prediction accuracy with a single-step genomic best linear unbiased prediction model integrating genome-wide association study results, Animals, 15(9): 1268.
https://doi.org/10.3390/ani15091268

Sadiq Q., Nazim M., Haq T., Fatima M., Hussain A., Ali M., Mathpal B., and Alwahibi M., 2024, Salt stress effects on growth, physiology, and ionic concentrations in hydroponically grown barley genotypes, Journal of King Saud University-Science, 36: 103448.
https://doi.org/10.1016/j.jksus.2024.103448

Sonia, Kaur V., Yadav S., Arya S., Aravind J., Jacob S., and Gautam R., 2023, Development and evaluation of barley mini-core collection for salinity tolerance and identification of novel haplotypic variants for *HvRAF*, Plant and Soil, 497: 317-337.
https://doi.org/10.1007/s11104-023-06397-6

Soud N., Fahmy A., El-Sharkawy A., and Hussein M., 2024, Molecular and physiological insights of salt tolerance in hulled barley (*Hordeum vulgare* L. var. nudum), Egyptian Pharmaceutical Journal, 23(3): 491-497.
https://doi.org/10.4103/epj.epj_310_23

Spindel J., Begum H., Akdemir D., Collard B., Redoña E., Jannink J., Jannink J., and McCouch S., 2016, Genome-wide prediction models that incorporate de novo GWAS are a powerful new tool for tropical rice improvement, Heredity, 116: 395-408.
https://doi.org/10.1038/hdy.2015.113

Spindel J., Begum H., Akdemir D., Virk P., Collard B., Redoña E., Atlin G., Jannink J., and McCouch S., 2015, Genomic selection and association mapping in rice (*Oryza sativa*): effect of trait genetic architecture, training population composition, marker number and statistical model on accuracy of rice genomic selection in elite, tropical rice breeding lines, PLoS Genetics, 11(6): e1005350.
https://doi.org/10.1371/journal.pgen.1004982

Thabet S., and Alqudah A., 2023, New genetic insights into improving barley salt tolerance by regulating mineral accumulation, cellular ion homeostasis, and membrane trafficking, Environmental and Experimental Botany, 208: 105252.
https://doi.org/10.1016/j.envexpbot.2023.105252

Tu Y., Fu L., Wang F., Wu D., Shen Q., and Zhang G., 2021, GWAS and transcriptomic integrating analysis reveals key salt-responding genes controlling Na^+ content in barley roots, Plant Physiology and Biochemistry, 167: 596-606.
https://doi.org/10.1016/j.plaphy.2021.08.038

Việt N., Bullet L., Dolstra O., Malosetti M., Benjamin B., Bullet K., Graner A., Visser R., Van Der Linden B., Springer-Verlag Ó., and Heidelberg B., 2013, Association mapping of salt tolerance in barley (*Hordeum vulgare* L.), Theoretical and Applied Genetics, 126: 2335-2351.
https://doi.org/10.1007/s00122-013-2139-0

Wang H., Li C., Li J., Zhang R., An X., Yuan C., Guo T., and Yue Y., 2024, Genomic selection for weaning weight in alpine merino sheep based on GWAS prior marker information, Animals, 14(13): 1904.
https://doi.org/10.3390/ani14131904

Wu D., Cai S., Chen M., Ye L., Chen Z., Zhang H., Dai F., Wu F., and Zhang G., 2013, Tissue metabolic responses to salt stress in wild and cultivated barley, PLoS ONE, 8(1): e55431.
https://doi.org/10.1371/journal.pone.0055431

Xu H., Chen H., Halford N., Xu R., He T., Yang B., Zhou L., Guo H., and Liu C., 2025, Ion homeostasis and coordinated salt tolerance mechanisms in a barley (*Hordeum vulgare* L.) doubled haploid line, BMC Plant Biology, 25: 52.
https://doi.org/10.1186/s12870-024-06033-0

Xu T., Meng S., Zhu X., Di J., Zhu Y., Yang X., and Yan W., 2023, Integrated GWAS and transcriptomic analysis reveal the candidate salt-responding genes regulating Na^+/K^+ balance in barley (*Hordeum vulgare* L.), Frontiers in Plant Science, 13: 1004477.
https://doi.org/10.3389/fpls.2022.1004477

Yildiz M., and Acar O., 2022, Determination of salt tolerance of some barley varieties based on physiological and biochemical properties, International Journal of Innovative Approaches in Agricultural Research, 6(4): 289-302.
https://doi.org/10.29329/ijiaar.2022.506.1

Zhang Y., Zhang M., Ye J., Xu Q., Feng Y., Xu S., Hu D., Wei X., Hu P., and Yang Y., 2023, Integrating genome-wide association study into genomic selection for the prediction of agronomic traits in rice (*Oryza sativa* L.), Molecular Breeding, 43: 81.
https://doi.org/10.1007/s11032-023-01423-y