Triticeae Genomics and Genetics, 2025, Vol.16, No.4, 175-183
http://cropscipublisher.com/index.php/tgg

Case Study Open Access

Identification of Key Transcription Factors Involved in Root Architecture of Barley

Zhengqi Ma, Wei Wang ✉
Institute of Life Sciences, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China
✉ Corresponding email: wei.wang@jicat.org

Triticeae Genomics and Genetics, 2025, Vol.16, No.4 doi: 10.5376/tgg.2025.16.0019
Received: 17 Jun., 2025
Accepted: 30 Jul., 2025
Published: 17 Aug., 2025

Preferred citation for this article:
Ma Z.Q., and Wang W., 2025, Identification of key transcription factors involved in root architecture of barley, Triticeae Genomics and Genetics, 16(4): 175-183 (doi: 10.5376/tgg.2025.16.0019)

Abstract Root structure plays a key role in the growth, development, nutrient absorption and stress resistance of barley (*Hordeum vulgare* L.). In recent years, transcriptomics and functional genomics studies have found that transcription factors are important molecules that regulate the formation and remodeling of root system architecture (RSA), affecting its development by regulating the gene expression network in the process of root initiation, elongation and branching. This study reviewed the main transcription factor families closely related to barley root development, such as NAC, MYB, WRKY and bHLH, and combined with the results of transcriptional expression analysis and functional verification, in-depth discussion of their role in regulating root morphology, and selected representative key transcription factors such as HvNAC005, HvWRKY23 and HvMYB1 as cases to explain their regulatory mechanisms on root development under salt stress, disease stress and phosphorus deficiency. This study hopes to provide theoretical support for the analysis of the molecular regulatory network of barley root traits and provide potential targets for breeding efficient and stress-resistant barley varieties.

Keywords Barley; Root system architecture; Transcription factor; Gene regulation; Stress response

1 Introduction

Whether barley can absorb enough water and nutrients depends mainly on its root structure. How well the roots grow directly affects how they grow, whether they can withstand adverse environments, and how much grain they can produce in the end. Recent studies have found that different barley varieties vary greatly in root characteristics, such as how deep the roots are, how far they extend, and how long they are. Some roots grow deep and efficiently, which can better absorb water and nutrients, especially when the environment is more difficult, and can significantly increase yields (Robinson et al., 2018; Jia et al., 2019).

Scientists have made a lot of progress in studying how cereal roots grow and the genetic and molecular mechanisms behind them. Some key transcription factors, such as those of the MADS-box family, and a regulatory factor called VERRNALIZATION1 (VRN1), have been found to affect not only the structure of roots and stems, but also the timing of flowering, and there may be a relationship between the two (Voss-Fels et al., 2018; Abdel-Ghani et al., 2019; Kirschner et al., 2021). In addition, through whole-genome association analysis and transcriptome research, a number of QTLs and candidate genes related to root growth, gravity response, and response to environmental stress have been found. This information will be very helpful for future breeding work (Ogrodowicz et al., 2023; Nguyen et al., 2024).

This study will combine the latest advances in genetic mapping, functional genomics, and transcriptome analysis to identify and characterize key transcription factors that affect barley root structure and elucidate the regulatory network that shapes root traits. Improved root structure helps improve resource efficiency and adapt to climate change. This study hopes to provide a reference for breeding strategies for cultivating barley varieties with optimized root systems, yield, and stress resistance.

2 Root Architecture Traits in Barley

2.1 Types of roots: primary, lateral, adventitious

The root system of barley is not a single structure, but is composed of several roots. The first to grow is the taproot, also called the seed root, which grows directly from the seed and is the basis of the entire root system. The number, length and growth angle of the seed roots vary greatly among different barley varieties (Robinson et al., 2016). The taproot will grow lateral roots outward, which allow the root system to explore a larger area of soil so that the plant can absorb more water and nutrients (Wang et al., 2021). In addition, there is a kind of root called adventitious root, which grows from the stem node. They mainly help plants to fix in the soil and absorb resources, especially when the plants grow larger and approach maturity, these roots are particularly important (Oyiga et al., 2019).

2.2 Root system response under different soil and nutrient conditions

The barley root system is particularly sensitive to soil and environmental changes. For example, in drought, the root growth of most varieties will slow down. However, some varieties can keep their roots longer or change their angles to go deeper into the soil to find water. Some root traits related to drought are controlled by specific genes, including some transcription factors and signal genes for responding to stress (Siddiqui et al., 2024). If the soil is acidic, it will also affect the root structure. Different varieties perform very differently in this environment. Some varieties have longer roots and more biomass, which shows that varieties that adapt to acidic soils can be cultivated (Abebe et al., 2024). In addition, traits such as root thickness, length and total root weight are affected by the amount of nutrients. Some studies have found some QTLs that can help plants adapt to low-fertilizer soils (Farooqi et al., 2023).

2.3 Influence on water absorption and crop productivity

How well the root system grows directly affects the ability of barley to absorb water and nutrients, which will be reflected in the yield. If the roots grow deep and at a steeper angle, they can usually draw water from deeper soil layers, which is particularly advantageous in drought conditions and leads to higher yields (Figure 1) (Jia et al., 2019). Longer roots and greater biomass are usually associated with better plant growth, more grains, and larger grains, all of which indicate that strong roots are important for yield (Manju et al., 2019). Of course, the relationship between roots and yield may vary in different environments, but in general, the number and angle of roots are more closely related to yield (Robinson et al., 2018). Optimizing root structure through breeding and genetic improvement is a promising direction. Doing so can make barley more adaptable to different environments and help increase yields (Wang, 2024).

3 Regulatory Role of Transcription Factors in Root Development

3.1 Overview of transcription factors in plant root systems

Transcription factors (TFs) are proteins that can bind to DNA. They can control the "on" or "off" of specific genes, and play a major role in root growth, cell differentiation, and plant response to various stresses (such as drought or pests and diseases) (Chen et al., 2022). Transcription factors recognize specific fragments on DNA and pull other proteins to work together, thereby affecting the structure, absorption capacity and environmental adaptability of roots (Strader et al., 2021).

3.2 Major TF families involved in barley root regulation: ARF, NAC, MYB, WRKY

In barley root development, some transcription factor families are particularly critical. For example, MYB is the largest one. It regulates the differentiation and cell cycle of root cells, and can also help plants cope with drought, salinity and nutrient deficiency. MYB also affects the signaling of plant hormones and is expressed in many root tissues. It is one of the core players in root gene regulation (Chen et al., 2022; Liu et al., 2023; Zhang et al., 2025). Transcription factors such as WRKY are also important, especially when plants are exposed to stress (such as lack of fertilizer), they can regulate the development of roots. These factors work together with other transcription factors to form a complex regulatory network to control root growth and adaptability (Bakshi and Oelmüller, 2014; Wani et al., 2021). There are also transcription factors such as ARF (auxin response factor) and NAC, which play a major role in the regulation of plant auxin and also play a key role in root development and stress response, and may have similar functions in barley.

3.3 Interaction with plant hormone signaling

Transcription factors often work together with hormone signaling pathways in plants to regulate root structure.

For example, MYB can respond to different hormone signals, such as auxin, cytokinin, and abscisic acid (ABA). It integrates these signals to affect the division, differentiation, and response of root cells to environmental changes (Chen et al., 2022; Zhang et al., 2025).

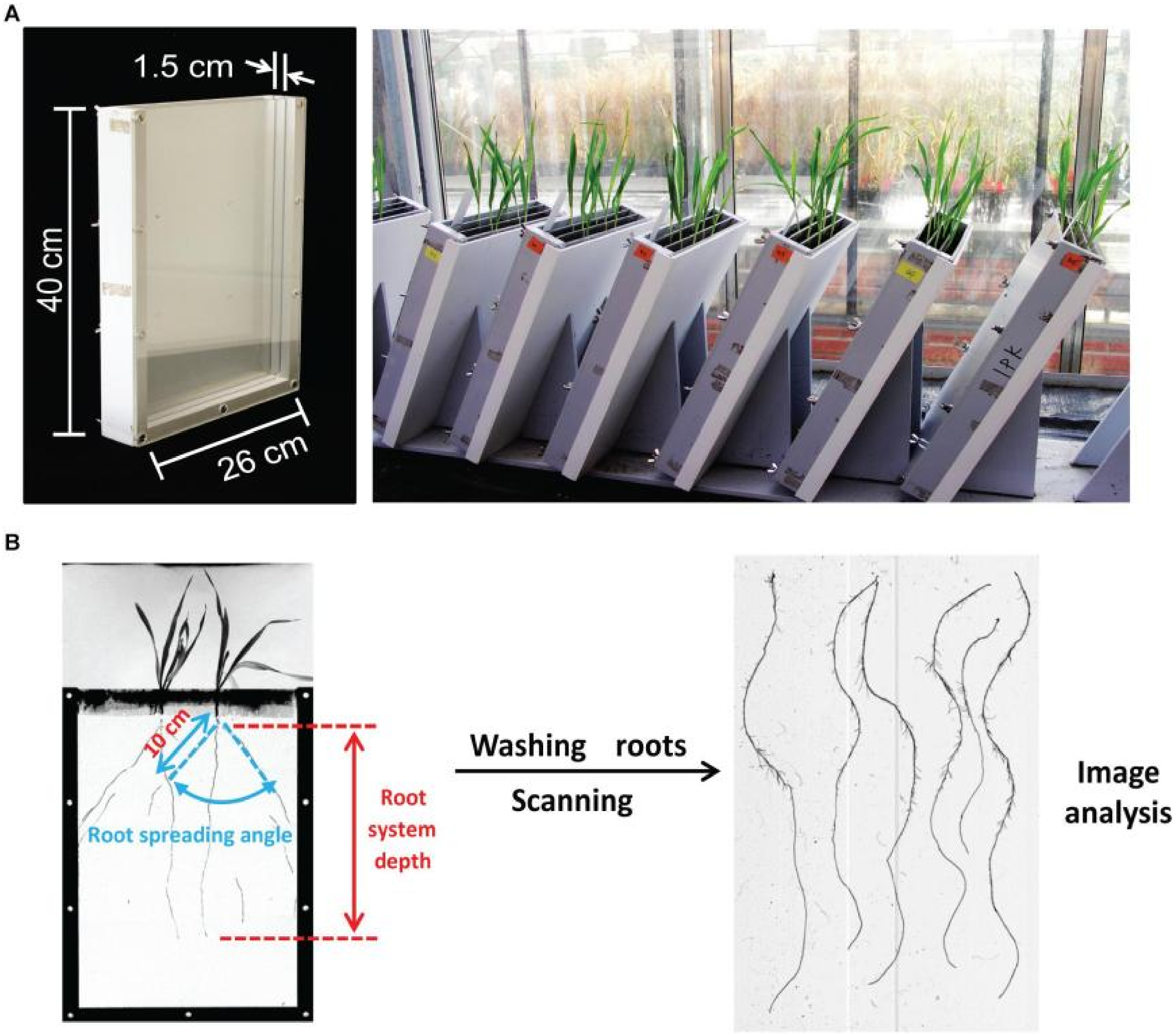


Figure 1 Root phenotyping and trait measurement (Adopted from Jia et al., 2019)

Image caption: (A) Three-compartment root observation box and appearance of barley seedlings grown in the greenhouse for 12 days. (B) Schematic illustration of the procedure for root trait measurements (Adopted from Jia et al., 2019)

WRKY is also involved in hormone-related regulation, especially ABA-related processes, which are equally important for root growth and stress response (Bakshi and Oelmüller, 2014). There are also transcription factors such as TGA and AP2/ERF, which are also involved in the signaling of ABA and ethylene hormones, and also affect root development and stress adaptation (Feng et al., 2020; Lu et al., 2023). Transcription factors such as MYB and WRKY help regulate barley root structure by cooperating with hormone signaling networks, enabling plants to adapt to various growth environments.

4 Methods for Identifying Key Transcription Factors

4.1 RNA-Seq and differential expression analysis

RNA sequencing (RNA-Seq) is a common technology that can be used to analyze the expression of genes in different tissues, developmental stages and environments. Researchers often find transcription factors (TFs) that may be related to root development or stress response by comparing the expression differences under normal conditions and stress conditions. For example, whole transcriptome analysis has found that when barley encounters abiotic stress, the expression levels of the MYB, NAC and GATA transcription factor families change. Researchers usually use real-time fluorescence quantitative PCR (qRT-PCR) to confirm these results (Zhang et al., 2004; Tombuloglu et al., 2013). There is also a method called DAP-seq (DNA affinity purification sequencing), which can more accurately find out which transcription factors bind to specific DNA sequences. For example, scientists have used it to find GATA-type transcription factors related to drought response in barley (Wang et al., 2023).

4.2 Co-expression network and GO/KEGG functional analysis

Some methods, such as WGCNA (weighted gene co-expression network analysis), can group genes with similar expression trends. This grouping method can help find regulatory modules and possible transcription factors related to root traits or stress resistance (Chen et al., 2023; Li et al., 2023). Next, researchers often use GO (gene ontology) and KEGG (genomic pathway) enrichment analysis to assign functional and pathway labels to these gene groups. This allows us to see whether these genes are involved in processes such as hormone signaling, stress response, or growth and development. These integrated methods can draw regulatory network diagrams. For example, some studies have found that the two transcription factors NAC and WRKY are core regulatory factors for barley to adapt to environmental changes (Xu et al., 2022).

4.3 Functional validation via gene editing and overexpression systems

In order to determine the role of a transcription factor, researchers often use gene editing technologies such as CRISPR/Cas9, or overexpress it to see what changes will occur in the plant. In barley, after overexpression of a transcription factor (such as Ant1), the accumulation of anthocyanins in the grain increased significantly, indicating that this gene does have an effect (Zhou et al., 2021). This method can help us confirm whether this gene is a key factor affecting root structure or stress resistance. In addition to CRISPR, some other methods are also commonly used, such as virus-induced gene silencing (VIGS) or transgenic experiments. They can also help us understand the specific role of transcription factors in plant development or stress response (Shang et al., 2020).

5 Case Studies of Functional Transcription Factors in Barley

5.1 HvNAC005: a key transcription factor regulating root development and stress response

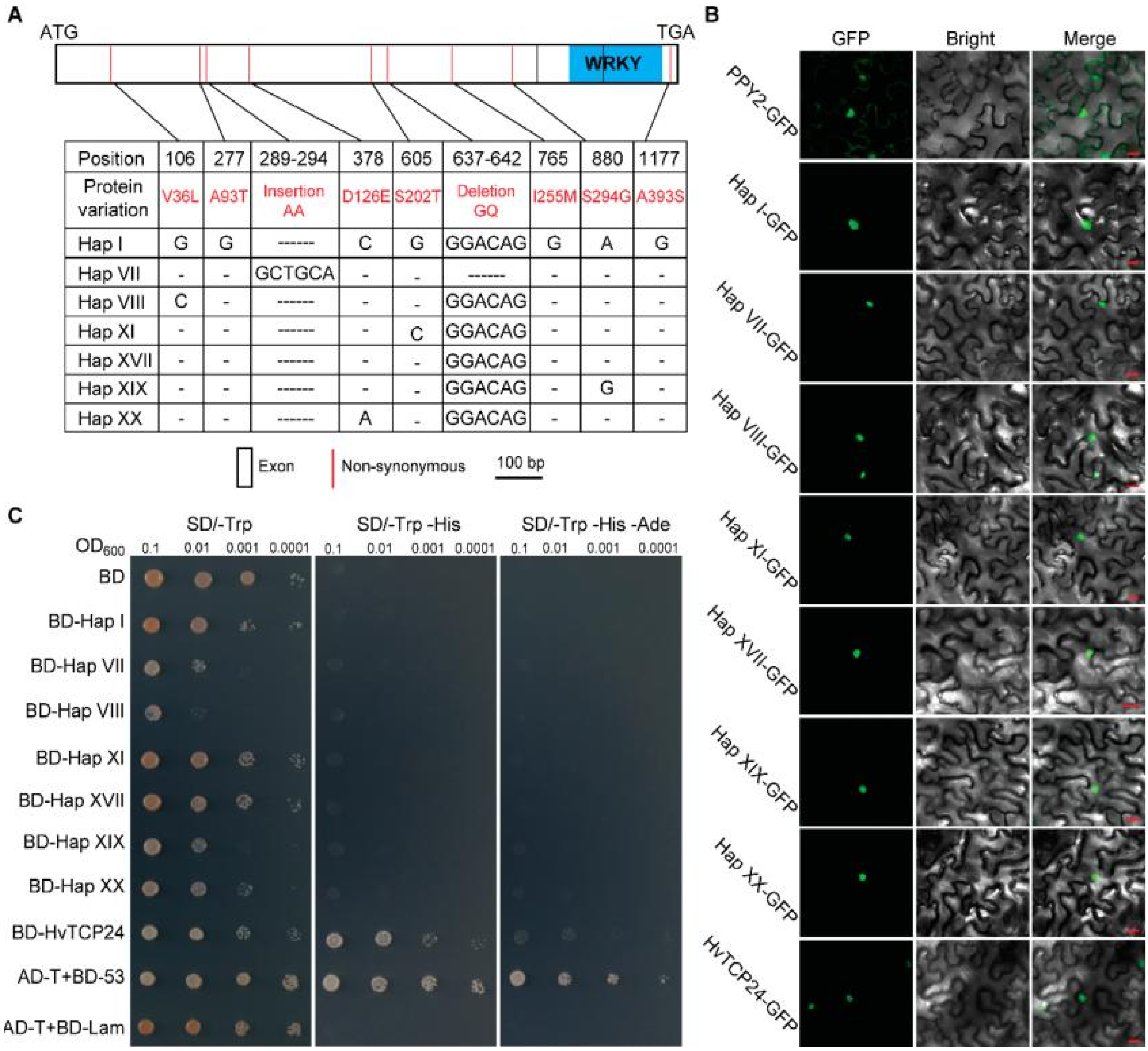
NAC-type transcription factors in barley, such as some members of the HvC3H family, are closely related to root development and plant coping with adversity. Genome analysis found that the expression levels of NAC and CCCH-type zinc finger transcription factors such as HvC3H1, HvC3H2 and HvC3H13 increased significantly under various stress conditions or after treatment with plant hormones. This shows that they play an important role in the adaptation and recovery of the root system to stress. The expression of these transcription factors varies at different growth stages and under stress environments. This feature makes them an important target for improving barley root performance and resistance in breeding (Ai et al., 2022).

5.2 HvWRKY23: mediating immune responses against root pathogen invasion

WRKY-type transcription factors are very important for barley to resist pathogens, especially for root diseases. Genomic studies have found more than a hundred *WRKY* genes in barley, and duplication and diversification among these genes have been found. Many *WRKY* genes are involved in immune response and stress resistance mechanisms. Their diversity may have been selected during the domestication of barley. Overall, the WRKY family is considered to be a key factor in helping barley roots cope with biotic and environmental stresses (Figure 2) (Pandey et al., 2018; Kan et al., 2021).

5.3 HvMYB1: regulating root hair development under phosphorus deficiency

MYB is another important class of transcription factors, especially the R2R3-MYB subgroup, which has been shown to regulate root hair development and help plants cope with nutrient deficiency. In barley, through transcriptome analysis, researchers have discovered many MYB transcription factors that show responsiveness when faced with stress, such as boron toxicity or other abiotic stresses. The MYB family has a direct effect on root hair formation and nutrient uptake, which also indicates that they play an important role in plant adaptation to low-P soils (Rubio-Somoza et al., 2006; Tombuloglu et al., 2013).



Position	106	277	289-294	378	605	637-642	765	880	1177
Protein variation	V36L	A93T	Insertion AA	D126E	S202T	Deletion GQ	I255M	S294G	A393S
Hap I	G	G	------	C	G	GGACAG	G	A	G
Hap VII	-	-	GCTGCA	-	-	------	-	-	-
Hap VIII	C	-	------	-	-	GGACAG	-	-	-
Hap XI	-	-	------	-	C	GGACAG	-	-	-
Hap XVII	-	-	------	-	-	GGACAG	-	-	-
Hap XIX	-	-	------	-	-	GGACAG	-	G	-
Hap XX	-	-	------	A	-	GGACAG	-	-	-

Figure 2 The subcellular localization and transactivation activity of WRKY9 haplotypes (Adopted from Kan et al., 2018)

Image caption: (A) Graphical representation of the full-length coding sequence of selected haplotypes. Only non-synonymous substitutions are indicated. The blue rectangle represents the WRKY domain. (B) Subcellular localization of WRKY9 haplotypes in N. benthamiana. Scale bar = 20 μm. (C) Transactivation activity of WRKY9 haplotypes in yeast. BD-HvTCP24, which contains a transactivation activity in yeast, serves as a positive control. SD, synthetic dextrose medium; Trp, tryptophan; His, histidine; Ade, Adenine. 0.1, 0.01, 0.001 and 0.000 1 denoted the different dilution series (Adopted from Kan et al., 2018)

6 Environmental Influence on Transcriptional Regulation of Root Architecture

6.1 Effects of drought, salinity, and nutrient limitations

The root structure of barley changes according to environmental stress, such as drought, excessive salt, or insufficient nutrients. Plants activate certain transcription factors to initiate responses in root cells. These responses change the morphology and structure of the roots, helping plants to better absorb water and nutrients or reduce the impact of adverse environments. For example, salt stress may activate some transcription factors to inhibit the growth of lateral roots. In the case of insufficient nitrogen or phosphorus, plants change the expression of related transcription factors and hormone signaling genes to make the roots longer or more branched (Ariel et al., 2010; Kumar et al., 2020; Roychoudhry and Kepinski, 2021). These changes allow roots to grow more flexibly, helping plants improve absorption efficiency and survival (Motte et al., 2019; Gouran and Brady, 2024).

6.2 TF expression plasticity under abiotic stress

The transcription factors in the roots show strong regulatory ability in the face of environmental changes. A transcription factor or a small gene module may play different roles at different times and locations. This "flexibility" allows them to selectively act in specific cells rather than reacting to the entire root. The same type of transcription factor may regulate different downstream genes under different stresses, depending on the type of stress and the type of root cell (Walker et al., 2017; Cai and Qian, 2024). For example, some transcription factors that regulate cytokinins (such as ARR10 and CRF6) and transcription factors related to auxin will quickly start or shut down depending on the amount of nutrients, and the structure of the root will also adjust accordingly (Ramireddy et al., 2014; Roychoudhry and Kepinski, 2021). It is precisely because these genes are expressed very flexibly that the roots can adapt well to various changing environments (Ramireddy et al., 2014).

6.3 Epigenetic and transcriptomic reprogramming in response to environmental cues

When the environment deteriorates, not only the expression of transcription factors will change, but the entire root system of the plant will also undergo deeper changes. This change includes reprogramming of overall gene expression and adjustments at the epigenetic level. These changes usually involve the way chromatin is opened, the way histones are modified, and the activity of non-coding RNA. These mechanisms work together to regulate which genes should be turned on and which should be turned off according to environmental signals (Roulé et al., 2021). Through single-cell and spatial transcriptome technologies, scientists have found that these regulations are often concentrated in specific cell types or developmental stages (Walker et al., 2017; Gouran and Brady, 2024). This precise multi-level control allows roots to quickly change their structure as needed in a short period of time to cope with the challenges of the external environment.

7 Concluding Remarks

Transcription factors play a key role in regulating root architecture. They receive information from the environment and developmental processes, and then regulate root growth, branching number, and nutrient absorption capacity. Transcription factor families such as ARF, NAC, MYB, and WRKY have been shown to regulate plant responses to drought, salinity, and nutrient deficiency. The gene expression networks they control determine the plasticity of the root system, that is, whether the roots can flexibly adjust to the environment. Because of this, barley and other cereal crops can adapt to various complex environments. In wheat, researchers have also discovered interactions between transcription factors and chromatin remodeling factors. This relationship makes it clearer that root development and absorption functions are actually completed by a whole set of complex regulatory mechanisms.

Although research has made a lot of progress, there is still a lot of room for further efforts. We need to use gene editing tools (such as CRISPR) or overexpression systems to verify whether the candidate transcription factors in barley have any effect. At the same time, higher-resolution technologies are also needed, such as transcriptome and epigenetic analysis of different cell types, so that we can know more clearly when and where these factors work. In the future, deep learning can be used for root phenotyping, combined with multi-omics data, so that gene regulation can be linked to the actual structure of the root. It is also possible to compare different cereal plants to find out which regulatory methods are universal and which are unique to barley. Single-cell transcriptomics technology and more advanced genetic manipulation methods will speed up our search and verification of key transcription factors.

Understanding the regulatory network of these transcription factors will help us transform plant roots. By precisely regulating these factors and their interacting partners, crop root structure can be optimized, making plants more resistant to water and fertilizer, and more resistant to drought, salt and disease. This is an important step for breeding. Especially in the context of increasingly obvious climate change, these advances are very important for achieving sustainable agriculture and food security with high yields, water and fertilizer savings. The discovery and study of these transcription factors in barley roots also provides new methods and directions for future breeding and agricultural improvement.

Acknowledgments

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

Conflict of Interest Disclosure

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

References

Abdel-Ghani A., Sharma R., Wabila C., Dhanagond S., Owais S., Duwayri M., Al-Dalain S., Klukas C., Chen D., Lübberstedt T., Von Wirén N., Graner A., Kilian B., and Neumann K., 2019, Genome-wide association mapping in a diverse spring barley collection reveals the presence of QTL hotspots and candidate genes for root and shoot architecture traits at seedling stage, BMC Plant Biology, 19: 216.
https://doi.org/10.1186/s12870-019-1828-5

Abebe G., Nebiyu A., Bantte K., and Menamo T., 2024, Root system architecture variation among barley (*Hordeum vulgare* L.) accessions at seedling stage under soil acidity condition, Planta, 259(6): 145.
https://doi.org/10.1007/s00425-024-04424-z

Ai Q., Pan W., Zeng Y., Li Y., and Cui L., 2022, *CCCH* Zinc finger genes in barley: genome-wide identification, evolution, expression and haplotype analysis, BMC Plant Biology, 22: 117.
https://doi.org/10.1186/s12870-022-03500-4

Ariel F., Diet A., Verdenaud M., Gruber V., Frugier F., Chan R., and Crespi M., 2010, Environmental regulation of lateral root emergence in *Medicago truncatula* requires the HD-Zip I Transcription factor HB1, Plant Cell, 22(7): 2171-2183.
https://doi.org/10.1105/tpc.110.074823

Bakshi M., and Oelmüller R., 2014, WRKY transcription factors, Plant Signaling & Behavior, 9(2): e27700.
https://doi.org/10.4161/psb.27700

Cai X.G., and Qian Q.S., 2024, Transcriptomic insights into wheat disease resistance, Molecular Pathogens, 15(4): 179-188.
https://doi.org/10.5376/mp.2024.15.0017

Chen L., Cui Y., Yao Y., An L., Bai Y., Li X., Yao X., and Wu K., 2023, Genome-wide identification of WD40 transcription factors and their regulation of the MYB-bHLH-WD40 (MBW) complex related to anthocyanin synthesis in Qingke (*Hordeum vulgare* L. var. *nudum* Hook. f.), BMC Genomics, 24: 166.
https://doi.org/10.1186/s12864-023-09240-5

Chen Z., Wu Z., Dong W., Liu S., Tian L., Li J., and Du H., 2022, MYB transcription factors becoming mainstream in plant roots, International Journal of Molecular Sciences, 23(16): 9262.
https://doi.org/10.3390/ijms23169262

Farooqi M., Moody D., Bai G., Bernardo A., St. Amand P., Diggle A., and Rengel Z., 2023, Genetic characterization of root architectural traits in barley (*Hordeum vulgare* L.) using SNP markers, Frontiers in Plant Science, 14: 1265925.
https://doi.org/10.3389/fpls.2023.1265925

Feng K., Hou X., Xing G., Liu J., Duan A., Xu Z., Li M., Jing Z., and Xiong A., 2020, Advances in AP2/ERF super-family transcription factors in plant, Critical Reviews in Biotechnology, 40: 750-776.
https://doi.org/10.1080/07388551.2020.1768509

Gouran M., and Brady S., 2024, The transcriptional integration of environmental cues with root cell type development, Plant Physiology, 196: 2150-2161.
https://doi.org/10.1093/plphys/kiae425

Jia Z., Liu Y., Gruber B., Neumann K., Kilian B., Graner A., and Von Wirén N., 2019, Genetic dissection of root system architectural traits in spring barley, Frontiers in Plant Science, 10: 400.
https://doi.org/10.3389/fpls.2019.00400

Kan J., Gao G., He Q., Gao Q., Jiang C., Ahmar S., Liu J., Zhang J., and Yang P., 2021, Genome-wide characterization of WRKY transcription factors revealed gene duplication and diversification in populations of wild to domesticated barley, International Journal of Molecular Sciences, 22(10): 5354.
https://doi.org/10.3390/ijms22105354

Kirschner G., Rosignoli S., Guo L., Vardanega I., Imani J., Altmüller J., Milner S., Balzano R., Nagel K., Pflugfelder D., Forestan C., Bovina R., Koller R., Stöcker T., Mascher M., Simmonds J., Uauy C., Schoof, H., Tuberosa R., Salvi S., and Hochholdinger F., 2021, *ENHANCED GRAVITROPISM 2* encodes a STERILE ALPHA MOTIF-containing protein that controls root growth angle in barley and wheat, Proceedings of the National Academy of Sciences of the United States of America, 118(35): e2101526118.
https://doi.org/10.1073/pnas.2101526118

Kumar V., Vogelsang L., Schmidt R., Sharma S., Seidel T., and Dietz K., 2020, Remodeling of root growth under combined arsenic and hypoxia stress is linked to nutrient deprivation, Frontiers in Plant Science, 11: 569687.
https://doi.org/10.3389/fpls.2020.569687

Li M., Cai K., Zheng N., Zhang G., and Ye L., 2023, Identification of the key transcription factors regulating the expression of the genes associated with barley malt quality during malting, Journal of Agricultural and Food Chemistry, 71(21): 8241-8251.
https://doi.org/10.1021/acs.jafc.3c00988

Liu L., Heidecker M., Depuydt T., Pérez N., Crespi M., Blein T., and Vandepoele K., 2023, Transcription factors KAN1, MYB44, and PIF4 regulate lincRNAs expressed in Arabidopsis roots, Plant Physiology, 193(3): 1933-1953.
https://doi.org/10.1093/plphys/kiad360

Lu C., Liu X., Tang Y., Fu Y., Zhang J., Yang L., Li P., Zhu Z., and Dong P., 2023, A comprehensive review of TGA transcription factors in plant growth, stress responses, and beyond, International Journal of Biological Macromolecules, 258(1): 128880.
https://doi.org/10.1016/j.ijbiomac.2023.128880

Manju Kaur V., Sharma K., and Jacob S., 2019, Assessment of genetic diversity in cultivated and wild species germplasm of barley based on morpho-agronomical and root architecture traits, Indian Journal of Plant Genetic Resources, 32(3): 360-367.
https://doi.org/10.5958/0976-1926.2019.00039.1

Motte H., Vanneste S., and Beeckman T., 2019, Molecular and environmental regulation of root development, Annual Review of Plant Biology, 70: 465-488.
https://doi.org/10.1146/annurev-arplant-050718-100423

Nguyen D., Kokáš F., Gonin M., Lavarenne J., Colin M., Gantet P., and Bergougnoux V., 2024, Transcriptional changes during crown-root development and emergence in barley (*Hordeum vulgare* L.), BMC Plant Biology, 24: 438.
https://doi.org/10.1186/s12870-024-05160-y

Ogrodowicz P., Mikołajczak K., Kempa M., Mokrzycka M., Krajewski P., and Kuczyńska A., 2023, Genome-wide association study of agronomical and root-related traits in spring barley collection grown under field conditions, Frontiers in Plant Science, 14: 1077631.
https://doi.org/10.3389/fpls.2023.1077631

Oyiga B., Palczak J., Wojciechowski T., Lynch J., Naz A., Léon J., and Ballvora A., 2019, Genetic components of root architecture and anatomy adjustments to water-deficit stress in spring barley, Plant, Cell & Environment, 43(3): 692-711.
https://doi.org/10.1111/pce.13683

Pandey B., Grover A., and Sharma P., 2018, Molecular dynamics simulations revealed structural differences among WRKY domain-DNA interaction in barley (*Hordeum vulgare*), BMC Genomics, 19: 132.
https://doi.org/10.1186/s12864-018-4506-3

Ramireddy E., Chang L., and Schmülling T., 2014, Cytokinin as a mediator for regulating root system architecture in response to environmental cues, Plant Signaling & Behavior, 9: 32.
https://doi.org/10.4161/psb.27771

Robinson H., Hickey L., Richard C., Mace E., Kelly A., Borrell A., Franckowiak J., and Fox G., 2016, Genomic regions influencing seminal root traits in barley, The Plant Genome, 9(1): 12.
https://doi.org/10.3835/plantgenome2015.03.0012

Robinson H., Kelly A., Fox G., Franckowiak J., Borrell A., and Hickey L., 2018, Root architectural traits and yield: exploring the relationship in barley breeding trials, Euphytica, 214: 1-16.
https://doi.org/10.1007/S10681-018-2219-Y

Roulé T., Crespi M., and Blein T., 2021, Regulatory long non-coding RNAs in root growth and development, Biochemical Society Transactions, 50(1): 403-412.
https://doi.org/10.1042/BST20210743

Roychoudhry S., and Kepinski S., 2021, Auxin in root development, Cold Spring Harbor Perspectives in Biology, 17(9): a039933.
https://doi.org/10.1101/cshperspect.a039933

Rubio-Somoza I., Martínez M., Díaz I., and Carbonero P., 2006, HvMCB1, a R1MYB transcription factor from barley with antagonistic regulatory functions during seed development and germination, The Plant Journal, 45(1): 17-30.
https://doi.org/10.1111/J.1365-313X.2005.02596.X

Shang Y., Yuan L., Di Z., Jia Y., Zhang Z., Li S., Xing L., Qi Z., Wang X., Zhu J., Hua W., Wu X., Zhu M., Li G., and Li C., 2020, A CYC/TB1 type TCP transcription factor controls spikelet meristem identity in barley (*Hordeum vulgare* L.), Journal of Experimental Botany, 71(22): 7118-7131.
https://doi.org/10.1093/jxb/eraa416

Siddiqui M., Jahiu M., Kamruzzaman M., Sanchez-Garcia M., Mason A., Léon J., and Ballvora A., 2024, Genetic control of root architectural traits under drought stress in spring barley (*Hordeum vulgare* L.), The Plant Genome, 17(2): e20463.
https://doi.org/10.1002/tpg2.20463

Strader L., Weijers D., and Wagner D., 2021, Plant transcription factors - being in the right place with the right company, Current Opinion in Plant Biology, 65: 102136.
https://doi.org/10.1016/j.pbi.2021.102136

Tombuloglu H., Kekec G., Sakcali M., and Unver T., 2013, Transcriptome-wide identification of R2R3-MYB transcription factors in barley with their boron responsive expression analysis, Molecular Genetics and Genomics, 288: 141-155.
https://doi.org/10.1007/s00438-013-0740-1

Voss-Fels K., Robinson H., Mudge S., Richard C., Newman S., Wittkop B., Stahl A., Friedt W., Frisch M., Gabur I., Miller-Cooper A., Campbell B., Kelly A., Fox G., Christopher J., Christopher M., Chenu K., Franckowiak J., Mace E., Borrell A., Eagles H., Jordan D., Botella J., Hammer G., Godwin I., Trevaskis B., Snowdon R., and Hickey, L., 2018, VERNALIZATION1 modulates root system architecture in wheat and barley, Molecular Plant, 11(1): 226-229.
https://doi.org/10.1016/j.molp.2017.10.005

Walker L., Boddington C., Jenkins D., Wang Y., Grønlund J., Hulsmans J., Kumar S., Patel D., Moore J., Carter A., Samavedam S., Bonomo G., Hersh D., Coruzzi G., Burroughs N., and Gifford M., 2017, Changes in Gene Expression in Space and Time Orchestrate Environmentally Mediated Shaping of Root Architecture[CC-BY]. Plant Cell, 29(10): 2393-2412.
https://doi.org/10.1105/tpc.16.00961

Wang W., 2024, Developing durable resistance to wheat diseases: integration of molecular breeding techniques, Molecular Pathogens, 15(3): 106-118.
https://doi.org/10.5376/mp.2024.15.0011

Wang J., Chen Y., Zhang Y., Zhang Y., Ai Y., Feng Y., Moody D., Diggle A., Damon P., and Rengel Z., 2021, Phenotyping and validation of root morphological traits in barley (*Hordeum vulgare* L.), Agronomy, 11(8): 1583.
https://doi.org/10.3390/agronomy11081583

Wang Y., Li H., Zhao C., Yang C., Xu Q., Yuan H., Yang H., and Zeng X., 2023, Identification of a novel transcription factor under long-term drought resistance in highland barley: a DNA affinity purification sequencing-based transcriptomic analysis, Chemical and Biological Technologies in Agriculture, 10: 1.
https://doi.org/10.1186/s40538-022-00376-2

Wani S., Anand S., Singh B., Bohra A., and Joshi R., 2021, WRKY transcription factors and plant defense responses: latest discoveries and future prospects, Plant Cell Reports, 40: 1071-1085.
https://doi.org/10.1007/s00299-021-02691-8

Xu Q., Huang S., Guo G., Yang C., Wang M., Zeng X., and Wang Y., 2022, Inferring regulatory element landscapes and gene regulatory networks from integrated analysis in eight hulless barley varieties under abiotic stress, BMC Genomics, 23: 843.
https://doi.org/10.1186/s12864-022-09070-x

Zhang D., Zhou H., Zhang Y., Zhao Y., Zhang Y., Feng X., and Lin H., 2025, Diverse roles of MYB transcription factors in plants, Journal of Integrative Plant Biology, 67(3): 539-562.
https://doi.org/10.1111/jipb.13869

Zhang H., Sreenivasulu N., Weschke W., Stein N., Rudd S., Radchuk V., Potokina E., Scholz U., Schweizer P., Zierold U., Langridge P., Varshney R., Wobus U., and Graner A., 2004, Large-scale analysis of the barley transcriptome based on expressed sequence tags, The Plant Journal, 40(2): 276-290.
https://doi.org/10.1111/J.1365-313X.2004.02209.X

Zhou C., Zeng Z., Suo J., Li X., Bian H., Wang J., Zhu M., and Han N., 2021, Manipulating a single transcription factor, Ant1, promotes anthocyanin accumulation in barley grains, Journal of Agricultural and Food Chemistry, 69(18): 5306-5317.
https://doi.org/10.1021/acs.jafc.0c08147