Tree Genetics and Molecular Breeding 2025, Vol.15, No.3, 117-127
http://genbreedpublisher.com/index.php/tgmb

Review and Perspectives Open Access

Functional Genomics of Root Development in *Populus* and Its Ecological Implications

Minghua Li, Hongpeng Wang, Shiying Yu

Biotechnology Research Center, Cuixi Academy of Biotechnology, Zhuji, 311800, Zhejiang, China

Corresponding email: shiying.yu@cuixi.org

Tree Genetics and Molecular Breeding, 2025, Vol.15, No.3 doi: 10.5376/tgmb.2025.15.0014

Received: 11 May, 2025

Accepted: 14 Jun., 2025

Published: 21 Jun., 2025

Preferred citation for this article:

Li M.H., Wang H.P., and Yu S.Y., 2025, Functional genomics of root development in *Populus* and its ecological implications, Tree Genetics and Molecular Breeding, 15(3): 117-127 (doi: 10.5376/tgmb.2025.15.0014)

Abstract This study summarizes the research progress of functional genes in the development of poplar root systems, introduces some important genes and signaling pathways that control the shape, differentiation process and response to the external environment of roots, integrates many methods such as transcriptome analysis, gene editing and epigenetic research, and clarifies the response of poplar root systems to drought, nutrient deficiency and interaction with microorganisms It also explores how these root traits are regulated within the body and discusses the possible assistance they may bring in afforestation, ecological restoration and other aspects. This study aims to provide a theoretical basis and technical reference for the study of poplar root systems, and also hopes to lay the foundation for breeding new varieties that are more adapted to the environment and have better traits in the future.

Keywords *Populus*; Root development; Functional genomics; Forestry applications; Environmental adaptation

1 Introduction

The root system of poplar (*Populus* spp.) is very important for its growth and also plays many roles in the ecosystem. Whether the roots grow well or not is directly related to whether they can absorb sufficient water and nutrients, and these will affect whether they can survive in various environments (Zhou et al., 2020). In forestry, people often use cuttings, a method of asexual reproduction, to grow poplar trees. Whether cuttings can successfully take root is the key to promoting high-quality varieties (Bannoud and Bellini, 2021; Ahkami, 2023). In addition, the roots of poplar trees have a complex relationship with the microorganisms in the soil. They are very helpful for maintaining soil health, the carbon cycle, and ecological restoration.

High-throughput sequencing, transcriptome analysis, gene editing and other technologies are widely used to understand how poplar roots form and develop, as well as how they respond to external environmental pressures (Ahkami, 2023; Shi et al., 2024b). Methods such as GWAS (genome-wide association studies), transcriptome sequencing, and gene family analysis have helped researchers identify many important genes and regulatory factors related to rooting ability, hormone signaling, and amino acid metabolism (Du et al., 2022; Han et al., 2022; Nagle et al., 2022; Li et al., 2025). These achievements have deepened the understanding of poplar root development and laid the foundation for poplar breeding and sustainable forest development.

This study expounds the key genes and signaling pathways that control root formation and growth, introduces the roles of these genes in the ecological environment, summarizes the molecular mechanisms and main regulatory networks that regulate root development, and explores the significance of these research results in explaining how poplar trees adapt to the environment and resist adverse conditions. And the possible impacts of root system research on ecological restoration, forestry production and germplasm resource innovation were analyzed. This study aims to provide ideas and references for a further understanding of the molecular basis and ecological roles of poplar root development.

2 Morphological and Developmental Features of Poplar Roots

2.1 Types of roots: primary, lateral, adventitious

The root system of poplar trees is generally divided into three types: main roots, lateral roots and adventite roots. adventitious roots (ARs) do not grow naturally from the roots but from places such as stems or leaves. They are particularly important for poplar asexual reproduction and response to environmental changes (Li et al., 2018; Xiao et al., 2020). The main roots and lateral roots grow naturally after the seeds germinate. The development of lateral roots is influenced by various factors, such as calcium signals, plant hormones and the external environment (Cai et al., 2019; An et al., 2023). Adventite roots can also grow flexibly under adverse conditions such as salt and diseases, helping trees survive better (Li et al., 2024; Zhang et al., 2024).

2.2 Anatomical traits and developmental stages

In the initial stage, both the main root and lateral roots of poplar trees have clear root tip meridians, root crowns, cortex and vascular tissues. The formation of adventitious roots is often accompanied by cell division and differentiation, and is also regulated by hormone signals. Genes such as the WOX family, *GLR3.3* and *CML* are highly expressed in the root apex region and can regulate root growth (Ahkami, 2023; Zhang et al., 2024). If the expression of these genes is artificially altered, the vascular tissue of the roots will be more developed and the xylem cells will increase, which can make the roots thicker and have more branches (Liu et al., 2022). The structure and growth of roots can also change with environmental variations under different conditions such as drought, nutrient deficiency or disease stress.

2.3 Natural variation among *Populus* species

Poplar trees of different species and strains vary greatly in the morphology of their roots and their adaptability. Studies have found that poplar trees of different genotypes show significant differences in the number, length and root weight of advancements, and these traits are closely related to genomic variations such as SNPS and Indel (Zhang et al., 2024). For instance, the advanced-roots of the varieties *P.* × *canadensis* ‘Guariento’ and *P. deltoides* ‘Zhongcheng5’ grow particularly well and are very suitable for breeding and rapid propagation (Zhang et al., 2024). In addition, the performance of roots of different varieties varies when facing changes in water, soil structure and nutrients. For example, traits such as the distribution pattern of roots, the thickness of fine roots and the root length per unit weight will all be different (Frymark-Szymkowiak and Kieliszewska-Rokicka, 2023; Frymark-Szymkowiak et al., 2023). These natural differences provide excellent materials for studying the functional genomics and ecological adaptability of poplar root systems.

3 Hormonal Regulation of Root Development

3.1 Auxin biosynthesis, transport, and signaling

Auxin plays a crucial role in the development of poplar roots, especially in the formation of adventite roots and lateral roots. Studies have found that genes such as *PagFBL1* (TIR1 receptor) and *Aux/IAA28* are highly expressed when poplar trees start to grow adventitious roots, which helps promote root formation and increase biomass (Shu et al., 2018). When *PagFBL1* is overexpressed, more adventitious roots grow. On the contrary, if it is expressed less, the roots grow slowly, indicating that the auxin signal must be activated for the roots to develop normally. Furthermore, some auxin responsive-related genes, such as *ARF*, *IAA14* and *SAUR*, are also activated at the beginning of advanced-root formation, thereby further promoting root growth (Cai et al., 2019; Zhang et al., 2023). Auxin transport direction (polar transport) is also important in lateral root formation, and changes in related genes can affect the shape and quantity of roots (Yao et al., 2023).

3.2 Crosstalk with cytokinin, ethylene, and abscisic acid

In addition to auxin, the roots of poplar trees are also jointly regulated by a variety of plant hormones. For instance, Cytokinin inhibits the formation of adventite roots through factors such as PtRR13. If this signal is too strong, roots will not grow out. However, after pruning, its level will decline, which instead helps hormones such as auxin and ethylene to function better, thereby promoting root growth. The genes related to Ethylene are also activated at the beginning of adventitious root development, indicating that it is also involved in the regulatory process of roots (Zhang et al., 2023). Abscisic acid (ABA) directly affects root growth and regulates root development together with other hormones such as brassinolide (BR) and gibberellin (GA) through some small RNAs (miRNAs) (Lian et al., 2018). Gibberellin mainly exerts a countereffect by inhibiting the initiation process of lateral roots, that is to say, it reduces the number of lateral roots (Du et al., 2023).

3.3 Molecular regulators involved in hormonal pathways

In the process of regulating the growth of poplar roots, many important genes and regulatory modules also play a role. For instance, the PagFBL1-PagIAA28 module is a key component in auxin signals and can directly promote the growth of adventite roots (Shu et al., 2018). miR167a is a small RNA, and its target is ARF8. This combination is important for both adventing roots and lateral roots. When miR167a is expressed in large quantities, lateral roots will also grow more (Cai et al., 2019). Some miRNAs related to ABA, such as peu-miR-n68 and peu-miR477b, are also involved in the signal interaction between ABA and BR, GA, thereby regulating root growth (Lian et al., 2018). There is also the bHLH transcription factor PsPRE1, which can regulate the related genes of multiple hormones, including auxin, gibberellin and salicylic acid. This not only helps adventite root development, but also enhances the stress resistance of poplar (Du et al., 2023). The gene *PtrXB38*, which is regarded as an eQTL hotspot, also promotes adventitious root formation by regulating genes related to auxin transport and signaling pathways (Yao et al., 2023).

4 Key Genes and Transcription Factors in Root Development

4.1 WOX, LBD, ARF, and NAC families

Some transcription factors have been found to be very important for root formation during the study of poplar root development. The WOX, LBD, ARF and NAC families are the most watched. Li et al. (2025) found that the expression of the ARF and LBD families would significantly decrease after exogenous addition of CLE13 signaling peptides, indicating that CLE signaling can regulate root growth and branching by influencing them. ARF plays a key role in the auxin signaling pathway and is directly involved in root differentiation and development (Yao et al., 2023). Nagle et al. (2022) hold that the NAC family is more extensively involved in cell differentiation, organ formation, and response to adverse conditions, exerting a considerable influence on the structure and function of roots.

4.2 Root meristem regulators and cell cycle genes

The continuous growth of poplar roots requires that the meristem at the root tip remain active all the time. CLE signaling peptides and their receptors are crucial in this process. They can regulate the information exchange between cells and maintain the activity of meristem (Li et al., 2025). Nagle et al. (2022) discovered through GWAS and QTL studies that many genes related to cell division, structural regulation, and hormone signaling can affect the development of adventite roots. Yao et al. (2023) discovered that the gene *PtrXB38* is a very important regulatory center. It can affect the transport and signal transmission of auxin, promote root formation and the activity level of meristem (Figure 1).

4.3 Genes controlling root elongation and branching

The growth and branching of roots are crucial to the root structure and environmental adaptability of the entire tree. There is a gene called *PsAAAP21*, which belongs to the AAAP family. It can help form adventite roots and regulate the transport of amino acids such as tyrosine, methionine and arginine, thereby enhancing the growth ability of roots (Du et al., 2022). In addition, GWAS analysis also found that genes related to hormone signaling, cell division, and reactive oxygen species regulation would affect root elongation and branching (Nagle et al., 2022). Some genes, such as *SWEET17*, have variations that are also closely related to the developmental ability of roots (Zhang et al., 2024). These genes have different functions, but the regulatory network they form is very complex, jointly determining how poplar roots grow and how strong their ability to adapt to the environment is.

5 Functional Genomic Tools and Resources in Poplar

5.1 Genome sequencing and annotation databases

In recent years, researchers have clarified the genomic structures of poplar varieties such as NL895 and 84K using PacBio high-fidelity sequencing and Hi-C technology (Qiu et al., 2019; Luo et al., 2024; Shi et al., 2024a). These new assembly results have distinguished the haplotypes of each chromosome and also enabled us to more accurately locate the gene positions and study the expression of different alleles. In addition to these genomic information, platforms like PoplarGene and PFGD have also been established, which include poplar gene function annotation, inter-gene interaction, expression level data, etc., and are very convenient to use.

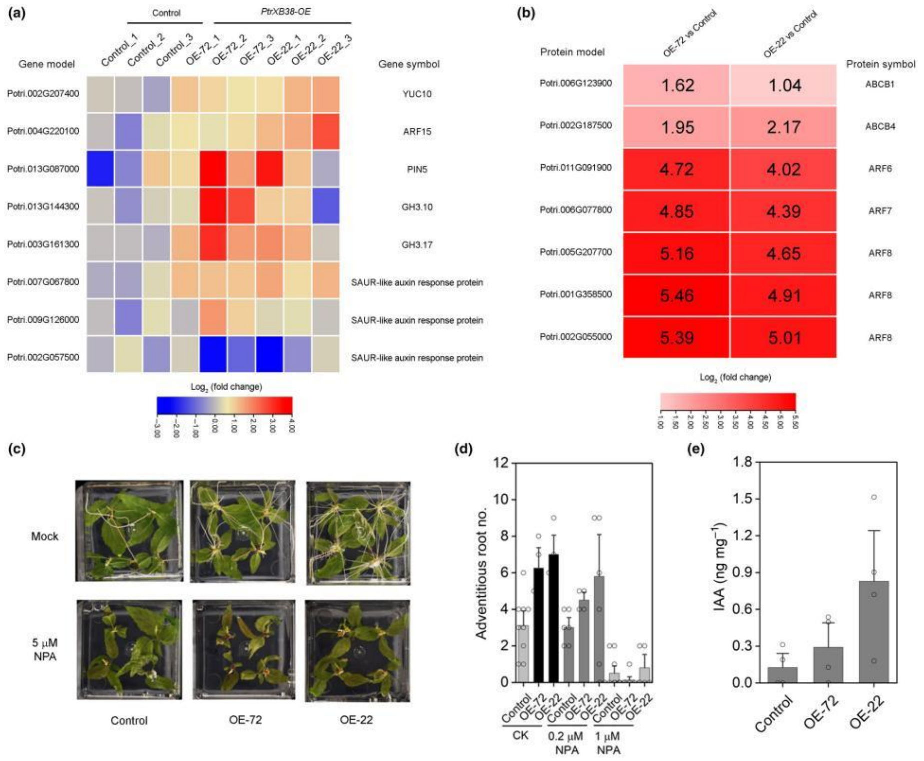

Figure 1 Auxin signaling and transport is essential for PtrXB38-mediated adventitious root formation in *Populus tremula* × *Populus alba* (Adopted from Yao et al., 2023)

Image caption: (a) Log-fold changes of transcript levels of auxin biosynthesis, signaling, transport, and response-related genes in 12-d-old root samples of *PtrXB38-OE* vs control plants, based on RNA-seq results. (b) Log-fold changes of protein abundance of auxin response factor in 12-d-old root samples of *PtrXB38-OE* vs control plants, based on quantitative proteomics. (c) Root formation of *PtrXB38-OE* plants upon auxin transport inhibitor treatment. (d) Adventitious root number of *PtrXB38-OE* plants with 0.2 and 1 μM NPA treatments. Bar charts represent mean ± SE ($n \geq 3$ independent plants). (e) IAA contents in the roots of *PtrXB38-OE* plants grown in ½-strength Murashige & Skoog medium. Bar charts represent mean ± SE ($n = 4$ independent plants) (Adopted from Yao et al., 2023)

5.2 RNA-Seq, ATAC-Seq, and single-cell transcriptomics

Whether analyzing different organs, studying a certain growth stage, or observing how poplar responds to stresses such as cold, drought, and salt, RNA-Seq is very useful. Databases like GEPSdb also integrate a lot of these RNA expression data, allowing for the review of the high or low expression level of a certain gene under what conditions at any time (Liu et al., 2021). Shi et al. (2024a) demonstrated that, in addition to traditional transcriptome techniques, ATAC-Seq and single-cell sequencing have now also begun to be applied to poplar trees, especially in the study of epigenetic and cell type specific expression of root systems. Although these techniques are still in their nascent stage in poplar trees, they have already shown great potential.

5.3 Gene editing (CRISPR/Cas9), VIGS, and transformation systems

CRISPR/Cas9 is now one of the most important tools used in poplar research. The *Populus* VariantDB v3.2 database provides a lot of useful information, such as the differences between different genomes, which are very helpful for designing editing targets. The transgenic system of poplar is also relatively mature and can efficiently introduce target genes, which is an important means for functional verification and variety improvement (Biselli et al., 2022). Furthermore, some reverse genetics tools, such as VIGS virus-induced gene silencing, have also been used to rapidly screen which genes are useful, helping researchers shorten the experimental cycle.

6 Root-Microbe Interactions: Genetic Insights

6.1 Mycorrhizal symbiosis and gene expression patterns

The roots of poplar trees and mycorrhizal fungi often establish a cooperative relationship, which is of great help to plants in absorbing nutrients and enhancing their stress resistance. Balestrini et al. ’s research in 2024 found that when the roots of poplar trees interact with arbuscular mycorrhizal (AM) fungi, certain specific genes are activated. These genes are related to processes such as nutrient transport, signal transmission and immune defense. Fröschel et al. (2020) discovered through genomic and proteomic studies that during the symbiotic process of plants, they adjust gene expression in different cellular layers to assist in fungal colonization and nutrient exchange, and also regulate defense responses to prevent excessive immunity.

6.2 Rhizosphere microbiome shaping by root exudates

Different poplar genotypes release different organic acids, sugars and secondary metabolites, which can attract beneficial bacteria while rejecting harmful ones. Demiwal et al. (2024) also found through transcriptome and metabolome analysis that root secretions can regulate the behavior of microorganisms, such as enabling them to express genes related to colonization, nutrient absorption, and signal recognition. The types and quantities of these secretions are controlled not only by the genes of the poplar itself but also by the surrounding environment (Yu and Hochholdinger, 2018).

6.3 Genomic response to beneficial and pathogenic microbes

When the roots of poplar trees come into contact with different types of microorganisms, such as beneficial probiotes or fungi, or harmful pathogens and nematodes, it activates different gene expression networks. Research has found that different cellular layers respond differently to microorganisms. For instance, outer cells are more likely to activate defense genes to fight against pathogenic bacteria; The inner cells mainly activate some genes related to symbiosis (Figure 2) (Fröschel et al., 2020). Furthermore, plants also adjust hormone signals and metabolic processes, promoting the activities of beneficial bacteria on the one hand and suppressing pathogens on the other hand (Demiwal et al., 2024). Genomic association analysis also indicates that the genetic background of plants can affect the types and functions of microorganisms around the roots (Wille et al., 2018; He et al., 2021; Martinez, 2023). These results have significant reference value for future genetic improvement and enhancing the cooperative ability between plants and microorganisms.

7 Root Plasticity and Environmental Responses

7.1 Root adaptation to drought, flooding, and nutrient limitation

The root system of poplar trees is very flexible and can adjust its structure and distribution pattern according to changes in the environment. *Populus euphratica* seedlings grow adventite roots when there is drought or too much water to help maintain stability and obtain oxygen. When the water level deepens, they also increase the number and length of their roots to adapt to the changes in moisture (Wang et al., 2021). Different soil environments can also cause changes in the morphology of root systems. When there is less clay water, the roots will work harder to grow outward. In sandy soil, to absorb more water and nutrients, roots will increase their total length. The roots of poplar trees also adjust the rate of formation and death of fine roots according to the amount of water and nutrients in the soil, especially during the growing season. This “transformable” ability enables poplar trees to maintain normal growth when facing drought, flooding or nutrient deficiency.

7.2 Epigenetic and transcriptional regulation under abiotic stress

When the root system of poplar trees encounters abiotic stress, it will adapt to these problems through genetic regulation. Transcriptome analysis revealed that under different water conditions, the expression levels of many genes in roots would increase or decrease. These genes are related to antioxidation, cell protection, cell wall adjustment, etc. Xu et al. (2021) found that the gene *XET* is “activated” by drought, and its promoter contains sequences responding to drought. After overexpression of this gene, the drought resistance of roots will be enhanced. There are also modules like miR476a-*RFL* that regulate mitochondrial function and auxin signaling, thereby promoting the formation of adventitious roots. Genomic and QTL studies have also identified key loci that control root morphology and function, indicating that these characteristics are jointly regulated by genetics and epigenetics (Liang et al., 2024).

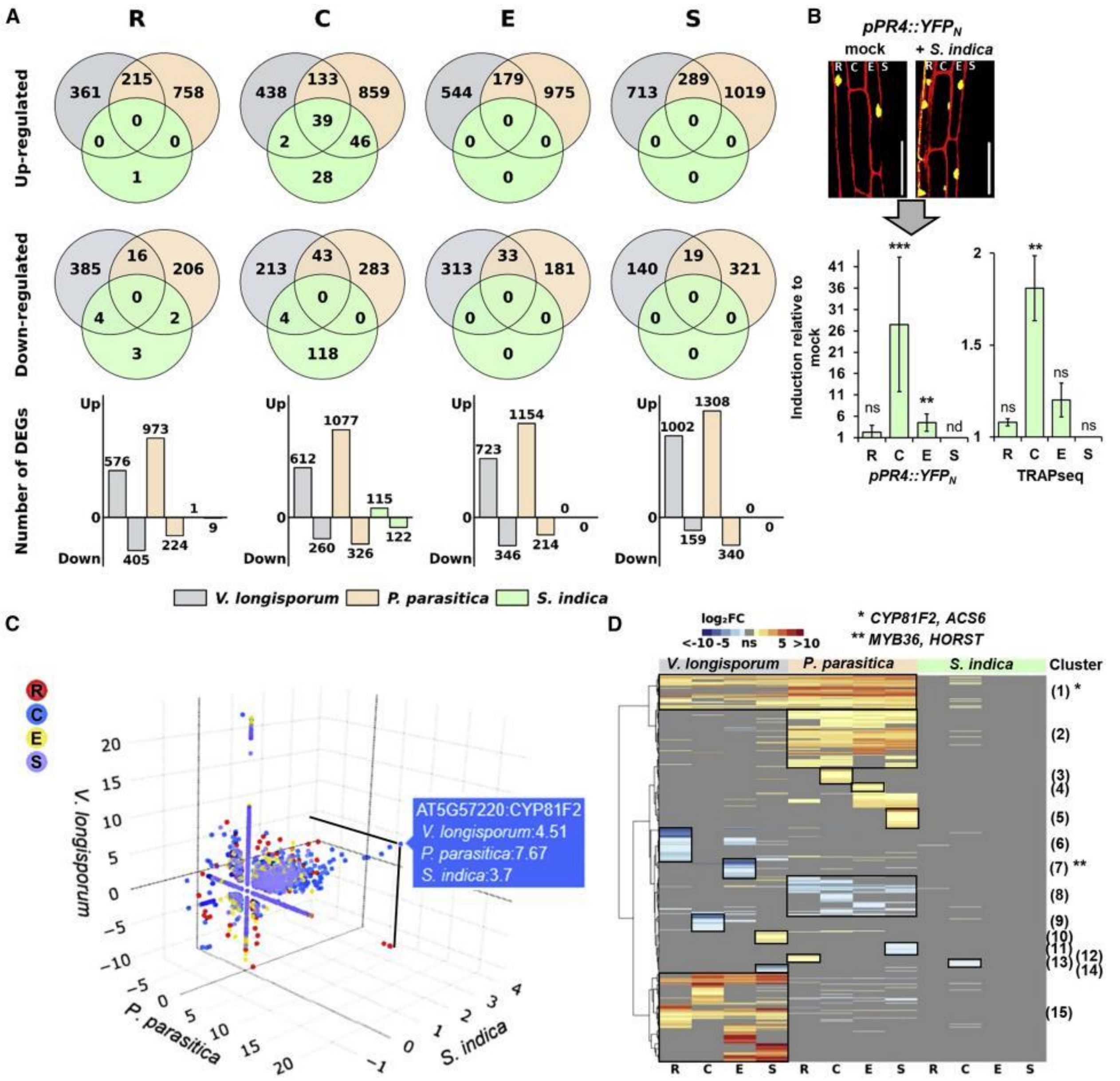

Figure 2 Cell-layer-specific translatomes upon microbial challenge (Adopted from Fröschel et al., 2020)

Image caption: (A) Venn diagrams comparing root cell-layer responses after inoculation with *V. longisporum* (2 dpi, gray), *P. parasitica* (2.5 hpi, rosé), and *S. indica* (3 dpi, green); (B) Verification of TRAP-seq data (right) by fluorescence localization studies applying a pPR4::YFPN reporter line (left); (C) 3D viewer of the entire dataset for the cell layers and microbial infections indicated; (D) Genome-wide hierarchical clustering of TRAP-seq data upon infection with the indicated microbes (Adopted from Fröschel et al., 2020)

7.3 Integrative omics in stress response profiling

The “multi-omics” approach enables us to have a more comprehensive understanding of how the root system of poplar trees responds to environmental stress. Xu et al. (2024) found that when poplar trees encounter novel stresses like nanoplastics, their roots will first use antioxidant enzymes to alleviate mild damage. If the pressure is too great, it will also trigger the synthesis of defense substances such as flavonoids. Under the background of climate change, such as in high-temperature or waterlogging conditions, through gene resequencing and transcriptome analysis, the genes and regulatory methods by which root systems adapt to these environmental changes can be discovered, indicating that the plasticity of roots is closely related to their evolutionary ability. Integrating these data is helpful for identifying regulatory key genes and metabolic pathways, and also provides new ideas for cultivating stronger poplar varieties in the future (Xu et al., 2024).

8 Case Study: Functional Characterization of *PtWOX5* in Lateral Root Formation

8.1 Background and identification of the candidate gene

The WOX gene family plays a very important role in the development of plant roots. Studies have found that in poplar trees, *PtWOX5* (such as *PtoWOX5a*) is particularly expressed at the root tips and lateral root tips during adventite and lateral root regeneration, suggesting that it may be involved in the maintenance of root meristem and the formation of new roots (Li et al., 2018). In an experiment where the main root was mechanically stimulated to induce lateral root growth, it was also observed that the expression of *WOX5-like* genes was activated at different stages of lateral root development, which further suggests that it may play a regulatory role in lateral root development (Baesso et al., 2020).

8.2 Experimental validation through overexpression and knockout

Through some genetic experiments, the function of this gene has also been confirmed. Researchers placed *PtoWOX5a* in the WOX5 mutant of *Arabidopsis thaliana* and found that it could restore the function of quiescent center (QC) cells in the mutant, indicating that this gene has similar functions in different plants. When *PtoWOX5a* was overexpressed in poplar trees, both roots and leaves changed: Adventist roots increased, roots became shorter, root tips became larger, leaves became fewer, and leaf area became smaller. These phenomena suggest that *PtWOX5* may affect the root development process by regulating genes related to cell division (such as *CYCD* genes) (Li et al., 2018). In addition, after being stimulated by external pressure, the expression of *PtWOX5* during lateral root development also changes, which also supports its role in regulating lateral root formation (Baesso et al., 2020).

8.3 Ecological relevance in reforestation and soil stabilization

PtWOX5 regulates root growth and also has practical significance for ecological restoration and soil stabilization and slope protection. It can enhance the formation of advmaturing roots and lateral roots, making poplar trees more likely to take root and expand their root systems more quickly. This is particularly useful in places like degraded land, riverbanks or slopes, as it can help trees fix the soil more quickly and reduce erosion (Li et al., 2018; Baesso et al., 2020). Li et al. (2018) and Baesso et al. (2020) hold that regulating the *PtWOX5* gene can provide new ideas and methods for forestry breeding and ecological engineering.

9 Ecological Implications of Root Traits in *Populus*

9.1 Role of root systems in carbon sequestration

The roots of poplar trees can adapt to different soil moisture environments by adjusting the length density, thickness and specific length of the roots. This change is beneficial for it to absorb water and nutrients better, and it can also make the roots grow deeper and more numerous, thereby increasing the weight of the roots. This not only helps trees grow better, but also allows more carbon to remain in the soil, which is very helpful for carbon fixation and storage (Xia et al., 2022; Tan et al., 2023). The roots of poplar trees can also form mutually beneficial relationships with nitrogen-fixing bacteria, mycorrhizal fungi and other microorganisms. These microorganisms are helpful for trees to absorb more nutrients, keep more carbon in the soil and maintain the carbon balance of the entire forest system (Schaefer et al., 2024; Fu et al., 2025).

9.2 Root architecture and soil water conservation

The roots of poplar trees make adjustments when the soil is dry (Han, 2024). When the surface is dry, more fine roots will grow deeper into the soil to absorb more water (Tan et al., 2023). The shape and structure of poplar tree roots can also change with the environment, such as increasing the root length or making the root tissue tighter, which is beneficial for more effective water absorption and transportation (Grünhofer et al., 2022; Schaefer et al., 2024). The roots of poplar trees can also work together with microorganisms in the soil to help improve soil structure and enhance soil water retention capacity (Xia et al., 2022; Fu et al., 2025).

9.3 Applications in afforestation and climate-resilient forestry

The root systems of different poplar species have different shapes and capabilities. This natural variation provides many options for afforestation and ecological restoration. Selecting varieties with well-developed root systems and strong adaptability can make trees more likely to survive and grow faster, and is suitable for the restoration of degraded land (Sun et al., 2019; Bannoud and Bellini, 2021). The cooperation between poplar roots and beneficial microorganisms can not only enhance their resistance to adverse conditions, but also increase the yield and ecological service functions of forests (Fu et al., 2025). These advantages are very useful for addressing climate change, increasing the carbon storage capacity of forests and conserving soil and water (Tan et al., 2023; Schaefer et al., 2024).

10 Concluding Remarks

In recent years, poplar (*Populus*), as an important research tree species, has made considerable progress in the study of root development. Scientists have begun to reveal how poplar roots grow and how they adapt to different environments through whole-genome sequencing, transcriptome analysis and epigenetic studies. Pan-genome research has found that some “private genes” and structural differences among different varieties are important for their adaptation to local climate and environment. These genes can affect the shape and function of poplar roots and also make them exhibit different growth characteristics. In addition, poplar trees have a strong ability to reproduce asexually through cuttings and other means, which is closely related to the growth of advancements. Therefore, many current studies are focusing on how these roots develop. More and more functional genes have been identified, laying a foundation for understanding the stress resistance and ecological functions of poplar root systems.

With the advancement of sequencing technology, some new methods have also been applied to the study of poplar root systems, such as high-throughput sequencing, single-cell omics, epigenetic analysis and machine learning, etc. These tools help scientists understand more systematically which genes control the development and morphology of roots. Super pan-genome, GWAS and multi-omics joint analysis are also used to discover important genes, and machine learning can be used to establish predictive models. Gene editing technologies, such as CRISPR/Cas9, enable researchers to quickly verify the function of a gene and also improve the traits of trees more rapidly. These methods have enabled us to have a clearer understanding of the poplar root system and also provided new means for enhancing its resistance and ecological functions in the future.

These research results are also of great help in practice. For instance, through genomic information, tree species with more developed root systems, greater drought resistance or better adaptation to saline-alkali land can be selected for afforestation on wasteland or restoration of degraded ecosystems. In addition, genetic engineering technology can also make poplar trees more resistant to pests and diseases, or restore soil in polluted areas. All these provide new possibilities for the development of forestry and environmental protection. In the future, by integrating various data and ecological models, we are expected to precisely regulate the growth pattern of poplar roots and apply it in more forest restoration and ecological management practices.

Acknowledgments

The authors thank Dr. Lian for his comments on the manuscript of this study.

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

Ahkami A., 2023, Systems biology of root development in *Populus*: review and perspectives, Plant Science, 335: 111818.
https://doi.org/10.1016/j.plantsci.2023.111818

An Y., Geng Y., Liu Y., Han X., Huang L., Zeng W., Zhang J., and Lu M., 2023, The glutamate receptor gene *GLR3.3*: a bridge of calcium-mediated root development in poplar, Horticultural Plant Journal, 10(6): 1449-1462.
https://doi.org/10.1016/j.hpj.2023.01.012

Baesso B., Terzaghi M., Chiatante D., Scippa G., and Montagnoli A., 2020, *WOX* genes expression during the formation of new lateral roots from secondary structures in *Populus nigra* (L.) taproot, Scientific Reports, 10: 18890.
https://doi.org/10.1038/s41598-020-75150-1

Balestrini R., Sillo F., Boussageon R., Wipf D., and Courty P., 2024, The hidden side of interaction: microbes and roots get together to improve plant resilience, Journal of Plant Interactions, 19: 2323991.
https://doi.org/10.1080/17429145.2024.2323991

Bannoud F., and Bellini C., 2021, Adventitious rooting in *Populus* species: update and perspectives, Frontiers in Plant Science, 12: 668837. https://doi.org/10.3389/fpls.2021.668837

Biselli C., Vietto L., Rosso L., Cattivelli L., Nervo G., and Fricano A., 2022, Advanced breeding for biotic stress resistance in poplar, Plants, 11(15): 2032. https://doi.org/10.3390/plants11152032

Bünger W., Jiang X., Müller J., Hurek T., and Reinhold-Hurek B., 2020, Novel cultivated endophytic *Verrucomicrobia* reveal deep-rooting traits of bacteria to associate with plants, Scientific Reports, 10: 8692. https://doi.org/10.1038/s41598-020-65277-6

Cai H., Yang C., Liu S., Qi H., Wu L., Xu L., and Xu M., 2019, MiRNA-target pairs regulate adventitious rooting in *Populus*: a functional role for miR167a and its target Auxin response factor 8, Tree Physiology, 39(11): 1922-1936. https://doi.org/10.1093/treephys/tpz085

Demiwal P., Tayade S., Yadav S., and Sircar D., 2024, A metabolomics perspective on root-derived plant immunity and phytohormone interaction, Physiologia Plantarum, 176(1): e14150. https://doi.org/10.1111/ppl.14150

Du J., Du C., Ge X., Wen S., Zhou X., Zhang L., and Hu J., 2022, genome-wide analysis of the *AAAP* gene family in *Populus* and functional analysis of *PsAAAP21* in root growth and amino acid transport, International Journal of Molecular Sciences, 24(1): 624. https://doi.org/10.3390/ijms24010624

Du J., Ge X., Wei H., Zhang M., Bai Y., Zhang L., and Hu J., 2023, *PsPRE1* is a basic helix-loop-helix transcription factor that confers enhanced root growth and tolerance to salt stress in poplar, Forestry Research, 3: 16. https://doi.org/10.48130/FR-2023-0016

Fröschel C., Komorek J., Attard A., Marsell A., López-Arboleda W., Berre L., Wolf E., Geldner N., Waller F., Korte A., and Dröge-Laser W., 2020, Plant roots employ cell-layer-specific programs to respond to pathogenic and beneficial microbes, Cell Host and Microbe, 29(2): 299-310. https://doi.org/10.1016/j.chom.2020.11.014

Frymark-Szymkowiak A., and Kieliszewska-Rokicka B., 2023, The fine root distribution and morphology of mature white poplar in natural temperate riverside forests under periodically flooded or dry hydrological conditions, Forests, 14(2): 223. https://doi.org/10.3390/f14020223

Frymark-Szymkowiak A., Kulczyk-Skrzeszewska M., and Tyburska-Woś J., 2023, Seasonal dynamics in mycorrhizal colonization and fine root features of the white poplar (*Populus alba* L.) in natural temperate riverside forests with two contrasting soils, Forests, 15(1): 64. https://doi.org/10.3390/f15010064

Fu R., Liu L., Wang Z., Hua Z., Bei S., Yu Y., and Li X., 2025, Synergy of diazotrophs with native soil microbes improves poplar traits, Industrial Crops and Products, 224: 120311. https://doi.org/10.1016/j.indcrop.2024.120311

Grünhofer P., Stöcker T., Guo Y., Li R., Lin J., Ranathunge K., Schoof H., and Schreiber L., 2022, *Populus* × *canescens* root suberization in reaction to osmotic and salt stress is limited to the developing younger root tip region, Physiologia Plantarum, 174(5): e13765. https://doi.org/10.1111/ppl.13765

Han M., Xu X., Li X., Xu M., Hu M., Xiong Y., Feng J., Wu H., Zhu H., and Su T., 2022, New insight into aspartate metabolic pathways in *Populus*: linking the root responsive isoenzymes with amino acid biosynthesis during incompatible interactions of *Fusarium solani*, International Journal of Molecular Sciences, 23(12): 6368. https://doi.org/10.3390/ijms23126368

Han Y.P., 2024, Application of CRISPR/Cas9 technology in editing poplar drought resistance genes, Molecular Plant Breeding, 15(2): 81-89. https://doi.org/10.5376/mpb.2024.15.0010

He X., Zhang Q., Li B., Jin Y., Jiang L., and Wu R., 2021, Network mapping of root-microbe interactions in *Arabidopsis thaliana*, NPJ Biofilms and Microbiomes, 7: 72. https://doi.org/10.1038/s41522-021-00241-4

Li J., Zhang J., Jia H., Liu B., Sun P., Hu J., Wang L., and Lu M., 2018, The *WUSCHEL-related homeobox 5a* (*PtoWOX5a*) is involved in adventitious root development in poplar, Tree Physiology, 38: 139-153. https://doi.org/10.1093/treephys/tpx118

Li M., Wang D., Fu Y., Zhao M., Li Z., Shen W., Pan L., Su X., and Zhao J., 2024, Poplar adventitious roots induced by stem canker pathogens: an experimental system for studying roots biology and light response-related processes, Journal of Visualized Experiments, 212: e67304. https://doi.org/10.3791/67304

Li Z., Chen F., Li M., Tang X., Liu Y., Huang M., Niu H., Liu C., Wang H., Xia X., and Yin W., 2025, Genome-wide identification and functional analysis of *CLAVATA3/EMBRYO SURROUNDING REGION-RELATED* (*CLE*) in three *Populus* species, International Journal of Molecular Sciences, 26(5): 1944. https://doi.org/10.3390/ijms26051944

Lian C., Yao K., Duan H., Li Q., Liu C., Yin W., and Xia X., 2018, Exploration of ABA responsive miRNAs reveals a new hormone signaling crosstalk pathway regulating root growth of *Populus euphratica*, International Journal of Molecular Sciences, 19(5): 1481. https://doi.org/10.3390/ijms19051481

Liang Z., Gong H., Lu K., and Zhang X., 2024, The genetic architecture of the root system during seedling emergence in *Populus euphratica* under salt stress and control environments, Applied Sciences, 14(6): 2225. https://doi.org/10.3390/app14062225

Liu R., Wen S., Sun T., Wang R., Zuo W., Yang T., Wang C., Hu J., Lu M., and Wang L., 2022, PagWOX11/12a positively regulates *PagSAUR36* gene that enhances adventitious root development in poplar, Journal of Experimental Botany, 73(22): 7298-7311.
https://doi.org/10.1093/jxb/erac345

Liu S., Lan Y., He T., Xiong R., Wu C., Xiang Y., and Yan H., 2021, GEPSdb: the gene expression database of poplar under stress, The Plant Genome, 15(1): e20163.
https://doi.org/10.1002/tpg2.20163

Luo J., Wang Y., Li Z., Wang Z., Cao X., and Wang N., 2024, Haplotype-resolved genome assembly of poplar line NL895 provides a valuable tree genomic resource, Forestry Research, 4: e015.
https://doi.org/10.48130/forres-0024-0013

Martinez C., 2023, Plant-microbe interactions: mining heritable root-associated microbiota across environments, Current Biology, 33(10): R413-R415.
https://doi.org/10.1016/j.cub.2023.03.068

Nagle M., Yuan J., Kaur D., Ma C., Peremyslova E., Jiang Y., Zahl B., De Rivera A., Muchero W., Fuxin L., and Strauss S., 2022, GWAS identifies candidate genes controlling adventitious rooting in *Populus trichocarpa*, Horticulture Research, 10(8): uhad125.
https://doi.org/10.1093/hr/uhad125

Qiu D., Bai S., Ma J., Zhang L., Shao F., Zhang K., Yang Y., Sun T., Huang J., Zhou Y., Galbraith D., Wang Z., and Sun G., 2019, The genome of *Populus alba* × *Populus tremula* var. *glandulosa* clone 84K, DNA Research, 26(5): 423-431.
https://doi.org/10.1093/dnares/dsz020

Schaefer E., Gehring C., Phillips R., Gadrat E., and Karst J., 2024, Variation of root functional traits indicates flexible below-ground economic strategies of the riparian tree species *Populus fremontii*, Functional Ecology, 38(9): 2003-2014.
https://doi.org/10.1111/1365-2435.14628

Shi T., Jia K., Bao Y., Nie S., Tian X., Yan X., Chen Z., Li Z., Zhao S., Ma H., Zhao Y., Li X., Zhang R., Guo J., Zhao W., El-Kassaby Y., Müller N., Van De Peer Y., Wang X., Street N., Porth I., An X., and Mao J., 2024a, High-quality genome assembly enables prediction of allele-specific gene expression in hybrid poplar, Plant Physiology, 195: 652-670.
https://doi.org/10.1093/plphys/kiae078

Shi T., Zhang X., Hou Y., Jia C., Dan X., Zhang Y., Jiang Y., Lai Q., Feng J., Feng J., Ma T., Wu J., Liu S., Zhang L., Long Z., Chen L., Street N., Ingvarsson P., Liu J., Yin T., and Wang J., 2024b, The super-pangenome of *Populus* unveil genomic facets for its adaptation and diversification in widespread forest trees, Molecular Plant, 17(5): 725-746.
https://doi.org/10.1016/j.molp.2024.03.009

Shu W., Zhou H., Jiang C., Zhao S., Wang L., Li Q., Yang Z., Groover A., and Lu M., 2018, The auxin receptor TIR1 homolog (PagFBL 1) regulates adventitious rooting through interactions with Aux/IAA28 in *Populus*, Plant Biotechnology Journal, 17(2): 338-349.
https://doi.org/10.1111/pbi.12980

Sun P., Jia H., Zhang Y., Li J., Lu M., and Hu J., 2019, Deciphering genetic architecture of adventitious root and related shoot traits in *Populus* using QTL mapping and RNA-Seq data, International Journal of Molecular Sciences, 20(24): 6114.
https://doi.org/10.3390/ijms20246114

Tan J., Yu W., Liu Y., Guo Y., Liu N., Fu H., Di N., Duan J., Li X., and Xi B., 2023, Response of fine-root traits of *Populus tomentosa* to drought in shallow and deep soil, Forests, 14(8): 1657.
https://doi.org/10.3390/f14081657

Wang T.Y., Wang P., Wang Z.L., Niu G.Y., Yu J.J., Ma N., Wu Z.N., Pozdniakov S.P., and Yan D.H., 2021, Drought adaptability of phreatophytes: insight from vertical root distribution in drylands of China, Journal of Plant Ecology, 14(6): 1128-1142.
https://doi.org/10.1093/jpe/rtab059

Wille L., Messmer M., Studer B., and Hohmann P., 2018, Insights to plant-microbe interactions provide opportunities to improve resistance breeding against root diseases in grain legumes, Plant, Cell and Environment, 42(1): 20-40.
https://doi.org/10.1111/pce.13214

Xia Z., He Y., Xu J., Zhu Z., Korpelainen H., and Li C., 2022, Rhizosphere microbe populations but not root traits induced by drought in *Populus euphratica* males, Soil Ecology Letters, 5: 220152.
https://doi.org/10.1007/s42832-022-0152-4

Xiao Z., Zhang Y., Liu M., Zhan C., Yang X., Nvsvrot T., Yan Z., and Wang N., 2020, Coexpression analysis of a large-scale transcriptome identified a calmodulin-like protein regulating the development of adventitious roots in poplar, Tree Physiology, 40(10): 1405-1419.
https://doi.org/10.1093/treephys/tpaa078

Xu C., Tao Y., Fu X., Guo L., Xing H., Li C., Yang Z., Su H., Wang X., Hu J., Fan D., Chiang V., and Luo K., 2021, The microRNA476a-*RFL* module regulates adventitious root formation through a mitochondria-dependent pathway in *Populus*, The New Phytologist, 230(5): 2011-2028.
https://doi.org/10.1111/nph.17252

Xu L., Liu C., Ren Y., Huang Y., Liu Y., Feng S., Zhong X., Fu D., Zhou X., Wang J., Liu Y., and Yang M., 2024, Nanoplastic toxicity induces metabolic shifts in *Populus* × *euramericana* cv. '74/76' revealed by multi-omics analysis, Journal of Hazardous Materials, 470: 134148.
https://doi.org/10.1016/j.jhazmat.2024.134148

Yao T., Zhang J., Yates T., Shrestha H., Engle N., Ployet R., John C., Feng K., Bewg W., Chen M., Lu H., Harding S., Qiao Z., Jawdy S., Shu M., Yuan W., Mozaffari K., Harman-Ware A., Happs R., York L., Binder B., Yoshinaga Y., Daum C., Tschaplinski T., Abraham P., Tsai C., Barry K., Lipzen A., Schmutz J., Tuskan G., Chen J., and Muchero W., 2023, Expression quantitative trait loci mapping identified PtrXB38 as a key hub gene in adventitious root development in *Populus*, The New Phytologist, 239(6): 2248-2264.
https://doi.org/10.1111/nph.19126

Yu P., and Hochholdinger F., 2018, The role of host genetic signatures on root-microbe interactions in the rhizosphere and endosphere, Frontiers in Plant Science, 9: 1896.
https://doi.org/10.3389/fpls.2018.01896

Zhang M., Zhou X., Xiang X., Wei H., Zhang L., and Hu J., 2024, Characterization and genetic differences analysis in adventitious roots development of 38 *Populus* germplasm resources, Plant Molecular Biology, 114: 9.
https://doi.org/10.1007/s11103-024-01418-z

Zhang Q., Shi M., Tang F., Su N., Jin F., Pan Y., Chu L., Lu M., Shu W., and Li J., 2023, Transcriptome analysis reveals the hormone signalling coexpression pathways involved in adventitious root formation in *Populus*, Forests, 14(7): 1436.
https://doi.org/10.3390/f14071436

Zhou Y., Zhang Y., Wang X., Han X., An Y., Lin S., Shen C., Wen J., Liu C., Yin W., and Xia X., 2020, The root-specific NF-Y family transcription factor, *PdNF-YB21*, positively regulates root growth and drought resistance by ABA-mediated IAA transport in *Populus*, The New Phytologist, 227(2): 407-426.
https://doi.org/10.1111/nph.16524