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Genome-Wide Identification of Drought-Responsive miRNAs in Maize Using Deep Sequencing and Network Analysis

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Abstract Drought stress is one of the main abiotic factors restricting corn production worldwide. microRNA (miRNA), as a key post-transcriptional regulatory factor, plays a significant role in the process of plants responding to adverse stress. This study utilized deep sequencing technology and network analysis methods to systematically identify miRNAs in corn that respond to drought stress, analyze their regulatory network mechanisms, and construct miRNA expression profiles of corn seedlings under drought treatment and normal irrigation conditions through high-throughput small RNA sequencing technology. A total of 312 known mirnas and 74 newly predicted mirnas were identified, among which 51 were significantly differentially expressed under drought stress. Further, the target genes were predicted through bioinformatics methods, and GO annotation and KEGG pathway enrichment analysis were conducted. The results showed that these mirnas were mainly involved in biological processes such as plant hormone signal transduction (such as the ABA pathway), oxidative stress response, and transcriptional regulation. This study comprehensively depicted the miRNA map of corn in response to drought stress and established a mirNA-mediated gene regulatory network framework, providing a theoretical basis for in-depth understanding of the molecular mechanism of corn drought resistance and potential target resources for molecular design breeding.

Keywords Corn (*Zea mays*); Drought stress; microRNA (miRNA); Deep sequencing; Gene regulatory network

1 Introduction

Corn (*Zea mays* L.), this seemingly ordinary crop, actually occupies an irreplaceable position in the global food and feed system. Whether it is for human consumption, livestock consumption, or raw materials used in industry, it deserves a place on the list. But there are also many problems, especially in today's increasingly unstable climate. Abiotic stresses like drought, which are often discussed, are almost the "invisible killers" in all corn-growing areas and have a very direct impact on plant growth and final yield (Tang et al., 2022). Worse still, with global warming, the frequency and intensity of droughts are both on the rise (Liu et al., 2019), which forces people to start thinking about a more realistic problem: How to cultivate drought-resistant corn varieties?

In recent years, molecular biology has developed rapidly, and research on drought resistance mechanisms has become increasingly in-depth. miRNA (microRNA), a small non-coding RNA, is not the most prominent role, but it plays a considerable behind-the-scenes role in regulating plants' responses to stress (Singroha et al., 2021). In corn bodies, they regulate a series of processes including abscisic acid signaling, reactive oxygen species scavenging, root development, etc. (Aravind et al., 2017; Jiao et al., 2022), playing a "bridging" role in enhancing drought resistance. With the aid of high-throughput sequencing and bioinformatics analysis, researchers have screened out many mirnas and their target genes related to drought, and have also sketched out a preliminary regulatory network map (Zhakypbek et al., 2025). But to be honest, these pictures are far from complete. There are still many aspects that remain unclear up to now, such as the specific responses of different tissues or the differential regulation among genotypes.

This study utilized deep sequencing and network analysis techniques to conduct a comprehensive genome-wide identification of mirnas responding to drought in maize. It reviewed the current research progress on drought stress and miRNA functions in maize and provided a detailed introduction to the experimental design and analysis methods. By integrating transcriptome and small RNA sequencing data, this study aims to clarify the regulatory networks involved in drought adaptation and the key miRNA-mRNA modules. The research results are expected

to deepen our understanding of the molecular mechanism of drought tolerance in corn and provide valuable genetic resources for breeding programs aimed at enhancing the drought resistance of corn.

2 Biological Characteristics and Regulatory Mechanisms of miRNAs

2.1 Biogenesis pathways and classification of miRNAs

miRNA may sound unremarkable, but in fact, it often plays a key role in regulating gene expression within plants. miRNA, which is usually only 20 to 24 nucleotides in length, is an endogenous non-coding RNA. Generally, it does not directly encode proteins, but it has a significant impact on the "switch" of gene expression. Its generation begins when the MIR gene is transcribed into pri-miRNA by RNA polymerase II, and this transcript has a typical stem-loop structure. Then, these PRI-mirnas will be processed in the cell nucleus by Dicer-like proteins, mainly DCL1, cleaved into pre-mirnas, and gradually transformed into double-stranded mature mirnas. Afterwards, miRNA binds to the AGO protein to assemble into a RISC complex, which acquires the ability to "quiet certain genes" - achieved by cutting mRNA or preventing it from being translated into proteins (Song et al., 2019; Wang et al., 2019; Zhan and Meyers, 2022). Of course, not all mirnas are exactly the same; their conservation levels, precursor structures, and processing methods vary significantly. Some miRNA families can be found in multiple species, while others only appear in specific groups.

2.2 Regulatory patterns of miRNAs in response to drought stress in plants

When drought occurs, the expression pattern of miRNA within plants is quite different. Behind this change lies the process of plants' self-adjustment. Not all mirnas are involved, but some mirnas, such as miR159, miR169, and miR393, have been repeatedly demonstrated to be involved in pathways such as ABA signaling, oxidative stress defense, and root regulation (Islam et al., 2022). These mirnas target the transcription factors or key signaling molecules that control the stress response and adjust the "neural response speed" of the entire system by adjusting up and down. However, such regulation is not uniform. The expression intensity and mode of miRNA may vary significantly across different tissues, varieties, and even at different growth stages. Nowadays, with the help of high-throughput sequencing technology, researchers have identified many mirnas in staple food crops such as corn and wheat that are induced or inhibited by drought, and their "node" status in the regulatory network is becoming increasingly clear.

2.3 Interactions between miRNAs and target genes and their modulation of signaling pathways

How exactly does miRNA shut up a gene? It relies on "matching oneself". Once it finds a complementary mRNA sequence to itself, it can bind to it, and then trigger mRNA degradation or at least prevent it from being translated. In plants, mirnas most frequently target various transcription factors, such as the "familiar faces" like MYB, NF-YA, SPL, ARF, and WRKY (Samad et al., 2017). These transcription factors themselves control a bunch of other genes. Therefore, when miRNA takes action, it is equivalent to influencing an entire series of signaling responses, such as ABA signaling, auxin regulation and ROS clearance mechanism (Sharma et al., 2025). What's more interesting is that miRNA and target genes usually show a state of "one rising and the other falling", where one side is elevated while the other is often suppressed. This reverse expression can achieve very fine regulation. Nowadays, by means such as degradation omics sequencing and RACE-PCR, researchers can relatively clearly confirm the relationship between these mirnas and their targets, and some have even become potential tools for studying drought-resistant breeding.

3 Application of Deep Sequencing in miRNA Identification

3.1 Overview of sRNA sequencing platforms and experimental procedures

Not everyone can realize at the beginning how much convenience the popularization of small RNA (sRNA) sequencing has brought to the research of plant miRNA. High-throughput platforms like Illumina HiSeq and NextSeq, although they may sound more technical, have actually become the "standard equipment" for analyzing miRNA. Take corn as an example. Researchers usually extract total RNA from the tissues of the control group and the drought treatment group, and then carry out a series of operations: screening out fragments of 18 to 32 nucleotides in length, adding linkers, reverse transcription, PCR amplification, and finally sending it for on-machine sequencing (Jiao et al., 2022; Cheng and Wang, 2025). Of course, setting up more time points and

adding biological repetition groups, although these operations are cumbersome, are to ensure that drought-responsive mirnas are not overlooked.

3.2 Data filtering, miRNA identification, and annotation methods

The raw data obtained cannot be directly analyzed. The first step must be to "clean it up" first. Sequences like adaptor sequences, low-quality reads, and small molecules that are clearly not mirnas (such as tRNA, rRNA, snoRNA) will all be filtered out. The remaining high-quality sRNA sequences are then compared with the reference genome. If one is lucky, they can find conserved mirnas that have been recorded in databases such as miRBase. When encountering the unknown, researchers have to resort to tools. Software such as miRDeep2, miRA or miRDeepFinder can predict new miRNA candidates based on sequence abundance, precursor structure and secondary structure (Evers et al., 2015). Sometimes, these predictions still need to be further confirmed, such as whether the miRNA precursors have typical stem-loop structures, whether the sequences are conserved, and how the expression levels vary among different samples. As for exactly which mrnas they target, tools such as psRNATarget and CleaveLand come in handy, and degradation omics sequencing is often required for verification (Xie et al., 2012; Sepulveda-Garcia et al., 2020).

3.3 Identification of differentially expressed miRNAs between drought-treated and control samples

Not every miRNA responds during drought; those with significant changes in expression are the focus of researchers. To identify these "responders", statistical tools such as DESeq2 are needed to compare the expression levels of mirnas in the drought group and the control group one by one (Sharma et al., 2025). In the research on corn, many mirnas showed significant up-regulation or down-regulation under drought conditions. Some were familiar faces, while new discoveries were made (Aravind et al., 2017; Liu et al., 2019). However, sequencing alone is not enough. qRT-PCR or Northern blotting is usually used as verification methods to confirm whether these differential expressions truly exist. This step is crucial because many of the miRNA-mRNA regulatory modules to be analyzed subsequently have been screened out from this batch of differentially expressed mirnas.

4 Functional Prediction and Analysis of Drought-Responsive miRNAs

4.1 Target gene prediction methods and bioinformatics tools

To figure out exactly what role a miRNA plays in drought response, the most direct way is to see who it regulates. Target gene prediction may sound highly technical, but in fact, the principle is not complicated - it relies on sequence complementarity and the accessibility of binding sites. Like in Corn, tools such as psRNATarget, psRobot and TargetFinder have become the "old three" that everyone commonly uses (Tang et al., 2022). However, predictions are predictions, but they cannot be implemented. Therefore, many times researchers will bring in degradation group sequencing data to cross-verify whether miRNA is indeed functioning (Yang et al., 2025). In addition, some people are more cautious and simply incorporate multiple sequence alignment (Clustal Omega), cluster analysis (R packages like seqinR and ape), and co-expression networks to help confirm whether the regulatory relationship under drought is "reliable". This is like a jigsaw puzzle. Only when each piece is pieced together can a reliable regulatory map be formed.

4.2 GO annotation and KEGG pathway analysis for functional enrichment

The predicted targets cannot merely be put up on a list; they must be explained exactly what they do during droughts. At this point, GO and KEGG come in handy. GO annotations categorize these genes into large boxes such as "Molecular functions" and "biological processes". Some common entries include cellular response regulation, water stress response, etc. (Liu et al., 2019; Jiao et al., 2022). KEGG, on the other hand, is more pastration-oriented and will tell you which signaling pathways are regulated by miRNA. Classic drought-resistant pathways such as plant hormone transmission, glutathione metabolism, and phenylpropanin synthesis are often on the list. To conduct these analyses, Blast2GO and AgriGO are frequently used tools.

4.3 Identification of key miRNAs involved in drought stress regulation

Some mirnas "step up" during drought and become very active, especially some classic ones such as miR164, miR159, miR156, miR319, miR160, as well as miR394 and miR408a, which are almost "familiar faces" in corn. They do not work on their own but "command the battle" by regulating transcription factors, such as MYB, NAC,

SPL, ARF, etc., which are responsible for regulating key links such as root development, hormone response, and ROS clearance. For instance, miR408a can affect the accumulation of ROS, and the result might be a negative regulatory effect. When miR164 pairs with MYB or NAC, it plays a role in promoting drought response in the ABA pathway (Figure 1) (Liu et al., 2019; Jiao et al., 2022). The clarification of these regulatory modules not only enables us to understand what they have done, but also provides a clear "bulltarget" for the future cultivation of drought-resistant varieties.

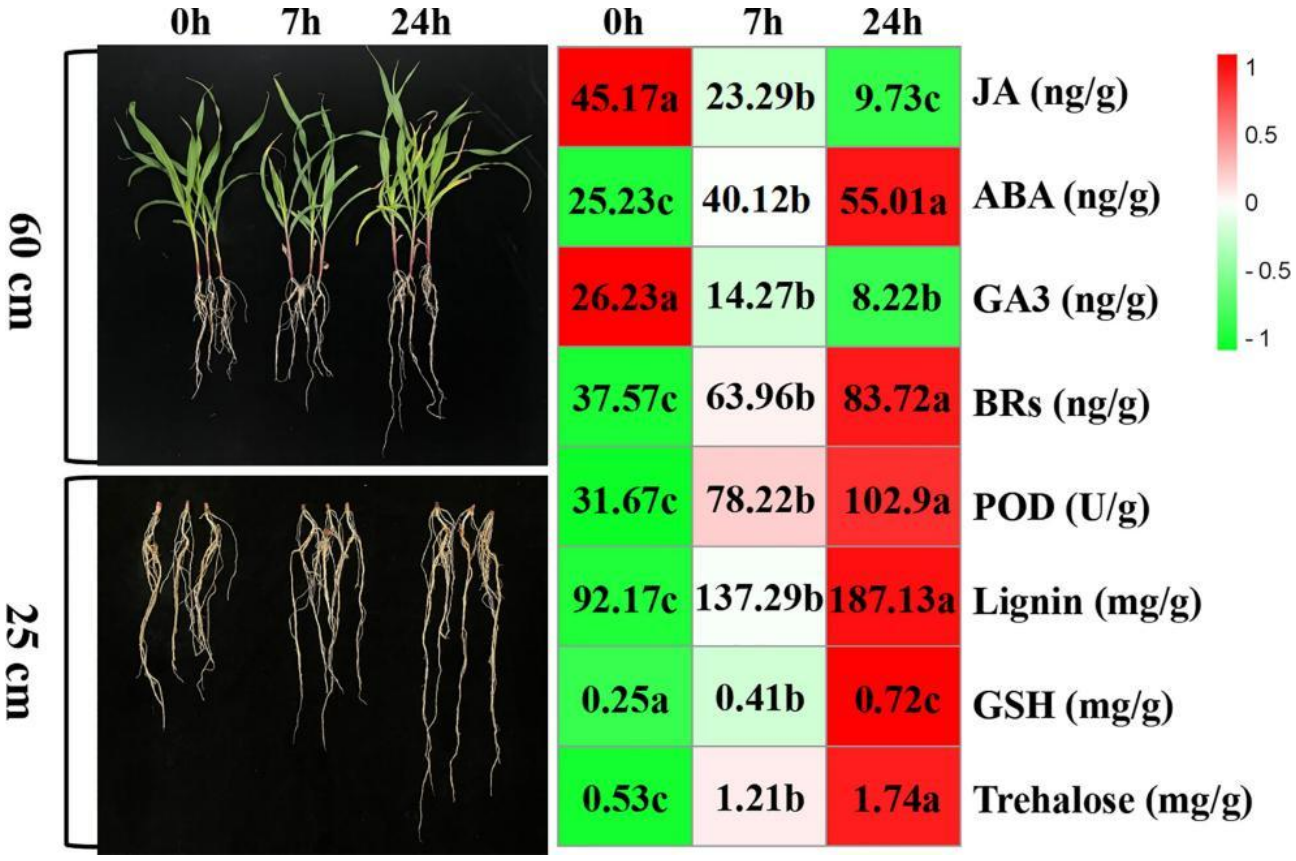

Figure 1 The morphology and physiochemical changes of maize variety “M8186” under drought stress. Values followed by different lowercase letters represent $p \leq 0.05$ (Adopted from Jiao et al., 2022)

5 Construction of miRNA Regulatory Networks and Systems Biology Analysis

5.1 Methods for constructing miRNA-target gene regulatory networks

When studying the drought response of corn, it is impossible to obtain a comprehensive picture by relying solely on a single miRNA or target gene. So, putting them on the Internet to look at "relationships" has become a common practice nowadays. Building this network is not entirely dependent on imagination; it requires a three-pronged approach of sequencing data, algorithmic prediction, and experimental verification. For instance, which mirnas showed significant expression changes after drought treatment were screened through tools such as psRNATarget and psRobot, and then degradation omics sequencing was used to verify whether they actually regulated the target genes (Aravind et al., 2017). Next, use software like Cytoscape to graph these interactive relationships, making it clear who controls and who regulates. Furthermore, some people will use WGCNA to analyze which mirnas and target genes are "clustered" in expression, which can dig out potential "core modules" (Tang et al., 2022).

5.2 Connections with ABA, ROS, transcription factors, and other signaling pathways

Under drought stress, mirnas do not play a solo role; they are almost always involved in complex networks such as hormones, REDOX reactions, and transcriptional regulation. For instance, the examples of miR164 regulating MYB and NAC transcription factors are often mentioned, and these happen to be involved in ABA-dependent drought responses (Liu et al., 2019; Jiao et al., 2022). For instance, miR408a, during drought, controls the

accumulation of ROS in its roots and to some extent becomes the "villain" in regulating resistance. Many mirnas target key transcription factors such as MYB, SPL, and ARF, which serve as the links connecting growth, development, and stress responses. The entire network is actually interwoven with multiple pathways. Modules such as phenylpropanin metabolism, glutathione cycle, and carbohydrate metabolism are also frequently driven by miRNA, indicating that it is not a single pathway working alone, but rather a whole system working in coordination (Li, 2025).

5.3 Network topology analysis and identification of core regulatory modules

The network has been built. The next step is not to look at how many "points" there are, but to see which nodes are more "important". Like miR164, miR156, and miR159, they almost always take the center stage in all the diagrams because they regulate too many downstream areas. If you don't look at them, you'll miss a large part. Through the analysis of network topology structure, these "hub" mirnas can be identified, which are often the intersection points of multiple pathways (Aravind et al., 2017; Tang et al., 2022). Meanwhile, the WGCNA method can also identify several modules that are particularly closely related to drought. For instance, the miR164-MYB/NAC module is linked to the ABA pathway, and miR408a is associated with ROS balance. While miR156-SPL is more related to development and growth regulation (Yang et al., 2025). These modules, to put it bluntly, are the "high-incidence areas" of regulation. If genetic improvement is to be carried out in the future, they will be very promising targets.

6 Case Study: Experimental Validation and Functional Analysis of Specific miRNAs

6.1 Drought response mechanism of miR164 targeting NAC transcription factors

Not all transcription factors are related to drought, but proteins like NAC, which play the role of "dispatchers" in plants, are often targets of miR164. In some drought-tolerant corn varieties, the regulation between miR164 and NAC seems to be centered around the ABA hormone - as soon as ABA is activated, miR164 will suppress the expression of NAC. In this way, both the structure of the root system and the reaction speed can be "adjusted more precisely". However, the situation is not always stable. For instance, miR164 overly strongly inhibits NAC, which instead makes plants more sensitive to drought. However, once the effect of miR164 is weakened or the expression of NAC is simply increased, sometimes plants become more drought-tolerant (Figure 2). Experimental evidence of this "waxing and waning" relationship has already been obtained for corn and other cereal crops (Liu et al., 2019; Tang et al., 2022).

6.2 Role of miR398 in regulating ROS scavenging and cellular protection

When it comes to drought resistance, ROS (reactive oxygen species) cannot be overlooked. Once they accumulate in excessive amounts, plant cells won't be able to handle them. And miR398 plays a somewhat "subtle" role in this process. It will target those genes encoding SOD (copper/zinc superoxide dismutase) and control their expression on a regular basis. However, once drought stress occurs, miR398 will decline, the amount of SOD will increase, and the antioxidant capacity of cells will also be enhanced. In this way, the plants can last a little longer. This mechanism is not uncommon and has similar results in many plants. Some people conducted regulatory experiments and found that when miR398 was lowered, its resistance increased, indicating that regulating its level can affect the ROS clearance system (Li et al., 2022; Zheng et al., 2023).

6.3 Expression profiling of key miRNAs via qRT-PCR and degradome validation

Sequencing results alone cannot explain all the issues; experimental evidence is needed to confirm them. So qRT-PCR and degradation group analysis came in handy. In the study, qRT-PCR was used to verify whether miR164 and miR398 would "rise" or "fall" under drought conditions, and the results were indeed consistent with the sequencing data. The degradation group further confirmed exactly who they had cut - the target genes, the cutting sites, all of which were paired up one by one. These methods combined are like piecing together a graph of the miRNA regulatory network from different angles, especially in the area of drought response, providing very solid experimental support (Seeve et al., 2019; Jiao et al., 2022).

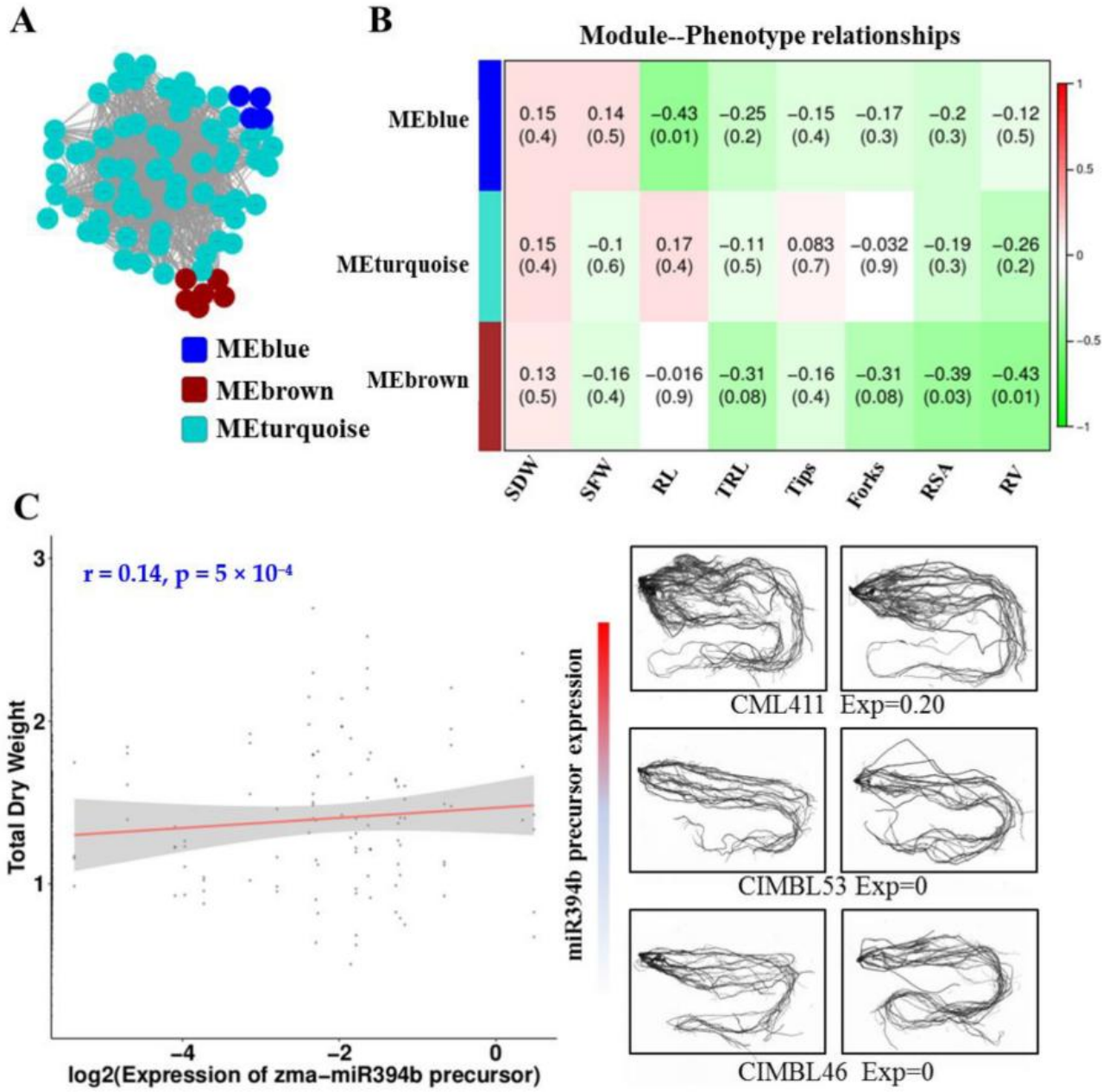

Figure 2 Co-expression network analysis in well water and water stress treatments. (A) Network visualization in Cytoscape. The nodes were colored by module membership. (B) Correlations between module eigengenes and root phenotypic traits. The numbers within the heatmap represent correlations and *p*-value (red, positively correlated; green, negatively correlated) for the module-trait associations (SDW, shoot dry weight; SFW, shoot fresh weight; RL, root length; TRL, total root length; Tips, root branches; Forks, root forks; RSA, root surface area; RV, root volume). (C) The connection between zma-miR394b precursor expression and total dry weight. On the left is the root phenotype of some lines from a natural group containing 368 lines. Red means that the expression of zma-miR394b precursor is higher (right) (Adopted from Tang et al., 2022)

7 Conclusions and Future Perspectives

The regulation of drought response by miRNA is neither simple nor straightforward. These small molecules in corn form a rather complex network, among which classic "partners" like miR164-MYB/NAC, miR159-MYB, miR156-SPL, and miR160-ARF often appear in pairs, with their expression levels fluctuating. The expression patterns of drought-tolerant and drought-intolerant varieties in this regard also differ significantly. Moreover, these regulatory relationships are not linear. For instance, some modules are closely bound to the ABA signaling pathway. Especially in some drought-resistant materials, the way miR164 regulates NAC and MYB is somewhat dependent on the rhythm of ABA. As for those newly identified mirnas, although they seem to have potential, it

remains to be seen how they will be verified and whether their effects will be stable in the future. Currently, commonly used methods such as high-throughput sequencing, degradation omics analysis, and qRT-PCR, although they have already been able to depict the interaction relationships between many key mirnas and target genes, the "usable" candidate resources are still being expanded.

By the way, although this field is bustling, there are still quite a few problems. Most current research often focuses on a specific organ or a certain point in time, and as a result, some important dynamic changes may be overlooked. Whether the newly discovered miRNA has real capabilities or not, there are still not many experiments to draw a conclusion at present - whether the mechanism is clear or not is another matter. The technical aspect cannot be solely resolved by existing methods. High-throughput validation still needs to be more precise, target prediction tools are not always reliable, and there are currently few studies that have effectively integrated omics data. Coupled with the influence of environmental factors and genotype differences, it is still somewhat difficult to directly apply the research results to the fields.

But then again, these mirnas themselves are treasures. Drought-resistant regulatory modules may become key resources in molecular breeding in the future. Whether they are used for labeling, gene editing or drought tolerance screening, the directions are quite clear. Especially for some mirnas that are only expressed in the root system or specific genotypes, they are even more worthy of close attention. The tasks to be done next are also very clear: the new mirnas need to continue to undergo functional verification. The verification methods should be more reliable, and it would be best to combine the relevant information of these mirnas with the breeding system. Only in this way can the selection and breeding process of drought-resistant corn be truly advanced.

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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

Aravind J., Rinku S., Pooja B., Shikha M., Kaliyugam S., Mallikarjuna M., Kumar A., Rao A., and Nepolean T., 2017, Identification characterization and functional validation of drought-responsive MicroRNAs in subtropical maize inbreds, Frontiers in Plant Science, 8: 941. https://doi.org/10.3389/fpls.2017.00941

Cheng J.H., and Wang W., 2025, Research progress on heat-resistant breeding of fresh-eating corn: screening and utilization of heat-resistant germplasm resources, Maize Genomics and Genetics, 16(3): 119-128. https://doi.org/10.5376/mgg.2025.16.0012

Evers M., Huttner M., Dueck A., Meister G., and Engelmann J., 2015, miRA: adaptable novel miRNA identification in plants using small RNA sequencing data, BMC Bioinformatics, 16: 370. https://doi.org/10.1186/s12859-015-0798-3

Islam W., Idrees A., Waheed A., and Zeng F., 2022, Plant responses to drought stress: microRNAs in action, Environmental Research, 215: 114282. https://doi.org/10.1016/j.envres.2022.114282

Jiao P., Wang C., Chen N., Liu S., Qu J., Guan S., and Ma Y., 2022, Integration of mRNA and microRNA analysis reveals the molecular mechanisms underlying drought stress tolerance in maize (*Zea mays* L.), Frontiers in Plant Science, 13: 932667. https://doi.org/10.3389/fpls.2022.932667

Li M.H., 2025, ATAC-seq reveals chromatin accessibility changes during maize seed development, Maize Genomics and Genetics, 16(4): 182-201. https://doi.org/10.5376/mgg.2025.16.0017

Li J., Song Q., Zuo Z., and Liu L., 2022, MicroRNA398: a master regulator of plant development and stress responses, International Journal of Molecular Sciences, 23(18): 10803. https://doi.org/10.3390/ijms231810803

Liu X., Zhang X., Sun B., Hao L., Liu C., Zhang D., Tang H., Li C., Li Y., Shi Y., Xie X., Song Y., Wang T., and Li Y., 2019, Genome-wide identification and comparative analysis of drought-related microRNAs in two maize inbred lines with contrasting drought tolerance by deep sequencing, PLoS ONE, 14(7): e0219176. https://doi.org/10.1371/journal.pone.0219176

Samad A., Sajad M., Nazaruddin N., Fauzi I., Murad A., Zainal Z., and Ismail I., 2017, MicroRNA and transcription factor: key players in plant regulatory network, Frontiers in Plant Science, 8: 565. https://doi.org/10.3389/fpls.2017.00565

Seeve C., Sunkar R., Zheng Y., Liu L., Liu Z., McMullen M., Nelson S., Sharp R., and Oliver M., 2019, Water-deficit responsive microRNAs in the primary root growth zone of maize, BMC Plant Biology, 19: 447.
https://doi.org/10.1186/s12870-019-2037-y

Sepúlveda-García E., Pulido-Barajas J., Huerta-Heredia A., Peña-Castro J., Liu R., and Barrera-Figueroa B., 2020, Differential expression of maize and teosinte microRNAs under submergence drought and alternated stress, Plants, 9(10): 1367.
https://doi.org/10.3390/plants9101367

Sharma P., Mishra S., Kaur A., Ahlawat O., Tiwari R., Kaur S., Sinha S., and Kumar S., 2025, Novel and conserved drought-responsive microRNAs expression analysis in root tissues of wheat (*Triticum asetivum* L.) at reproductive stage, Frontiers in Plant Science, 16: 1581542.
https://doi.org/10.3389/fpls.2025.1581542

Singroha G., Sharma P., and Sunkur R., 2021, Current status of microRNA-mediated regulation of drought stress responses in cereals, Physiologia Plantarum, 172(3): 1808-1821.
https://doi.org/10.1111/ppl.13451

Song X., Li Y., Cao X., and Qi Y., 2019, MicroRNAs and their regulatory roles in plant-environment interactions, Annual Review of Plant Biology, 70: 489-525.
https://doi.org/10.1146/annurev-arplant-050718-100334

Tang Q., Lü H., Li Q., Zhang X., Li L., Xu J., Wu F., Wang Q., Feng X., and Lu Y., 2022, Characteristics of microRNAs and target genes in maize root under drought stress, International Journal of Molecular Sciences, 23(9): 4968.
https://doi.org/10.3390/ijms23094968

Wang J., Mei J., and Ren G., 2019, Plant microRNAs: biogenesis homeostasis and degradation, Frontiers in Plant Science, 10: 360.
https://doi.org/10.3389/fpls.2019.00360

Xie F., Xiao P., Chen D., Xu L., and Zhang B., 2012, MiRDeepFinder: a miRNA analysis tool for deep sequencing of plant small RNAs, Plant Molecular Biology, 80: 75-84.
https://doi.org/10.1007/s11103-012-9885-2

Yang S., Liu J., Cao L., Chen J., and Duan P., 2025, Integrated analysis of transcriptome sRNAome and degradome involved in the drought-response of maize Zhengdan958, Open Life Sciences, 20(1): 20221044.
https://doi.org/10.1515/biol-2022-1044

Zhakypbek Y., Belkozhayev A., Kerimkulova A., Kossalbayev B., Murat T., Tursbekov S., Turysbekova G., Tursunova A., Tastambek K., and Allakhverdiev S., 2025, MicroRNAs in plant genetic regulation of drought tolerance and their function in enhancing stress adaptation, Plants, 14(3): 410.
https://doi.org/10.3390/plants14030410

Zhan J., and Meyers B., 2022, Plant small RNAs: their biogenesis regulatory roles and functions, Annual Review of Plant Biology, 74: 21-51.
https://doi.org/10.1146/annurev-arplant-070122-035226

Zheng Z., Yang J., Wang X., Zhang N., and Si H., 2023, Potato stu-miR398b-3p negatively regulates Cu/Zn-SOD response to drought tolerance, International Journal of Molecular Sciences, 24(3): 2525.
https://doi.org/10.3390/ijms24032525