Field Crop 2025, Vol.8, No.1, 41-50
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# Identification of Drought-Responsive Genes in Rapeseed Through Transcriptome Profiling

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Field Crop, 2025, Vol.8, No.1 doi: 10.5376/fc.2025.08.0005
Received: 08 Jan., 2025
Accepted: 18 Feb., 2025
Published: 28 Feb., 2025

**Preferred citation for this article**:
Huang Z.M., and Huang W.Z., 2025, Identification of drought-responsive genes in rapeseed through transcriptome profiling, Field Crop, 8(1): 41-50 (doi: 10.5376/fc.2025.08.0005)

**Abstract** The impact of drought on rapeseed is no joke. Once this important oil crop lacks water, its growth and yield will be greatly reduced. This time, we used RNA-Seq technology to carefully study the changes in gene expression of rapeseed under drought conditions and found that the situation is much more complicated than expected. Interestingly, different varieties of rapeseed cope with drought in very different ways. Some genes are busy regulating osmotic pressure, while others are particularly active in removing reactive oxygen species (ROS). We also noticed that some genes involved in signal transduction and cell structure maintenance are also critical. These findings may help us breed more drought-tolerant rapeseed varieties, but if they are really applied to breeding, they may have to combine more omics data. When it comes to practical applications, now with these transcriptome data, breeders at least know which direction to work towards. But this alone is not enough. In the future, it may be necessary to combine gene editing technology to precisely regulate key genes. After all, climate change is becoming more and more obvious, and breeding drought-tolerant crops really can't be delayed.

**Keywords** Drought stress; Rapeseed (*Brassica napus*); Transcriptome analysis; Drought tolerance genes; Gene editing technology

## 1 Introduction

Drought has a significant impact on agriculture, causing a significant reduction in crop yields every year (Bano et al., 2022). This is the biggest headache for farmers, after all, it is directly related to the problem of food (Zhang et al., 2021). However, plants are not vegetarians, they have their own set of coping methods. Studies have found that different crops respond to drought in a variety of ways (Zhang et al., 2019). Some are busy adjusting their internal moisture, while others change their growth rhythm. It is important to understand these tricks, after all, the climate is becoming more and more abnormal now (Yi et al., 2022). But to be honest, it is not that simple to completely solve the problem of drought, and it requires approaching from multiple angles.

Anyone who has grown rapeseed knows that this crop is most afraid of drought. A study last year showed that a slight lack of water would cause a sharp drop in yield (Xiong et al., 2022). However, it is not completely hopeless. Breeding experts are now trying to find more drought-resistant varieties (Tan et al., 2020). A closer look will reveal that drought has an all-round impact on rapeseed. Not only will the plants not grow well, but even photosynthesis will be affected (Wang et al., 2019). The most troublesome thing is that the metabolic process is also messed up, and naturally fewer seeds are produced in the end. Therefore, when the dry season comes, farmers are particularly troubled. Seeing that the rapeseed is growing well, a drought may make all their efforts in vain.

When it comes to studying how rapeseed resists drought, transcriptome analysis technology is now of great help (Chai et al., 2023). This technology is quite powerful and can help us find genes and long non-coding RNAs that are particularly active during drought (Raza et al., 2021a). However, in actual operations, the results obtained by different laboratories sometimes differ. The recent study by Yang et al. (2023) is quite interesting. They found that the gene trehalose-6-phosphate synthase (TPS) is particularly important in the process of drought resistance. But to be honest, this gene alone may not be enough, after all, drought resistance is a complex system engineering. The problem now is that although we have found some key genes and transcription factors, in order to truly apply them to breeding, we still have to clarify the relationship between these regulatory networks.

This study introduces the physiological and molecular effects of drought stress on rapeseed, the identification of key genes and regulatory networks involved in drought resistance, and the potential application of these findings in breeding drought-resistant rapeseed varieties. It emphasizes the progress that has been made and identifies future directions for improving rapeseed drought resistance. It aims to provide a comprehensive overview of the current status of rapeseed drought-responsive genes through transcriptome analysis.

## 2 Mechanisms of Drought Tolerance in Rapeseed

### 2.1 Physiological and biochemical responses

When faced with drought, rapeseed has a variety of ways to cope. Studies have found that varieties with strong drought resistance have a characteristic that they can better lock in water, and at the same time, indicators of cell damage, such as electrolyte leakage and malondialdehyde levels, are relatively low (Waititu et al., 2021). However, not all varieties are like this, and some performance is unsatisfactory. A recent study is quite interesting and found that trehalose-6-phosphate (T6P) is particularly critical in the process of drought resistance (Yang et al., 2023). It can help regulate carbon allocation and help increase yields. In addition, rapeseed with strong drought resistance has another ability, which is its strong ability to remove reactive oxygen (Schiessl et al., 2020), which can reduce oxidative damage. But how these mechanisms work together may require further study.

### 2.2 Molecular mechanisms and regulatory pathways

There are many ways to make rapeseed drought resistant at the genetic level. Recent studies have found that different varieties have obvious differences in gene expression when responding to drought (Liu et al., 2019). In particular, some genes in drought-resistant varieties are particularly active, mainly responsible for removing reactive oxygen and regulating osmotic pressure (Tan et al., 2020). When it comes to specific genes, several members of the trehalose-6-phosphate synthase family, such as *BnTPS6* and *BnTPS8*, are particularly active when encountering drought. But what's interesting is that the expression levels of these genes are different at different growth stages. What's more complicated is that long non-coding RNAs are also involved, and they are mixed with mRNA and transcription factors to form a very complex regulatory network (Tan et al., 2019). So if you really want to understand how rapeseed resists drought, you may have to sort out all these relationships.

### 2.3 Role of epigenetic modifications in drought response

When it comes to how rapeseed copes with drought, epigenetics is quite interesting. Wang et al. (2021) found that changes in DNA methylation and histone modification can adjust gene expression without changing the DNA sequence. It's like installing a fast adjustment switch on the gene, which can respond immediately when encountering drought. However, the performance of different genes is also different. For example, genes encoding heat shock proteins and β-2 tubulin are particularly closely related to histone modifications (Boldura et al., 2015). Another interesting discovery is that long non-coding RNAs often appear together with genes related to plant hormone signals, indicating that epigenetic regulation is indeed critical in the process of drought resistance. But to say how it works specifically, we may have to continue our research.

## 3 Transcriptome Profiling Techniques for Identifying Drought-Responsive Genes

### 3.1 High-throughput sequencing approaches

Nowadays, the means of studying gene expression are becoming more and more advanced. RNA sequencing technology (RNA-seq) is a good example, which can detect the transcription of the entire genome at one time (Li, 2024). This technology is particularly useful in studying plant drought resistance, for example, it can find out which genes become particularly active or silent during drought (Shah et al., 2018). Yang et al. (2023) used this method to study rapeseed last year and found that drought can cause changes in the expression of thousands of genes. Interestingly, not only protein-coding genes have changes, but also long non-coding RNAs (lncRNAs) that do not encode proteins are also very active (Tan et al., 2020). But then again, although a lot of data has been measured, more experiments may be needed to truly understand how these genes specifically affect drought resistance.

### 3.2 Data analysis and bioinformatics tools

The processing of high-throughput sequencing data now mainly relies on various bioinformatics tools. Raza et al. (2021b) mentioned a common process, first using HISAT2 for sequence alignment, then using StringTie to assemble transcripts, and finally using DESeq2 to analyze differential expression. However, in actual operation, each step may encounter some minor problems. After analyzing the differentially expressed genes, you still have to figure out what these genes do. The GO and KEGG pathway analysis used by Li et al. (2021) is good and can help us understand the biological functions of these genes. Interestingly, through co-expression network analysis, we found that the interaction between lncRNAs and mRNAs is quite complex, which is very helpful for understanding drought resistance mechanisms. But to be honest, although these analysis tools are powerful, sometimes the results are still a bit difficult to interpret.

### 3.3 Challenges in transcriptome profiling for drought stress studies

Although technology has advanced a lot in the study of drought-responsive genes, there are still many headaches. Liu et al. (2022) found that different rapeseed varieties and different growth stages responded to drought very differently. Just doing a time series experiment requires an awful lot of data, which makes analysis very difficult. What's more complicated is that transcriptome data alone may not be enough. Boldura et al. (2015) pointed out earlier that metabolome data should be combined to get a more comprehensive view. But the problem is that after finding the key genes, functional verification must be done, which is a time-consuming and expensive step. And to be honest, some genes do not perform exactly the same under different experimental conditions, which is even more troublesome.

## 4 Identification of Drought-Responsive Genes in Rapeseed

### 4.1 Key drought-responsive genes and their functional roles

In the study of drought resistance mechanisms in rapeseed, several key genes have been identified. The BnaC08g41070 gene, located near an important association site, showed correlation with drought response (Tan et al., 2017). Notably, members of the trehalose-6-phosphate synthase gene family (*BnTPS6*, *BnTPS8*, *BnTPS9*, and *BnTPS11*) were significantly upregulated under drought stress, suggesting their potential role in carbon allocation and drought resistance (Figure 1) (Yang et al., 2023). In addition, *BnNRT2.1a* and *BnNRT2.5* in the NRT2 gene family were found to be associated with nitrate metabolism under drought conditions, but their specific regulatory mechanisms still need to be further elucidated. These findings provide important clues for understanding the molecular mechanisms of rapeseed drought resistance, although the synergistic network between genes remains to be resolved.

### 4.2 Transcriptomic signatures of drought stress in rapeseed

When rapeseed encounters drought, the changes in gene expression are quite amazing. Research by Tan et al. (2019; 2020) showed that the drought-tolerant variety Q2 and the sensitive variety Qinyou8 behaved very differently under drought conditions. In Q2, 5 546 genes were downregulated and 6 997 were upregulated, while the changes in Qinyou8 were more dramatic-7 824 were downregulated and 10 251 were upregulated. Behind these numbers, there is a complex regulatory network. Transcription factors and lncRNAs seem to play an important role in this. However, it is interesting that the difference between the two varieties is so large, indicating that drought resistance may involve multiple levels of gene regulation. Which specific pathways are the most critical may require more in-depth analysis.

### 4.3 functional categories of drought-responsive genes

Different genes perform different functions when rapeseed responds to drought. Xue et al. (2022) divided these genes into several categories according to their functions. For example, some genes are specifically responsible for transmitting signals, such as those near BnaC07g44670D, which are mainly responsible for plant hormone signal transduction. Interestingly, genes that produce proline and ubiquitin ligase E3 are particularly active in drought resistance. Tong et al. (2020) found that the NRT2 gene family is also very important and is specifically responsible for the transport of nutrients. As for the TPS genes, the trehalose they produce can not only regulate carbon distribution, but also directly improve drought resistance. However, how these genes work together may require more research.

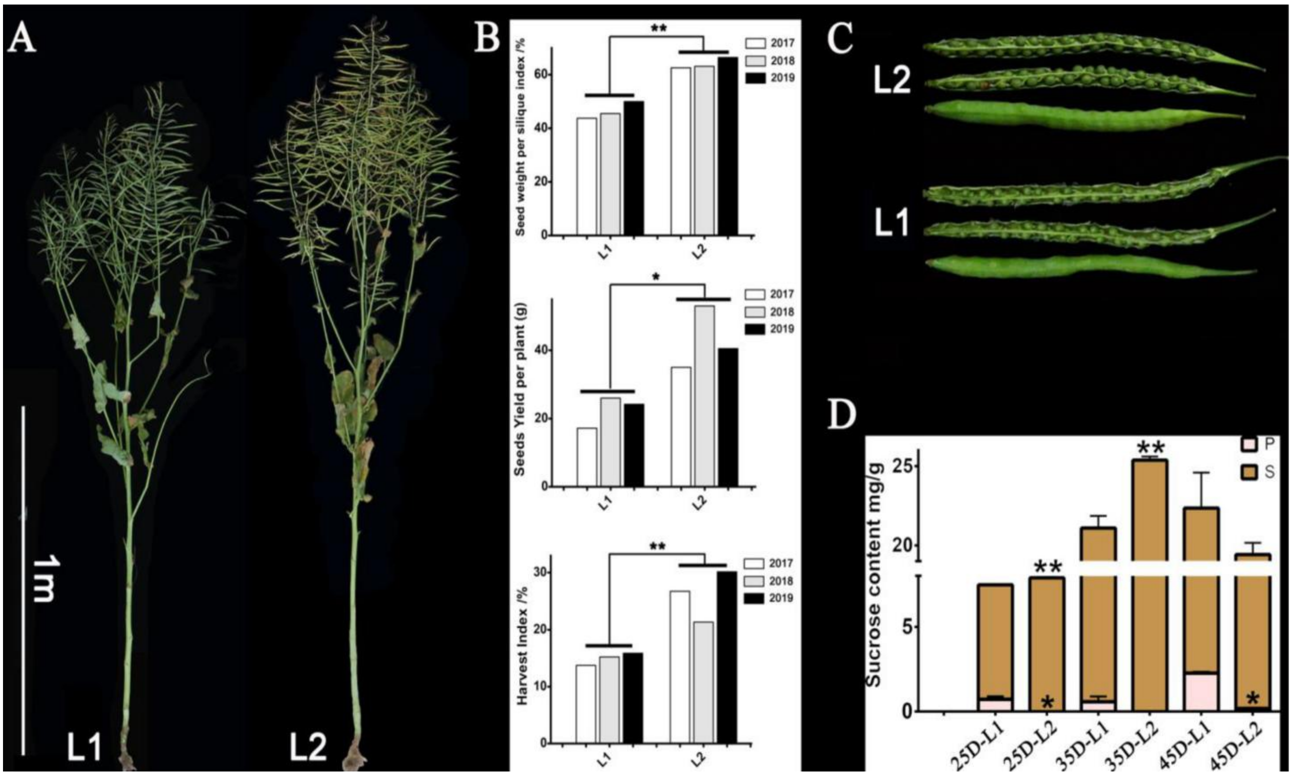

Figure 1 The phenotype of the plant materials associated with source-/sink-related yield traits and drought response. (A) The plant phenotype of materials with extremely high (L2) and low (L1) yield traits. (B) The statistical analysis of source-/sink-related yield traits between materials of L1 and L2. (C) The silique phenotype of materials with extremely high (L2) and low (L1) yield traits. (D) Dynamic content of sucrose in source-/sink-tissues of extreme materials during different developmental stages. L1: Low yield-related material; L2: High yield-related material; The number of 15, 25, 35, and 45 mean corresponding days after flowering; S: seeds; P: pericarps; **: significant difference at $p < 0.01$; *: significant difference at $p < 0.05$ (Adopted from Yang et al., 2023)

## 5 Case Study

### 5.1 Background of the case study

Speaking of rapeseed, this thing is really a treasure. You may not know that many of the vegetable oils we usually eat, feed for livestock, and even biodiesel used in cars rely on it (Zhou et al., 2022). However, everyone who has farmed knows that this crop has a natural enemy-drought. Of course, it is not to say that other disasters are not important, but drought is indeed the most troublesome. In the past, people always thought that drought-resistant breeding mainly relied on experience, but now it is different. By analyzing those genes that are "active" in drought, we gradually figured out how rapeseed copes with water shortages. Although the specific mechanism has yet to be studied, these findings have pointed out a clear way for breeding work. In the final analysis, if you want to stabilize the yield of rapeseed, you can't just rely on the old method. You have to understand from the root how it "fights wits and courage" with drought.

### 5.2 Transcriptome profiling under drought conditions

To understand how plants cope with drought, it is not enough to just look at the appearance, you have to see what their genes are doing-to put it bluntly, it is to study which RNAs are activated or silenced during drought (Tan et al., 2020). This experiment used two types of rapeseed: drought-tolerant Q2 and drought-sensitive Qinyou8. Not only did they measure the response during drought, but they also looked at the changes after watering was restored. The results are quite interesting. In Q2, about 5 500 genes were downregulated and 7 000 were upregulated; and Qinyou8 was even more exaggerated, with more than 7,800 downregulated and more than 10,000 upregulated (Figure 2). However, the numbers are just appearances. What is more important is the discovery of those inconspicuous long-chain non-coding RNAs-although they are not directly involved in encoding proteins, they play an important role in drought response and even form a complex regulatory network. This may explain why the drought resistance of the two rapeseeds is so different.

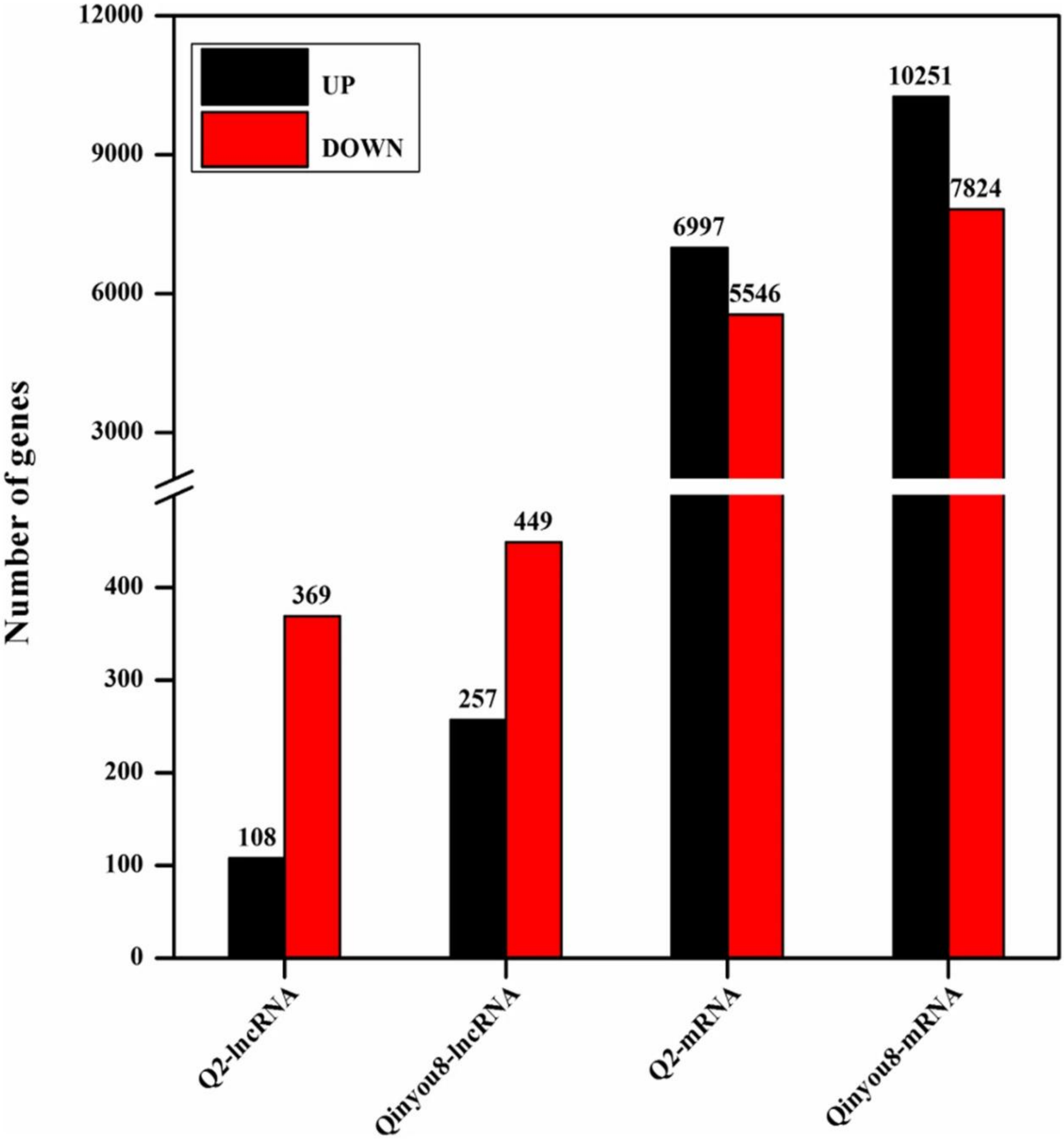

Figure 2 The numbers of differentially expressed lncRNAs and mRNAs in two genotypes (Q2 and Qinyou 8) in response to drought stress and re-watering treatments (Adopted from Tan et al., 2020)

### 5.3 Key findings and implications for breeding

When it comes to rapeseed drought resistance, recent studies have found some interesting things. Take genes such as *LEA3* and *VOC*, for example. They are particularly active during droughts-this is no small matter. Experiments have shown that overexpressing these genes not only improves drought resistance, but also unexpectedly improves seed size and oil content (Liang et al., 2019). On the other hand, if the expression of these genes decreases, both oil content and drought resistance will suffer (Figure 3). Interestingly, those inconspicuous lncRNAs are also working secretly. They work in partnership with some key genes, especially those related to plant hormone signals and stress resistance. Although the specific operation remains to be studied, these findings do remind breeders: if you want to cultivate rapeseed varieties that are both drought-resistant and high-yielding, it is not enough to just focus on conventional genes, but these regulatory factors must also be taken into account.

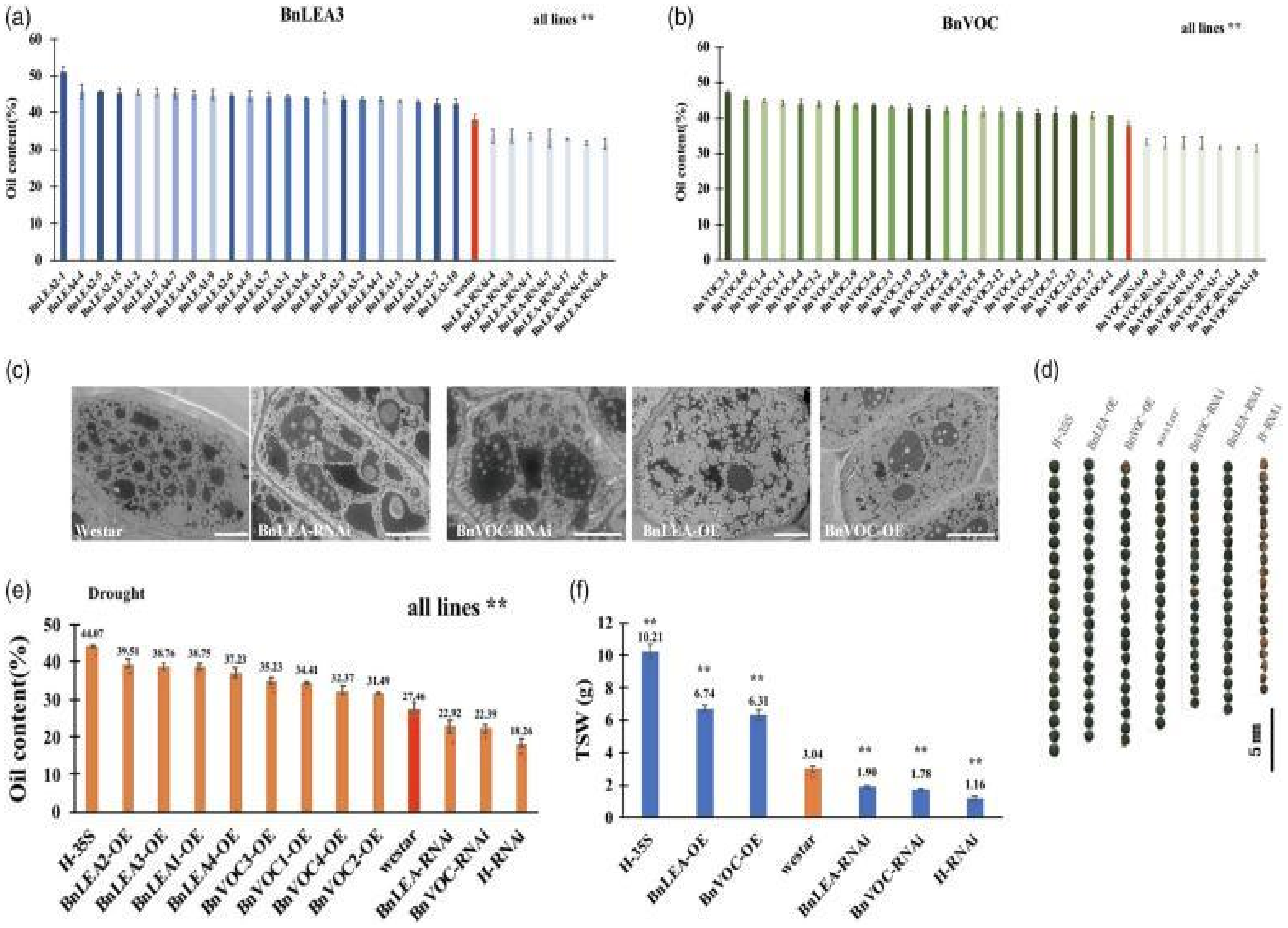

Figure 3 Transgenic *B. napus* showed changes in oil content and seed size. (a and b): Oil contents of transgenic *B. napus* lines. (c): TEM observation of transgenic and WT seeds. Bar=10 μm. (d): Seed sizes of transgenic plants, hybrids (H-35S: OE hybrids; H-RNAi: RNAi hybrids) and WT. (e): Average oil contents of transgenic and hybrid plants under drought conditions. (f): TSWs of transgenic and hybrid plants. All the results are represented as the mean ± standard deviation (STD; n=3). Statistically significant differences were determined using a two-tailed paired Student's t-test compared with WT plants under similar conditions, and the results are indicated by $^{**}P<0.01$ (Adopted from Liang et al., 2019)

## 6 Challenges in Identifying Drought-Responsive Genes

### 6.1 Complexity of drought stress response in rapeseed

How rapeseed copes with drought is not a simple matter. Different rapeseed varieties can behave very differently when faced with water shortage (Tan et al., 2019). For example, some genotypes will activate a large number of mRNAs and lncRNAs, while others may not react as strongly. Of course, this is just the tip of the iceberg. In fact, from gene expression to protein activity to various metabolites, the entire plant is busy adjusting its state. What's more complicated is that various transcription factors and signaling pathways are involved, especially those related to plant hormones (Tan et al., 2020). So don't underestimate it just because it's a rapeseed plant. Its system for coping with drought may be more sophisticated than we can imagine.

### 6.2 Limitations of current transcriptome profiling approaches

The transcriptome analysis technology currently used is indeed very powerful, but it is still a little short of fully understanding the drought resistance genes of rapeseed (Shamloo-Dashtpagerdi et al., 2015). For example, microRNAs and protein kinases are obviously very important in the process of drought resistance, but conventional detection methods often miss them. There is also a headache-different varieties of rapeseed, or even the same variety planted in different places, can have very different gene expressions (Zhang et al., 2019). What's more troublesome is that the rapeseed genome itself is very complex. Although those homologous genes look similar, their expression and regulatory mechanisms may be completely different (Moebes et al., 2022). Therefore, it is not realistic to rely on existing technology to catch all drought resistance genes.

### 6.3 Strategies to overcome challenges in data analysis

To solve these problems, we can try a multi-pronged approach. For example, if we analyze the data of transcriptome, proteome and metabolome together, we can see a more comprehensive drought resistance mechanism (Boldura et al., 2015). In particular, proteome data can help us find those key regulatory proteins that have been modified, and this information cannot be obtained by transcriptome alone. Now that computer technology is so advanced, using machine learning to analyze massive data is also a good way (Tan et al., 2017). Although algorithms are sometimes confusing, they can indeed dig out some regulatory networks that are easily missed by manual analysis. By the way, experimental methods must also keep up. Sometimes changing the RNA extraction method or improving the cDNA synthesis step may result in very different results. These details may seem insignificant, but they are particularly important for improving detection sensitivity.

## 7 Future Directions in Drought Stress Research

### 7.1 Integration of multi-omics approaches

To explain how rapeseed responds to drought, it is not enough to look at just one level. Now researchers are accustomed to looking at the data of genome, transcriptome, proteome and metabolome together-this method really works (Shamloo-Dashtpagerdi et al., 2015). For example, just looking at the transcriptome, we can find which genes are particularly active during drought and which are wilted (Tan et al., 2020). But if we combine the proteome and metabolome data, the whole picture will be much more complete. Interestingly, this method also finds some "black hands behind the scenes", such as long non-coding RNA (Tan et al., 2019). Although they do not directly encode proteins, they can work hand in hand with mRNA and play a role in the drought resistance process. If we clarify these relationships, we may find new breakthroughs in improving drought resistance.

### 7.2 Application of CRISPR and gene editing technologies

Now, people who are doing research on rapeseed drought resistance are talking about gene editing technologies such as CRISPR, which is indeed quite promising. For example, genes such as *ERD15* and *RAB18* (Zhang et al., 2019) are usually inconspicuous, but they are particularly active when encountering drought. If you use CRISPR to adjust them, drought resistance may be improved. However, it is not enough to just focus on these star genes. Recently, some people have found that if the genes related to trehalose-6-phosphate synthesis are also adjusted, the drought resistance effect may be better (Yang et al., 2023). In fact, regulatory proteins such as transcription factors and protein kinases (Kamali and Singh, 2023; Han, 2024) are all good editing targets. Although it is still in the exploratory stage, this path does bring new hope to drought-resistant breeding.

### 7.3 Leveraging big data and artificial intelligence

In recent years, big data and AI technology have indeed brought many new ideas to the study of rapeseed drought resistance. Look at those high-throughput sequencing data, which are often massive amounts of information, and manual analysis is simply too much to handle (Yan et al., 2021). This is when machine learning comes in handy, and it can find patterns that we may have overlooked from these data. Speaking of GWAS research, although many SNP sites related to drought resistance have been found (Tan et al., 2017; Shahzad et al., 2021), to string together these scattered information, AI still has to help analyze. More practically, some AI models can now predict the drought resistance of new varieties (Boldura et al., 2015). Of course, these predictions may not be 100% accurate, but at least they can point the direction for breeding work, saving too many detours.

## 8 Conclusion

There have been some new discoveries in the study of rapeseed drought resistance genes. Take *trehalose-6-phosphate synthase* (*TPS*) for example. Genes such as *BnTPS6* and *BnTPS8* are particularly active in drought, and seem to be closely related to drought resistance. But what's interesting is that different varieties of rapeseed behave differently-the long non-coding RNAs (lncRNAs) in drought-resistant varieties are obviously more active. In fact, the most surprising thing is that genes like ERD15 and RAB18 not only work in drought resistance, but also respond to other environmental stresses. This shows that the mechanism by which plants cope with drought may be much more complicated than we thought. Although further research is needed to understand how it works, these findings at least give us a clearer understanding of rapeseed drought resistance.

This study has indeed opened up some new ideas for rapeseed breeding. Think about it, those TPS genes and lncRNAs (long non-coding RNAs) that are particularly active in drought are simply ready-made molecular markers. Breeding experts can now use them directly to screen varieties with strong drought resistance, without having to rely on luck as before. Interestingly, genes like *ERD15* are not only drought-resistant, but can also cope with other environmental stresses. This means that it may be possible to cultivate "all-round" rapeseed varieties-not afraid of drought, but also able to resist other adverse environments. Although it will take time to achieve this goal, at least there is a clear direction now. Applying these findings to actual breeding should greatly accelerate the selection and breeding process of high-quality rapeseed varieties.

Where should we go next? I think we can start from the following aspects. First, we need to verify the candidate genes for drought resistance one by one. CRISPR gene editing technology is so mature now. It should be useful to knock out a few genes or overexpress them to see how drought resistance changes. Interestingly, these genes may not work alone. They may have some "secret operations" with other stress response pathways, especially those genes that can cope with multiple stresses. It may be more valuable to sort out these relationship networks than to study a single gene alone. There is also a practical problem: Are the current research samples too single? If we can collect more different varieties of rapeseed and test them under various environmental conditions, we may be able to find more abundant drought resistance gene resources. After all, nature is the most powerful breeding expert.

**Acknowledgments**
The authors thank all members of this study for their valuable suggestions, support, and encouragement.

**Conflict of Interest Disclosure**

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

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