

# The Transcriptomics of Sesame

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Transcriptome is an inevitable link between genomic genetic information and biological function, and is one of the most active disciplines in the post genomic era. The transcriptome sequencing technology has been widely utilized in basic research fields, such as medicine, drug development and agricultural science. Researchers in plant science have been focusing on the application of RNA sequencing technology to study gene expression patterns under different environmental conditions or different growth and development stages, in order to understand the regulatory mechanism of gene expression and explore candidate genes related to specific traits. In fact, sesame is an oil crop with a large planting area in China. As an important food and medicine, it plays a vital role in human life. Therefore, studying the gene expression pattern of sesame under specific conditions is very important for the development and utilization of sesame germplasm resources.

sesame

genomics

transcriptomics

## 1. Application of Transcriptomics in Abiotic Stress

Abiotic stress is a general term for all abiotic conditions that are unfavorable to plant growth, such as salinity, water, extreme temperatures, heavy metals, ultraviolet radiation, etc. [1]. When plants face adverse growth conditions, abiotic stress will hinder their growth and productivity, and plants adapt to an unfavorable living environment by changing their own morphology, physiology and biochemical level. Recently, researchers have mainly focused on the study on the abiotic stress of sesame in salt, water and heat (**Table 1**).

**Table 1.** The summary of omics studies on stress response in sesame.

Stress	Varieties	Tissues	Descriptions	Reference
Salt stress	WZM3063 (ST), ZZM4028 (SS)	shoot of seedling	Transcriptome and metabolome profiles in the seedlings of salt-tolerant and sensitive sesame genotypes were performed in the early phase of salt stress.	[2]
	WZM3063 (ST), ZZM4028 (SS)	shoot of seedling	miRNAs and their targets were identified from two contrasting sesame genotypes by a combined analysis of small RNAs and degradome sequencing.	[3]
Drought stress	ZZM0635 (DT), ZZM4782 (DS)	root	Decipher the response of tolerant and sensitive genotypes to progressive drought and rewatering based on transcriptome.	[4]

Stress	Varieties	Tissues	Descriptions	Reference
	ZZM3330 (DT), ZZM3743(DS)	leaf	Transcriptional and metabolic profiling in two sesame genotypes with contrasting ability to cope with drought stress.	[5]
	TEX-1 (DT), VEN-1 (DS)	root	Transcriptome analysis of two sesame genotypes with contrasting responses under PEG-induced osmotic stress.	[6]
Waterlogging stress	Zhongzhi 13 (WT), ZZM0563 (WS)	root	RNA-seq-based analysis between waterlogging-tolerant and -susceptible genotypes.	[7]
	ZZM2541 (WT), Ezhi3 (WS)	root	High-resolution temporal transcriptome analysis of two contrasting sesame genotypes over a 48 h period for waterlogging and drainage treatments.	[8]
Heat stress	Taizhi3 (HT), SP19 (HS)	leaf	Transcriptome analysis of two sesame cultivars with different heat tolerance.	[9]
Disease stress	Yuzhi 11 (DT), RXBS (DS)	seedlings	Transcriptome profiles of resistant and susceptible sesame germplasm resources inoculated with <i>Fusarium oxysporum</i> f. sp. <i>Sesami</i> .	[10]
	GT-10 (DT), RT-373 (DS)	root	Transcriptome analysis of resistant and susceptible sesame genotypes during <i>Macrophomina phaseolina</i> infection.	[11]

## 1.1. Salt Stress

Salt stress not only affects the external morphology, but also influences the internal physical and chemical properties of plants. It is commonly known that sesame is moderately tolerant to salt stress, and salt-tolerant varieties are urgently needed in the saline areas of the main sesame production countries. Through the comparison of two sesame genotypes, it was found that the germination and survival rates of salt-tolerant sesame were higher than those of salt-sensitive sesame. A total of 1275 and 1946 DEGs were identified in four treatment groups of salt-tolerant and salt-sensitive sesame, respectively. In total, 59 genes were highly up-regulated in salt-tolerant sesame after salt treatment, which were identified as candidate genes for improved salt tolerance in salt-sensitive sesame [2]. Subsequently, 18 small RNA libraries of salt-tolerant and salt-sensitive genotypes under control and salt-stress conditions were constructed, and 442 miRNAs were identified. Among them, 116 miRNAs were involved in the salt-stress response, and they showed different expression levels under salt-stress by analyzing the regulatory network of miRNA-mRNA [3]. These theoretical studies are crucial for cultivating new salt-tolerant sesame varieties and understanding the molecular mechanism of the adaptive response to salt stress.

## 1.2. Water Stress

Water is an indispensable substance in life, and it has the greatest impact on plants. Through the response to drought between two sesame genotypes (tolerant and sensitive), Dossa et al. [4] observed that the tolerant

genotype relied on well-functioning taproots that could provide water to the above ground tissues. In addition, the tolerant genotype strongly activated genes related to antioxidant activity, osmotic protection, and hormone signaling pathways. The candidate genes with a higher tolerance constituted useful resources for improving drought tolerance in sesame. You et al. [5] discovered a core set of drought-responsive genes by analyzing the transcriptome data of leaves from two sesame genotypes (drought-tolerant and drought-sensitive). They included 684 up-regulated and 1346 down-regulated genes, which were expressed differently in these two genotypes. Furthermore, Song et al. [6] performed polyethylene glycol (PEG)-induced osmotic stress to explore the transcriptional changes in the roots of drought-tolerant and drought-sensitive sesame. A total of 1251 and 541 genes were detected differentially expressed in PEG-treated and untreated roots, respectively. During osmotic stress, multiple members of the WRKY, bZIP, MYB and NAC families were also found to be over-expressed in roots of the drought-tolerant genotype.

Like most typical dry-land crops, sesame is highly sensitive to waterlogging stress, and soil waterlogging will lead to hypoxia and high CO<sub>2</sub> in the roots, slow down photosynthesis, and ultimately damage the normal growth and yield of crops [12]. The comparative analysis was utilized to explore the waterlogging stress response in two sesame genotypes, and a total of 19,316 genes were expressed during waterlogging. Among these, 66 genes were found to be potential candidates for improving sesame tolerance to waterlogging [7]. Dossa et al. [13] treated the flowering sesame for 36h with water, and then drained them for 12 h. The samples were collected at 22 time points under the waterlogging/draining treatment and 10 time points under the control condition. Subsequently, 47 core waterlogging-responsive genes were identified through these transcriptome data. Moreover, a temporal transcriptional network model was constructed to predict the putative causal relationships between TFs and downstream waterlogging-responsive genes, and some interactions were verified by yeast one-hybrid assays [8].

Therefore, the research on drought and waterlogging stress is mainly in order to obtain changes in their plant morphology, physiology and biochemistry; this is to find out the mechanism of drought and waterlogging stress, and lay a foundation for subsequent research on sesame genetics and breeding.

### 1.3. Heat Stress

Heat stress causes serious damage to almost all stages of growth in the plant. It not only hinders the growth and development of the plant, but also causes irreversible damage to intracellular homeostasis, and even leads to death [14]. Su et al. [9] identified a total of 6736 DEGs by treating the seedlings of two sesame cultivars (heat-tolerant and heat-sensitive). They found that the heat-tolerant genotype had 5526 DEGs, of which 2878 were up-regulated and 2648 were down-regulated, while the heat-sensitive genotype had 5186 DEGs, of which 2695 were up-regulated and 2491 were down-regulated. These DEGs included heat shock proteins related to stress tolerance, and genes related to carbohydrate and energy metabolism, signal transduction, endoplasmic reticulum protein processing, amino acid metabolism, and secondary metabolism. The high temperature climate of this summer seriously affected the growth of surface vegetation, leading to serious ecological problems in many places. Thus, it is more urgent to study related heat-tolerant genes and transcription factors at the transcriptome level, so

that the sesame could better adapt to a high temperature climate. It provides a theoretical basis for the breeding of temperature-resistant sesame to adapt to the future global warming.

## 2. Application of Transcriptomics in Biotic Stress

Apart from abiotic stress, plant growth and development are also greatly affected by biotic stress. When plants are attacked by bacteria, animals and other stresses, they will change the expression of genes and enzyme activities in the body to complete the induction and transmission of these signals, and the realization of biological effects. Previous studies have been reported that there are more than 170 pathogens causing diseases in sesame, of which the most serious diseases are sesame fusarium wilt and charcoal rot [15]. The following studies are about these two diseases: two sesame varieties, resistant and susceptible genotypes, were infected by *Fusarium oxysporum*; the KEGG analysis indicated that the “phenylpropanoid biosynthesis” pathway may play a more vital role in infected sesame, while the differences in fusarium wilt symptoms between resistant and susceptible genotypes may depend on whether plants can activate this pathway in an efficient manner [10]; by sequencing the transcriptome of two sesame varieties with different incidence rates 72 h after infection with *Macrophomina phaseolina*, 1153 and 1226 DEGs were identified in the resistant and susceptible genotypes, respectively. The resistant genotype showed the highest expression of genes at 24 h post-inoculation (hpi), while the susceptible genotype illustrated those at 48 hpi. It is speculated that the biosynthesis of flavonoids, carotenoids and caffeine via the phenylpropanoid pathway and salicylic acid biosynthesis at 24 hpi may contribute to sesame charcoal rot resistance [11]. These studies on diseases will help us to deeply understand the disease resistance of sesame varieties, and provide a theoretical basis for scientifically preventing and controlling important diseases and ensuring a bumper harvest of sesame.

## 3. Application of Transcriptomics in Organ Development

Gene expression is tissue specific, and the study of gene expression in different tissues and organs at different developmental stages is of great significance for understanding plant development and regulatory mechanisms, and for the better transformation and utilization of plants [16]. Here, the basic information of gene expression in different tissues during the development stage is presented (Table 2). Wang et al. [17] sequenced the seeds and carpels of three high-oil and low-oil sesame cultivars, and found that the number of expressed genes tends to decrease in seeds, but that it fluctuates in the carpels 10 to 30 days post-anthesis (DPA). The enrichment of genes involved in lipid biosynthesis can distinguish between high-oil and low-oil genotypes (30 DPA), suggesting that oil biosynthesis in seeds plays a key role at later stages. Furthermore, Wang et al. [18] detected two sesame cultivars with different seed coat colors (Zhongzhifeng 1, white seeds; Zhongzhi 33, black seeds) at the developmental stages (5, 8, 11, 14, 17, 20, 23, 26 and 30 DPA). Using 5 DPA as the control, 11 to 20 DPA groups were used to identify candidate genes related to melanin biosynthesis in sesame. In total, 1572 up- and down-regulated DEGs were identified. In addition, Li et al. [19] constructed a QTL mapping of seed coat color in sesame, and 17 QTLs were detected on four linkage groups. In the meantime, the DEGs between a white- and a black-seeded variety were enriched significantly in 37 pathways. Zhou et al. [20] compared the oil content and fatty acid compositions

between Zhongzhi 16 and Mishuozhima, and identified a total of 8404 DEGs in the seeds. Combined with WGAS, 20 candidate genes were identified and SiTSP1 was found as a key regulatory gene of fatty acids and triacylglycerol metabolism in sesame.

**Table 2.** Summary of transcriptome-based organ development studies in sesame.

Traits	Varieties	Tissues	Number of DEGs	Number of Candidate Genes	Reference
Oil content	ZZM4728, ZZM3495, ZZM2161	seeds, carpels	794, 1807, 528 and 1667 of DEGs at 10, 20, 25,30 DPA	23 sesame homologous lipid genes	[17]
Seed coat colors	Zhongfengzhi 1, Zhongzhi 33	seed	the maximum DEGs at 11 DPA (20,253)	20 genes	[18]
Seed coat colors	Yuzhi DS899, JS012	seed	2148, 5176, 3725, 2984 and 5115 of DEGs at 5, 10, 15, 20,25 DAF	28 genes	[19]
Oil content and fatty acid composition	Zhongzhi 16, Mishuozhima	seed	8404 DEGs	20 genes	[20]
Leaf size	Zhongzhi 13, ZZM2289	leaf	-	26 genes	[21]
Root size	Baizhima, 697	root	1831 and 1066 up and down regulated genes	10 genes	[22]
Male sterility	W1098A, W1098B	flower buds	1502 DEGs	49 homologous genes	[23]

Except for the most important seeds, other tissues have also been studied. Sheng et al. [21] combined QTL-seq and SSR marker mapping methods to identify 56 candidate genomic regions controlling leaf size in RIL populations, crossed between large-leaf and small-leaf sesame varieties. In total, 12 were identified as expressing lower and 14 as expressing higher in the large leaf parent at both the 8th and 20th leaf stages, respectively, and three candidate genes (SIN\_1004875, SIN\_1004882 and SIN\_1004883) that are associated with leaf growth and development were revealed. Su et al. [22] studied the root of 40 different sesame varieties grown in soil and hydroponic systems, and found that similar genotypes usually clustered in small or large root groups. A total of 2897 DEGs were identified, and these genes were mostly enriched in flavonoid, phenylpropanoid and gingerol biosynthesis, and starch and sucrose metabolism, etc., demonstrating that these pathways play vital roles in the growth and development of sesame roots. Liu et al. [23] analyzed the sterile flower buds of two near-isogenic DGMS lines, and identified 1502 significant DEGs, of which 751 were up-regulated genes. Many DEGs were also found to be involved in ethylene, and jasmonic acid synthesis and signaling pathways; their expression was up-regulated or down-regulated in sterile shoots, respectively. However, most NAC and WRKY transcription factors

related to DEGs were up-regulated in sterile shoots. These studies have laid a foundation for an in-depth understanding of genetic characteristics and the variability of different tissues in sesame, and will be utilized as genetic resources for the structural improvement of plants.

## 4. Research on Non-Coding RNAs

The applications of transcription illustrated above were mainly related to coding proteins, and the following was the introduction of non-coding regions. Noncoding RNAs (ncRNAs) are RNAs that cannot be translated into proteins but have catalytic activity, such as tRNAs, rRNAs, snRNAs, miRNAs and lncRNAs [24]; ncRNAs have important biological functions, ranging from regulating gene expression and principal cellular functions, to affecting genome structure. When the sesame genome was completely assembled, a total of 207 miRNAs, 870 tRNAs, 268 snRNAs, and 386 rRNA fragments were identified at the same time [25]. miRNA plays a vital role in the response to abiotic stress by the post-transcriptional regulation of target gene expression in plants. Zhang et al. [3] identified 351 known miRNAs and 91 novel miRNAs from 18 sesame libraries, and 116 miRNAs were found to be involved in the salt-stress response through the comparison between the salt-treated group and the control group. Subsequently, Zhang et al. [26] sequenced a total of 220 miRNAs in seed development and constructed a regulatory co-expression network through transcriptomics, small RNAs and degradome. The FAD2, LOC10515945, LOC105161564, and LOC105162196 genes were observed for regulating the accumulation of unsaturated fatty acid biosynthesis. lncRNA plays a major role in various biological regulation processes involving complex mechanisms, and in the regulation of the stress response. Gong et al. [27] identified a total of 2482 lncRNAs from different sesame genotypes under salt stress by high-throughput RNA sequencing, of which 599 were intergenic lncRNAs, 293 were antisense lncRNAs, and 786 lncRNAs had the potential to encode proteins. Most lncRNAs were expressed at low levels, and about 700 differentially expressed lncRNAs were characterized as salt responsive. Functional annotation showed that differentially expressed lncRNAs under salt stress may regulate protein coding genes involved in multiple important pathways, such as glycolysis/gluconeogenesis, flavonoid biosynthesis, biotin metabolism, and monoterpenoid biosynthesis. At present, the study of biological functions and the mechanisms of ncRNAs in plants is mainly focused on model plants, such as *Arabidopsis* [28][29]. The research on miRNAs and lncRNAs in sesame is still at the initial stage. It is expected that more new ncRNAs, mature technologies and the use of the mechanism of ncRNAs to promote molecular breeding will be found in the near future.

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