Review

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Review

Research Progress on Multi-Omics of Plant Response to Abiotic Stress

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Abstract

Multi-omics research, a powerful approach for studying biological systems, encompasses genomics, transcriptomics, proteomics, metabolomics, and other omics technologies. It reduces the limitations and biases associated with single-omics approaches by enabling cross-validation and integration of multiple data types, thereby providing a more comprehensive understanding of the physiological and biochemical processes in organisms. This research approach has been widely adopted in the study of plant responses to abiotic stress. During plant growth, diverse abiotic stressors such as drought, salinity, and extreme temperatures can adversely affect physiological and metabolic processes. Under such adverse conditions, the molecular components within plant undergo complex and dynamic changes. Therefore, the responses to abiotic stress have become a central focus in plant science research. Clarifying the molecular pathways at the levels of gene expression, proteins, and metabolites is of great significance for breeding, cultivation, and enhancing plant adaptability to environmental challenges. This knowledge can significantly improve plant resilience and survival, ultimately enhancing their agronomic performance and economic value. This review summarizes recent advances in the application of integrative multi-omics approaches to plant abiotic stress research, aiming to provide a valuable reference for future studies in this field.

Keywords: multi-omics; abiotic stress; botany; genome; transcriptome; proteome; metabolome

1. Introduction

Adversity refers to a range of environmental factors that negatively affect plant growth and survival, commonly referred to as stress. The physiological processes that enable plants to cope with such stress are known as stress physiology. In natural environments, plants are frequently exposed to suboptimal conditions. Under both biotic and abiotic stress, key plant growth factors become imbalanced, deviating from the optimal range required for normal development. In severe cases, it can cause severe physiological damage to the physiological state of plants, and even result in plant death [1].

Plants have an instinctive response to stress. For example, plant leaves may curl under drought stress, and if the damage is severe, physiological functions may be irreversibly impaired. By analyzing environmental stress, researchers can reveal the physiological and biochemical changes of plants under harsh environmental conditions, improve their ability to resist environmental stress, and thus achieve higher yield and quality [2–4].Intrinsic mechanisms allow plants to perceive stress signals and initiate signal transduction cascades that regulate gene expression, ultimately translating related proteins to cope with stress conditions [5]. To adapt to adverse environments, plants undergo physiological and biochemical adjustments, eventually manifesting their responses through changes in metabolite profiles[4,6].

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Given the complexity of plant metabolism and regulatory networks, research limited to a single omics layer is insufficient to fully elucidate stress response mechanisms. Comprehensive analysis of gene transcription, protein translation, post-translational modification, and metabolism has become a major focus in current plant stress research. Advances in sequencing technologies and bioinformatics have enabled the high-throughput and sensitive analysis of plant stress responses at multiple biological levels [7].

Omics research represents a core approach in functional genomics and systems biology, employing high-throughput and large-scale analytical technologies to dissect biological complexity at multiple molecular levels. It is conventionally divided into transcriptomics, proteomics, and metabolomics, which focus on profiling RNA transcripts, proteins, and small-molecule metabolites, respectively. In the context of plant responses to abiotic stress, multi-omics association analysis enables the precise identification of stress-responsive genes and regulatory elements, and facilitates the elucidation of underlying molecular pathways involved in stress perception, signal transduction, and adaptive responses.

Beyond classical omics types, recent advances have led to the emergence of specialized fields such as miRNAomics, epigenomics, and interactomics, which further refine our understanding by capturing post-transcriptional regulation, epigenetic modifications (e.g., DNA methylation, histone modifications), and dynamic biomolecular interactions. The integrative application of these omics approaches provides a comprehensive framework for decoding the complex regulatory networks that govern plant stress tolerance. Insights from these analyses provide valuable guidance for improving stress resilience in crops through molecular breeding, genetic engineering, and the development of climate-resilient cultivation strategies, thereby contributing to agricultural sustainability and ecological conservation.

2. Integrated Overview of Multi-Omics Approaches

2.1. Genomics

Genomics is an interdisciplinary field of biology that focuses on the comprehensive study of the genome—the complete set of DNA, including all of an organism's genes. It primarily investigates genome structure, function, and evolution, and enables the precise mapping and characterization of genes within the genome [8].

Genomics provides a global and quantitative perspective on gene composition, organization, and regulation, as well as the interactions among genes and their collective influence on phenotypes [9]. It also facilitates comparative genomic analyses across species or cultivars, which are instrumental in uncovering evolutionary relationships and functional conservation [10].

A major component of genomics involves whole-genome sequencing and assembly, which relies on high-throughput DNA sequencing technologies and advanced bioinformatics pipelines to generate complete, annotated genomic datasets[11]. These efforts have significantly advanced our understanding of genome-wide regulatory networks, and laid the foundation for functional genomics, genome-wide association studies (GWAS), and molecular breeding strategies[12].

For example, the sequencing and analysis of the rice (*Oryza sativa*) genome have revealed numerous genes related to drought and salt tolerance, such as DREB and NHX gene families, which play critical roles in abiotic stress responses [13]. Similarly, the recent completion of the wheat (*Triticum aestivum*) genome provided insights into gene families involved in heat tolerance and grain quality[14]. These genomics-driven discoveries exemplify how comprehensive genome analysis can accelerate our understanding of plant adaptation to harsh environments and guide the development of stress-resistant cultivars.

2.2. Transcriptomics

Transcriptomics refers to the comprehensive study of gene expression profiles within cells at various developmental stages or under different environmental conditions, such as plants exposed

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to heat or drought stress [15]. This field encompasses both coding and non-coding RNA molecules and involves sequencing the complete set of RNA transcripts (the transcriptome) present in a biological sample [16,17].

Transcriptomics serves as a crucial tool for elucidating cellular phenotypes, regulating transcriptional activity, identifying key functional genes, and predicting the roles of previously uncharacterized genes. Common analytical methods include marker-based high-throughput techniques such as Serial Analysis of Gene Expression (SAGE) and Massively Parallel Signature Sequencing (MPSS) [18]. Additionally, hybridization-based technologies like DNA microarrays enable the direct detection of gene expression and single nucleotide polymorphisms (SNPs) at high resolution [19].

More recently, RNA sequencing (RNA-seq) has emerged as a powerful approach for transcriptome profiling, allowing accurate quantification of gene expression and identification of SNPs. RNA-seq is widely applied in basic plant research, clinical diagnostics, and drug discovery [20].

2.3. Proteomics

The proteome encompasses all proteins expressed by the genome of a cell, tissue, or organism, and the term was first proposed by Marc Wilkins [21]. Proteomics is the systematic study of these proteins, aiming to elucidate their composition, abundance, modifications, structures, interactions, and dynamics within the organism. This field is typically divided into several branches, including expression proteomics, structural proteomics, subcellular proteomics, and quantitative proteomics [22].

Key proteomic technologies include two-dimensional gel electrophoresis (2-DE), isotope labeling methods such as isobaric tags for relative and absolute quantitation (iTRAQ) [23,24], and protein microarrays[25]. The foundational techniques of 2-DE were developed by O'Farrell, Klose, and Scheele in 1975. Through these advanced methods, proteomics enables in-depth analysis of protein expression patterns, protein-protein interactions, and post-translational modifications, thereby revealing fundamental biological processes and mechanisms of life.

When integrated with genomics, proteomics provides crucial validation of gene expression and functional annotation, helping to confirm the roles of genes in various biological contexts [24,26].

2.4. Metabolomics

Metabolites, as the end products of gene transcription and protein activity, play crucial regulatory roles in cellular signaling, energy transfer, and intercellular communication [27]. The metabolome refers to the complete set of low molecular weight metabolites present in an organism or cell at a given time. Key analytical techniques used for metabolite separation and identification include gas chromatography (GC), liquid chromatography (LC), capillary electrophoresis (CE), mass spectrometry (MS), and nuclear magnetic resonance (NMR) spectroscopy.

As downstream products of genomic and proteomic processes, metabolites provide a more direct and accurate reflection of the physiological and pathological status of organisms than genomics or proteomics alone. Changes in metabolite profiles under specific environmental or stress conditions can effectively characterize the biochemical and physiological state of organisms, thereby providing precise phenotypic information [28]. Metabolomics research thus reveals dynamic changes in biological systems influenced by environmental factors and closely correlates with observable phenotypes [29].

2.5. Epigenomics

The epigenome refers to the complete set of epigenetic modifications across the genome of cells, tissues, or organisms, which regulate gene expression without altering the underlying DNA sequence [30]. Epigenomics is the science that systematically investigates these modifications, including DNA

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methylation, histone modifications, chromatin remodeling, and non-coding RNAs [31]. These mechanisms play crucial roles in gene regulation, development, and environmental responses in plants.

Epigenomic research technologies include bisulfite sequencing for DNA methylation [32], chromatin immunoprecipitation followed by sequencing (ChIP-seq) for histone modifications [33], assay for transposase-accessible chromatin using sequencing (ATAC-seq) to assess chromatin accessibility [34], and RNA-seq for profiling non-coding RNAs [35]. These methods allow high-throughput identification and mapping of epigenetic marks across the genome.

By using epigenomics techniques, we can better understand how plants perceive and respond to abiotic stresses such as drought, salinity, and temperature changes. Epigenetic regulation not only influences gene expression during stress but also contributes to stress memory and potential transgenerational inheritance [36]. Combined with other omics approaches, epigenomics provides critical insights into the complex regulatory networks underlying plant adaptation and resilience.

2.6. Interactomics

The interactome refers to the complete set of molecular interactions within a cell, tissue, or organism, particularly focusing on protein–protein interactions (PPIs), but also encompassing protein–DNA, protein–RNA, and protein–metabolite interactions . Interactomics is the systematic study of these interactions, aiming to elucidate the dynamic networks that underpin cellular functions, signaling pathways, and stress responses.

Interactomics research employs a variety of techniques, including yeast two-hybrid screening [37], co-immunoprecipitation (Co-IP) [38], affinity purification coupled with mass spectrometry (AP-MS) [39], bimolecular fluorescence complementation (BiFC) [40], and proximity labeling methods such as BioID and TurboID [41]. These technologies enable the identification of direct and indirect molecular associations with high specificity and throughput.

By using interactomics approaches, researchers can reconstruct interaction networks that govern plant development, signal transduction, and adaptation to abiotic stress conditions such as drought, salinity, and temperature fluctuations. Interactomics also provides insight into the functions of previously uncharacterized proteins by placing them within known biological pathways. When integrated with transcriptomics, proteomics, and phosphoproteomics, interactomics significantly enhances our understanding of the molecular mechanisms underlying plant stress tolerance.

2.7. miRNAomics

miRNAomics focuses on microRNAs (miRNAs), a class of non-coding small RNAs approximately 21–24 nucleotides in length that primarily regulate gene expression post-transcriptionally. In plants, miRNAs play a crucial role in regulating growth and development, hormone signaling, and responses to environmental stress. Their mechanisms of action typically involve guiding the cleavage of specific mRNAs or inhibiting their translation [42].

With the advancement of high-throughput sequencing technologies and bioinformatics, researchers can now more efficiently identify and analyze both conserved and novel miRNAs under various stress conditions [43]. Studies have shown that miRNA expression undergoes significant changes when plants are exposed to drought, salinity, low temperature, high temperature, and oxidative stress, reflecting how plants adapt to external pressures by adjusting their internal regulatory networks [44].

Integrating miRNAomics with transcriptomics, proteomics, and other multi-omics data facilitates a deeper understanding of how miRNAs collaborate with other molecular layers to regulate gene expression and physiological responses. Ultimately, miRNAomics provides a key target for crop genetic improvement. Through precision breeding and gene editing techniques, crop resilience to climate change and environmental stresses has been improved.

2.8. Relationship Between Omics

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The plant response to abiotic stress involves a highly coordinated network of molecular events, wherein different omics layers-genomics, transcriptomics, proteomics, and metabolomics—operate in an interrelated and hierarchical manner. Genes serve as the blueprint for proteins, which in turn orchestrate cellular metabolism, while metabolites reflect the final physiological outcomes. Exploring the interactions among these layers is crucial for understanding the complexity of stress responses.

Transcriptomic and proteomic integration enables correlation analysis between gene expression and protein abundance, providing insights into transcriptional regulation, post-transcriptional modification, and protein stability. For example, combined transcriptome and proteome analyses in *Arabidopsis thaliana* under drought stress revealed that while many transcripts were differentially expressed, only a subset showed concordant changes at the protein level, indicating significant post-transcriptional regulation [45].

Proteomics and metabolomics represent the functional output of gene expression and are instrumental in identifying stress-responsive proteins and metabolites. Their integration with transcriptomic data allows for more comprehensive functional characterization of stress-related pathways. In rice under salt stress, multi-omics analysis demonstrated that transcriptional upregulation of stress-responsive transcription factors was accompanied by increased accumulation of compatible solutes such as proline and glycine betaine, linking regulatory gene networks with metabolic adjustments [46].

Such integrative multi-omics approaches highlight the importance of examining stress responses not only at the molecular level but also across different time points and developmental stages to fully understand plant adaptation mechanisms. Plants achieve dynamic adaptation and physiological regulation in response to environmental stress by coordinating responses across multiple omics levels—including the transcriptome, metabolome, and proteome—at different temporal scales and developmental stages. For example, Jia et al. found that under progressive drought stress, the transcriptomes and metabolomes of Astragalus membranaceus exhibited significant differences at different developmental stages, indicating stage-specific response mechanisms. Kim et al. reviewed that during leaf senescence, multiple omics levels are coordinately regulated, influencing stress resistance and metabolic activities. Michaletti et al. analyzed the metabolome and proteome of spring wheat leaves to reveal key regulatory pathways under drought stress at different time points. Pan et al. utilized integrated multi-omics data to elucidate the metabolic adaptation strategies of two perennial ryegrass species at different growth stages under drought stress, demonstrating the complex effects of time and developmental stage on stress responses [47–50].

Compared to single-omics approaches, multi-omics integration offers a more holistic perspective, reduces interpretational bias, and bridges the gap between genotype and phenotype. Functional analyses such as differential expression profiling, pathway enrichment, and network reconstruction help delineate the molecular basis of plant stress tolerance. Metabolomics, in particular, plays a pivotal role in connecting upstream molecular events with downstream physiological responses, reinforcing its value as a complement to transcriptomic and proteomic data [51].

3. Joint Study of Omics in Response to Abiotic Stress in Plants

3.1. Plant Response to Salt Stress

While low salt concentrations may enhance seed germination, excessive soil salinity is generally detrimental to plant growth and inhibits germination [52]. Krishnamurthy et al. investigated mangroves and found that their roots are directly exposed to high salinity, showing a unique adaptation to salt stress. Using transcriptomic analysis, 47 key salt-tolerance-related genes were identified as upregulated. Among these, most differentially expressed genes (DEGs) involved in ethylene and auxin signaling pathways were upregulated, while those associated with ABA signaling were downregulated. These findings suggest that ABA-independent signaling pathways also play a significant role in the salt tolerance mechanism of mangroves (Table 1) Based on metabolomic

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analysis, mangroves accumulate high levels of proline, betaine, and soluble sugars to cope with salt-induced osmotic stress [53].

Table 1. Multi-omics analysis of responses of different plants to salt stress.

Stress of adversity	Species	Relevant omics	Key genes, proteins, or metabolites	References
	Oryza sativa L.	Genomics/Transcriptomics	*OsPP2C8* 、 *phosphatase 2C family*、*bZIP*、*bHLH*	[101,104]
Salt stress	*Avicennia officinalis*	Transcriptomics/Metabolomics	*Zinc finger11*、*MYBs*、*BZIPs*、*ARF6*、*proline*、*glycinebetaine*、*polyols*、*sugars*	[53]
	Cicer arietinum L.	Transcriptomics/Metabolomics	*AP2-EREBPs*、*MYBs*、*HBs*、*WEKYs*、*UDP-glucose*、*Fucose*、*citrulline*、*yloglucan*	[59]
	Glycine max (L.) Merr.	Transcriptomics/Proteomics	*GmPAP3*、*GmWRKY*	[62,113]
	Arachis hypogaea L.	Transcriptomics/Metabolomics	*AhHKT1*、*1,5-Anhydroglucitol*、*proline* 、*Lactobionic Acid*	[58]
	Triticum aestivum	Transcriptomics/Metabolomics	*Ta.NCL2*、*Ta.GLR*、*Ta.ABAC15*、*Ta.CIPK31* 、*Ta. SOS1*	[54]
	Helianthus tuberosus L.	Transcriptomics/Proteomics	*peroxidase 5-like*、*alkaline leaf peroxidase*、*Condensin-2 complex subunit D3*、*Dihydroxy-acid dehydratase*	[60]

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	Sesamum indicum L.	Transcriptomics/Metabolomics	*bHLHs*、*bZIPs*、*LEA*、*MYBs*、*NACs*、*maltose*、*raffinose*、*erythritol*	[61]
	Castor Bean	Transcriptomics/Genomics	*RSM1*、*OPS*、*bHLHs*、*ERFs*、*HD-ZIPs*、*NACs*、*WRKYs*、*MYBs*	[64]
	Zeamays. L	Transcriptomics/Proteomics	*ABH1*、*ABI5*、*ZEP*、*Ethylene-responsive transcription factor 2*	[65]
	Ipomoea batatas L.Lam	Transcriptomics/Genomics	*GNAT TFs*、*bZIPs*、*BLH-1*、*Hsp70*、*AhpC/TSA gene family*	[103,114]

However, the patterns of gene expression in response to salt stress vary among plant species, reflecting different molecular mechanisms of adaptation. In wheat, Amirbakhtiar et al. identified 5128 differentially expressed genes (DEGs) under salt stress. To better understand the biological processes involved, KEGG pathway enrichment analysis was performed, revealing that these DEGs were mainly associated with transporters, phenylpropanoid biosynthesis, transcription factors, plant hormone signal transduction, and the MAPK signaling pathway[54].

Further functional annotation using MapMan showed that genes encoding hexokinase, cell wall-modifying enzymes, and sucrose synthase were upregulated in the sucrose metabolism pathway [55]. Salt stress often leads to sugar accumulation, and the increased levels of glucose, sucrose, and fructose under high salinity play important roles in carbon storage, osmotic adjustment, cellular homeostasis, and reactive oxygen species (ROS) scavenging [56]. The osmotic and ionic stress induced by salt in wheat may be sensed by ion channels and Na^+/H^+ antiporters on the membrane, which in turn trigger downstream signaling cascades, as evidenced by the upregulation of genes encoding these membrane-associated proteins [57].

In recent years, advances in multi-omics approaches have significantly deepened our understanding of the mechanisms by which different plant species respond to salt stress. By integrating transcriptomic, proteomic, metabolomic, and epigenomic data, researchers have identified a large number of genes, pathways, and regulatory factors associated with salt tolerance.

In peanuts, a joint analysis of transcriptomics and metabolomics revealed that 95 transcripts and one key metabolite were involved in transpiration regulation and sodium ion (Na^+) accumulation during the recovery phase of salt stress, elucidating a coordinated molecular response mechanism [58]. Similarly, RNA sequencing of chickpea root tissues under long-term salt stress showed that most differentially expressed genes were associated with cellular metabolic processes, indicating metabolic reprogramming under stress[59].

In sunflowers, proteomics and transcriptomics analyses identified 5,432 differentially expressed genes and 43 proteins, many of which were associated with carbohydrate metabolism, redox

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regulation, ribosomal activation, and ion binding. These results suggested that the activation of ribosomal and carbohydrate metabolic pathways may contribute to sunflower salt tolerance [60]. Similar molecular responses were observed in sesame, further supporting the conservation of these adaptive mechanisms [61].

In kidney beans, integrated genomic and transcriptomic analyses confirmed that 63 PvbHLH transcription factors were involved in adapting to salt stress. In soybeans, proteome and transcriptome data indicated that GmPAP3 alleviated salt stress by scavenging reactive oxygen species (ROS)[62], while GmWRKY transcription factors played a broad role in salt stress responses in both roots and aboveground parts [63]. These findings contributed to the construction of a novel transcriptional regulatory model under salt stress and assisted in the screening of salt-tolerant candidate genes.

Additionally, studies on the epigenome are also emerging. In castor bean, a joint analysis of transcriptomics and histone methylation revealed that dynamic changes in histone methylation are closely associated with gene expression under salt stress [64]. In maize, post-transcriptional and translational omics analyses revealed significant differences between endosperm and embryo after salt treatment, suggesting that the endosperm can actively sense and transmit salt stress signals [65].

3.2. Response of Plants to Drought Stress

Drought stress is a major abiotic factor that adversely impacts plant growth and developmental processes. Soil water deficiency and related environmental conditions can lead to a water imbalance in plants, where transpiration exceeds water uptake. Severe dehydration disrupts cellular membrane integrity, increasing membrane permeability and causing leakage of intracellular solutes [66]. Drought stress significantly suppresses leaf expansion and overall plant biomass accumulation.

Overexpression of JAZ7 has been shown to enhance drought tolerance in *Arabidopsis thaliana*[67]. To explore the underlying molecular mechanisms, a combination of tandem mass tag (TMT)-based quantitative proteomics and targeted metabolomics analyses was performed across three genotypes: JAZ7-overexpressing (OE), JAZ7-knockout (KO), and wild-type (WT) plants. Proteomic profiling identified 225 differentially abundant proteins in the OE plants, with most involved in disease defense, energy metabolism, and general metabolic processes. Notably, under drought conditions, the proteome of OE plants exhibited substantial changes compared to KO and WT plants, suggesting a JAZ7-dependent regulation of drought-responsive proteins (Table 2).

Table 2. Multi-omics analysis of responses of different plants to drought stress.

Stress of adversity	Species	Relevant omics	Key genes, proteins, or metabolites	References
drought stress	*Hordeum vulgare* L.	Transcriptomics/Proteomics/Metabolomics	*HSP40*、*HSP70*、*HSP70*、*Fructokinase*、*Caffeoyl-CoA O-methyltransferase*、*proline*、*Ascorbic acid*、*PAL1-Methyladenosine*、*2-Ethoxyethanol*	[74,76]

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	Arabidopsis thaliana	Proteomics/Metabolomics	*JAZ7*、*Proteins involved in disease defense*、 *energy and metabolic functions*、*Secondary metabolic pathways such as amino acids and antioxidant metabolites, flavonoids*、*flavonols*、 *and flavonoid biosynthesis are abundant*	[68]
	Zeamays. L	Genomics/Transcriptomics/Proteomics	*RAPs*、*ERFs*、*BRH1*、*BRs*、*Xyloglucan endotransglucosylase/hydrolase*、 *heat shock proteins*、*MDA*、*SOD/ubiquitin fusion degradation protein*、*asparagine synthetase*、*aldehyde dehydrogenase*	[70,71,77,78]
	Sesamum indicum L.	Transcriptomics/Metabolomics	*Dehydrin*、*Glycosyl transferase family 8*、*ABA*、*GABA*、*saccharopine*、*2-aminoadipate*、*allantoin*、*proline*	[69]
	Astragalus membranaceus Bge. var. mongolicus	Transcriptomics/Metabolomics	*Sucrose*、*prolin*）、*malate*	[47]

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	Lolium multiflorum L.	Transcriptomics/Proteomics/Metabolomics、	*LTP3*、*MYBs*、*bHLHs*、*bZIPs*、*CAT*、*SOD*、*APX* 、*tyrosine aminotransferase*、*Stearidonic acid*	[50]
	Triticum aestivum L.	Proteomics/Metabolomics	*RuBisCO large subunit-binding protein subunit beta*、 *ATP synthase CF1 beta subunit*、*proline*、*methionine*、*glutamate*	[49]
	Setaria italica (L.) P. Beauv.	Transcriptomics/Metabolomics	*MYBs*、*WRKYs*、*AP2/ERF*、*PAL*、*cinnamic acid*	[75]

After drought stress, the metabolic changes in WT and OE plants were similar, but these metabolites decreased in KO plants. Most of these metabolites were amino acids and antioxidant metabolites. In addition, under drought treatment, secondary metabolic pathways such as flavonoids, flavonols, and flavonoid biosynthesis were abundant, but only a few proteins were involved in the metabolism of pentose phosphate, fructose, and flavonoids. Therefore, targeted proteomics and activity analysis of metabolomics results are needed. This also indicates the necessity of complementary analysis between proteomics and metabolomics [68].

After drought stress, the metabolic changes observed in wild-type (WT) and overexpressing (OE) plants were similar, whereas these metabolites decreased in knockout (KO) plants. Most of the affected metabolites were amino acids and antioxidants. Additionally, drought treatment led to an abundance of secondary metabolic pathways, including flavonoids, flavonols, and flavonoid biosynthesis; however, only a limited number of proteins were involved in the metabolism of pentose phosphate, fructose, and flavonoids. Therefore, targeted proteomic studies and activity assays based on metabolomic data are necessary. This underscores the importance of integrating proteomics and metabolomics analyses for a comprehensive understanding[68].

You et al. conducted transcriptomic and metabolomic analyses on two genotypes of sesame. They found that, under drought conditions, drought-resistant genes were significantly enriched and expressed. These genes were mainly involved in endoplasmic reticulum protein processing, plant hormone signal transduction, photosynthesis, lipid metabolism, and amino acid metabolism. Metabolomic analysis revealed that metabolites such as abscisic acid, proline, arginine, lysine, aromatic and branched-chain amino acids, GABA, glycosides, 2-aminoadipic acid, and allantoin accumulated at higher levels under drought conditions. Comprehensive analysis showed that ABA metabolism and signaling pathways, as well as amino acid metabolism (especially the glycoside pathway), played important roles in sesame drought tolerance[69].

Transcriptomic and metabolomic analyses of *Astragalus membranaceus* revealed that the expression of drought-responsive genes was highly dependent on stress severity. Different drought levels elicited genotype-specific responses, which were primarily associated with the expression of

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genes involved in glycolysis, the tricarboxylic acid (TCA) cycle, and glutamate-mediated proline biosynthesis [47].

The study of transcriptomics plays an important role in revealing changes in metabolic pathways in plants under drought conditions, and has strong theoretical implications for guiding plant molecular breeding. For example, this has been demonstrated in plants such as maize[70,71], peanuts [72], rye [50], and cabbage[73].

Recent studies have also identified genes including RLK-LRR, glycosidase, HSP and others. in barley play key roles in drought stress response [74]. The genes and metabolites related to the synthesis pathway of phenylpropanoids in millet during the germination period of millet [75].

Using 2D-PAGE combined with matrix-assisted laser desorption/ionization time-of-flight (MALDI-TOF) and MALDI-TOF/TOF analysis, 121 drought-responsive proteins were identified in the leaves of two barley genotypes from different sources, and 182 drought-responsive proteins were found in the roots. In addition, GC/MS-TOF analysis was conducted to find that the accumulation levels of several proteins and metabolites showed high structural accumulation levels in drought-resistant barley lines, including HSP70, CLP, APX, GST, proline, carbohydrates, ascorbic acid, and some molecular chaperones, indicating that structural biochemical susceptibility mechanisms are the main drought resistance mechanisms rather than induction mechanisms [76].

The advantage of integrative omics analysis is that it enables the identification of biological patterns that cannot be revealed by a single omics approach. For example, combining proteomics and metabolomics facilitates the detection of coordinated changes in proteins and metabolites, and helps uncover their interrelationships in plant drought resistance.

Zeng et al. used iTRAQ to analyze protein expression in two maize varieties, Chang7-2 and TS141, and observed the differences. The significant upregulation of Xyloglucan endoglucosidase/hydrolase in the root system of Chang7-2 facilitated cell wall remodeling under drought stress. The low content of malondialdehyde (MDA) reflected the stronger resistance of Chang7-2 cell membrane to osmotic stress caused by drought; the activity of antioxidant enzymes, such as SOD, was higher than that in TS141, indicating stronger antioxidant capacity, which provides practical guidance for the breeding of drought-resistant maize varieties [77].

Recent studies have identified several key drought-responsive proteins in maize, among which proteins differentially expressed in MO17 are mainly involved in sugar metabolism and oxidative phosphorylation pathways, while those in YE8112 is mainly involved in endoplasmic reticulum protein processing and tryptophan metabolism pathways [78].

Drought can lead to a severe decrease in the total protein content of wheat, mainly including proteins related to photosynthesis, sugar metabolism, detoxification processes, and so on. Based on proteomic and metabolomic analysis, Michaletti found in their proteomic and metabolomic analysis of spring wheat that Kavir was less affected by drought stress compared to the Bahar strain, with only two pathways (such as purine metabolism) showing significant changes, offering insights into potential targets for crop improvement [49].

3.3. Response of Plants to Temperature Stress

Temperature stress, encompassing both cold and heat extremes, is a major abiotic factor limiting plant growth, development, and agricultural productivity worldwide. Exposure to low temperatures induces a range of physiological and molecular alterations, including membrane rigidification, accumulation of reactive oxygen species (ROS), and disruption of metabolic homeostasis[79]. In contrast, high temperatures often destabilize protein structures, inhibit enzymatic activity, and impair reproductive processes [80].

Multi-omics approaches have greatly enhanced our understanding of the molecular mechanisms underlying plant responses to temperature stress. For instance, transcriptomic analysis by Guan et al. using RNA-seq in two weedy and two cultivated rice lines revealed that cold-tolerant genotypes exhibited significantly higher expression of cold-responsive genes, such as those encoding basic helix-loop-helix (bHLH) and leucine-rich repeat (LRR) proteins, compared to cold-sensitive

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counterparts [81]. Cold-tolerant lines also showed more extensive transcriptional changes in genes related to protein metabolism, post-translational modification, protein folding, and defense signaling, providing valuable genetic targets for molecular breeding and genetic engineering to improve cold tolerance (Table 3).

Table 3. Multi-omics analysis of responses of different plants to temperature stress.

Stress of adversity	Species	Relevant omics	Key genes, proteins, or metabolites	References
temperature stress	*Oryza sativa* L.	Transcriptomics/Metabolism omics	*bHLHs*、*LRR*、*MYBs*、*WRKYs*、*MYSs*、*Glucose-6-phosphate*、*Glutathione*、*phenylpropanoids*、*polyhydroxy acids*	[71,115]
	Medicago falcata	Transcriptomics/Metabolomics	*ERF, MYB, bHLH*、*NAC*	[82]
	Camellia sinensis L. cv. 'Suchazao'	Transcriptomics/Metabolomics	*Hsp70*、*Hsp90*、*late embryogenesis abundant(LEA)*、*anthocyanin*	[84]
	Capsicum annuum L.	Transcriptomics/Metabolomics	*NAC2,*、*HSP20*、*WRKY40*、*HSP90*、*HSP70*、*D-glucoronic*、*flavonoids*	[87]
	Nicotiana tabacum	Transcriptomics/Metabolomics	*C4H*、*PAL*、*lignin*、*HCT*、*L-phenylalanine*	[100]
	Camellia sinensis	Transcriptomics/Metabolomics	*CBFs*、*HSFs*、*CYPs*、*GSTU18*、*Fatty*	[86]

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			acid desaturase、*Calcium-binding protein CML45*	
	Momordica charantia L.	Genomics/Metabolomics	*McERF*、*McMYB*、*McWRKY*、*L-Valine*、*NAD*、*Sucrose*	[116]
	Brassica napus L.	Metabolomics/Transcriptomics	*bHLH*、*ERF*、*MYB*、*WRKY*、*D-+-sucrose*、*dihydromyricetin*	[117]
	Solanum lycopersicum L.	Transcriptomics/Metabolomics	*ACS*、*IDH*、*Citrate*、*succinate*	[99]

The integration of next-generation sequencing (NGS) and single-molecule real-time (SMRT) sequencing has further enabled a more comprehensive transcriptomic profiling. In alfalfa, Cui et al. identified over 11,000 differentially expressed genes (DEGs) in response to cold stress, with enrichment in pathways related to pathogen recognition and carbon metabolism [82]. Transcription factors such as WRKY, ERF, MYB, bHLH, and NAC were identified as central regulators orchestrating the cold stress response, reflecting a coordinated immune and metabolic adaptation mechanism [83].

Metabolomics provides an essential complement to transcriptomic findings by uncovering downstream biochemical changes. For example, in Camellia sinensis, anthocyanin biosynthesis was found to vary with temperature stress type: ultra-low temperatures enhanced the accumulation of anthocyanin monomers, whereas moderate heat suppressed biosynthetic enzyme activity [84]. Similar transcriptome-metabolome integration studies in tobacco and green tea have shown increased lignin biosynthesis under cold conditions, suggesting a protective structural adaptation [85,86].

High temperature stress elicits distinct molecular responses. In chili peppers, Wang et al. compared a heat-tolerant and a heat-sensitive variety using combined transcriptomic and metabolomic analyses [87]. Their study identified common heat-responsive genes with significantly higher expression levels in the tolerant genotype and highlighted the critical role of glutathione metabolism in combating heat-induced oxidative damage. Furthermore, stress proteomics in Camellia species revealed that heat shock proteins (Hsp70 and Hsp90) were more prominently involved in heat stress responses than in cold stress, indicating differential mechanisms of protein homeostasis [88].

Notably, multi-omics integration—encompassing transcriptomics, proteomics, and metabolomics—enables a systems-level understanding of temperature stress responses. This approach facilitates the identification of key regulatory genes, signaling proteins, and metabolic

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pathways, as well as their dynamic interactions. For example, in a recent study on maize seedlings under heat stress [89], joint transcriptomic and proteomic analyses identified coordinated regulation of genes involved in photosynthesis, calcium signaling, and antioxidant pathways, offering promising targets for breeding thermotolerant cultivars.

Taken together, these integrated multi-omics strategies provide comprehensive insights into the complex molecular networks mediating plant adaptation to temperature extremes and serve as a foundation for the development of climate-resilient crop varieties.

3.4. Response of Plants to Heavy Metal Stress

Rapid industrialization and urbanization have led to a significant increase in heavy metal pollutants in soil, threatening plant health and ecosystem stability [90]. Consequently, plants have developed and activated a variety of metabolic pathways to mitigate the toxic effects of heavy metal stress Among these, Zn, Cu, and Mo are essential micronutrients for plant growth, while others such as Cd, Pb, and Hg are toxic even at low concentrations [91]. Excessive heavy metals can affect plant metabolism and disrupt cellular structure and physiological functions. Since heavy metal ions can interfere with proper protein folding and function, leading to alterations in protein expression profiles, proteomic analysis is essential for understanding plant responses under heavy metal stress [92].

In the study of heavy metal stress in rice and Arabidopsis, Li et al. analyzed the genes encoding heavy metal-related proteins (HMPs) under various heavy metal stress conditions. The expression profiles showed that only 8 out of 46 OsHMPs have various heavy metal stress conditions in rice tissues, while only 9 out of 55 AtHMPs in Arabidopsis. These findings suggest that the expression of HMPs is stress-inducible, triggered by exposure to heavy metal conditions [93]. Furthermore, the application of omics approaches offers valuable insights into the mechanisms of heavy metal detoxification and phytoremediation.

Proteomic and metabolomic analyses were conducted to investigate changes in orchid roots and their associated mycorrhizal fungi under heavy metal-contaminated soil conditions. The results showed elevated exudation of citric acid, succinic acid, and malic acid from the roots. In the non-mycorrhizal root segments, proteins related to carbon metabolism and stress responses were upregulated. In the mycorrhizal root segments, proteins involved in pathogen defense, cytoskeletal remodeling, and sugar metabolism showed increased abundance. The integrated proteomic and metabolomic analyses revealed distinct metabolic strategies employed by orchid roots to cope with heavy metal stress [94].

Luo and Zhang conducted a proteomic analysis of Brassica napus under cadmium (Cd) stress and identified 73 differentially expressed proteins. The most affected metabolic pathways were related to cell wall modification, redox, and lipid and protein metabolism [95]. From a genomic perspective, Shivi Tyagi identified 10 TaCAT genes in bread wheat (Triticum aestivum L.) under arsenic metal stress, among which molecular cloning and overexpression of TaCAT3-B gene in E. coli showed tolerance to different concentrations of AsIII and AsV treatment [96]. In addition, Proteomic analyses were performed to investigate the response of tomatoes[97] and cocoa seedlings [98] to cadmium (Cd). The results showed that plants modulate protein expression under heavy metal stress to reduce the damage caused by stress (Table 4).

Table 4. Multi-omics analysis of responses of different plants to heavy metal stress.

Stress of adversity	Species	Relevant omics	Key genes, proteins, or metabolites	References

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heavy metal stress	*Bipinnula fimbriata*	Proteomics/Metabolomics	*Ribosomal protein*、*Glutamate decarboxylase*、*Beta-tubulin*、*Peroxidase*	[94]
	Oryza sativa L.	Proteomics/Genomics/Transcriptomics	*OsHMP37*、*OsHMP09*、*OsHMP18*、*OsHMP22/Plasma membrane H+-ATPase*、*Phosphate transporter 5*、*Phospholipase D*、*Sucrose synthase*、*GTP-binding protein*	[93]
	Brassica napus)	Transcriptomics/Metabolomics	*Defense-like proteins*、*DAI-related protein 5*	[95]
	Solanum lycopersicum	Proteomics/Metabolomics	*cysteine*、*expansin*、*aldehyde dehydrogenase*、*aldolase*	[97]
	Arabidopsis thaliana	Genomics/Transcriptomics	*AtHMP20*、*AtHMP23*、*AtHMP25*、*AtHMP31*、*AtHMP35*、*AtHMP46*	[93]

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	Triticum aestivum L.	Genomics	*TaCAT*	[96]

3.5. Response of Plants to Multiple Abiotic Stresses

Plants in natural environments often face the combined effects of various abiotic stresses, such as drought, salinity, high and low temperatures, which pose complex challenges to growth and development [1]. Traditional studies have primarily focused on single stress conditions; however, multi-omics research has revealed that plant responses to combined stresses are not simply additive but involve distinct regulatory networks[99,100]. Studies integrating transcriptomic, metabolomic, and proteomic data have revealed that core pathways—such as the antioxidant defense system, osmoregulation, and energy metabolism—are significantly activated under combined stress conditions [58,68,70].

Moreover, key transcription factors including the Hsf family, WRKY, and NAC, along with signaling pathways involving hormones, calcium ions, and reactive oxygen species, exhibit highly overlapping expression patterns under diverse stresses, establishing core regulatory mechanisms for broad-spectrum stress tolerance [63,101,102]. Notably, the heat shock transcription factor HsfA2b regulates not only heat stress but also salt and drought tolerance [101]. The identification of these common pathways provides promising targets for gene editing and molecular breeding to enhance crop resilience to multiple stresses [103,104].

Systems biology approaches integrating multi-omics data further reveal dynamic interactions among genes, transcripts, proteins, and metabolites during stress responses[7,48]. In particular, joint transcriptomic and metabolomic analyses facilitate the identification of key metabolic nodes and pathways [47,99]. However, research on synergistic multi-omics responses under combined stresses remains limited. Future studies urgently require the application of high spatio-temporal resolution omics technologies combined with advanced bioinformatics tools to systematically elucidate signal integration mechanisms, providing a theoretical basis for developing broad-spectrum stress-tolerant crops[1,7].

4. Understanding the Molecular Response Process and Its Significance

Understanding the molecular response mechanisms of plants under abiotic stress conditions can help us enhance crop stress tolerance and yield through advanced molecular breeding strategies. Some plant species have evolved complex genetic, physiological, and biochemical adaptation mechanisms that enable them to survive in extreme environments.

Under abiotic stress conditions such as drought, salt stress, low or high temperature, the expression patterns of key regulatory genes (including those encoding transcription factors, protein kinases, and phosphatases) undergo significant changes. These regulatory factors modulate the expression of downstream genes and protein functions, thereby initiating protective responses. For example, studies have shown that genes encoding enzymes involved in osmoregulation, late embryogenic abundant (LEA) proteins, aquaporins, reactive oxygen species scavengers, and molecular chaperones exhibit significant expression differences. These genes collectively maintain cell membrane integrity, ion homeostasis, and balanced cellular functions [102,105].

Transcriptome analysis provided crucial insights into the genome-wide transcriptional reprogramming of plants under environmental stress [106]. However, studies have also shown poor consistency between mRNA levels and actual protein abundance, highlighting the necessity of conducting proteomics research [107]. Proteomics can identify and quantify functional proteins responding to stress, directly revealing biological functional changes at the translational and post-translational levels. In addition, spatial proteomics focuses on specific cells or subcellular compartments, enabling us to analyze organ-specific stress response processes, such as signal regulation in chloroplasts or mitochondria under oxidative stress.

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For example, comparative proteomic analyses in rice under salt stress have revealed upregulation of vacuolar H^+-ATPase and Na^+/H^+ antiporters, highlighting their role in ion compartmentalization and detoxification [108]. Similarly, drought-stressed maize has shown enhanced accumulation of heat shock proteins and ROS detoxifying enzymes localized to chloroplasts [109]. By integrating transcriptomics and proteomics, researchers can reconstruct stress-responsive regulatory networks and identify candidate biomarkers or targets for crop improvement. Overall, such multi-omics strategies deepen our understanding of stress sensing, signal transduction, and adaptive responses, bridging molecular knowledge with agricultural application.

In recent years, research has revealed that various miRNAs play key regulatory roles in plant responses to stress. For example, miR398 regulates reactive oxygen species (ROS) scavenging by targeting the superoxide dismutase genes CSD1 and CSD2, thereby enhancing plant tolerance to drought and salt stress [42]. miR159 targets MYB transcription factors, participating in the regulation of the ABA signaling pathway, and enhances stomatal regulation capacity under drought stress in Arabidopsis [44]. Under salt stress, miR393 influences root structure by regulating the auxin receptor TIR1, thereby improving rice's adaptability to salt stress [46]. Additionally, miR164 targets the NAC transcription factor, participating in regulation under various stress conditions, significantly enhancing Arabidopsis' tolerance to drought, salt, heat, and cold stress [105]. miR390 influences ARF transcription factor expression by regulating the TAS3 tasiRNA pathway, not only delaying leaf senescence but also enhancing plant drought tolerance[48]. These studies reveal the multi-level roles of miRNAs in regulating plant stress responses, providing an important theoretical foundation for improving plant stress tolerance through genetic engineering. Table 5 summarizes the important candidate genes and miRNAs reported in recent years and their stress adaptation performance in transgenic plants.

Table 5. Key Candidate miRNAs Involved in Abiotic Stress Tolerance and Their Transgenic Examples.

Stress Type	Gene/miRNA	Function/Target	Transgenic Plant	Improved Trait Observed	Reference
Drought, Salt, Heavy metal	miR398	Targets CSD1/2 (superoxide dismutase), regulates oxidative stress	*Arabidopsis thaliana*	Enhanced tolerance to drought and salt stress by reducing ROS damage	[42]
Drought	miR159	Targets MYB transcription factors, regulates ABA signaling	*Arabidopsis thaliana*	Improved drought tolerance via stomatal regulation	[44]
Salt	miR393	Targets TIR1 auxin receptor, modulates auxin signaling	Rice (*Oryza sativa*)	Increased salt tolerance by modulating root architecture	[46]
Drought, Salt, Heat, Cold	miR164	Targets NAC transcription factors, regulates stress responses	*Arabidopsis thaliana*	Enhanced tolerance to multiple abiotic stresses	[105]

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Leaf senescence, drought	miR390	Involved in TAS3 tasiRNA pathway, regulates ARF transcription factors	*Arabidopsis thaliana*	Delayed leaf senescence and improved drought tolerance	[48]
Cold	miR319, miR394	Targets TCP, LCR regulatory pathways	Melon /Arabidopsis	Downregulation under cold correlates with cold response	J Integr Plant Biol (2017)

5. Challenges and Future Directions

5.1. Impact on Secondary Metabolites

Given the aforementioned challenges, abiotic stress factors exert profound and multifaceted effects on plant secondary metabolites. Stress conditions influence plant growth and development through complex interactions involving primary and secondary metabolic processes [110]. Under such adverse environmental conditions, primary metabolic activities such as photosynthesis and respiration are often inhibited, leading to reduced synthesis of essential organic molecules and insufficient energy supply for normal cellular functions. This inhibition not only delays plant growth but may also cause irreversible physiological damage.

To counteract these adverse effects, plants typically upregulate the synthesis of secondary metabolites, which act as important defensive compounds. These include alkaloids, phenols, flavonoids, and terpenoids, which function as antioxidants, metal chelators, or osmotic protectants, helping plants mitigate the harmful effects of abiotic stress. Notably, many stress-induced secondary metabolites possess significant pharmacological activity and have been widely applied in pharmaceuticals and nutritional supplements. Therefore, investigating the regulatory mechanisms of secondary metabolism under stress conditions not only deepens our understanding of plant adaptive responses but also provides crucial theoretical foundations for related biotechnological applications.

5.2. Role of Multi-Omics Correlation Analysis

Given the complexity of plant stress response mechanisms, traditional studies focused on a single omics level often struggle to effectively enhance plant stress tolerance, particularly when relying solely on genetic modifications of individual genes. In this context, multi-omics association analysis emerges as a powerful research strategy, integrating data from different molecular levels to provide a comprehensive perspective on plant stress adaptation mechanisms.

For example, combining transcriptomics and proteomics allowed for more precise identification and validation of key stress-responsive genes at both the transcriptional and translational levels [111]. When further integrated with metabolomics data, this approach facilitates the accurate screening of metabolites involved in stress resistance pathways, enabling targeted genetic and metabolic engineering with improved efficiency and reduced costs.

Specifically, genomics reveals the genetic blueprint; transcriptomics, with its high-throughput and high-precision characteristics, can capture dynamic gene expression information without the need for a reference genome. Proteomics expands our understanding of post-transcriptional regulation, revealing the expression profiles of functional proteins and their interactions. Metabolomics, as an interdisciplinary field integrating biology, analytical chemistry, and bioinformatics, maps the changes in small-molecule metabolites that directly reflect physiological states.

In recent years, the synergistic development of these omics technologies has significantly advanced research into plant responses to abiotic stress. Multi-omics studies are evolving toward

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higher quantification and high-throughput approaches, making it possible to construct comprehensive gene–mRNA–protein–metabolite regulatory networks. Such integrated analyses not only aid in deciphering complex regulatory circuits and identifying key functional genes and metabolic pathways but also enable the application of research findings to plant breeding and cultivation practices[48,112].

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