

Review

# MicroRNA and cDNA-Microarray as Potential Targets against Abiotic Stress Response in Plants: Advances and Prospects

Tariq Pervaiz <sup>1,2</sup>, Muhammad Waqas Amjid <sup>3</sup>, Ashraf El-kereamy <sup>2</sup>, Shi-Hui Niu <sup>1,\*</sup> and Harry X. Wu <sup>1,4,5,\*</sup>

- <sup>1</sup> Beijing Advanced Innovation Center for Tree Breeding by Molecular Design, National Engineering Laboratory for Tree Breeding, College of Biological Sciences and Technology, Beijing Forestry University, Beijing 100083, China; tariqzoqi2009@gmail.com
- <sup>2</sup> Department of Botany and Plant Sciences, University of California Riverside, Riverside, CA 22963, USA; ashrafe@ucr.edu
- <sup>3</sup> State Key Laboratory of Crop Genetics and Germplasm Enhancement, Cotton Germplasm Enhancement and Application Engineering Research Center (Ministry of Education), Nanjing Agricultural University, Nanjing 210095, China; waqasamjid@hotmail.com
- <sup>4</sup> Umeå Plant Science Centre, Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, Linnaeus väg 6, SE-901 83 Umeå, Sweden
- <sup>5</sup> CSIRO National Research Collection Australia, Black Mountain Laboratory, Canberra, ACT 2601, Australia
- \* Correspondence: arrennew@bjfu.edu.cn (S.-H.N.); harry.wu@slu.se (H.X.W.)

**Abstract:** Abiotic stresses, such as temperature (heat and cold), salinity, and drought negatively affect plant productivity; hence, the molecular responses of abiotic stresses need to be investigated. Numerous molecular and genetic engineering studies have made substantial contributions and revealed that abiotic stresses are the key factors associated with production losses in plants. In response to abiotic stresses, altered expression patterns of miRNAs have been reported, and, as a result, cDNA-microarray and microRNA (miRNA) have been used to identify genes and their expression patterns against environmental adversities in plants. MicroRNA plays a significant role in environmental stresses, plant growth and development, and regulation of various biological and metabolic activities. MicroRNAs have been studied for over a decade to identify those susceptible to environmental stimuli, characterize expression patterns, and recognize their involvement in stress responses and tolerance. Recent findings have been reported that plants assign miRNAs as critical post-transcriptional regulators of gene expression in a sequence-specific manner to adapt to multiple abiotic stresses during their growth and developmental cycle. In this study, we reviewed the current status and described the application of cDNA-microarray and miRNA to understand the abiotic stress responses and different approaches used in plants to survive against different stresses. Despite the accessibility to suitable miRNAs, there is a lack of simple ways to identify miRNA and the application of cDNA-microarray. The elucidation of miRNA responses to abiotic stresses may lead to developing technologies for the early detection of plant environmental stressors. The miRNAs and cDNA-microarrays are powerful tools to enhance abiotic stress tolerance in plants through multiple advanced sequencing and bioinformatics techniques, including miRNA-regulated network, miRNA target prediction, miRNA identification, expression profile, features (disease or stress, biomarkers) association, tools based on machine learning algorithms, NGS, and tools specific for plants. Such technologies were established to identify miRNA and their target gene network prediction, emphasizing current achievements, impediments, and future perspectives. Furthermore, there is also a need to identify and classify new functional genes that may play a role in stress resistance, since many plant genes constitute an unexplained fraction.

**Keywords:** abiotic stress tolerance; drought stress; salinity stress; cold stress; miRNA target gene expression; adaptation



**Citation:** Pervaiz, T.; Amjid, M.W.; El-kereamy, A.; Niu, S.-H.; Wu, H.X. MicroRNA and cDNA-Microarray as Potential Targets against Abiotic Stress Response in Plants: Advances and Prospects. *Agronomy* **2022**, *12*, 11. <https://doi.org/10.3390/agronomy12010011>

Academic Editor: Alfonso Albacete

Received: 17 November 2021

Accepted: 15 December 2021

Published: 22 December 2021

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## 1. Introduction

Plants are subjected to a wide range of abiotic stresses that are primarily hostile to plant growth, leading to plant death worldwide. Abiotic stresses have an extensive impact on various physiological, molecular, and metabolic responses. Much progress has been made in unravelling the complex stress response mechanisms, particularly in identifying stress-responsive genes with the help of biotechnological tools [1,2]. MicroRNAs (miRNAs), play a critical role in post-transcriptional regulation through base-pairing with other miRNA targets, including transcription factors (TFs) [1,3]. Understanding the role of miRNAs in abiotic stresses may be helpful in the development of innovative ways for improving plant responses against abiotic stresses. MicroRNAs are involved in multiple cellular and metabolic pathways under abiotic stresses, such as flowering, morphogenesis, signal transduction [4–6], and gene feedback regulation [7]. MicroRNAs are a group of single-stranded non-protein-coding short length RNA of approximately 18–25 nucleotides in length with a highly conserved class [8–10]. MicroRNAs are formed by antecedence with distinctive stem-loop assemblies [11]. In the plants, miRNAs are important regulators of gene expression at various stages of plant development; for instance, 959 founding members representing 178 miRNA families were identified in rapeseed (*Brassica napus*), earth mosses (*Physcomitrella patens*), arabidopsis (*Arabidopsis thaliana*), maize (*Zea mays*), black cottonwood (*Populus trichocarpa*), barrel clover (*Medicago truncatula*), rice (*Oryza sativa*), soybean (*Glycine max*), sorghum (*Sorghum bicolor*), and sugar cane (*Saccharum officinarum*) [12,13] (Tables 1 and 2). Usually, intronic miRNAs are coordinately expressed in host plant miRNAs, suggesting that they are also initiated from mutual transcripts. Host gene expression by situ analysis was used to probe the temporal and spatial localization of intronic miRNAs. These non-coding small RNAs are proposed to perform crucial roles in plant adaptation and immunity to adverse environmental conditions [14,15].

**Table 1.** Examples of miRNAs identified in model plants under drought, cold and salinity stresses.

Stress Condition	Plant Species	Inducible Genes	Known Responsive miRNAs	Functions	References
Drought stress	<i>Arabidopsis thaliana</i>	Rd29A (At5g52310) CCAAT-binding transcription factors	miR164, miR169, miR389, miR393, miR396, miR397, miR402	Pathogen immune response Drought tolerance Oxidative stress tolerance Pathogen immunity response Syncytium formation response to parasitic nematodes	[16–19]
	<i>Medicago truncatula</i>	CCAAT Binding Factor (CBF) Growth Regulating Factor (GRF) Cu/Zn superoxide dismutases (CSD1, CSD2) TIR-NBS-LRR domain protein	miR169, miR396 miR398, miR2118	Drought tolerance Syncytium formation response to parasitic nematodes Oxidative stress tolerance Photoperiod-sensitive male sterility	[16,20]
	<i>Oryza sativa</i>	SalT (LOC_Os01g24710) TIR1 OsLEA3 (LOC_Os05g46480)	miR393 miR402	Salt/cold tolerance	[6,17,18,21]
Cold stress	<i>Arabidopsis thaliana</i>	Rd29A (At5g52310) CBF3 (At4g25480)	miR165, miR172, miR169, miR396, miR397, miR402	Drought/cold tolerance Drought tolerance Heat stress tolerance	[16,17]
	<i>Oryza Sativa</i>	OsWRKY71 (LOC_Os02g08440) OsMAPK2(LOC_Os03g17700) Os05g47550, Os03g42280 Os01g73250, Os12g16350 Os03g19380	miR319, miR389, miR393, miR1320, miR1435 miR1884b, CHY1 CP12-2	Drought/salt tolerance Cold tolerance Pathogen immunity response	[17,21–23]

Table 1. Cont.

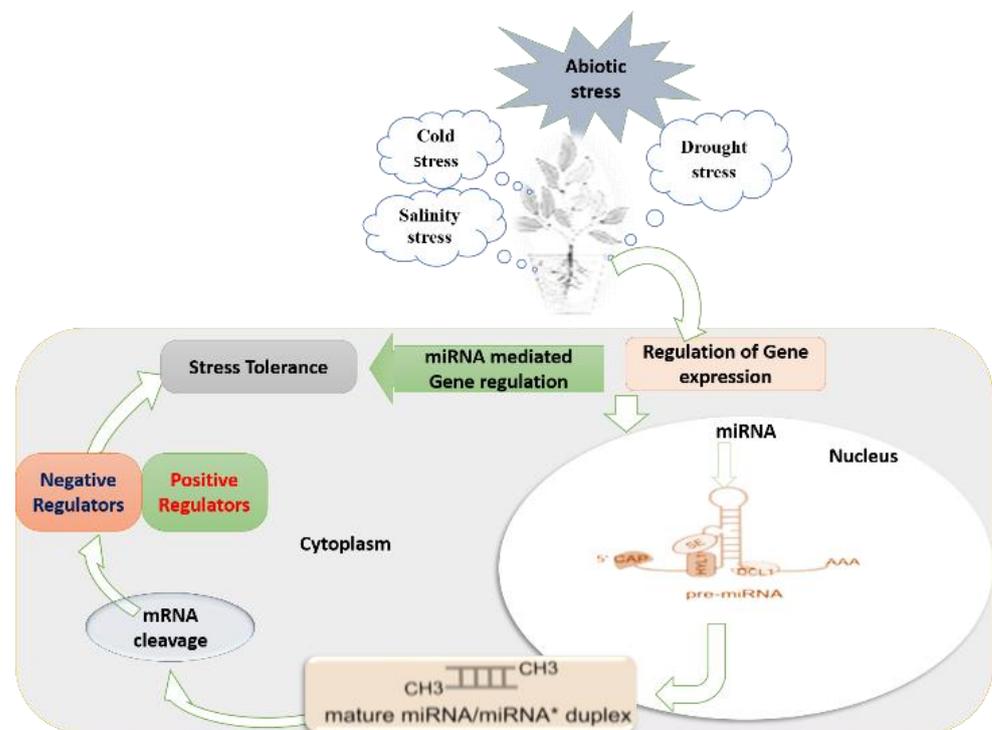
Stress Condition	Plant Species	Inducible Genes	Known Responsive miRNAs	Functions	References
Salinity stress	<i>Arabidopsis thaliana</i>	<i>Rd29A</i> (At5g52310) <i>COR15A</i> (At2g42540)	<i>miR389</i> , <i>miR393</i> ,	Oxidative stress tolerance Heat stress tolerance	[24]
	<i>Populus trichocarpa</i>	Dihydropyrimidinase	<i>miR162</i> , <i>miR164</i> , <i>miR166</i> , <i>miR167</i> , <i>miR168</i> , <i>miR172</i> , <i>miR395</i> , <i>miR396</i>	Pathogen immune response Drought tolerance Drought/cold tolerance Sulfate-deficiency response	[25–27]
	<i>Glycine max</i>		<i>miR1507a</i> , <i>miR395</i>	Sulfate-deficiency response	[28]
	<i>Oryza sativa</i>	<i>SalT</i> (LOC_Os01g24710) <i>OsLEA3</i> (LOC_Os05g46480)	<i>miR156</i> , <i>miR158</i> , <i>miR159</i> , <i>miR397</i> , <i>miR398</i> , <i>miR482.2</i> , <i>miR530a</i> , <i>miR1445</i>	Drought tolerance Pathogen immune response Heat stress tolerance	[22,29–31]
	<i>Zea mays</i>		<i>miR402</i>	Seed germination and seedling growth of <i>Arabidopsis</i> under stress	[18]

Table 2. Microarray analysis of genes involved in the drought, salinity and cold stress responses in *Arabidopsis*.

Phenotype of Mutants	Genes	Function	AGI Code	Coded Proteins	Microarrays	References
Increased tolerance to drought	<i>AtPARP2</i>	DNA repair	At2g31320	Poly (ADPribose) polymerase	24K Affymetrix	[32–34]
Hypersensitive to drought stress	<i>AHK1/ATHK1</i>	positive regulator of drought and salt stress responses	At2g17820	Histidine kinase	22K Agilent	[32,35,36]
Increased tolerance to drought stress	<i>AREB1/ABF2</i>	regulate the ABRE-dependent expression	At1g45249	bZIP TF	22K Agilent	[33,37,38]
Increased tolerance to salt stress	<i>AtbZIP60</i>	encodes a predicted protein of 295 aa	At1g42990	bZIP TF	44K Agilent	[37,39]
Increased tolerance to drought stress	<i>AtMYB60</i>	regulates stomatal movements and plant drought tolerance	At1g08810	MYB TF	7K cDNA	[40]
Increased sensitivity to drought stress	<i>AtMYB41</i>	control of primary metabolism and negative regulation	At4g28110	MYB TF	24K Affymetrix	[41,42]
Increased tolerance to drought and salt stress	<i>AHK2</i>	positive regulators for cytokinin signaling	At5g35750	Histidine kinase	Agilent	[35,36]
Increased tolerance to drought and salt stress	<i>AHK3</i>	perception of cytokinin, downstream signal transduction	At1g27320	Histidine kinase	22K Agilent	[35,36]
Increased tolerance to drought and freezing stress	<i>DREB1A/CBF3</i>	stress-inducible transcription factor	ERF/AP2 TF	ERF/AP2 TF	1.3K cDNA	[43]
Increased tolerance to drought stress	<i>DREB2A</i>	heat shock-stress responses.	At5g05410	ERF/AP2 TF	22K Agilent 7K cDNA	[44]
Hypersensitive to salt	<i>HOS10</i>	coordinating factor for responses to abiotic stress and for growth and development.	At1g35515	MYB TF	24K Affymetrix	[32,45]
Increased tolerance to drought stress	<i>ZFHD1</i>	mediates all the protein-protein interactions	At1g69600	Zinc finger HD TF	22K Agilent	[36,39]

Numerous miRNAs/target gene expression modules are responsive to abiotic stresses in *Arabidopsis*; therefore, altering the molecular profile of certain expression modules might help plants adapt to abiotic stresses [46,47]. To date, miRNAs have become an important field of intense study in recent years. Functional analysis of conserved miRNAs revealed their association with numerous developmental and biological processes. They

regulate diverse metabolic events, including meristem boundary formation, organ separation and auxin signaling, the transition from the vegetative to the reproductive stage (juvenile-to-adult), and stress tolerance (Figure 1). The first reported miRNA in *Arabidopsis thaliana* to regulate the auxin signaling pathway was miR398, and miR398 was the first-ever reported miRNA related to stress tolerance. At the same time, the expression of miR398 was down-regulated under various oxidative activities and environmental stresses (Figure 1) [48,49], which further validate the substantial involvement of miRNAs in adverse environmental conditions [15]. MicroRNAs are significantly hardboard during plant development by negative gene expressions at the post-transcriptional level [50,51], and hence are considered as a popular molecular tool in modern biotechnology to study signal transduction, environmental extremes, response to stresses, protein degradation, biogenesis, and pathogen incursion [50,52,53]. Recently, several miRNAs have been mutually recognized by experimental and computational tactics in many crops [54]. In contrast, hundreds of identified miRNAs are documented as conserved across several species, suggesting that miRNAs might be used to develop abiotic stress tolerance in plants through genetic modifications [52,55].



**Figure 1.** Schematic summary of miRNA-mediated regulatory mechanisms under abiotic stress in plant cells, with the particular formation process of miRNAs and miRNA mediated gene regulation: (1) miRNA gene is transcribed to a long sequence of primary miRNA (pri-miRNA). Primary miRNAs (pri-miRNAs) are transcribed from nuclear-encoded MIR genes by RNA polymerase II (Pol II), leading to precursor transcripts with a characteristic hairpin structure. (2) The pri-miRNA is cleaved to a stem-loop intermediate called miRNA precursor or pre-miRNA.

The second important function of miRNAs is in post-transcriptional regulation by targeting mRNAs for repressing or cleavage translation [16]. Many detrimental environmental factors adversely affect the plant's metabolic activities which, as a result, inhibit plant growth and development. However, it is quite challenging to differentiate and quantify the impact of various stresses on the plants through visual identification of hazardous factors, such as ozone, wound, and drought. Therefore, the development of sensitive and reliable techniques for diagnostics based on determining altering genes expression in DNA microarray is required [56]. Thus, the use of high-throughput sequencing (HTS)

and genome tilling miRNA are focused on discovering the function of epigenetic mechanisms in ecological adaptation and genome idiomatic expressions. However, epigenomics, expression-pattern, and functional characterization urge us to elucidate the communal regulatory pathways by miRNAs that control abiotic stress resistance in plants [57]. Small RNA cloning and high-throughput deep sequencing technologies can obtain the expression profiles of both known and unknown miRNAs. The study of post-transcriptional regulation is also crucial in improving stress tolerance and suggesting next-generation targeting for classical breeding and genetic improvement.

DNA microarrays are a commonly developed tool in functional genomics. Analysis of the microarray expression profiles is a positive approach to improve in-depth understanding of genes involved in regulatory networks and signal transduction associated with resistance against multiple abiotic stresses [58,59]. With the continued progress of genome sequencing, DNA-microarray technology has become the pioneer in biotechnology and has bridged the gap between functional genomics and sequencing data. Microarrays are classified into two main classes according to the nature of immobilized probes: (1) DNA microarrays created with DNA-fragments which are normally produced by employing PCR techniques [60–62] and spotted cDNA-microarrays (most commonly used) and (2) oligonucleotide microarrays produced with longer (up to 120-mer) or shorter (10 to 40-mer) oligonucleotides premeditatedly corresponding to explicit coding targets. These cDNA-microarrays have certain advantages, particularly for regulating gene expression patterns. However, oligonucleotide-microarrays are restricted to low sequence complication array elements. The hybridization specificity for a compound probe is amended with arrays containing DNA fragments that are significantly longer than oligonucleotides [61,63]. The spotted cDNA-microarray was the earliest and widely used technology, which comprised several PCR-amplified probes of cDNA-fragments dropped, cross-linked, and dried in a matrix pattern of spots on a treated glass surface. The targets for these samples are preferentially identified cDNA solutions derived from reverse-transcribed mRNAs obtained from two cell samples populations [64,65]. There are two modifications to the DNA array series that may contain cDNAs that are immobilized to a firm base, such as oligonucleotides or glass/nylon membranes, that are perceived on glass slides (20 to 80-mer) [63]. The most hotly debated topics are the data normalization techniques, the purpose of which is to reduce the sample variations resulting from the technical features of microarray processing that may obscure biological differences in a specific experiment [66]. The review presents a perspective analysis and bridges the gap between previous and recent advancements in MicroRNAs and cDNA-Microarray as potent targets to cope with abiotic adversities in plants.

## 2. MicroRNAs and Microarray Target Prediction against Abiotic Stress

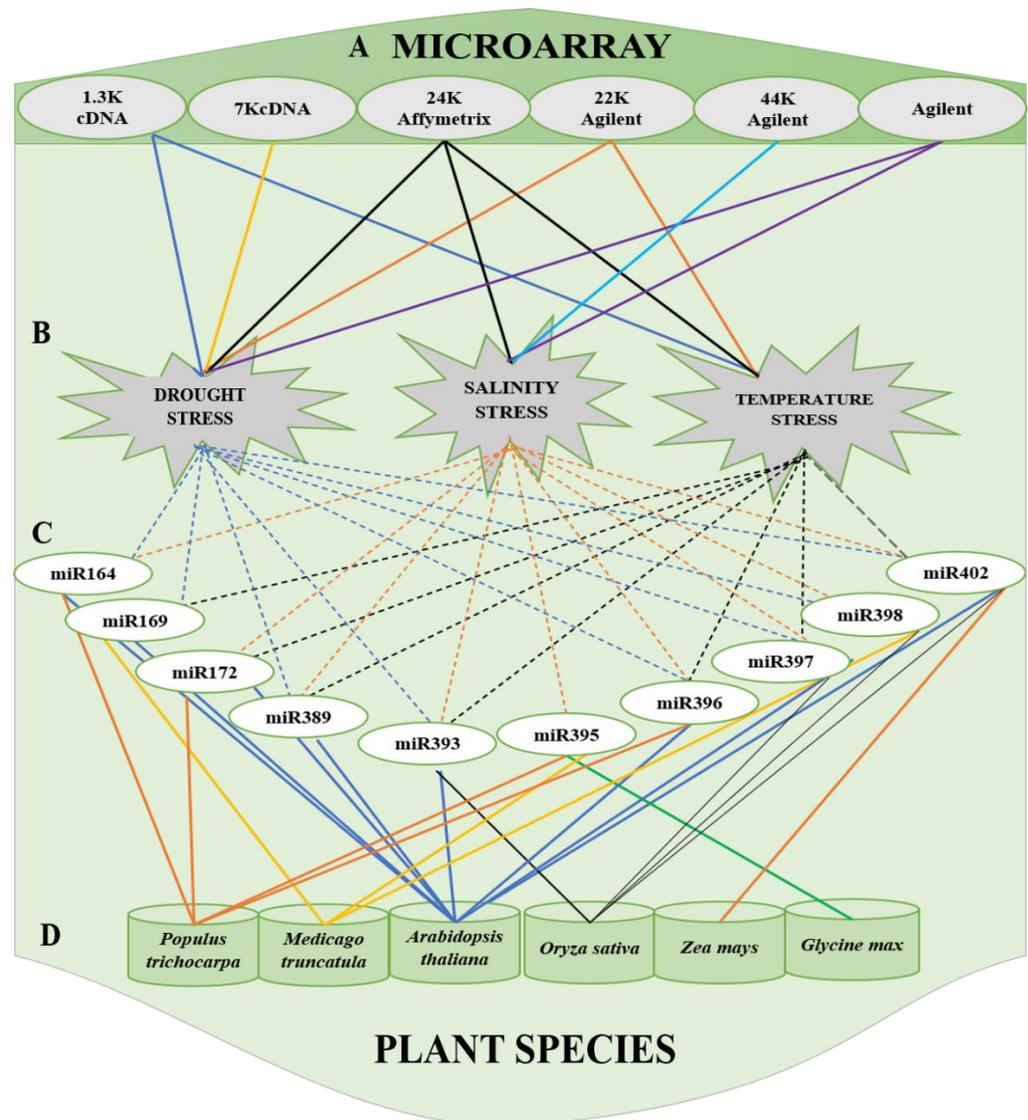
Perusing plant stress responses is an inclusive concern, which has been threatened by global warming and other abiotic factors. Currently, numerous miRNAs related to stress-responses have been identified as being triggered under high salinity, low temperature, and drought [58,67,68] (Tables 1–3, Figure 2). The stress-induced miRNAs depend upon the type of stress, tissues or organs, and plant genotype. Stress-sensitive miRNAs can either be negative regulators by downregulation or positive regulators by upregulation of the accumulation of positive regulators [57]. MicroRNA regulates gene modulation in a sequence-specific mode and plays a significant role against stress. Understanding and recognizing abiotic stress-associated microRNAs can help to establish schemes and improve tolerance against extreme stress [69,70]. Various advancements in miRNA identification—for example, deep sequencing, cloning, and prediction by bioinformatics methods, including miRNA-regulated network, miRNA target prediction, miRNA identification, expression profile, features (disease or stress, biomarker) association, tools based on machine learning algorithms, NGS, and tools specific for plants—have been developed to study the expression patterns of miRNA against stress [70–72]. High-throughput sequencing (HTS) evaluated the miRNA landscape of Arabidopsis entire seedlings subjected to heat, drought, and

salinity stress, and 121, 123, and 118 miRNAs with a larger than 2-fold changed abundance, respectively, were discovered [46]. cDNA-microarray includes 3628 distinctive sequences retrieved from the Yukon ecotype of *Thellungiella salsuginea*, earlier stress-induced cDNA libraries, and reported transcript profiles in response to simulated drought, cold, and salinity [73]. Many stress-inducible genes are responsible for low temperature and dehydration; their sequences have been used to prepare cDNA-microarray with descriptive exposure of the *T. salsuginea* genome developed with stress-associated gene expression [41,73,74]. In addition, microarray revealed a larger number of stress-related genes (1886) as differentially regulated in *RG1* mutants [75]. Using full-length cDNA or Gene Chips array transcription profiling experiments on *A. thaliana* reveals an extensive alteration occurrence in transcription against salinity, cold, and drought stress [74,76] (Table 2).

**Table 3.** miRNAs regulated by drought stress, salinity stress, and cold stress in plants.

Stress Condition	Plant Species	miRNA	Key Functions	Response	References
Drought stress	<i>Medicago truncatula</i>	miR398a,b miR408 miR399k miR2089 miR2111a-f,h-s miR2111g miR4414a	Oxidative stress tolerance Salt/drought/cold/oxidative osmotic-stress responses Phosphate-deficiency response	Up-regulated	[20,77–80]
		miR398b,c miR2111u,v miR5274b miR1510a-3p, 5p miR1510a	Heat stress tolerance Drought responsive Oxidative-stress tolerance triggering phasiRNA production from numerous NB-LRRs	Down-regulated	[77,79,80]
	<i>Glycine max</i>	miR5554a-c	Drought responsive		[79]
Salinity stress	<i>Glycine max</i>	miR169d miR395a miR395b,c miR1510a-5p miR1520d,e,l,n,q	Drought tolerance Sulfate-deficiency response triggering phasiRNA production from numerous NB-LRRs	Up-regulated	[20,81,82]
		gma-miR159b,c gma-miR169b,c gma-miR1520c	Pathogen immune response Drought/Salt tolerance	Down-regulated	[82]
	<i>Phaseolus vulgaris</i>	pvu-miR159.2	Plant–nematode interaction		
Cold stress	<i>Phaseolus vulgaris</i>	pvu-miR2118	regulate the expression of genes encoding the TIR-NBS-LRR resistance protein	Up-regulated	[31]

Cold- or drought-inducing genes were clustered based on the RNA gel blot and microarray analyses. The clusters were (1) cold-specific, (2) cold-inducible, and (3) drought-specific inducible genes. Recently, microRNAs have appeared as gene expression regulators that have also been associated with stress responses. However, the association between stress responses and miRNA expression is just beginning to be unfolded and documented. Fourteen stress-inducible miRNAs were established using microarray, in which the results of three main environmental stresses in *Arabidopsis* were plotted. Of them, 10 were cold regulated and had high salinity, while four were detected for drought miRNAs [83,84] (Tables 1 and 2). Seki M., et al. [43] reported 20 genes related with cold and drought-inducible genes, five which were drought-specific, and four novel genes, including *FL5-2D23*, *FL5-3J4*, *FL2-56*, and *FL6-55*, and two genes that were cold-specific inducible, including a novel (*FL5-90*) gene. Additionally, in rice, two siRNAs were previously reported as miR441 and miR446 [70,85,86]. They were testified to be down-regulated due to water deficiency; miR169g is the individual gene tempted by the scarcity of water which belongs to the miR169 family (Table 1). Moreover, the miRNAs responsive to abiotic stress inducements were comprised of 21 miRNAs belonging to 11 miRNA families which were up-regulated by UV-B stress in *Arabidopsis* [51,87,88].



**Figure 2.** Summary of commonly used (A) microarrays (cDNA, Affymetrix, and Agilent) to stress and (B) miRNAs, categorized based on the stress, that respond to drought stress, salinity and temperature stress and (C) miRNAs reported in (D) plant species: *Populus trichocarpa*, *Medicago truncatula*, *Arabidopsis thaliana*, *Oryza sativa*, *Zea mays* and *Glycine max*.

High-throughput sequencing (HTS) microarray techniques have been employed for gene expression profiling under environmental stresses [42,89–91]. Several members of stress-regulated gene families were reported, such as *bZIP* to drought, *AP2* family to drought and cold, *MYB* to dehydration, *NAC* and *bHLH* to drought, ABA, and salinity, and *zinc finger* to drought and cold [92–94]. In addition, up-to-date, numerous drought-sensitive genes have been acknowledged in populus and pine [95,96].

### 3. Drought Responsive miRNAs and cDNA-Microarray

Drought stress is the foremost ecological factor that profoundly influences plant growth and development. Drought or soil water scarcity and perturbations is a main abiotic stress condition that causes yield reduction or complete crop loss [69]. It may be enduring in climatic zones with low or random water accessibility, due to meteorological changes during plant growth [97,98]. Therefore, preliminary physiological modifications in drought stress lead to radical gene expression variations [99]. A transcriptomic study in *Pinus taeda* was conducted in order to understand how plants were treated for mild drought

and recuperation cycles [100]. To understand the role of microRNA, an oligonucleotide microarray was employed to control a rice microRNA expression profile against drought stress. Furthermore, it was confirmed that *mir169g* was stimulated by drought along with the *mir169* family, and the introduction of *mir169g* was more prominent in roots than in shoots [16,93]. Among the *miR169* family, only *miR169g* in *Oryza sativa* was regulated by drought [16]. Many genes associated with drought stress responses have been identified (Table 3) through cloning and characterization of cDNAs [101]. The examination of gene regulation through the drought stress response illuminated the roles of genes involved against abiotic stresses [67]. Moreover, microRNAs induced in drought was identified, and *mir169g* was reported as the only family member of *mir169* which was induced under drought condition. The presence of *mir169g* was more pronounced in plant roots than in shoots. Several microRNAs in rice were modified against stress conditions on the microarray. RNA-seq analysis revealed two adjacent Dehydration-responsive elements (DREs) upstream of the *MIR169g*. *Mir169g* was substantially up-regulated and *mir169* was the only family member caused via drought. The expression of *mir169g* might be directly synchronized by the *CBF/DREBs* [16,41].

Water uptake mechanisms are improved under stress, and the crop cells can confer drought avoidance to retain water and regulate the water deficit. The molecular response of higher plant mechanisms to water stress was analyzed by identifying various genes that are sensitive to drought stress at the transcriptional levels [102]. Comprehensive study on transcriptome analysis has presented important evidence on gene expression and pathways expressed differently in cotton cultivars, which are useful in developing drought tolerance [15,42]. MicroRNAs are known to significantly regulate the function against stress, but miRNAs associated with drought have not been recognized (Figure 2). Moreover, it is unclear that miRNAs could contribute to drought lenience capabilities in some plants (such as cowpeas) [103,104].

Expression microarrays provided novel insights into the physiological and metabolic pathways of dehydration tolerance, which led to the detection of candidate genes that might be helpful to speed up the breeding of tolerant varieties [99,100], and exhibited a photosynthetic acclimatization trend in response to moderate drought. Because of the novelty of the technology, performing DNA-microarray experiments remains a challenge [105,106]. *PHENOPSIS* was developed as an automated controlled drought screen to measure various *Arabidopsis* accessions efficiency and identify resistant ecotypes [107]. cDNA-microarrays have been designed for aquaporins (AQPs) to determine the expression patterns of 35 *Arabidopsis* AQPs in roots, flowers, and leaves, however, no leaf specific AQPs were identified. Plasma membrane intrinsic protein (PIP) transcripts were reported, usually down-regulated under moderate drought in the leaves, apart from *AtPIP2;5-6* and *At-PIP1;4*, which were expressed constitutively and were unaffected by drought stress [108]. Liu, et al. [84] reported seven drought regulated miRNAs by microarray analysis in *Arabidopsis thaliana* (*miR167*, *miR165*, *miR31*, *miR156*, *miR168*, *miR171*, and *miR396*) and confirmed this by spotting their expression patterns in their promoter sequences and analyzing the cis-elements. Moreover, an additional subset of c.150 gene expression was discovered during recovery from the stress. Identifying co-regulated gene groups has made it possible to identify common sequence patterns between promoters of certain genes and to detect transcription factors that control their expression [30,67,76] (Tables 1 and 2).

The plant stress-responsive pathways are not linear, but are dynamically integrated circuits consisting of several passages involving various tissues, cellular compartments, cofactors, and signaling molecules to organize a precise response to particular signals [109,110]. Microarray research showed that transgenic drought resistance was associated with several stress tolerant pathway genes, such as *DREB1A/CBF3*, *RD29A*, and *COR15A*, and was up-regulated. Protein phosphorylation/dephosphorylation is the main signaling event, which is being stimulated by osmotic stress. *Arabidopsis* 2-Oligo Microarray (Agilent) was used to analyze transcription profiles of the *SRK2C* gene, and protein kinase activated by osmotic stress (Table 1, Figure 2) [111].

#### 4. miRNAs and cDNA-Microarray Associated with Cold Stress

Cold stress (frost and chilling) decreases crop yields worldwide through tissue degradation and delayed growth. Most temperate plants have evolved cold resistance through cold-acclimatization [112]. Signaling pathways were being used in response to winter stress. The functional genes transform reactions, and reports suggest that the signaling pathways for leaf senescence and plant defense responses may overlap [113]. The most characteristic region of cold-stress responsive genes includes transcription factors, such as *CBF/DREB* and stress-inducible candidate genes, identified as *KIN* (cold-induced), *COR* (cold-regulated), and *LTI* genes (induced by low temperature) or *RD* (dehydration) [114]. Several *HSPs* (heat shock proteins) are also reported for their functions against cold stress. *HSPs*, which perform as molecular chaperons, play an important regulatory function in protecting from stress by restoring normal protein conformation and thus maintaining cellular homeostasis in plants [115]. The number of the miRNA target genes in expression is intricate during stress and plant growth. These miRNAs are co-regulated by both developmental signals and ecological factors (Table 3). The cold-responsive miRNAs were detected by microarray analysis in *Arabidopsis thaliana* (miR165, miR31, miR156, miR168, miR171, miR396) and recommended by identifying their expression patterns in their promoter sequences and evaluating the cis-components (Table 3, Figure 1) [116,117]. Furthermore, high-intensity light (HL) responsive genes were assessed with the drought-inducible genes reported with a similar microarray system, which exposed an impenetrable intersection between drought and HL-induced genes. Moreover, 10 genes were identified as being involved in the regulation by HL, drought, salinity, and cold stress (Tables 1 and 2). These genes are comprised of *ERD10*, *RD29A*, *KIN1*, *LEA14*, *COR15a*, and *ERD7*, and most of them are considered to be concerned in the defense of cellular components [78,118,119]. Along with the HL-inducible genes, some are also identified and encouraged by other stresses (heat, drought, and cold), including *AtGolS*, *LEA*, *RAB*, *RD*, *COR*, *ERD*, *HSP*, *KIN*, lipid-transfer proteins, and *fibrillins* [76,120,121].

DNA microarrays almost in all genes of the unicellular *Synechocystis sp* PCC6803 were used to investigate the gene expression sequential software [122]. A cDNA-microarray was used to test the profile expression in cold stress, and 328 temperature-regulated transcripts were reported. *OsMYB3R-2* was studied further and was shown to be a dominant regulator against stress [123]. In this study, there was an attempt to use a 3.1K cDNA-microarray to express the cold-regulated transcripts in the *Capsicum annumum*. Several TFs, including the *EREBP* (*CaEREBP-C1* to *C4*) family of four genes, a protein of the ring domain, a *bZIP* protein (*CaBZ1*), *RVA1*, a *WRKY* (*CaWRKY1*), and *HSF1* protein have been observed among the cold stress-regulated genes. These genes included *CaBZ1*, *CaEREBP-C3*, *NtPRp27*, the *SAR8.2* protein precursor, putative trans-activator factor, malate hydrogenase, putative protein of auxin-repressed, xyloglu-canendo-1, 4-D-gucanase precursor, *LEA* protein 5 (*LEA5*), homologous *DNAJ* protein, *PR10* and *Stns LTP* [124,125]. cDNA microarray z1300 full-length cDNAs were used in *Arabidopsis* to identify cold stress-inducing genes and target genes of *DREB1A/CBF3*. Six genes were documented based on microarray and, in RNA gel blot analyses, it was observed that a novel *DREB1A* controls cold- and drought-inducible genes [43,126]. Furthermore, microarray with full-length cDNA was performed by 1300 full-length cDNAs and cDNA microarray to discover cold-induced genes. Previous reports exhibited the target genes of *DREB1A/CBF3* and stress-inducible gene expressions were controlled by transcription factors [76]; in contrast, stress-sensitive genes' expressions were reported as specific to the growth stage [42]. Full-length cDNA microarray is convenient for analyzing the *Arabidopsis* gene expression patterns under cold stress, and can also be used to identify the functional genes of stress-related TFs that are likely to act as DNA elements by merging the genomic sequence data with the expression data [76,127]. Additionally, cold stress is also induced by the increase in the proline content in plants (osmoprotectant). Microarray and RNA gel blot research found that the proline can induce the expression of several genes with the proline-responsive elements in their promoters (*PRE*, *ACTCAT*) [120,127,128]. Microarray analysis was carried out to detect the cold-inducible

*AP2* gene family transcription factor *RAV1* [129], which could control plant growth under stress. *RAV1* is down-regulated by epibrassinolide, and transgenic *Arabidopsis* overexpressing *RAV1* exhibits a rosette leaf and adjacent root growth retardation, although the early-flowering phenotype showed antisense to *RAV1* plants [130,131].

### 5. miRNAs and cDNA-Microarray Response to Salinity Stress

Salt intrusion from saline soils and irrigation water is one of the most severe and harmful risks to reduce agricultural production and adverse effects on cultivated land and the geographical distribution of plant species [70,132,133], coupled with oxidative stress [134]. The most imperative cations in saline soils are calcium, potassium, magnesium, and sodium, and the main anions in saline soils are chloride, bicarbonate, sulfate, nitrate, and carbonates. Other electrolytes causative to salinity are borane, molybdenum, strontium, silicon dioxide, aluminum cation, and barium ion [135,136]. Higher concentrations of sodium chloride (NaCl) typically affect plant development, metabolism, and physiology at various metabolic phases (ion toxicity, nutrient imbalance, and oxidative stress) [70,137]. Despite such advances in scientific research, it remains unclear about the underlying molecular mechanism of salinity responses in plants. However, based on the combination of microarray and inhibition subtractive hybridization (SSH), changes in the transcriptome profile caused by salt induction were studied and evaluated [138]. Investigation of complete transcriptomics suggests that these processes, such as the synthesis of osmolytes and ion carriers and the regulation of transcription and translation mechanisms, have distinctive reactions under salinity stress. In particular, the introduction of transcripts of specific TFs, ribosomal genes, RNA-binding proteins, and translation initiation and elongation factors has been testified [139,140].

Using cDNA microarray in *Synechocystis*, 19 genes were reported to be instantaneously regulated under salinity stress. The salt- and osmo-regulated genes, and some putative sensor molecules, have been implicated during salinity stress signaling [35]. Several differentially regulated miRNAs have been reported against salinity stress. In *A. thaliana*, several microRNAs are regulated against salinity stress, such as miR156, miR158, miR159, miR165, miR167, miR168, miR169, miR171, miR319, miR393, miR394, miR396, and miR397 (Table 3, Figure 2) [84]. In *Populus trichocarpa*, miR1445, miR1447, miR1446a-e, miR530a, and miR1711-n were down-regulated (Table 3) [141]. Arenas-Huertero et al. [31] reported, in *Proteus vulgaris*, the production of miRS1 and miR159.2 expression in response to salinity. Furthermore, miR169g and family members of miR169n were induced in saline-rich conditions [142]. However, there is a need to discover and annotate novel functional genes which have a probable function against salinity stress. Subsequently, a large number of genes in plants still have unknown functions [143]. Recent studies revealed that specific down-regulation of the bacterial-type *phosphoenolpyruvate carboxylase* (*PEPC*) gene *Atppc4* by artificial microRNA enhanced the salinity tolerance in *A. thaliana*. The increased salinity tolerance might be linked to enhanced *PEPC* activity [10,144]. Transcript control for salinity-tolerant rice with microarrays, like 1728 cDNAs from salinity-stressed roots libraries, was studied in response to high salinity (Table 3) [144–146].

A tiling path microarray was used to examine the high-throughput expression profiling patterns under various environmental stresses for all of the known miRNAs [16,70] (Tables 1 and 4). The analysis revealed that the effects of miRNAs under low-temperature, drought, and high salinity with miRNA chips represent, approximately, all of the reported miRNAs cloned or recognized in *A. thaliana* (L.). High salinity stress agitates homeostasis in water potential. Extreme changes in water homeostasis and ions lead to molecular breakdown, stunted growth, and even the death of cells or whole plants [16,147].

**Table 4.** Software and tools used for the detection of plant miRNA and cDNA microarray data analysis.

Software and Tools	Function	Website	Reference	Accessed
Software and tools used for detection of plant miRNA and data analysis				
MiPred	Random forest (RF)-based miRNA predictor, which can distinguish between real and pseudo-miRNA precursors	<a href="http://server.malab.cn/MiPred/">http://server.malab.cn/MiPred/</a>	[72]	5 November 2021
miBridge	Algorithm and database	<a href="http://sitemaker.umich.edu/mibridge/home">http://sitemaker.umich.edu/mibridge/home</a>	[148]	5 November 2021
miRTar	A novel rule-based model learning method for cell line specific microRNA target prediction	<a href="http://miRTar.mbc.nctu.edu.tw">http://miRTar.mbc.nctu.edu.tw</a>	[72]	5 November 2021
PolymiRTS	Linking polymorphisms in microRNAs and their target sites	<a href="http://compbio.uthsc.edu/miRSNP">http://compbio.uthsc.edu/miRSNP</a>	[149]	25 November 2021
miRGator	microRNA portal for deep sequencing, expression profiling and mRNA targeting	<a href="http://mirgator.kobic.re.kr">http://mirgator.kobic.re.kr</a>	[150]	10 November 2021
Bowtie	Aligns efficiently, and short-read aligners	<a href="http://bowtie-bio.sourceforge.net">http://bowtie-bio.sourceforge.net</a>	[72]	5 November 2021
miRBase	Provides handy and useful ID conversion tools	<a href="http://www.mirbase.org/">http://www.mirbase.org/</a>	[72]	25 November 2021
miRDB	miRNA target databases	<a href="http://www.mirdb.org">http://www.mirdb.org</a>	[151]	25 November 2021
mirDIP	Integrative database of microRNA target predictions	<a href="http://ophid.utoronto.ca/mirDIP">http://ophid.utoronto.ca/mirDIP</a>	[152]	25 November 2021
miRanda	Predict or collect miRNA targets	<a href="http://34.236.212.39/microrna/home.do">http://34.236.212.39/microrna/home.do</a>	[72]	25 November 2021
RNAhybrid	microRNA target prediction	<a href="https://bibiserv.cebitec.uni-bielefeld.de/rnahybrid">https://bibiserv.cebitec.uni-bielefeld.de/rnahybrid</a>	[72]	8 November 2021
miTALOS	Analyzes tissue specific microRNA function.	<a href="http://mips.helmholtz-muenchen.de/mitalos">http://mips.helmholtz-muenchen.de/mitalos</a>	[153]	5 November 2021
RNA22	microRNA target predictions	<a href="https://cm.jefferson.edu/rna22">https://cm.jefferson.edu/rna22</a>	[154]	5 November 2021
psRNATarget	Small RNA target analysis server	<a href="http://plantgrn.noble.org/psRNATarget/">http://plantgrn.noble.org/psRNATarget/</a>	[155]	5 November 2021
miRandola	Curated knowledge base of non-invasive biomarkers	<a href="http://mirandola.iit.cnr.it/">http://mirandola.iit.cnr.it/</a>	[155]	5 November 2021
ChIPBase	Decoding transcriptional regulatory networks of non-coding RNAs and protein-coding genes from ChIP-seq data	<a href="http://rna.sysu.edu.cn/chipbase/">http://rna.sysu.edu.cn/chipbase/</a>	[155,156]	1 October 2021
MirGeneDB	Curated miRNA gene database	<a href="http://mirgenedb.org/">http://mirgenedb.org/</a>	[157]	28 November 2021
TarHunter	Predicting conserved microRNA targets and target mimics in plants	<a href="http://tarhunter.genetics.ac.cn">http://tarhunter.genetics.ac.cn</a>	[158]	28 November 2021
TissueAtlas	Tissue specificity miRNA database	<a href="https://ccb-web.cs.uni-saarland.de/tissueatlas/">https://ccb-web.cs.uni-saarland.de/tissueatlas/</a>	[72]	28 November 2021
miRNAme Converter	miRNA ID converter	<a href="http://163.172.134.150/miRNAmeConverter-shiny">http://163.172.134.150/miRNAmeConverter-shiny</a>	[159]	28 November 2021

Table 4. Cont.

Software and Tools	Function	Website	Reference	Accessed
Software and tools used for detection of plant microarray and data analysis				
Array Designer	Design primers and probes for oligo and cDNA expression microarrays.	<a href="http://www.premierbiosoft.com/dnamicroarray/index.html">http://www.premierbiosoft.com/dnamicroarray/index.html</a>	[160]	1 November 2021
Stanford Microarray Database SMD	Stores raw and normalized data from microarray experiments	<a href="http://smd-www.stanford.edu/download/">http://smd-www.stanford.edu/download/</a>	[161]	1 November 2021
eArray	Designing Agilent arrays	<a href="http://earray.chem.agilent.com/earray/login.do">http://earray.chem.agilent.com/earray/login.do</a>	[160]	1 November 2021
Significance Analysis of Microarrays	Adjustments for multiple testing, statistical analysis for discrete, quantitative, and time series data, gene set enrichment analysis	<a href="http://www-stat.stanford.edu/~tibs/SAM/">http://www-stat.stanford.edu/~tibs/SAM/</a>	[162]	5 November 2021
Visual OMP	Design software for RNA, DNA, single or multiple probe design, microarrays, Taq Manassays, genotyping, single and multiplex PCR, secondary structure simulation, sequencing, genotyping.	<a href="http://www.dnasoftware.com/Products/VisualOMP">http://www.dnasoftware.com/Products/VisualOMP</a>	[160]	5 November 2021
caArray	Open-source, web and programmatically accessible microarray data management system that supports the annotation of microarray	<a href="http://caarray.nci.nih.gov/">http://caarray.nci.nih.gov/</a>		5 November 2021
Gene Expression Model Selector	Diagnostic models and biomarker discovery	<a href="http://www.gems-system.org/">http://www.gems-system.org/</a>	[163]	18 November 2021
Gene index	Gene Index Project is to use the available EST and gene sequences, along with the reference genomes, to provide an inventory of likely genes and variants.	<a href="http://compbio.dfci.harvard.edu/tgi/plant.html">http://compbio.dfci.harvard.edu/tgi/plant.html</a>	[160]	5 November 2021
Genesis	Java package of tools to simultaneously visualize and analyze a whole set of gene expression experiments	<a href="http://genome.tugraz.at/genesisclient/genesisclient_description.shtml">http://genome.tugraz.at/genesisclient/genesisclient_description.shtml</a>		18 November 2021
RMA Express	Standalone GUI program for Windows, OS X and Linux to compute gene expression summary values for Affymetrix	<a href="http://rmaexpress.bmbolstad.com">http://rmaexpress.bmbolstad.com</a> <a href="http://www.r-project.org">http://www.r-project.org</a> <a href="http://www.bioconductor.org">http://www.bioconductor.org</a>		18 November 2021
dCHIP	Model-based expression analysis for Affymetrix gene expression arrays	<a href="http://www.dchip.org">http://www.dchip.org</a>	[164]	18 November 2021
TM4	Microarray Data Manager (MADAM), TIGR Spotfinder, Microarray Data Analysis System (MIDAS), and Multi experiment Viewer (MeV)	<a href="http://www.tm4.org/">http://www.tm4.org/</a>	[164]	18 November 2021

Table 4. Cont.

Software and Tools	Function	Website	Reference	Accessed
Able Image Analyser	Software for image analysis. It enables dimensional measurements: distance, area, angle in digital images	<a href="http://able.mulabs.com">http://able.mulabs.com</a>	[160]	18 November 2021
ImaGene	Unique, robust, room-temperature preservation solutions for nucleic acids, biospecimens and bioreagents for in the living ectors	<a href="http://www.biodiscovery.com/index/imagene">http://www.biodiscovery.com/index/imagene</a>	[160]	13 November 2021
Spotfinder	Custom-designed cDNA array, the chips are scanned using a microarray scanner	<a href="http://www.tm4.org/spotfinder.html">http://www.tm4.org/spotfinder.html</a>	[164]	18 November 2021
SNOMAD	Web-based tool and has various normalization options for two-channel and single-channel experiments	<a href="http://pevsnerlab.kennedykrieger.org/snomadinput.html">http://pevsnerlab.kennedykrieger.org/snomadinput.html</a>	[164]	18 November 2021
Multiexperimet Viewer	Cloud-based application supporting analysis, visualization, and stratification of large genomic data	<a href="http://www.tm4.org/mev.html">http://www.tm4.org/mev.html</a>		18 November 2021
Onto-Express and Pathway-Express	Automatically translates DE gene transcripts from microarray experiments into functional profiles characterizing the impact of the condition studied	<a href="http://vortex.cs.wayne.edu/projects.htm">http://vortex.cs.wayne.edu/projects.htm</a>	[164]	13 November 2021
DAVID/EASE	Database for annotation, visualization and integrated discovery (DAVID) is an online tool for annotation and functional analysis. Expression analysis systematic explorer (EASE)	<a href="http://david.abcc.ncifcrf.gov">http://david.abcc.ncifcrf.gov</a>	[164]	13 November 2021

Oligo-DNA microarrays were developed in common wheat, and these microarrays were designed to include approximately 32,000 distinctive genes characterized by several expressed sequence tags (ESTs). To classify the salinity-stress responsive genes, the expression profiles of transcripts that responded to stress were examined using microarrays. It was concluded that 5996 genes were verified by more than a 2-fold change in expression. These genes were categorized into twelve groups based on gene expression patterns [165]. Transcription-regulator activity, DNA binding, and the genes' assigned transcription factor functions were preferentially classified as immediate response genes. In wheat, candidate genes were identified as involved in salinity-stress tolerance [165,166]. These genes are active in the regulation of transcription [112,143] and the signal transduction that is engaged in metabolic pathways [167] or acting as ion transporters [168]. cDNA library in yeast (*Saccharomyces cerevisiae*) was examined using a synthetic medium augmented with excessive salt concentrations (900 mM). A few clones showed comparatively improved growth. The notorious clones bore the *Guanylyl transferase* (OsMPG1) mannose-1-phosphate gene [133]. Extreme salinity stress was significantly linked with the transcription factors of four tomato genes from the family of *zinc finger*. There has been prior evidence of the relationship between *zinc finger* transcription factors and plant salinity tolerance [169,170]. Overexpression of *OSISAP1* in transgenic tobacco resulted in tolerance to salinity, dehydration, and cold stress in the new sprouts [171].

A microarray containing 384 genes associated with stress responses was used in *Medicago truncatula* genotypes (*Jemalong A17* and *108-R*) to compare rooting gene expression during salt stress. The homolog of flora *TFIIIA*-related TF, *MtZpt2-1*, and *COLD-REGULATED1* genes were known to regulate the previous genes and were acknowledged in *Jemalong A17* stress-tolerant genotypes. Two *MtZpt2* Transcription factors (*MtZpt2-1* and *MtZpt2-2*) have shown increased expression in the roots compared to *108-R* [172]. Salinity stress is attributed to diverse stresses that persuade overlapping patterns in gene expression. For example, in an investigation of 8100 *A. thaliana* genes, approximately 2400 genes were reported to have a widespread expression in exposure to salt, oxidative and cold stress [92]. In addition, 23 genes were reported against NaCl stress. This also accounted for a small percentage of DEGs, including encoding transcription factors *WOX2* and *BZIP3*, calcium-binding protein *CML42*, ubiquitin-protein ligase *UBC17*, and *IDA-like 5* protein [92]. Most prominently, synthesized *isiA* encoded a novel chlorophyll (*Chl*)-binding protein [173] (Table 3).

## 6. Potential Role of Bioinformatics in the Prediction of miRNA and cDNA Microarray

Next-generation sequencing methods are crucial in gene expression profiling, epigenomics, genomics, and transcriptomics. These tools can sequence multiple DNA molecules within a short period. The recent introduction of innovative “-omics” technologies, such as metabolomics, proteomics, and genomics allows for analyzing and identifying the genetic elements that contribute to system complexity [72,90,174,175]. Bioinformatics tools developed for miRNA prediction include miRNA target prediction, analysis, and structure prediction. For example, miRanda, RNAhybrid, RNA22, and TarHunter detect miRNA expression and perform analysis based on miRNA-Seq data (Table 4). Existing plant miRNA prediction tools lack a cross-species conservation filter and eTM prediction function. TarHunter features a strict cross-species conservation filter and the capability of predicting eTMs [158]. Despite ongoing progress, bioinformatics prediction of microRNA targets remains difficult, since current tools have a lack of accuracy and sensitivity. [72,176]. Microarrays are an effective method for determining the quantity of RNA in a sample. Since microarray data have computational complexity and contain hundreds of genes, statistical and bioinformatics methods are required for data interpretation [160]. These specialized tools provide statistical analysis, sample comparisons, and functional interpretation of data generated in a series following visualization and normalization in a microarray study, such as Array Designer, eArray, Visual OMP, caArray, and dCHIP (Table 4). The software, including Able Image Analyser, Gene pix pro-6.0, and GeneChip operating software, are used for analyzing images in order to obtain the intensity at each spot and quantify the expression for each transcript. Additionally, this also provides different types of discoveries by comparing gene expression data with already reported biological information, such as protein–protein interactions, pathway analysis, transcription factor binding sites, and network analysis tools, including Array Designer, eArray, Significance Analysis of Microarrays, Gene Expression, and Model Selector (Table 4) [164].

## 7. Conclusions and Future Perspectives

MicroRNAs (miRNAs) have been considered a potential target in genetic engineering against abiotic stresses in plants. Thus, miRNAs can also be utilized in the initial monitoring and transmission of abiotic stresses, and to elucidate the genetic and physiological responses against stress in plants. This review summarized current developments and the history of miRNAs and microarray with diverse functions in several stress responses, predominantly abiotic stresses. Many traditional approaches have identified significant numbers of miRNAs in plants from various organisms. Microarray-based genomic technologies for ecological studies have received great attention, particularly in plants, to disclose the role of stress-responsive loci in plants. DNA microarrays provide a novel insight into the cell and provide a solution for several problems from the viewpoint of analytical calculation, despite the inconceivable amount of work done in

the last two decades to reduce the different sources of uncertainty on the subsequent measurements. The review will provide valuable insight to plant researchers, especially plant breeders and stress physiologists, to design a comprehensive strategy to cope with environmental stresses.

The elucidation of miRNA responses to abiotic stresses may lead to the development of technologies for the early detection of plants' environmental stressors. MicroRNAs and cDNA-microarrays are powerful targets for engineering abiotic stress tolerance in transgenic plants. The field of bioinformatics is developing rapidly, and it is inevitable to progress in plant genomics and breeding without integrating the latest bioinformatics tools. Multiple advanced sequencing and bioinformatics tools were established to identify miRNAs and their target gene network and prediction. As the understanding of the function of miRNAs under stress deepens, the potential use of miRNA mediated genes to enhance plant tolerance will also increase. In the future, the large-scale microarrays might be substituted with small biosensors which contain a unique or a small number of novel microbes deposited on an electronic platform. We would like to conclude by illustrating the existing gap between the detection of stress-regulated miRNAs and microarray to validate their role. In conclusion, we recommend the utilization of miRNAs for the identification and classification of new functional genes conferring a significant functional role in stress tolerance and to exploit the unexplained fraction of genes further.

**Author Contributions:** T.P. and M.W.A.: have made substantial contributions to formulate, Drafting and retrieve data, A.E.-k.; revised and improved the technical language S.-H.N.; Revised and improved the MS, H.X.W.; Final approval and revised for publication. All authors have read and agreed to the published version of the manuscript.

**Funding:** This work is funded by the National Natural Science Foundation of China (31870651).

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Not applicable.

**Conflicts of Interest:** The authors declare no conflict of interest.

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