

Review



Progressive Genomic Approaches to Explore Drought- and Salt-Induced Oxidative Stress Responses in Plants under Changing Climate

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Abstract: Drought and salinity are the major environmental abiotic stresses that negatively impact crop development and yield. To improve yields under abiotic stresses conditions, drought- and salinity-tolerant crops are key to support world crop production and mitigate the demand of the growing world population. Nevertheless, plant responses to abiotic stresses are highly complex and controlled by networks of genetic and ecological factors that are the main targets of crop breeding programs. Several genomics strategies are employed to improve crop productivity under abiotic stress conditions, but traditional techniques are not sufficient to prevent stress-related losses in productivity. Within the last decade, modern genomics studies have advanced our capabilities of improving crop genetics, especially those traits relevant to abiotic stress management. This review provided updated and comprehensive knowledge concerning all possible combinations of advanced genomics tools and the gene regulatory network of reactive oxygen species homeostasis for the appropriate planning of future breeding programs, which will assist sustainable crop production under salinity and drought conditions.

Keywords: salt; drought; plants; ROS; genomics; approaches; integration

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1. Introduction

Global crop productivity is restricted due to abiotic stresses such as drought, salinity, flooding, nutrient deficiency, and environmental toxicity. Among these abiotic stresses, salinity and drought are the most severe constraints for sustainable agriculture on a global scale. Nearly 7% of terrestrial land is affected by salinity [1], while drought is widespread and increasingly common in recent years due to climate change. Altogether, salinity- and drought-affected lands cover approximately 10.5 and 60 million km², respectively [2]. Furthermore, climatic changes worsen the frequency and intensity of water shortages in subtropical areas of Asia and Africa. As stated by the UN climatic report



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Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations. [http://www.solcomhouse.com/drought.htm; accessed date on 12 July 2021], rising temperatures are melting the Himalayan glaciers that feed Asia's largest rivers (Indus, Ganges, Brahmaputra, Yangtze, Mekong, Salween, and Yellow), and those glaciers may disappear by 2035. Additionally, long-term trends indicate that the progressive proliferation of salinity has caused the dilapidation of arable land [3]. For instance, in California, over the last century, 4.5 out of 8.6 million hectares of wetted agricultural land have become salt-affected [4]. Currently, it has become a pertinent problem for crop production [5], mostly in arid and semiarid areas.

Based on numerous estimations, the world population will increase to over 9.7 billion by 2050, which will continue to exacerbate current global food insecurity issues. It is estimated that, over the past 50 years, improved crop productivity has brought about an increase in world food production by up to 20% per capita and decreased the proportion of food-insecure people existing in developing countries from 57% to 27% of the world population [6]. As a result, crops will need to cope with abiotic stresses such as drought and salinity and double productivity to further diminish food insecurity and support the growing human population in more ecologically sustainable ways.

Both drought and salinity stresses induce cellular dehydration, which causes osmotic stress, removal of water from the cytoplasm into the apoplast, and eventually evaporation into the atmosphere [2]. Moreover, early responses to salt stress and drought are comparable in plants. For example, plant cells prevent water loss by increasing the ionic constituents and decreasing the osmotic potential in stressed cells. Due to the similar mechanisms of the stress response in plants, it appears that drought and salinity tolerance mechanisms might be functionally interchangeable [7]. It is well known that stress response mechanisms involve several particular physiological and biochemical pathways that allow plants to adapt to unfavorable conditions. A number of abiotic stress factors, such as salinity, drought, high temperatures, and osmotic stresses, lead to the overproduction of reactive oxygen species (ROS), which cause serious cellular damage and hamper photosynthesis. To protect or repair these injuries, plant cells use an intricate defense system, including a number of antioxidative stress-related defense genes that, in turn, prompt changes in the biochemical plant machinery [8]. ROS production and antioxidant regulation all occur in a synergistic, additive, or antagonistic way and are associated with the control of oxidative stress.

Nevertheless, plant stress response mechanisms are controlled by convoluted networks that are determined by environmental and genetic factors that are often difficult to untangle, thereby impeding traditional breeding approaches [9]. Considering that the conventional breeding strategies for crop improvement are largely aimed at improving yield to meet the demands of an ever-growing world population, breeders have to implement innovative approaches in agriculture to combine high-yield and abiotic stress-tolerant traits in crops [10]. Recent scientific advances and the abovementioned challenges in agriculture have directed the development of high-throughput techniques to pursue and take advantage of plant genome research for the improvement of stress-tolerant crops. Thus, these genomics approaches focus on the entire genome, involving genic and intergenic positions, to attain new insights into the functional and molecular responses of plants, which will sequentially offer specific techniques for crop plant improvement. Recently, many scientists have revealed promising outcomes toward understanding the molecular mechanisms of abiotic stress tolerance in prospective crops using progressive molecular biology practices [10–21]. The mechanisms involved in crop salt and drought stress responses are discussed in Figure 1. In this review, we described in detail how to mine the functional genes involved in drought and salt response in plants, using methods such as traditional QTL, transcriptomic analysis, and GWAS. Then, we explored approaches such as epigenetic regulators, gain-of-function, RNAi, TALENs, ZFNs, CRISPR, base editing, and primer editing for functional verification with an example of target genes generated by the aforementioned approaches. Finally, we summarized the methods for generating salt and drought-tolerant crops. The review aimed to offer comprehensive knowledge for improving salt- and drought-tolerant crops using modern genomics strategies regarding



ROS regulatory networks. The overview of earlier studies on the advancement of genomics approaches will help in the investigation of upcoming research instructions for improving salt- and drought-tolerant crops.

Figure 1. The mechanisms involved in crop salt and drought stress responses.

2. Mining Approaches for Salt and Drought Stress Response Genes

To improve drought and salinity stress tolerance in crops, we first require comprehensive knowledge concerning the complex mechanisms of plants that respond to stresses. Detecting the genes/markers/QTL regions associated with drought and salinity stress responses is the first crucial step toward reaching the required understanding for breeding drought and salinity stress-tolerant crop varieties. For the discovery of a gene, various strategies are available in both model and nonmodel crops; here, some of the most advanced are discussed briefly.

2.1. Quantitative Trait Loci (QTL) Analysis

A quantitative trait locus (QTL) is a gene or a region of DNA that is associated with the variation of a quantitative/phenotypic trait that must be polymorphic to affect the biological population. QTL mapping has been a powerful tool for dissecting genetic variants underlying quantitative traits in numerous biological studies and breeding programs. There are two primary concerns when using QTL mapping. One is the power for QTL identification under a controlled false-positive rate, and the other is the accuracy of QTL localization [22]. QTL mapping has been applied as a technique for identifying genomic regions significantly correlated with grain output and various genetically intricate characteristics in cereal crops. This technique is particularly powerful when genetic variation is studied concerning numerous complex traits, where it is possible to identify and differentiate genomic regions that contribute to different characteristics of interest. The data relevant to QTL mapping can be conducive to enhancing the genetic potential of crops via marker-assisted breeding [23]. Currently, scientists can link the molecular mechanisms of genes found in QTLs to demonstrate the genetic and physiological basis of traits such as grain yield. A nice example of this cooperation of QTL mapping, trait scoring, and breeding can be found in using green coloration as a metric of drought resistance in sorghum. The genetic dissection of molecular QTLs associated with green coloration during drought lends convenience to demonstrate the basic mechanisms of physiology and investigate the molecular causes of drought tolerance in sorghum and different grasses [24]. Reducing the genomic sizes of QTLs facilitates enhanced targeting of pertinent genomic regions. Improving the fine mapping of QTLs improves the efficiency with which breeders can understand the significance and mechanisms of QTLs relevant to their traits of interest [24]. Enhanced QTL mapping is particularly relevant when deconvolving complex genomic regions. For example, hypostasis of alleles within QTLs, QTL-QTL genetic interactions, context-dependent activities of QTLs, and the QTL marker position itself impact the articulation of a complex trait such as the yield of grain under drought stress [25]. Interestingly, fine mapping of QTLs revealed that an individual main QTL controlling membrane potential vastly improved marker-assisted selection for salinity-stressed barley [26]. Thus, fine QTL mapping is required for marker-aided QTL pyramiding to improve drought tolerance [27]. Identification of QTLs for abiotic stress tolerance suggests augmentations that can be used for further genomics studies toward the detection of noble genes of salt and drought tolerance to develop a new variety [28]. Several examples of QTLs (quantitative trait loci) for improving crop plant production under salinity and drought stresses are discussed in Table 1.

Table 1. Known QTLs (quantitative trait loci) for improving crop plant production under salinity and drought stresses.

| Stresses | Crops | Major Effect/Finding | References |
|--------------------------------------|--------------------------|---|------------|
| Drought stress | Cowpea | Detected QTL relevant to salt-tolerant and sensitive varieties | [29] |
| Drought stress | Wheat | Detected genetic loci to major morpho-physiological traits, components of yield, and grain yield | [30] |
| Salinity | Barley | Detected QTLs related to stomatal and photosynthetic traits associated with salinity tolerance | [31] |
| Drought | Sorghum | Identified QTLs associated with flowering and drought resistance | [24] |
| Drought | Rice | Improved crop yield under drought tolerance | [25] |
| Drought and submergence tolerance | Rice (TDK1) | Drought and submergence tolerance and yield stability | [25] |
| Drought and flood | Rice | Detected drought and salinity tolerance varieties based on developmental and physiological traits | [32] |
| Salinity | Rice (Pusa Basmati 1121) | Detected two QTLs for drought and one QTL for salt stress | [32] |
| Drought | Upland rice | Identified QTLs relevant to leaf rolling, leaf drying, leaf relative water content, and relative growth rate under water stress | [33] |

2.2. Forward Genetics and the Candidate Gene Strategy

Crop plants with stress tolerance have been generated by the transference of genes/loci from definite donor parents, either through a forwarding genetics method that includes the determination of a gene function linked with a phenotype or the identification of novel stress-tolerant donor lines created by the use of mutagenesis. In contrast, reverse genetic breeding approaches could offer an understanding of gene functions and struc-

ture/sequence information to predict traits for adapting stress-tolerant cultivars using transgenic and advanced breeding tools. In genomic studies, researchers have implemented these approaches for the genetic improvement of various model and nonmodel species toward salt and drought stress tolerance [34–41].

2.3. Transcriptomics Analysis

Transcriptome analysis refers to the study of the transcriptome of the entire set of RNA transcripts that are generated by a genome, under given times and circumstances or in a specific cell. Transcriptomic analysis techniques play a crucial role in the identification of candidate gene functions and pathways that respond to specific environments [42]. In the last decade, universal transcriptome analysis approaches have been particularly advantageous for functional genomic studies that offer comprehensive molecular mechanisms of certain phenomena. Primarily, a global transcriptome study was initiated with suppression subtractive hybridization (SSH) and cDNA-AFLP and acquired a quantum dive to RNA-seq with the progression of NGS platforms [10]. The information content of an organism is held in its genome and articulated through transcription. The basic purposes of transcriptomics are to record the transcription of all species, including mRNAs, noncoding RNAs, and small RNAs; to determine the transcriptional configuration of genes in terms of their start sites, 5' and 3' ends, splice variants, and other posttranscriptional modifications; and to calculate the varying expression patterns of every transcript throughout development and under diverse conditions [40,41]. Currently, transcriptome profiling has progressed into nearly all organisms and represents how information attained from sequence data can be converted into a wide knowledge of gene functionality [42]. Plant stress-response mechanisms frequently employ the use of transcription factors (TFs). A TF is a protein that targets, typically, multiple genes that comprise a regulon and influences their expression patterns. Thus, TFs are a powerful tool for the genetic regulation of many downstream genes and processes, including abiotic stress responses [43]. In the case of salt and drought stress, transcripts related to the upregulation of vital biochemical pathways required for cellular osmotic balance, abscisic acid, and cellular water uptake are controlled by TFs [44]. The role and example of various transcription families through transcriptome analysis relevant to salt and drought stress tolerance are discussed in Table 2.

| SL No. | TF Family | Gene ID | Crop Variety | Target Stresses | References |
|--------|------------------|------------------------|------------------------------|------------------------|------------|
| 1 | AP2/EREBP | TaERF3 | Triticum aestivum | Drought, Salt | [45] |
| 2 | bZIP | GmbZIP1, | Glycine max | Drought, Salinity, | [46] |
| 3 | MYB/MYC | StMYB1R-1 | Solanum tuberosum | Drought | [47] |
| 4 | NAC | OsNAC5, GmNAC20 | Oryza sativa, Glycine max | Drought | [48,49] |
| 5 | WRKY | TaWRKY44 AREB1, | Triticum aestivum | Drought, Salt | [50] |
| 6 | AREB/ABF | AREB2/ABF4 and ABF3 | Arabidopsis thaliana, | Drought | [51] |

Table 2. Identification of different TF families through transcriptome analysis relevant to salt and drought stress tolerance.

2.4. Association Mapping

In genetics studies, association mapping (also well known as linkage disequilibrium mapping) refers to the regular genome-wide distribution of several genes together with other measurable loci (markers) in predicting marker-trait relatives [52] applied in various crops, including rice, barley, maize, sorghum, and wheat, to identify the significant genes or markers that confer a given trait [53]. Numerous genes have been indicated as being connected with abiotic resistance by applying association mapping [54]. It has also been applied to inquire about the limitations within focused parameters and molecular markers in different crops [55]. Association mapping is extremely efficient in experimental varieties with complex or unknown genotypes or those that have a large regeneration time.

Association mapping of drought-related varieties in barley was applied to terminate a conventional biparental system of QTL mapping [56]. Furthermore, association mapping has been used to progress the development of QTL maps [57]. A detailed discussion on the association mapping for the sustainability of crop production under salinity and drought stresses is available in Table 3.

Table 3. Association mapping for improving crop production under salinity and drought stresses.

| Stresses | Crops | Target Gene | Major Findings | References |
|----------|-----------------------------------|---|---|------------|
| Salinity | Cowpea (Vigna unguiculata (L.) | | Association mapping for salt tolerance at germination and seedling stages and the identification of SNP markers associated with salt tolerance in cowpea | [58] |
| Drought | Wheat | RM223 | Demonstrated a strong power of joint association analysis and linkage mapping for the identification of important drought response genes in wheat | [59] |
| Salinity | Cotton (Gossypium hirsutum L.) | | Provided reference data for the use of MAS for salt tolerance in cotton | [55] |
| Salinity | Cotton (Gossypium arboretum) | (<i>Cotton_A_</i> 37775 and <i>Cotton_A_</i> 35901) | Provided fundamental information to produce novel salt-tolerant cultivars | [54] |
| Drought | Pearl Millet | PMiGAP | Development of high-yielding drought- and submergence-tolerant rice varieties using marker-assisted introgression | [60] |

2.5. Genome-Wide Association

GWAS (genome-wide association study) is a potent presumption-free method used to identify and dissect the genetic regions associated with a certain trait. Typically, GWAS is performed by scoring the phenotypes and sequencing many individuals to link genotype to phenotype, thereby linking genetic variants to a given trait (Figure 2) [61].



Figure 2. Connection of genotype to phenotype variation.

GWAS applies large markers and several populations of non-cross-executed lines to provide larger mapping exploration than traditional QTL mapping based on a crossevolved segregating population, leading to the detection of unknown or unexpected genes. It has been applied to separate complicated genetic parameters in leading crops such as rice and wheat under salt and drought stress. Additionally, GWAS has been effectively conducted to designate QTLs for particular characteristics in wheat (e.g., grain yield, morphology relevant to leaf rust disease, and end-usage quality), thereby applying various systems of molecular markers to bolster breeding resources [62,63]. GWAS has detected more than 2000 loci for simple human diseases to date [64]. Therefore, compared with QTL mapping, GWAS delivers an in-depth, cost-efficient mode of gene investigation and detection of molecular markers.

GWAS focused on the flowering period of saline-treated rice identified 11 loci bearing 22 important SNPs linked to stress responses. The potential genetic determinant of germination was identified on chromosome one, close to the saline conditional QTL regulating Na⁺ and K⁺ levels. Approximately 1200 candidate genes linking development to sodium and potassium ion allowances were detected [65]. Thus, GWAS offered an informed list of candidates for saline tolerance-connected gene cloning and uncovered responsive genetic elements relevant to salt stress [66]. GWAS is also important to perceive the genetic architecture of complex characteristics to improve drought tolerance [67]. Recently, "No-Genome-Required-GWAS" approaches have provided easy and efficient identification of genetic variants underlying phenotypic variation in plants [68]. Details on genome-wide association mapping for identifying QTLs under salinity and drought stresses are discussed in Table 4.

Table 4. Genome-wide association mapping for identifying QTLs under salinity and drought stresses.

| Heat proneSpring wheatYield stability[69]Heat proneSpring wheatIdentified QTL containing promising candidate genes related toIdentified QTL containing promising candidate genes related toDroughtRice (indica and japonica)drought[70]tolerance by osmotic stress adjustmentProvided a comprehensive view of AS under salt stress and[71]Salt stressArabidopsis thalianarevealed novel insights into the[71]potential roles of AS in plant response to salt stress[65]SalinityRiceCandidate genes can be identified by QTL[65]DroughtBarley (Hordeum spontaneum)in wild progenitors with expected ecological and economic applications[72] | References | Major Effect/Finding | Crop Variety | Stresses |
|---|-----------------|---|------------------------------|-------------|
| DroughtRice (indica and japonica)Identified QTL containing promising candidate genes related to drought[70]DroughtRice (indica and japonica)tolerance by osmotic stress adjustment Provided a comprehensive view of AS under salt stress and revealed novel insights into the potential roles of AS in plant response to salt stress[71]SalinityRiceCandidate genes can be identified by QTL[65]DroughtBarley (Hordeum spontaneum)in wild progenitors with expected ecological and economic applications[72] applications | [69] | Yield stability | Spring wheat | Heat prone |
| DroughtRice (indica and japonica)drought[70]tolerance by osmotic stress adjustmenttolerance by osmotic stress adjustmentProvided a comprehensive view of AS under salt stress andSalt stressArabidopsis thalianarevealed novel insights into the[71]potential roles of AS in plant response to salt stresspotential roles of AS in plant response to salt stress[65]SalinityRiceCandidate genes can be identified by QTL[65]DroughtBarley (Hordeum spontaneum)in wild progenitors with expected ecological and economic applications[72]applicationsA compact of can didate genes can be identified by and contained[72] | related to | Identified QTL containing promising candidate genes related t | , , | - |
| Salt stress Arabidopsis thaliana Provided a comprehensive view of AS under salt stress and revealed novel insights into the [71] [71] Salt stress Arabidopsis thaliana revealed novel insights into the potential roles of AS in plant response to salt stress [65] Salinity Rice Candidate genes can be identified by QTL [65] Drought Barley (Hordeum spontaneum) in wild progenitors with expected ecological and economic applications [72] A server set of served id to server dide to server a dide to | [70] | drought | Rice (indica and japonica) | Drought |
| Salt stress Arabidopsis thaliana Provided a comprehensive view of AS under salt stress and revealed novel insights into the potential roles of AS in plant response to salt stress [71] Salinity Rice Candidate genes can be identified by QTL [65] Drought Barley (Hordeum spontaneum) in wild progenitors with expected ecological and economic applications [72] | | tolerance by osmotic stress adjustment | | |
| Salt stress Arabidopsis thaliana revealed novel insights into the potential roles of AS in plant response to salt stress [71] Salinity Rice Candidate genes can be identified by QTL [65] Drought Barley (Hordeum spontaneum) Exploring the genomic basis of reproductive success under stress in wild progenitors with expected ecological and economic applications [72] | ess and | Provided a comprehensive view of AS under salt stress and | | |
| Salinity Rice Candidate genes can be identified by QTL [65] Drought Barley (Hordeum spontaneum) Exploring the genomic basis of reproductive success under stress in wild progenitors with expected ecological and economic applications [72] | [71] | revealed novel insights into the | Arabidopsis thaliana | Salt stress |
| Salinity Rice Candidate genes can be identified by QTL [65] Drought Barley (Hordeum spontaneum) Exploring the genomic basis of reproductive success under stress in wild progenitors with expected ecological and economic applications [72] | ess | potential roles of AS in plant response to salt stress | | |
| Drought Barley (Hordeum spontaneum) Exploring the genomic basis of reproductive success under stress in wild progenitors with expected ecological and economic applications [72] | [65] | Candidate genes can be identified by QTL | Rice | Salinity |
| Drought Barley (<i>Hordeum spontaneum</i>) in wild progenitors with expected ecological and economic [72] applications | der stress | Exploring the genomic basis of reproductive success under stress | | |
| applications | momic [72] | in wild progenitors with expected ecological and economic | Barley (Hordeum spontaneum) | Drought |
| Λ and set of an didate mass of a set of the set of t | | applications | | |
| A core set of candidate genes encoding proteins with a putative | putative | A core set of candidate genes encoding proteins with a putativ | | |
| Drought Willow (paper-mulberry) function in drought response was [73] | [73] | function in drought response was | Willow (paper-mulberry) | Drought |
| identified | | identified | | |
| Salinity Wild barlow Across many traits, QTLs that increased phenotypic values were | lues were | Across many traits, QTLs that increased phenotypic values we | Wild barlow | Salinity |
| identified | [/+]. | identified | whice barriey | Samily |
| Salinity Rice Unveiled genomic regions/candidate genes regulating salinity | z salinity [75] | Unveiled genomic regions/candidate genes regulating salinity | Rico | Salinity |
| stress tolerance in rice | [75] | stress tolerance in rice | Kite | Samily |
| Drought Alfalfa (Medicage cative L) Improved alfalfa cultivars with enhanced resistance to drought | drought [76] | Improved alfalfa cultivars with enhanced resistance to drough | Alfalfa (Medicago satima L) | Drought |
| and salt stresses | [70] | and salt stresses | Allalla (Meulcugo Sullou L.) | Dibugin |
| Drought-induced alterations to DNA methylation that may | at may | Drought-induced alterations to DNA methylation that may | Rico | Drought |
| influence epigenetics | | influence epigenetics | Kite | Dibugin |
| Drought Wheat Thirty-seven of the significant marker-traits were detected under | ted under [67] | Thirty-seven of the significant marker-traits were detected under | Wheat | Drought |
| the drought-stressed condition | [07] | the drought-stressed condition | willeat | Diougin |
| Drought Wheat Identified a QL on chromosome 4H [78] | [78] | Identified a QL on chromosome 4H | Wheat | Drought |

2.6. Next-Generation Sequencing

Sequencing technologies include several techniques that generally consist of template preparation, sequencing and imaging, and data analysis [79]. Next-generation sequencing (NGS) integrates technologies that inexpensively and efficiently produce millions of short DNA sequence reads mainly in the range of 25 to 700 bp in length [80]. These technologies have made it possible for scientists to investigate crops at the genomic and transcriptomic levels to assist diversity analysis and marker-assisted breeding [80]. The relevance of NGS appears to be endless, permitting quick presses forward in numerous fields associated with the biological sciences. NGS has also afforded a wealth of knowledge for biology studies via end-to-end whole-genome sequencing of a broad diversity of organisms [81]. Whole-genome sequence studies have focused particularly on detailed information on genomics criteria, including regulatory sequences, coding and noncoding genes, GC content,

and repetitive elements, which would be utilized in functional characterization, such as microarray or tiling arrays. Additionally, NGS can be used to address many remaining biological questions by means of resequencing targeted areas of concern or whole genomes (as is being performed for the human genome [82]), *de novo* assemblies of bacterial and lower eukaryotic genomes, cataloging the transcriptomes of cells, tissues, and organisms (RNA sequencing), genome-wide profiling of epigenetic markers and chromatin structure using additional seq-based methods (ChIP-seq, methyl-seq, and DNase-seq), and species classification and/or gene discovery by metagenomics studies [50].

3. Functional Genomics Approaches

After identifying a QTL/allel/gene, the next sensible step is to characterize the gene before incorporation into a cultivar by studying several physiological, molecular, and biochemical pathways of genes. Thus, functional genomics approaches were extensively implemented to determine the gene functions and the connections between genes in a regulatory network that would be utilized to produce improved crop varieties. Consequently, there have been multiple tools developed for the characterization of gene function; some of the most exploited are described briefly.

3.1. Epigenetic Regulators

In wider definitions, the term 'epigenetics' frequently refers to a type of overall nongenetic (unrelated to DNA sequence per se) heredity at various levels. That is, epigenetics illustrates a number of dissimilar methods of genetic regulation whose temporal and heritable constituents have not in all cases been decided [83]. For example, methylation of DNA generally interferes with gene expression by way of gene silencing [84]. The reduction of methylation in resistance-associated genes activates chromatin and the expression of genes, which offers long-term or enduring resistance under stress conditions [85]. Epigenetics sustains the identity of stress memory in plants, which helps pre-exposed plants fight comparable stress throughout subsequent exposures. Histone modifications, DNA methylation and demethylation, and ATP-dependent chromatin remodeling are some of the epigenetic changes performed by plants during drought stress [86]. Epigenetic responses to drought stress have been studied in numerous plants, particularly the stress memory and gene activation marker H3K4me3, which has been used to carry out genome-wide ChIPseq analyses in Arabidopsis [87]. Furthermore, the HAT genes in rice (OsHAC703, OsHAG703, OsHAF701, and OsHAM70) [88] and the HvMYST and HvELP3 genes in barley were also shown to be involved in epigenetic regulation in drought responses [89]. DNA methylation and histone modifications may have a similar result on stress-inducible genes, as salinity stress influences the expression of a range of transcripts in soybean [48]. Work in rice underlined that hypomethylation in reaction to salt stress may be associated with changes in the expression of DNA demethylases [90]. The transcriptional adaptor ADA2b (a modulator of histone acetyltransferase activity) is responsible for hypersensitivity to salt stress in Arabidopsis thaliana [91].

3.2. Gain-of-Function Lines

Gain-of-function methods have been extensively used for the study of gene function in plants and are considered among the most useful tools for gain-of-function phenotypes. Gain-of-function lines are generated through the arbitrary activation of endogenous genes by transcriptional enhancers and the regular expression of individual transgenes by transformation [9]. This method employs the phenotype of gain-of-function lines that overexpress a selected gene family and can be executed without meddling from other gene family members that allow the categorization of functionally unwanted genes [10]. Alternatively, the overexpression of a mutant gene can be expressed due to the presence of higher levels of nonfunctional protein causing a superseding negative interface with the wild-type protein. To overcome this event, a mutant type could be used to compare the wild-type protein allies, resulting in a mutant phenotype. Conversely, heterologous expression of a gene in the yeast-hybrid system is an alternative way to characterize genes. In the first gain-of-function approach, a strong promoter or enhancer element is arbitrarily inserted into the plant genome with the help of T-DNA [11], which stimulates a gene near the site of the harbor. Other gain-of-function approaches involve cDNA overexpression and open reading frame (ORF) overexpression, whereas full-length cDNAs or ORFs have been cloned into a strong promoter downstream. Under the switch of the CaMV35S promoter, various abiotic stress response genes have been characterized by the use of ectopic overexpression of cDNAs [11–14].

3.3. Gene Silencing and RNA Interference Techniques for Salinity and Drought Stress

Suppression of a gene is referred to as gene silencing in plants and fungi and interference RNA (RNAi) in animals and is generally thought of as a controlling mechanism of gene expression mostly in eukaryotic cells [92]. RNA interference (RNAi) has been considered one of the most crucial discoveries in molecular genetics during the last several years for posttranscriptional gene silencing (PTGS) cosuppression [93]. RNA silencing hints at a nucleotide sequence-specific procedure that prompts mRNA degradation or translation termination at the posttranscriptional level in plants arbitrated by small RNAs (sRNAs), which are divided into two classes: microRNAs (miRNAs) and small interfering RNAs (siRNAs). However, RNAi was properly adapted into antisense-stranded RNA as an operative technique to constrain gene expression [94]. Silencing a gene through transgenic expression of sRNAs has been extensively implemented for abiotic stress-related gene function functional efforts. Currently, the virus-induced gene silencing (VIGS) technique for posttranscriptional gene silencing is extensively used for rapid and efficient gene function studies related to salt and drought stresses [95–98]. It can also be used for both forward and reverse genetic studies. Target gene silencing techniques for improving crops under salinity and drought stresses are discussed in Table 5.

Table 5. Target gene-silencing techniques for improving crop variety under salinity and drought stresses.

| Stresses | Crops | Silencing Gene | Major Findings | References |
|-------------------------------|--------------------------------|-------------------------------|---|------------|
| Cold, drought, salt stress | Rice | OsNAC5 | RNAi lines became less tolerant of these stresses than control plants | [58] |
| Salinity | Arabidopsis | sos1 | <i>thsos1</i> -RNAi lines of <i>Thellungiella</i> were highly salt-sensitive | [99] |
| Salinity | pepper | CaATG8c | The silencing of <i>CaATG8c</i> made pepper seedlings more sensitive to salt stress | [100] |
| Salinity | Alternanthera philoxeroides | ApSI1 | Significantly decreased tolerance to salinity | [101] |
| Drought | Alternanthera philoxeroides | ApDRI15 | Plants were more sensitive to drought stress than the control plants | [101] |
| Drought | Tomato | SpMPK1, SpMPK2, and SpMPK3 | Reduced drought tolerance in tomato plants | [102] |
| Drought | wheat | Era1 and Sal1 | Played imperative roles in conferring drought tolerance | [103] |
| Drought, salt stress | Cotton | GH3.17 | Enhanced drought and salt stress | [104] |
| Salinity | Cotton | GhWRKY6 | Downregulation of <i>GhWRKY6</i> increased salt tolerance | [105] |

3.4. Genome Engineering (TALENs, ZFNs, CRISPR/Cas)

Recently, several functional genomics-based strategies have been developed for genetic engineering. To improve crops for sustainable food production, targeted genome engineering has become a substitute for conventional plant breeding and transgenic (GMO) strategies, including transcription regulators, epigenetic modifiers, DNA integrators, TAL effector nucleases (TALENs), zinc-finger nucleases (ZFNs), clustered regularly interspaced short palindromic repeats (CRISPR)/Cas (CRISPR-associated proteins), and base editors and prime editors. Until recently, the existing methods have been considered to be unwieldy. Both TALENs and ZFNs could be used to mutagenize genomes at exact loci. However, the problem is that these systems need two altered DNA-binding proteins flanking a sequence of interest, each with a C-end FokI nuclease unit [106]. For plant research, these techniques have not been extensively implemented. Recently, a technique based on the bacterial clustered regularly interspaced short palindromic repeats (CRISPR)/Cas (CRISPR-associated proteins) type-2 prokaryotic adaptive invulnerable system has been developed as an alternate process for genome engineering [106]. The CRISPR/Cas (clustered regularly interspaced short palindromic repeats/CRISPR-associated proteins) system was first identified in bacteria and archaea and can cleave exogenous DNA substrates [107]. CRISPR/Cas has since been modified to be used as a gene-editing technology. However, CRISPR/Cas9 has largely overtaken the other aforementioned gene editing practices. Investigators express similar stories: a few years ago, they started working on projects using both TALENs and CRISPR/Cas9 side-by-side but rapidly established CRISPR systems [108]. Graphical presentations of the CRISPR/Cas9 techniques are available in Figure 3.



Figure 3. CRISPR/Cas9 is a powerful tool for genome editing of Cas9 to a guide RNA that directs the complex to a place on the DNA double helix and contains the code for the addition of a new DNA sequence at the double-stranded break. Source: adapted and modified from [www.stockadobe.com; accessed date on 12 July 2021].

The beginning of CRISPR has made it conceivable to rewrite host DNA by introducing some major amendments. These modifications include gene replacement, deletions, inversion, knockouts, and translocations [109]. Using CRISPR/Cas9 tools, several genes, such as OsERF922, OsPDS, OsERF922, ERFs, OsHAK1, Badh2, OsRR22, and TMS5, were knocked out, and a predictable phenotype was attained [110–116]. More promising are the potential forecasts of this technique for producing plants with specifically tailored purposes, i.e., biofuel production, synthetic biology, disease resistance, phytoremediation, etc. [117]. This technique also offers a new method for abiotic stress breeding programs [113]. Several examples of CRISPR/Cas9 technology-mediated improvements to plant tolerance to abiotic stress are discussed in Table 6.

| Target Genes | Crops | Target Stresses | References |
|---------------------|---------------------------|---|------------|
| TaDREB2 and TaERF3 | Wheat | Abiotic stress response | [118] |
| ScNsLTP | Sugarcane | Drought and chilling resistance | [119] |
| MaAPS1 and MaAPL3 | Banana | Cold and salt | [120] |
| MeKUP | Cassava | Salt, osmosis, cold, and drought resistance | [121] |
| MeMAPKK | Cassava | Drought resistance | [122] |
| GhPIN1–3 and GhPIN2 | Cotton | Drought resistance | [123] |
| GhRDL1 | Cotton | Drought resistance | [124] |
| CpDreb2 | Papaya | Drought, heat, and cold resistance | [125] |
| ÓsDST | Indica mega rice cultivar | Salt and Drought | [126] |
| SINPR1 | Tomato | Drought | [127] |
| Leaf1,2 | Rice | Drought | [128] |

Table 6. CRISPR/Cas9 technology-mediated improvements to plant tolerance to abiotic stress.

3.5. CRISPR-Mediated Base Editing and Prime Genome Editor

It is well known that CRISPR is a powerful genome-editing technique. CRISPR can change genes and edit DNA sequences by producing double-strand breaks in double-helical DNA, leaving the cell to repair the breakage (Figure 4).



Figure 4. A new tool (prime editor) of DNA manipulation that couples two enzymes, Cas9 (brown) and reverse transcriptase (yellow), to a guide RNA (red) that directs the complex to an exact place on the DNA double helix and contains the code for the addition of a new DNA sequence at the double-stranded break. [Figure modified from: https://www.synthego.com/guide/crispr-methods/prime-editing; accessed date on 12 July 2021].

The control mechanisms over the repair process are the main limitations in basic research and plant sciences. However, several groups recently reported the "base editing" system, a new approach for site-directed mutagenesis of genomic DNA. Base editing tools are highly efficient, reduce the rate of off-target effects, and do not require DNA double-strand cleavage or donor template repair. These methods make use of a Cas9 nickase fused to various deaminases. Specific C-to-T or A-to-G transitions in genomic DNA are catalyzed by these fusion proteins. The base editor and Target-AID (target-activation-induced cytidine deaminase) systems are two representative architectures of cytidine base [127,128]. Therefore, engineering of single-plasmid CRISPR-mediated base editors (CBEs), and glycosylase base editors (GBEs) is capable of achieving both base transitions (A-to-G, C-to-T) and transversions (C-to-G) [129]. Base editing has become a widely applicable tool for gene disruption in a variety of bacteria [17,22,28,130]. Nevertheless, the new invention "prime editor" makes the successful addition or deletion of exact sequences within the genome possible with minimum off-target effects [129].

The creators claim that their tools can precisely target approximately 89% of recognized pathogenic human genetic variants. Prime editing may have fewer bystander mutations than base editing, especially when multiple Cs or As are present in the editing activity window [131]. It is also less constrained by the availability of protospacer adjacent motif (PAM) than other methods such as homology directed repair (HDR), non-homologous end joining (NHEJ), or base editing, because the PAM-to-edit distance can be greater than 30 bp on average [26]. Nevertheless, there is a large suite of base editors that have been developed with improved efficiency, product purity, and DNA specificity, as well as broad applicability [25]. Although prime editing has the potential to replace base editors, the technology is still in its early stages and is typically less efficient than current generation base-editing systems with superior on and off-target DNA editing profiles [20]. Consequently, a suitable editing strategy for specific applications must be chosen based on various criteria for gene-editing, such as the desired edit, the availability of PAMs, the efficiency of editing, and off-target/bystander mutations.

4. The Development of Salt- and Drought-Tolerant Crops with High Yielding Capacity

The generation of crop varieties with a high level of tolerance to salinity and drought is vital for creating full yield potential and sustainable production. Generally, there are two methods to integrate enhanced traits such as drought and salinity stresses in plants: genetic engineering and breeding programs.

4.1. Genetics Engineering

The advent of modern genetic engineering strategies offers the generation of plants with rising abiotic stress tolerance. Under abiotic stress conditions, several genes of crop plants in different pathways lead to upregulation of expression. Stress-responsive genes and their controlling genes can be transferred and expressed in different species using an Agrobacterium-mediated transformation system involving molecular, biochemical, and physiological changes that direct an increase in plant growth, development, and yield under stress environments [16]. Currently, the use of stress-inducible promoters for the expression of stress response genes has confirmed a time-specific and optimal level of expression. Salinity and drought are major environmental stresses that adversely affect the growth and development of crops; thus, a number of genes encoding proteins involved in the biosynthesis of stress defensive elements, including glycine betaine, mannitol, and heat shock proteins, have been used for abiotic stress tolerance, as well as several transcription factors, such as MAPK, bZIP, AP2/EREBP, WRKY, and DREB1 [17,18]. However, overexpressed transgenes can function as positive regulators of tolerance to a single stress or multiple stresses, such as salinity, drought or both. Therefore, the newly developed transgenic plant might have to be tolerant to single or multiple stresses, have high yields, and be devoid of harmful pleiotropic traits. Posttranslational modifications, orthologous gene

expression of effectors from wild relatives or halophytes, gene expression by regulating miRNA activity, osmoprotectants, gene pyramiding, engineering of transcription factors, chaperones, late embryogenesis, metabolic pathways, abundant proteins, epigenetics, and even chaperones have been implemented to produce a new generation of transgenic plants [130]. Successful salinity- and drought-tolerant transgenic crops were produced and approved for cultivation as food and feed [23,27–29].

4.2. Gene Introgression

Introgressionics is designated as an extensive systematic improvement of plant genomes and populations through bearing introgressions of genomic fragments from wild crop relatives relative to the genetic background of established crops to develop new cultivars with promising traits [24]. Through introgression, greater genomic plasticity can be attained in a crop using exotic genetic material that was previously nonexistent within the genome [104]. For crop improvement, genetic engineering strategies are relatively faster than traditional breeding programs, as well as cloning of genes responsible for imperative traits and introgression into plants [104]. To develop salt- and drought-tolerant varieties, a particular breeding program can be established through an understanding of the physiological and genetic mechanisms of these stresses. MAS improves the speed and efficacy of breeding because genetic markers are unaffected by the environment, are efficient to use in early generations [105], and can be useful for the introgression of target genes. Successful stories of introgression in various crops for many traits, including both abiotic and biotic stress tolerance/resistance, have been implicated from wild relatives in cultivation without affecting yield and quality [24,106,107].

4.3. Marker-Assisted Breeding and Transference of Genes

Marker-assisted breeding is a process that permits breeders to track traits over generations of breeding using genetic markers associated with a given trait. In marker-assisted breeding, DNA markers associated with desirable traits are used to identify and choose plants containing the genetic locus that confers the desirable trait. DNA markers have a high probability of increasing the capability and accuracy of traditional plant breeding via marker-assisted selection (MAS). MAS allows for quicker and more efficient selection of desired crops, as cultivators can reliably test for the presence of a genetic marker associated with a trait rather than waiting to assess the trait itself. The most efficient and extensively applied method for MAS is marker-assisted backcrossing [132]. Marker-assisted breeding is in contrast to the direct addition of a gene or multiple genes to enhance a trait, such as genetic modification. Using genetic markers in breeding depends on the phenological acclimatization of the acceptor genotype, and the introduction of a new marker or allele may be necessary to increase the yield. With the advent of molecular markers and MAS technology, numerous studies have capitalized on such technology to identify genes or QTLs affecting sequence tagging in different plant species during different developmental stages, to identify genes or QTLs that were introduced into different plant varieties, and to gain an overall deeper and more efficient understanding of QTLs that contribute to complex traits [133]. Marker-assisted breeding for improving crop quality under salinity and drought stresses is discussed in Table 7.

| Stresses | Crops | Target Genes | Major Effect/Finding | References |
|-------------------|--------|--------------|--|------------|
| Drought and Salt | Cotton | | Significant associations between polymorphic markers and drought and salt tolerant traits were observed using | [48] |
| Salinity | Rice | RM223 | Transferring genes from one variety to another and their use in MAS | [134] |
| Drought | Rice | | Developed high-yielding rice cultivars suitable for water-limited environments through marker-assisted breeding | [135] |
| Salinity | Rice | NAL1 | through marker-assisted breeding High yield through optimizing NAL1 transportation efficiency of photosynthetic products by marker-assisted selection | |
| Drought and flood | Rice | | Developed high-yielding drought- and submergence-tolerant rice varieties using marker-assisted introgression | [25] |
| Drought | Rice | | Provided a higher yield advantage | [137] |
| Drought | maize | | Improved grain yield under drought stress conditions | [138] |
| Drought and salt | Wheat | TaCRT-D | Increased plant stress tolerance and the functional markers of TaCRT-D for marker-assisted selection in wheat breeding | [139] |
| Salinity | Rice | | Developed new salt-tolerant rice germplasm using speed-breeding | [140] |
| Drought | Rice | | Stimulated 10–36% higher yield among different inbred lines | [141] |

Table 7. Marker-assisted breeding results for improving crop quality under salinity and drought stresses.

Current advances in genomics and genome sequencing in rice have made it feasible to locate and precisely map a certain number of genes via linkage to DNA markers. MAS can be applied to control the presence or absence of genes and has also been applied to assess the contributions of such genes conferring traits that have been introduced into extensively developed varieties [26]. Coupling genomic resources with the utility of MAS, breeders can now gain unprecedented insight into the genetic regulation of complex traits. MAS is a large advantage for developing new crop varieties because crops with ineligible gene aggregations can be dispelled from the selection process. This offers breeders the opportunity to focus on a reduced number of candidate lines for breeding targets in successive generations [131]. It has been shown that association mapping along with population formation and screening of cotton germplasm can improve QTL assignment and MAS [131]. Combining MAS and GS (genomic selection) with adequate genetic variety, databases, analytical instruments, and well-established climate and soil data is a powerful way to produce modern varieties with high drought resistance that can be readily inaugurated into appropriate agricultural programs [27]. These methods could produce a high number of lines of a crop appropriate for propagating crops in a range of drought and salinity stress ecosystems. Furthermore, incorporating these data can lead to the creation of varieties that can be further optimized to control largely heritable principal secondary characteristics. MAS delivers precise, rapid, and profitable progress toward the development of crop varieties that can be applied to abiotic stress tolerance [26]. A graphical presentation of the development of a new crop variety by marker-assisted selection is available in Figure 5.



Figure 5. Development of a new crop variety by marker-assisted selection. Source: modified from: [http://b4fa.org/bioscience-in-brief/plantbreeding/how-do-you-develop-a-new-cropvariety-by-marker-assisted-selection-mas/; accessed date on 12 July 2021]. Note: Marker 1 and Marker 2 confer susceptible and resistance alleles, respectively; f1 and f2 indicate the first and second filial generations of offspring, respectively.

5. Involvement of Genes in the Regulation of ROS in Abiotic Stress Tolerance

Reactive oxygen species (ROS) are assumed to play roles in many noteworthy signaling reactions in plant metabolism. Under drought and salinity environments, interrupting photosynthesis and increasing photorespiration intermittently alter the regular homeostasis of cells and influence the production of ROS in mitochondria, chloroplasts, and peroxisomes (Figure 6) [142,143].



Figure 6. Sites and typical regulation of ROS in plant cells. PSII; Photosystem II, PSI; Photosystem I, MDA; Malondialdehyde, APX; Ascorbate Peroxidase, PGA; 3-Phosphoglyceric acid, H₂O₂; Hydrogen peroxide, SOD; Superoxide dismutases, CAT; Catalase, MDAR; Monodehydroascorbate reductase, NADH; Nicotinamide adenine dinucleotide, Alternative oxidase.

In addition to organelles, the plasma membrane together with the apoplast is the main site for ROS production in response to endogenous signals and exogenous environmental stimuli [144]. Overproduction of ROS in plant cells is extremely reactive and noxious to proteins, lipids, and nucleic acids, which finally results in cellular damage and death initiated by stressful environments [142]. ROS-scavenging enzymatic antioxidants (SOD, APX, CAT, GPX, MDHAR, DHAR, GR, GST, and PRX) and nonenzymatic antioxidants (GSH, AsA, carotenoids, tocopherols, and flavonoids) are located in different sites of plant cells, and they directly or indirectly play a key role in ROS homeostasis via different unique pathways to avoid oxidative damage. In addition, soluble sugars as well as disaccharides, raffinose family oligosaccharides, and fructans play a dual role in ROS maintenance [145]. Consequently, crop plants have executed several interrelated signaling pathways to operate different groups of genes (Figure 7), which are induced under stress conditions to generate different classes of proteins, for example, protein kinases, enzymes, transcription factors, molecular chaperones, and other efficient proteins, subsequent to various physiological and metabolic reactions to improve tolerance to multiple environmental stresses.



ABIOTIC STRESS TOLERANCE

Figure 7. A general view of major genes that are intricate in abiotic stress resistance through ROS maintenance in crops. MAPK, mitogen-activated protein kinase; CDPK, calcium-dependent protein kinase; CIPK, calcineurin B-like protein-interacting protein kinase; PK, protein kinase; PP, protein phosphatase; SRO, similar to RCD.

It is well known that antioxidants stimulate gene expression linked with responses to various environmental signals to exploit protection through the regulation of cellular ROS levels and redox state [146]. The characteristics and roles of selected genes and their processes under salinity and drought stresses are discussed in detail in Tables 8 and 9.

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| Genes | Origin | Transformation Receptor | Protein Function | Major Functions | Signaling Hormone | Approaches Used | References |
|---------------------|-----------------|----------------------------|-------------------------------------|--|---|---------------------------------------|------------|
| GhMKK1 | G. hirsutum | N. benthamiana | МАРКК | Influences oxidative, ROS scavenging, salt and drought tolerance | Abscisic acid (ABA) | Reverse genetics | [147] |
| DSM1 | O. sativa | O. sativa | МАРККК | Influences oxidative, ROS scavenging, drought tolerance | ABA | RNA interference, Reverse genetics | [148] |
| DSM2 | O. sativa | O. sativa | МАРККК | Influences oxidative, ROS scavenging, drought tolerance | ABA | RNA interference, Reverse genetics | [149] |
| MEKK1 | Arabidopsis | Arabidopsis | МАРККК | Influences oxidative, ROS scavenging, abiotic stress tolerance | ABA | Reverse genetics | [150] |
| GhMAPKKK49 | G. hirsutum | G. hirsutum | МАРККК | ROS scavenging, salt, drought, and wounding stresses | ABA, gibberellins (GB), methyl jasmonate (JA), salicylic acid (SA), 6-benzyl amino purine, a-naphthyl acetic acid, and ethylene (ET) | Transcriptome | [151] |
| MKK1, MKK2, MKK6 | Arabidopsis | | MAPKK | Stimulate oxidative, ROS scavenging, abiotic stresses | SA | RNA interference | [150,152] |
| OsCPK4 | O. sativa | O. sativa | Calcium-dependent protein kinase | ROS scavenging, drought, and salt stress | SA | Reverse genetics | [153] |
| OsCPK12 | O. sativa | O. sativa | Calcium-dependent protein kinase | ROS scavenging, influences oxidative salt stress | ABA | RNA interference, Reverse genetics | [154] |
| SiCDPK24 | Setaria italica | Arabidopsis | Calcium-dependent protein kinase | ROS scavenging, drought stress | ABA | Reverse genetics | [155] |
| TaCIPK29 | T. aestivum | N. benthamiana | ĈBL-interacting protein | ROS scavenging, salt stress | ABA and ET | Reverse genetics | [156] |
| MdCIPK6L | Apple | Arabidopsis | CBL-interacting protein kinase | ROS scavenging, salt, osmotic/drought and chilling stresses | ABA | Reverse genetics | [157] |

Table 8. Characterized genes involved in abiotic stress tolerance through ROS regulation in crops.

| Genes | Origin | Transformation Receptor | Protein Function | Major Functions | Signaling Hormone | Approaches Used | References |
|----------|-------------------|----------------------------|--------------------------------|--|----------------------|--|------------|
| MdSOS2L1 | Apple | tomato | CBL-interacting protein kinase | ROS scavenging, salt stresses | ABA | Reverse genetics | [158] |
| AtCIPK5 | Arachis diogoi | Arabidopsis | CBL-interacting protein kinase | Salt and osmotic stress tolerance | NA | Reverse genetics | [159] |
| SIT1 | O. sativa | O. sativa | Lectin receptor-like kinase | ROS production, salt sensitivity | ET | Reverse genetics | [160] |
| OsMPK6 | O. sativa | O. sativa | МАРК | ROS scavenging, salt stresses | SA | RNA interference | [161] |
| ZmMPKL1 | Zea mays | Zea mays | МАРК | ROS production, drought sensitivity | ABA | CRISPR/Cas9, Reverse genetics | [162] |
| МеМАРК | Cassava | NA | МАРК | osmotic, salt, cold, oxidative stressors | ABA | Transcriptome | [163] |
| ZmMKK3 | Zea mays | N. benthamiana | МАРК | ROS scavenging, osmotic tolerance | ABA | Reverse genetics | [164] |
| OsPP18 | O. sativa | O. sativa | Protein phosphatase 2C | ROS scavenging, drought and oxidative stress | ABA | RNA interference, Reverse genetics | [165] |
| DST | O. sativa | O. sativa | zinc finger C2H2 | ROS scavenging, drought and salt stress | Cytokinins | RNA interference, Reverse genetics | [166,167] |
| ZFP36 | O. sativa | O. sativa | zinc finger C2H2 | ROS scavenging, stress and oxidative stress | ABA | RNA interference, Reverse genetics | [168] |
| OsTZF1 | O. sativa | O. sativa | Zinc Finger Protein CCCH | ROS scavenging, drought, high-salt stress | ABA | RNA interference | [169] |
| OsWRKY30 | O. sativa | O. sativa | WRKY | ROS scavenging, drought tolerance | SA | Reverse genetics | [170] |
| GhWRKY6 | G. hirsutum | Arabidopsis | WRKY | ROS production, drought and salt stress | ABA | Transcriptome, VIGS, Reverse genetics | [105] |
| EcNAC1 | Helianthus annus | Helianthus annus | NAC | ROS scavenging, salt stress | ABA | Reverse genetics | [171] |
| NTL4 | Arabidopsis | Arabidopsis | NAC | ROS production, drought stress | ABA | RNA interference, Reverse genetics | [172] |
| EcbHLH57 | Eleusine coracana | N. benthamiana | bHLH | ROS scavenging, salt, oxidative and drought stress | ABA | Reverse genetics | [173] |

Table 8. Cont.

| Genes | Origin | Transformation Receptor | Protein Function | Major Functions | Signaling Hormone | Approaches Used | References |
|---------|---------------------|----------------------------|---|---|----------------------|------------------------------------|------------|
| JERF3 | O. sativa | O. sativa | Ethylene response factor (ERF) | Drought and osmotic stress | ET | Reverse genetics | [174] |
| MnSOD | N. plumbaginifolia | M. sativa | MnSOD | ROS scavenging drought stress | NA | Reverse genetics | [175] |
| OsAPX2 | Medicago sativa | Medicago sativa | APX | ROS scavenging, salt tolerance | ABA | Reverse genetics | [176] |
| PgGPX | Pennisetum glaucum | O. sativa | GPX | ROS scavenging, salinity and drought stress | SA | Reverse genetics | [177] |
| MsALR | M. sativa | N. benthamiana | NADPH-dependent aldose/aldehyde reductase | Antioxidative metabolism, drought and oxidative stress | NA | Reverse genetics | [178] |
| AtMIOX4 | Arabidopsis | Arabidopsis | MIOX | ROS scavenging, salt tolerance | ABA | Reverse genetics | [179] |
| MtPP2C | Medicago truncatula | NA | PP2C | ROS scavenging, drought and cold stress responses | ABA | Transcriptome | [180] |
| OsAHL1 | O. sativa | O. sativa | AHL | ROS scavenging, drought resistance | ABA, SA | GWAS, Reverse genetics | [181] |
| OsHK3 | O. sativa | NA | НК | ROS scavenging, salinity and drought stress | ABA | RNA interference | [182] |
| IcSRO1 | Ipomoea cairica | Arabidopsis | SRO | ROS scavenging, salt and drought tolerance | ABA | Transcriptome, Reverse genetics | [183] |
| OsCATB | O. sativa | O. sativa | CATB | ROS production, drought stress | ABA | Transcriptome | [184] |
| RBOHH | O. sativa | O. sativa | NADPH Oxidase | ROS production, drought stress | ET | CRISPR/Cas9, Reverse genetics | [185] |

Table 8. Cont.

| Functional Category | List of Genes | Type of Stress | Biological Function and Signaling Pathway | Tools Used | References |
|---------------------|---|--|--|---|---------------|
| | | Protein kina | se | | |
| МАРККК | MEKK1, MEKK2, MEKK3, MEKK4, MAPKKK18, GhMAP3K40, OsMAPKKK63, GhMAPKKK49 DSM1_DSM2 | Influences oxidative, abiotic, and biotic stress. | Growth and development; ABA | RNA interference, reverse genetics | [150,186,187] |
| | MKK1, MKK2, MKK6, GhMKK1, | Influences oxidative, salt and drought | Growth and development; SA | Transcriptome, reverse genetics | |
| МАРКК | MKK3, GhMKK3 | Influences oxidative, salt, and drought stresses | Growth and development; SA | RNA interference, reverse genetics | [150,188] |
| | MKK4, MKK5 GhMKK4, GhMKK5, | Influences oxidative, drought | Growth and development; JA | RNA interference, reverse genetics | |
| | MKK7, MKK8, MKK9, MKK10, RhMKK9, GhMKK9, ZmMKK10 | Salt and/or drought | Growth and development; ET | Reverse genetics | |
| | VvMKK2, VvMKK4 | Influences oxidative, salt, and drought | Growth and development; SA | Reverse genetics | [177] |
| MAPK | MPK3, MPK6, MPK10 OsMPK6, ZmMPK3, RhMPK6, ZmMPK6-2, OsMPK3, 7mMPK3 | Influences oxidative, abiotic, and biotic stresses | Cell cycle regulation, cell division; JA and ET | RNA interference, reverse genetics | [150,189] |
| | MPK4, MPK5, MPK11, MPK12, MPK13, OsMPK4ZmMPK4-1, OsMPK5, OsMPK5, ZmMPK5 | Influences oxidative, salt, and/or drought | Cell cycle regulation; SA | RNA interference, reverse genetics | [150] |
| | MPK1, MPK2, MPK7, MPK14, ZmMPK7, OsMPK2AtMPK7, OsMPK7, GhMPK7 | Influences oxidative, salt, drought | Circadian-rhythm-regulated; JA, SA | RNA interference, reverse genetics | [150] |
| | MPK8, MPK9, MPK15/16/17/18/19/20 GhMPK17, ZmMPK17 | Influences oxidative, salt, drought | Cell cycle regulation; JA | RNA interference, reverse genetics | [161] |
| CDPK | OsCPK4 OsCPK12 SiCDPK24 FaCDPK4, FaCDPK11 StCDPK3, StCDPK23 | Influences oxidative, salt, drought | Responses to developmental and environmental cues; SA, ABA | Transcriptome, RNA interference, reverse genetics | [190] |
| CIPK | TaCIPK29 MdCIPK6L MdSOS2L1 AtCIPK5 | ROS scavenging, salt and osmotic stress tolerance | tissue and organ development; ABA | Reverse genetics | [167–170] |

Table 9. A summary of identified genes and their processes under salinity and drought stresses.

Table 9. Cont.

| Functional Category | List of Genes | Type of Stress | Biological Function and Signaling Pathway | Tools Used | References |
|---------------------|---|-----------------------------|--|--|----------------|
| | Transcrip | otion factor | | | |
| bZIP | ABF3, BF4 ABF3, ABF4 FtbZIP5, PtrABF OsbZIP23, OsbZIP12, OsbZIP71, OsbZIP46 OsbZIP72, ZmbZIP4 | Salt, drought | Light signaling, seed maturation, flower development; ABA | Transcriptome, RNA interference reverse genetics | [191–200] |
| bHLH | OSbZIP62, IabZIP MYC2, AtbHLH17, AtbHLH68, AtbHLH122, FtbHLH2, FtbHLH3, PebHLH35, OsbHLH148 | Salt, drought | Growth, development, response to various stresses; JA, ABA | Transcriptome, RNA interference, reverse genetics | [201–208] |
| NAC | ANACOT9, ANACO35, ANACO72, ANACO42, TaNAC29, OsNAC6, OsNAC5, OsNAC9, OsNAC10, TaRNAC1, GmNAC109, CaNAC035 | Salt, drought | Plant growth and development range from the formation of shoot apical meristem, floral organ development, reproduction, lateral shoot development; ABA | Transcriptome, RNA interference, reverse genetics | [209–219] |
| AP2/ERF | CBF1, CBF2, CBF3, AtERF53, AtERF74, AhDREB1, OsDREB1, OsEREBP1, OsERF7, GmERF3, ZmDREB2A, SIERF5 | Salt, drought | Regulation of plant growth and development; ABA | Transcriptome, RNA interference reverse genetics | [220–230] |
| МҮВ | AtMYB44, AtMYB96, AtMYB20, OsMYB4, OsMYB6, OsMYB48-1, OsMYB91, GmMYB76, GmMYB92, GmMYB177 | Abiotic stresses | Circadian rhythm, regulation of primary and secondary metabolism; ABA, JA | Transcriptome, RNA interference reverse genetics | [231–239] |
| WRKY | OsWRKY11, OsWRKY45, TaWRKY1, TaWRKY33, cWRKY023, ZmWRKY33, VvWRKY2 | Salt, drought | Growth and development; ABA | Transcriptome, RNA interference reverse genetics | [240-245] |
| | | ROS-sc | avenging | | |
| SOD | FSD1, FSD2, FSD3 CSD1, CSD2, CSD3 MSD1 | Salt, drought | Antioxidant defense against oxidative stress; ABA | RNA interference, Reverse genetics | [246] |
| | CmSOD CsSOD | Oxidative stress Drought | ABA JA and gibberellin (GA3) | reverse genetics Transcriptome | [247] [248] |

Table 9. Cont.

| Functional Category | List of Genes | Type of Stress | Biological Function and Signaling Pathway | Tools Used | References |
|---------------------|------------------------------------|--|---|---------------------------------|------------|
| АРХ | APX1-APX7 | Salt and or drought | Growth regulation; ABA | Transcriptome | [246] |
| | OsAPX1, OsAPX2 | Oxidative, Salt, drought | ĂBA | Transcriptome | [249] |
| | OsAPX3, OsAPX4 | Salt and drought | ABA | Transcriptome | [249] |
| | OsAPX5, OsAPX6 and OsAPX7 | salinity | ABA | Transcriptome | [250] |
| | AgAPX1 | Drought | NA | Reverse genetics | [251] |
| | TbAPX | Salt | ABA | Reverse genetics | [252] |
| | CytAPX | Salt | ABA | Reverse genetics | [253] |
| CAT | CAT2, CAT3, ScCAT1 | Salt and/or drought | ABA | Transcriptome | [254] |
| | HuCAT3 | Salt and drought | NA | Transcriptome | [255] |
| | VsCat | Salt | Salt | CRISPR/C as9 | [198] |
| | CsCAT3 | Tolerance to heat, cold, salinity and osmotic condition | ABA | Transcriptome, Reverse genetics | [256] |
| GPX | GPX1, GPX2, GPX5, GPX6 and GPX7 | Abiotic stress | Plant development, multiple signaling pathways | Transcriptome | [257,258] |
| | PgGPx | Salinity and Drought | NA J | Reverse genetics | [177] |
| | CĨGPX | Salinity and Drought | ABA | Transcriptome | [258] |
| | NnGPX | Salt | NA | Reverse genetics | [259] |
| | OsGPX5 | Salt | ABA | Transcriptome, RNA interference | [260] |
| MDHAR | MDAR2-4 | Salt | Stress protection; ABA | Transcriptome | [256] |
| | AeMDHAR | Salt | NA | Reverse genetics | [261] |
| | AtMDAR1 | Ozone, salt and drought stress | ABA | Reverse genetics | [262] |
| | TrMDHAR | salt | ABA | Transcriptome | [261] |
| DHAR | SIDHAR1 and SIDHAR2 | salt | Stress protection; NA | Transcriptome | [263] |
| | DHAR1 and DHAR3 | Salt | ABA | Transcriptome | [256] |
| | LcDHAR | Salt and drought | NA | Transcriptome, Reverse genetics | [264] |
| | TrDHAR | Salt | ABA | Transcriptome | [265] |

6. Conclusions

The adverse effects of climatic change and an increasing population pose a momentous challenge to crop production and food security, particularly in developing countries. Thus, it is a prerequisite to understand plant response mechanisms to abiotic stresses, namely, salinity and drought, at the molecular level to improve crop productivity. To overcome these circumstances, conventional breeding systems are no longer appropriate avenues to bolster crop production. In this review, we mainly discussed advanced molecular genomics tools focusing on plant genes in response to abiotic stress mechanisms to update our knowledge on the rapid development of high-yielding crop varieties under salt and drought stresses. Moreover, we summarized the recent studies of plant genes and differentiated them according to their molecular functions in response to salt and drought and reported recent advances in these stress-response mechanisms. Finally, the integration of any two or all three genomics approaches would be used to generate salinity- and drought-tolerant crops.

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