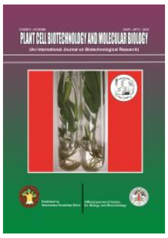

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Breeding Techniques and Approaches for Developing Abiotic Stress-tolerant Crop Cultivars: A Comprehensive Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Abiotic stresses, such as drought, salinity, extreme temperatures, and nutrient deficiencies, pose significant challenges to crop production worldwide. These stresses lead to substantial yield losses and threaten food security. Developing crop cultivars with enhanced tolerance to abiotic stresses is crucial for maintaining agricultural productivity and ensuring sustainable food production. This comprehensive review article discusses the various breeding techniques and approaches employed in developing abiotic stress-tolerant crop cultivars. We highlight the importance of understanding the molecular mechanisms underlying stress tolerance and the utilization of genetic resources for breeding programs. Conventional breeding methods, such as hybridization, mutation breeding, and marker-assisted selection, have been widely used to develop stress-tolerant cultivars. However, the integration of advanced technologies, including genomics, transcriptomics, proteomics, and metabolomics, has revolutionized the breeding process. These omics approaches provide valuable insights into the complex genetic architecture of stress tolerance traits and facilitate the identification of key genes and pathways involved in stress responses. Genetic engineering and genome editing techniques, such as CRISPR/Cas9, offer precise and targeted manipulation of stress-related genes, enabling the development of cultivars with enhanced stress tolerance. Additionally, the utilization of wild relatives and landraces as sources of stress tolerance traits has proven beneficial in broadening the genetic base of crop species. We also emphasize the importance of phenotyping platforms and high-throughput screening methods for accurate evaluation of stress tolerance in breeding programs. Furthermore, the integration of breeding strategies with agronomic practices, such as water management, soil amendments, and precision agriculture, is essential for optimizing the performance of stress-tolerant cultivars under field conditions. This review provides a comprehensive overview of the current state of knowledge, challenges, and future prospects in developing abiotic stress-tolerant crop cultivars. It aims to guide researchers, breeders, and stakeholders in their efforts to enhance crop resilience and ensure food security in the face of changing climatic conditions.

Keywords: Abiotic stress; breeding techniques; crop improvement; genetic resources; stress tolerance.

1. INTRODUCTION

Abiotic stresses, including drought, salinity, extreme temperatures, and nutrient deficiencies, are major constraints to crop production and productivity worldwide. These stresses adversely affect plant growth, development, and yield, leading to significant economic losses and threatening global food security [1]. With the increasing world population and the impact of climate change, the development of crop cultivars with enhanced tolerance to abiotic stresses has become a pressing need. Breeding for abiotic stress tolerance is a complex process that requires a comprehensive understanding of the physiological, biochemical, and molecular mechanisms underlying stress responses in plants. It also necessitates the utilization of diverse genetic resources, advanced breeding techniques, and integrated approaches to develop resilient crop cultivars [2,116-118].

This review article provides a comprehensive overview of the breeding techniques and approaches employed in developing abiotic stress-tolerant crop cultivars. We discuss the impact of various abiotic stresses on crop production and highlight the molecular mechanisms of stress tolerance in plants. The review also explores the genetic resources available for breeding programs, including germplasm collections, wild relatives, and landraces. We then delve into conventional breeding approaches, such as hybridization, mutation breeding, and marker-assisted selection, and their applications in developing stress-tolerant cultivars. The integration of advanced omics technologies, including genomics, transcriptomics, proteomics, and metabolomics, in breeding for abiotic stress tolerance is also discussed. We further examine the role of genetic engineering and genome editing techniques, such as CRISPR/Cas9, in precise manipulation of stress-related genes. The importance of phenotyping platforms and high-throughput screening methods for accurate evaluation of stress tolerance is emphasized. Additionally, we discuss the integration of breeding strategies with agronomic practices to optimize the performance of stress-tolerant cultivars under field conditions. The review concludes by highlighting the challenges and future perspectives in developing abiotic stress-tolerant crop cultivars and their potential impact on ensuring food security in the face of changing climatic conditions.

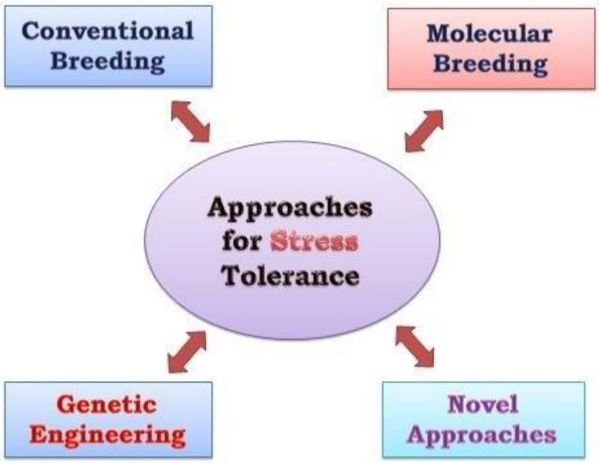

Fig. 1. Overview of breeding approaches for developing abiotic stress-tolerant crop cultivars

Table 1. Major abiotic stresses affecting crop production

Abiotic Stress	Crops Affected	Yield Loss (%)	Regions Affected
Drought	Maize, Wheat, Rice	20-50	Global
Salinity	Rice, Wheat, Barley	10-30	Coastal areas
Heat	Wheat, Maize, Soybean	10-40	Tropical and subtropical
Cold	Rice, Maize, Soybean	5-20	Temperate regions
Nutrient deficiency	Maize, Wheat, Rice	10-30	Developing countries
Flooding	Rice, Maize, Soybean	10-30	South and Southeast Asia
Soil acidity	Maize, Wheat, Barley	10-20	Tropical and subtropical
Soil alkalinity	Maize, Wheat, Rice	5-15	Arid and semi-arid regions
Ozone	Soybean, Wheat, Rice	5-15	Industrial areas
UV radiation	Maize, Wheat, Rice	5-10	High-altitude regions

Table 2. Key genes involved in drought stress tolerance

Gene	Crop	Function	Reference
DREB1A	Arabidopsis, Rice, Wheat	Transcription factor	[17]
NCED3	Arabidopsis, Maize, Tomato	ABA biosynthesis	[58]
OsNAC6	Rice	Transcription factor	[61]
OsSNAC1	Rice	Transcription factor	[70]
TaNAC2	Wheat	Transcription factor	[71]
ZmDREB2A	Maize	Transcription factor	[67]
ZmNF-YB2	Maize	Transcription factor	[107]
ZmVPP1	Maize	Vacuolar H+-pyrophosphatase	[107]
AtAVP1	Arabidopsis, Cotton, Tomato	Vacuolar H+-pyrophosphatase	[107]
AtERD10	Arabidopsis, Rice, Wheat	Late embryogenesis abundant protein	[84]

2. ABIOTIC STRESSES AND THEIR IMPACT ON CROP PRODUCTION

Abiotic stresses are non-living environmental factors that adversely affect plant growth, development, and productivity. These stresses include drought, salinity, extreme temperatures (heat and cold), nutrient deficiencies, and toxicities. Abiotic stresses can occur individually or in combination, leading to complex stress scenarios that pose significant challenges to crop production [3]. In this section, we discuss the major abiotic stresses and their impact on crop yield and quality.

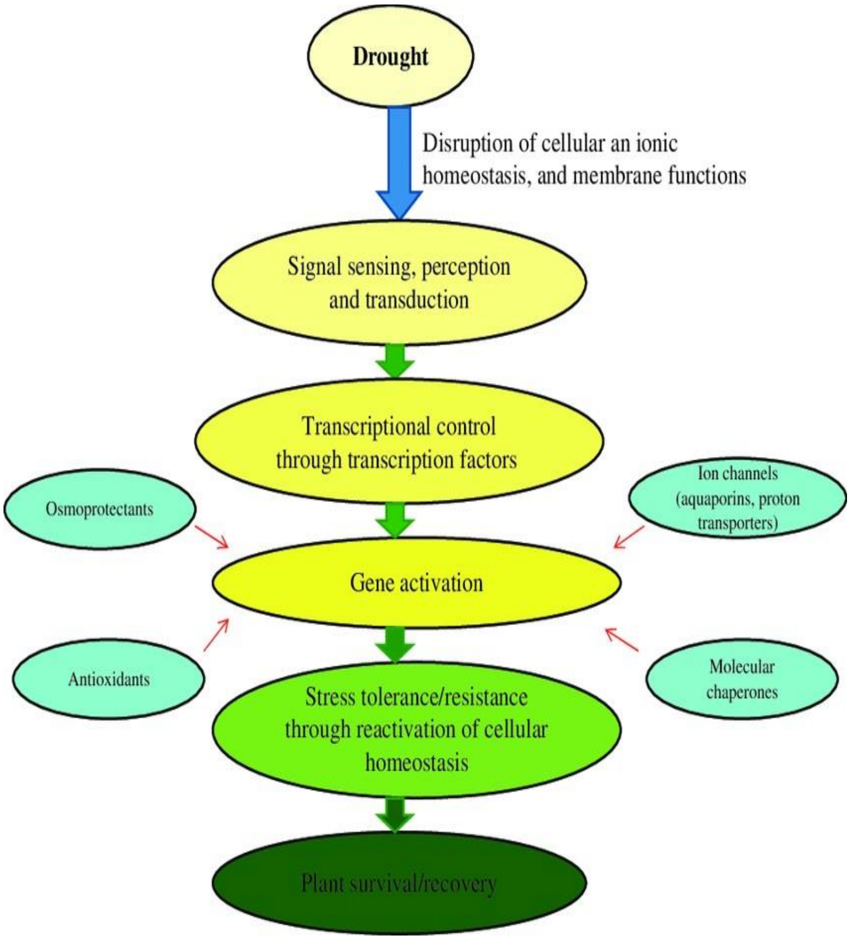

Fig. 2. Molecular mechanisms of drought stress tolerance in plants

Table 3. Major abiotic stresses affecting crop production

Abiotic Stress	Crops Affected	Yield Loss (%)	Regions Affected
Drought	Maize, Wheat, Rice	20-50	Global
Salinity	Rice, Wheat, Barley	10-30	Coastal areas
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Flooding	Rice, Maize, Soybean	10-30	South and Southeast Asia
Soil acidity	Maize, Wheat, Barley	10-20	Tropical and subtropical
Soil alkalinity	Maize, Wheat, Rice	5-15	Arid and semi-arid regions
Ozone	Soybean, Wheat, Rice	5-15	Industrial areas
UV radiation	Maize, Wheat, Rice	5-10	High-altitude regions

2.1 Drought Stress

Drought stress is one of the most prevalent and devastating abiotic stresses affecting crop production worldwide. It occurs when the available water in the soil is insufficient to meet the transpiration demands of the plant, leading to reduced growth, wilting, and yield losses [4]. Drought stress affects various physiological and biochemical processes in plants, such as photosynthesis, stomatal conductance, and osmotic adjustment. Prolonged drought can lead to irreversible damage to plant tissues and even plant death. Breeding for drought tolerance involves the identification and introgression of genes and traits that enable plants to maintain growth and yield under water-limited conditions [5].

2.2 Salinity Stress

Salinity stress is another major abiotic stress that affects crop production, particularly in arid and semi-arid regions. High salt concentrations in the soil can disrupt the osmotic balance of plant cells, leading to ion toxicity, nutrient imbalances, and oxidative stress [6]. Salinity stress reduces plant growth, leaf area, and photosynthetic efficiency, ultimately resulting in yield losses. Breeding for salinity tolerance focuses on identifying genotypes with enhanced ability to exclude or compartmentalize salt ions, maintain osmotic balance, and protect cellular structures from oxidative damage [7].

2.3 Temperature Stress

Temperature stress, including both high and low temperatures, can significantly impact crop growth and productivity. Heat stress occurs when the ambient temperature exceeds the optimal range for plant growth and development. It can cause protein denaturation, enzyme inactivation, and membrane damage, leading to reduced photosynthesis, accelerated senescence, and yield losses [8]. Breeding for heat tolerance involves the identification of genotypes with improved thermotolerance, enhanced antioxidant capacity, and the ability to maintain cellular integrity under high temperatures [9].

Cold stress: on the other hand, occurs when the temperature falls below the optimal range for plant growth. It can lead to chilling injury, freezing damage, and reduced metabolic activities. Cold stress affects membrane fluidity, enzyme activity, and photosynthetic efficiency, resulting in stunted growth and yield reductions [10]. Breeding for cold tolerance focuses on identifying genotypes with enhanced cold acclimation ability, increased accumulation of cryoprotectants, and improved membrane stability [11].

2.4 Nutrient Deficiencies

Nutrient deficiencies are another form of abiotic stress that can limit crop growth and productivity. Essential plant nutrients, such as nitrogen, phosphorus, potassium, and micronutrients, play crucial roles in various physiological and biochemical processes. Deficiencies of these nutrients can lead to chlorosis, stunted growth, reduced photosynthesis, and yield losses [12]. Breeding for nutrient-use efficiency involves the identification of genotypes with enhanced nutrient uptake, translocation, and utilization abilities. This can be achieved through the introgression of genes and traits associated with improved root architecture, enhanced nutrient transporters, and efficient metabolic pathways [13].

Table 4. Key genes involved in drought stress tolerance

Gene	Crop	Function	Reference
DREB1A	Arabidopsis, Rice, Wheat	Transcription factor	[17]
NCED3	Arabidopsis, Maize, Tomato	ABA biosynthesis	[58]
OsNAC6	Rice	Transcription factor	[61]
OsSNAC1	Rice	Transcription factor	[70]
TaNAC2	Wheat	Transcription factor	[71]
ZmDREB2A	Maize	Transcription factor	[67]
ZmNF-YB2	Maize	Transcription factor	[107]
ZmVPP1	Maize	Vacuolar H+-pyrophosphatase	[107]
AtAVP1	Arabidopsis, Cotton, Tomato	Vacuolar H+-pyrophosphatase	[107]
AtERD10	Arabidopsis, Rice, Wheat	Late embryogenesis abundant protein	[84]

Table 5. Crop tolerance level

Crop	Cultivar	Tolerance level (EC)	Yield improvement (%)	Reference
Rice	CSR27	8-10 dS/m	20-30	[101]
Rice	CSR36	8-10 dS/m	20-30	[101]
Rice	FL478	12-14 dS/m	30-40	[102]
Wheat	Kharchia 65	8-10 dS/m	10-20	[109]
Wheat	KRL 19	8-10 dS/m	10-20	[109]
Barley	CM 72	12-14 dS/m	20-30	[109]
Soybean	Lee 68	6-8 dS/m	10-20	[109]
Soybean	S-100	6-8 dS/m	10-20	[109]
Tomato	Edkawy	8-10 dS/m	20-30	[62]
Alfalfa	Mesa Sirsa	10-12 dS/m	20-30	[109]

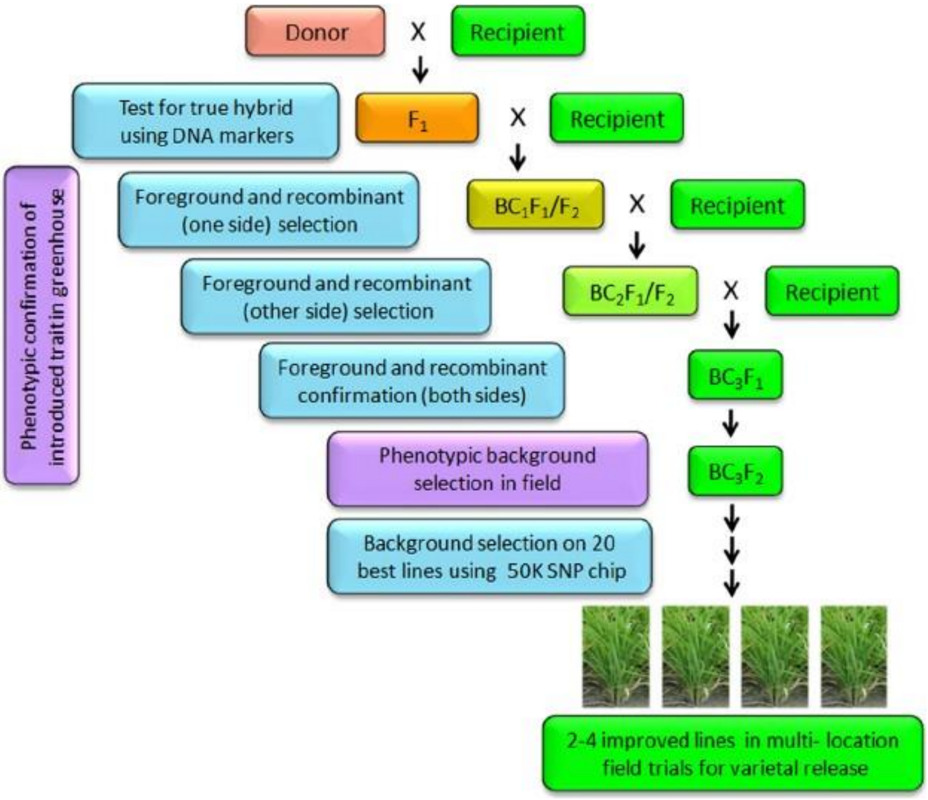

Fig. 3. Schematic representation of marker-assisted selection for stress toleranceSalt-tolerant crop cultivars developed through conventional breeding

Table 6. Wild relatives and landraces used as sources of abiotic stress tolerance traits

Crop	Wild relative/Landrace	Stress tolerance trait	Reference
Rice	*Oryza rufipogon*	Drought tolerance	[29]
Rice	*Oryza glumaepatula*	Heat tolerance	[108]
Wheat	*Aegilops tauschii*	Drought tolerance	[106]
Wheat	*Triticum dicoccoides*	Heat tolerance	[106]
Maize	*Zea diploperennis*	Drought tolerance	[107]
Maize	*Zea nicaraguensis*	Waterlogging tolerance	[107]
Soybean	*Glycine soja*	Salt tolerance	[109]
Soybean	*Glycine tomentella*	Drought tolerance	[109]
Tomato	*Solanum pimpinellifolium*	Salt tolerance	[62]
Potato	*Solanum commersonii*	Cold tolerance	[106]

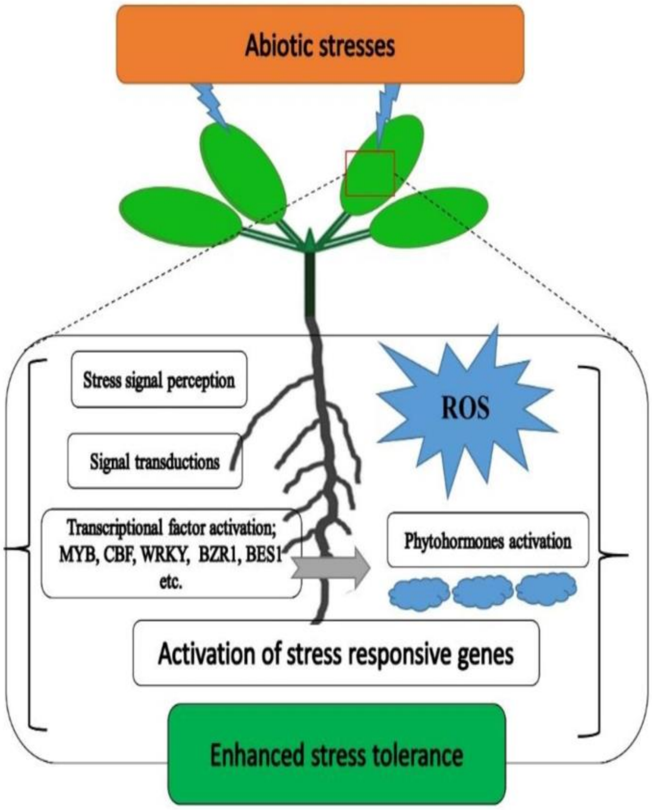

Fig. 4. Transgenic approaches for enhancing abiotic stress tolerance in crops

3. MOLECULAR MECHANISMS OF ABIOTIC STRESS TOLERANCE

Understanding the molecular mechanisms underlying abiotic stress tolerance is crucial for developing resilient crop cultivars. Plants have evolved complex signaling pathways and regulatory networks to perceive, transduce, and respond to various abiotic stresses. These mechanisms involve the activation of stress-responsive genes, the synthesis of protective compounds, and the modulation of physiological and biochemical processes [14]. In this section, we discuss the key molecular mechanisms of abiotic stress tolerance in plants.

3.1 Stress Perception and Signaling Pathways

Plants perceive abiotic stresses through specialized sensors and receptors located on the cell surface or within the cell. These sensors detect changes in the environment, such as osmotic pressure, ion concentrations, and temperature fluctuations, and initiate signaling cascades to transduce the stress signal [15]. The signaling pathways involve the activation of protein kinases, phosphatases, and transcription factors that regulate the expression of stress-responsive genes. For example, the mitogen-activated protein kinase (MAPK) cascade and the calcium-dependent protein kinase (CDPK) pathway are important signaling modules that mediate stress responses in plants [16].

3.2 Transcriptional Regulation of Stress-Responsive

Genes Transcriptional regulation plays a crucial role in the activation of stress-responsive genes under abiotic stress conditions. Transcription factors (TFs) are key regulators that bind to specific DNA sequences in the promoter regions of target genes and modulate their expression. Several TF families, such as DREB (dehydration-responsive element-binding), AREB/ABF (ABA-responsive element-binding factors), NAC (NAM, ATAF, and CUC), and WRKY, have been identified as important regulators of abiotic stress responses in plants [17]. These TFs control the expression of genes involved in stress perception, signaling, and adaptation, such as those encoding chaperones, antioxidants, and osmolytes [18].

Table 7. Molecular markers used in marker-assisted selection for stress tolerance

Marker type	Crop	Stress tolerance trait	Reference
SSR	Rice	Drought tolerance	[53]
SNP	Maize	Drought tolerance	[47]
SSR	Wheat	Heat tolerance	[105]
CAPS	Rice	Submergence tolerance	[25]
SSR	Barley	Salt tolerance	[30]
SNP	Soybean	Drought tolerance	[107]
SSR	Pearl millet	Drought tolerance	[81]
AFLP	Tomato	Salt tolerance	[62]
SSR	Chickpea	Drought tolerance	[81]
SNP	Pigeonpea	Drought tolerance	[81]

Table 8. Transcription factors regulating stress-responsive genes

Transcription factor family	Crops	Stress tolerance trait	Reference
DREB	Arabidopsis, Rice, Wheat	Drought, Salt, Cold	[17]
NAC	Rice, Wheat	Drought, Salt	[61,71]
MYB	Arabidopsis, Rice, Wheat	Drought, Salt, Cold	[18]
WRKY	Arabidopsis, Rice, Soybean	Drought, Salt, Heat	[18]
bZIP	Arabidopsis, Maize, Soybean	Drought, Salt, Cold	[18]
AP2/ERF	Arabidopsis, Rice, Maize	Drought, Salt, Flooding	[18]
HSF	Arabidopsis, Rice, Tomato	Heat	[22]
NF-Y	Arabidopsis, Maize, Soybean	Drought, Heat	[107]
bHLH	Arabidopsis, Rice, Wheat	Drought, Salt, Cold	[18]
AREB/ABF	Arabidopsis, Rice, Soybean	Drought, Salt	[17]

Table 9. Proteomics studies identifying stress-responsive proteins in crop species

Crop	Stress	Proteins identified	Reference
Rice	Drought	LEA proteins, HSPs, Aquaporins	[56]
Wheat	Drought	LEA proteins, HSPs, Enzymes	[56]
Maize	Drought	LEA proteins, HSPs, Defensins	[56]
Soybean	Drought	LEA proteins, Dehydrins, Enzymes	[56]
Rice	Salt	Ion transporters, Enzymes, HSPs	[56]
Wheat	Salt	Ion transporters, Enzymes, Dehydrins	[56]
Maize	Salt	Ion transporters, LEA proteins, Enzymes	[56]
Tomato	Salt	Ion transporters, Aquaporins, Enzymes	[56]
Rice	Heat	HSPs, Enzymes, Transcription factors	[56]
Wheat	Heat	HSPs, Enzymes, LEA proteins	[56]

Table 10. Metabolites associated with abiotic stress tolerance in crops

Metabolite	Crops	Stress tolerance trait	Reference
Proline	Rice, Wheat, Maize	Drought, Salt	[19]
Glycine betaine	Wheat, Barley, Soybean	Drought, Salt	[19]
Trehalose	Rice, Maize, Tomato	Drought, Salt, Heat	[19]
Mannitol	Wheat, Barley, Potato	Drought, Salt	[19]
Fructans	Wheat, Barley, Ryegrass	Drought, Cold	[19]
Polyamines	Rice, Wheat, Maize	Drought, Salt, Heat	[19]
Flavonoids	Soybean, Tomato, Alfalfa	Drought, Salt, UV	[19]
Carotenoids	Maize, Tomato, Carrot	Drought, Salt, Heat	[19]
Tocopherols	Soybean, Sunflower, Rapeseed	Drought, Salt, Ozone	[19]
Ascorbic acid	Rice, Wheat, Maize	Drought, Salt, Cold	[19]

3.3 Physiological and Biochemical Adaptations

Plants employ various physiological and biochemical adaptations to cope with abiotic stresses. These adaptations help maintain cellular homeostasis, protect cellular structures, and ensure the continuation of vital metabolic processes under stress conditions. One of the key adaptations is the accumulation of compatible solutes, such as proline, glycine betaine, and sugars, which act as osmolytes and protect cells from osmotic stress [19]. Plants also synthesize antioxidants, such as ascorbic acid, glutathione, and carotenoids, to scavenge reactive oxygen species (ROS) generated under stress conditions and prevent oxidative damage [20].

Other physiological adaptations include the modulation of stomatal conductance to regulate water loss, the adjustment of photosynthetic pigments to optimize light capture, and the alteration of root architecture to enhance water and nutrient uptake [21]. Additionally, plants employ molecular chaperones, such as heat shock proteins (HSPs), to maintain protein stability and prevent protein aggregation under stress conditions [22].

4. GENETIC RESOURCES FOR ABIOTIC STRESS

Tolerance Genetic resources are the foundation for breeding programs aimed at developing abiotic stress-tolerant crop cultivars. These resources include a wide range of germplasm, such as cultivated varieties, landraces, wild relatives, and mutant populations. The genetic diversity present in these resources provides valuable traits and alleles that can be harnessed to improve stress tolerance in crop plants [23]. In this section, we discuss the various genetic resources available for breeding abiotic stress-tolerant crops.

4.1 Germplasm Collections and Diversity Germplasm

Collections are repositories of plant genetic resources that are maintained and conserved for research and breeding purposes. These collections include a diverse range of accessions from different geographical origins, agroecological zones, and cultivation practices [24]. Germplasm collections serve as a valuable source of genetic variation for abiotic stress tolerance traits. For example, the International Rice Genebank Collection at the International Rice Research Institute (IRRI) contains over 130,000 accessions of rice, including cultivated varieties, landraces, and wild relatives, with diverse adaptations to different abiotic stresses [25].

Exploring the genetic diversity present in germplasm collections is crucial for identifying novel alleles and traits associated with abiotic stress tolerance. Genotyping and phenotyping of germplasm accessions using high-throughput technologies, such as genotyping-by-sequencing (GBS) and high-throughput phenotyping platforms, can facilitate the identification of promising genotypes for breeding programs [26].

4.2 Wild Relatives and Landraces

Wild relatives and landraces are important genetic resources for abiotic stress tolerance breeding. Wild relatives are the ancestors and closely related species of cultivated crops that have evolved under natural selection pressures, including abiotic stresses. They often possess novel alleles and traits that have been lost during the domestication and breeding process of cultivated varieties [27]. Landraces, on the other hand, are locally adapted traditional varieties that have been grown and selected by farmers over generations in specific agroecological niches. They often possess unique adaptations to local abiotic stress conditions [28].

Introgression of abiotic stress tolerance traits from wild relatives and landraces into cultivated crop varieties can be achieved through conventional breeding methods, such as backcrossing and marker-assisted selection. For example, the introgression of drought tolerance traits from the wild relative *Oryza rufipogon* into cultivated rice has led to the development of drought-tolerant rice varieties [29]. Similarly, the use of salt-tolerant landraces, such as 'Pokkali' and 'Nona Bokra,' in rice breeding programs has contributed to the development of salt-tolerant rice cultivars [30].

4.3 Mutant Libraries and Populations

Mutant libraries and populations are valuable genetic resources for functional genomics and breeding of abiotic stress-tolerant crops. Mutants are generated through the application of physical or chemical mutagens, such as gamma radiation or ethyl methanesulfonate (EMS), which induce random mutations in the genome [31]. These mutations can lead to the creation of novel alleles and traits associated with abiotic stress tolerance. Mutant libraries and populations provide a platform for identifying genes and pathways involved in stress responses through forward and reverse genetics approaches [32].

Tilling (Targeting Induced Local Lesions IN Genomes) is a powerful reverse genetics approach that combines chemical mutagenesis with high-throughput screening to identify mutants with desired alleles [33]. Tilling has been successfully used to identify mutants with enhanced abiotic stress tolerance in various crop species, such as wheat, rice, and soybean [34]. These mutants serve as valuable resources for understanding the molecular mechanisms of stress tolerance and for breeding stress-resilient crop varieties.

5. CONVENTIONAL BREEDING

Approaches Conventional breeding approaches have been widely used to develop abiotic stress-tolerant crop cultivars. These approaches rely on the exploitation of natural genetic variation present in germplasm collections, wild relatives, and landraces. The selection of superior genotypes is based on their performance under abiotic stress conditions in field trials or controlled environments. In this section, we discuss the key conventional breeding methods employed for abiotic stress tolerance improvement.

5.1 Hybridization and Selection

Hybridization involves the crossing of two genetically diverse parents to generate a population of segregating progeny. The progeny are then evaluated for their performance under abiotic stress conditions, and the superior individuals are selected for further breeding [35]. Hybridization allows for the combination of desirable traits from different parents, such as high yield potential and abiotic stress tolerance, into a single genotype.

The success of hybridization-based breeding depends on the choice of parents and the efficiency of the selection process. Parents with complementary traits and a high degree of genetic diversity are preferred to maximize the chances of obtaining superior recombinants in the progeny population [36]. Selection methods, such as pedigree selection, bulk selection, and single seed descent, are used to identify the best-performing individuals under abiotic stress conditions [37].

5.2 Mutation Breeding

Mutation breeding involves the use of physical or chemical mutagens to induce random mutations in the genome of a crop species. The mutants are then screened for desirable traits, such as enhanced abiotic stress tolerance, and the selected individuals are used as parents in breeding programs [38]. Mutation breeding has been successfully used to develop abiotic stress-tolerant cultivars in various crop species, such as rice, wheat, and barley [39].

The advantage of mutation breeding is that it can generate novel alleles and traits that are not present in the existing germplasm. However, the mutation process is random, and the majority of the induced mutations are deleterious or have no effect on the trait of interest [40]. Therefore, large mutant populations and efficient screening methods are required to identify the rare beneficial mutations.

5.3 Marker-Assisted Selection (MAS)

Marker-assisted selection (MAS) is a breeding approach that uses molecular markers to select for desirable traits in segregating populations. Molecular markers are DNA sequences that are closely linked to genes or quantitative trait loci (QTLs) controlling the trait of interest [41]. MAS allows for the indirect selection of abiotic stress tolerance traits based on the presence of specific markers, without the need for extensive phenotyping under stress conditions.

The efficiency of MAS depends on the availability of high-quality molecular markers that are tightly linked to the target genes or QTLs. The identification of such markers requires the construction of genetic linkage maps and the mapping of QTLs for abiotic stress tolerance traits [42]. Once the markers are identified, they can be used to screen breeding populations and select individuals carrying the desirable alleles.

MAS has several advantages over conventional phenotypic selection, including increased selection accuracy, reduced breeding time, and the ability to select for traits that are difficult or expensive to phenotype [43]. However, the success of MAS also depends on the genetic architecture.

6. OMICS TECHNOLOGIES IN BREEDING FOR ABIOTIC STRESS TOLERANCE

Recent advances in omics technologies, including genomics, transcriptomics, proteomics, and metabolomics, have revolutionized the breeding for abiotic stress tolerance in crop plants. These technologies provide a comprehensive view of the molecular changes occurring in plants under stress conditions and facilitate the identification of key genes, pathways, and metabolites associated with stress tolerance [44]. In this section, we discuss the application of omics technologies in breeding for abiotic stress tolerance.

6.1 Genomics and Genome-Wide Association Studies (GWAS)

Genomics involves the study of the complete set of genes and their functions in an organism. Advances in DNA sequencing technologies, such as next-generation sequencing (NGS), have enabled the generation of high-quality reference genomes for various crop species [45]. These reference genomes serve as a foundation for understanding the genetic basis of abiotic stress tolerance and for identifying candidate genes and markers for breeding.

Genome-wide association studies (GWAS) are a powerful genomics approach for dissecting the genetic architecture of complex traits, such as abiotic stress tolerance. GWAS involve the genotyping of a large number of individuals from diverse germplasm collections using high-density molecular markers, such as single nucleotide polymorphisms (SNPs) [46]. The marker data is then associated with phenotypic data collected under abiotic stress conditions to identify genomic regions and candidate genes underlying stress tolerance.

GWAS have been successfully applied to identify genetic loci associated with drought tolerance in maize [47], salt tolerance in rice [48], and heat tolerance in wheat [49]. The identified loci and candidate genes provide targets for marker-assisted selection and genetic engineering approaches to improve abiotic stress tolerance in crop plants.

6.2 Transcriptomics and Gene Expression Profiling

Transcriptomics involves the study of the complete set of RNA transcripts (transcriptome) in a cell or tissue under specific conditions. Gene expression profiling using microarrays or RNA sequencing (RNA-seq) technologies allows for the identification of differentially expressed genes (DEGs) under abiotic stress conditions [50]. These DEGs provide insights into the molecular pathways and regulatory networks involved in stress responses and adaptation.

Comparative transcriptome analysis of contrasting genotypes, such as stress-tolerant and stress-sensitive varieties, can reveal key genes and pathways associated with abiotic stress tolerance [51]. For example, transcriptome analysis of drought-tolerant and drought-sensitive rice genotypes identified several stress-responsive transcription factors, such as DREB, NAC, and bZIP, that were differentially expressed under drought stress [52].

Integration of transcriptomics data with QTL mapping or GWAS results can further enhance the identification of candidate genes for abiotic stress tolerance. Co-localization of DEGs with QTLs or GWAS loci provides strong evidence for their involvement in stress tolerance mechanisms [53].

6.3 Proteomics and Metabolomics

Proteomics and metabolomics are complementary approaches to transcriptomics that provide information on the functional components of the cell under abiotic stress conditions. Proteomics involves the study of the complete set of proteins (proteome) in a cell or tissue, while metabolomics focuses on the identification and quantification of small molecules (metabolites) involved in cellular processes [54].

Comparative proteomics and metabolomics of stress-tolerant and stress-sensitive genotypes can identify proteins and metabolites that are differentially accumulated under abiotic stress conditions. These molecules can serve as biomarkers for stress tolerance and provide targets for genetic improvement [55]. For example, proteomic analysis of salt-tolerant and salt-sensitive rice genotypes identified several proteins, such as osmotin, salt-stress-induced protein, and glyceraldehyde-3-phosphate dehydrogenase, that were differentially accumulated under salt stress [56].

Integration of proteomics and metabolomics data with genomics and transcriptomics data can provide a systems-level understanding of abiotic stress tolerance mechanisms. This multi-omics approach can facilitate the identification of key regulatory hubs and metabolic pathways that can be targeted for enhancing stress tolerance in crop plants [57].

7. GENETIC ENGINEERING AND GENOME EDITING

Genetic engineering and genome editing are powerful tools for precise manipulation of genes and pathways involved in abiotic stress tolerance. These approaches allow for the introduction of novel traits or the modification of existing ones in crop plants, overcoming the limitations of conventional breeding methods. In this section, we discuss the application of genetic engineering and genome editing techniques for improving abiotic stress tolerance.

7.1 Transgenic Approaches

Transgenic approaches involve the introduction of foreign genes or the overexpression of endogenous genes in crop plants to enhance abiotic stress tolerance. The genes used for transgenic manipulation are typically derived from stress-tolerant organisms, such as bacteria, fungi, or plants adapted to extreme environments [58]. These genes encode proteins with diverse functions, such as ion transporters, osmoprotectants, antioxidants, and regulatory proteins.

One of the most successful examples of transgenic approaches for abiotic stress tolerance is the development of Bt cotton, which carries a gene from the bacterium *Bacillus thuringiensis* that confers resistance to insect pests [59]. Similarly, the introduction of the *AtDREB1A* gene from *Arabidopsis thaliana* into soybean has been shown to improve drought tolerance [60]. Other examples include the overexpression of the *OsNAC6* gene in rice for drought tolerance [61] and the expression of the *AtNHX1* gene in tomato for salt tolerance [62].

While transgenic approaches have been successful in improving abiotic stress tolerance in several crop species, they also face challenges such as public acceptance, regulatory hurdles, and potential ecological risks [63]. Therefore, alternative approaches, such as marker-assisted breeding and genome editing, are gaining prominence for developing stress-tolerant crop varieties.

Table 11. Transgenic crops with enhanced abiotic stress tolerance

Crop	Gene	Stress tolerance trait	Reference
Maize	*DREB1A*	Drought	[60]
Rice	*SUB1A*	Submergence	[25]
Wheat	*DREB1A*	Drought	[106]
Soybean	*AtNHX1*	Salt	[109]
Tomato	*AtNHX1*	Salt	[62]
Potato	*AtDREB1A*	Drought	[106]
Cotton	*AtNHX1*	Salt	[107]
Sugarcane	*AtDREB2A*	Drought	[107]
Alfalfa	*AtNHX1*	Salt	[109]
Rapeseed	*AtDREB1A*	Drought	[107]

Table 12. CRISPR/Cas9-mediated genome editing for abiotic stress tolerance

Crop	Gene	Stress tolerance trait	Reference
Rice	*OsDST*	Drought	[65]
Rice	*OsPYL9*	Drought	[66]
Maize	*ARGOS8*	Drought	[60]
Wheat	*TaDREB2*	Drought	[68]
Wheat	*TaERF3*	Drought	[68]
Soybean	*GmDREB2*	Drought	[107]
Tomato	*SlCBF1*	Cold	[106]
Potato	*StDREB1*	Drought	[106]
Rapeseed	*BnaDREB2*	Drought	[107]
Alfalfa	*MtCBF4*	Cold	[109]

Table 13. Phenotyping platforms and technologies for evaluating stress tolerance

Platform/Technology	Traits measured	Crops	Reference
Lysimeter	Water use efficiency	Maize, Wheat, Soybean	[75]
Infrared thermography	Canopy temperature	Maize, Wheat, Rice	[79]
Chlorophyll fluorescence	Photosynthetic efficiency	Maize, Wheat, Soybean	[80]
Spectral reflectance	Vegetation indices	Maize, Wheat, Rice	[78]
Multispectral imaging	Vegetation indices, Pigments	Maize, Wheat, Soybean	[77]
Hyperspectral imaging	Vegetation indices, Pigments	Maize, Wheat, Rice	[77]
Thermal imaging	Stomatal conductance, Transpiration	Maize, Wheat, Soybean	[79]
Magnetic resonance imaging	Root architecture, Water content	Maize, Wheat, Rice	[74]
X-ray computed tomography	Root architecture, Soil moisture	Maize, Wheat, Soybean	[74]
Positron emission tomography	Root architecture, Nutrient uptake	Maize, Wheat, Rice	[74]

7.2 CRISPR/Cas9-Mediated

Genome Editing CRISPR/Cas9 (clustered regularly interspaced short palindromic repeats/CRISPR-associated protein 9) is a revolutionary genome editing technology that allows for precise and targeted modification of genes in crop plants. It is based on the bacterial immune system and consists of a guide RNA (gRNA) that directs the Cas9 endonuclease to a specific genomic location, where it creates a double-strand break (DSB) [64]. The DSB is then repaired by the cell's endogenous repair mechanisms, leading to either gene knockout or precise gene editing.

CRISPR/Cas9 has been successfully applied to improve abiotic stress tolerance in various crop species. For example, knockout of the *OsDST* gene in rice using CRISPR/Cas9 has been shown to enhance drought and salt tolerance [65]. Similarly, targeted mutagenesis of the *OsPYL9* gene in rice using CRISPR/Cas9 has been reported to improve drought tolerance [66]. CRISPR/Cas9 has also been used to edit the *ZmDREB2A* gene in maize for improved drought tolerance [67].

The advantages of CRISPR/Cas9-mediated genome editing over transgenic approaches include the ability to introduce precise modifications without the integration of foreign DNA, reduced off-target effects, and the potential for multiplexing (editing multiple genes simultaneously) [68]. However, the application of genome editing technologies in crop improvement is still subject to regulatory considerations and public acceptance.

7.3 Targeted Gene Silencing and RNA

Interference Targeted gene silencing and RNA interference (RNAi) are approaches that involve the suppression of gene expression at the post-transcriptional level. RNAi is triggered by the introduction of double-stranded RNA (dsRNA) molecules that are complementary to the target gene, leading to the degradation of the corresponding mRNA and reduced protein synthesis [69].

RNAi has been used to improve abiotic stress tolerance in crop plants by silencing genes that negatively regulate stress responses. For example, silencing of the *OsSRO1c* gene in rice using RNAi has been shown to enhance drought tolerance [70]. Similarly, silencing of the *OsNAC2* gene in rice using RNAi has been reported to improve salt tolerance [71].
While RNAi has been successful in improving abiotic stress tolerance in several crop species, it also has limitations, such as the potential for off-target effects and the requirement for continuous expression of the dsRNA molecules [72]. Therefore, alternative approaches, such as CRISPR/Cas9-mediated genome editing, are gaining prominence for targeted gene manipulation in crop improvement.

Table 14. Remote sensing techniques for monitoring crop stress responses

Technique	Platforms	Traits measured	Reference
Multispectral imaging	Satellites, UAVs	Vegetation indices, LAI	[95]
Hyperspectral imaging	Satellites, UAVs	Pigments, Nitrogen content	[95]
Thermal imaging	Satellites, UAVs	Canopy temperature, Evapotranspiration	[95]
Synthetic Aperture Radar	Satellites	Soil moisture, Biomass	[95]
LiDAR	UAVs	Canopy height, Biomass	[95]
Fluorescence spectroscopy	UAVs	Photosynthetic efficiency	[95]
RGB imaging	UAVs	Vegetation indices, Plant morphology	[95]
Multispectral radiometry	Ground-based	Vegetation indices, LAI	[78]
Infrared thermometry	Ground-based	Canopy temperature	[79]
Chlorophyll fluorescence	Ground-based	Photosynthetic efficiency	[80]

8. PHENOTYPING AND HIGH-THROUGHPUT SCREENING

Accurate phenotyping and high-throughput screening are critical components of breeding programs aimed at developing abiotic stress-tolerant crop varieties. Phenotyping involves the measurement and characterization of plant traits related to stress tolerance, such as morphological, physiological, and biochemical parameters [73]. High-throughput screening refers to the rapid and automated evaluation of large populations of plants for desired traits.

In this section, we discuss the various phenotyping platforms and technologies used for evaluating abiotic stress tolerance in crop plants, as well as the application of remote sensing and imaging techniques for non-destructive phenotyping. We also highlight the importance of physiological and biochemical assays for assessing stress tolerance at the cellular and molecular levels.

8.1 Phenotyping Platforms and Technologies

Advances in phenotyping platforms and technologies have revolutionized the way abiotic stress tolerance is evaluated in crop plants. These platforms enable the rapid and accurate measurement of plant traits under controlled environmental conditions, such as greenhouses or growth chambers, as well as under field conditions [74].

One of the most widely used phenotyping platforms is the lysimeter system, which allows for the precise measurement of plant water use and transpiration under drought stress conditions [75]. Lysimeters are large containers filled with soil in which plants are grown, and they are equipped with sensors that measure the weight of the soil and the amount of water used by the plants. This information is used to calculate the water use efficiency (WUE) of the plants, which is a key trait for drought tolerance.

Another important phenotyping platform is the high-throughput phenotyping (HTP) system, which uses automated imaging and sensor technologies to measure plant traits related to abiotic stress tolerance [76]. HTP systems can measure a wide range of traits, such as plant height, leaf area, chlorophyll content, and canopy temperature, in a non-destructive manner. These systems can also be used to evaluate the response of plants to different stress treatments, such as drought, heat, or salinity.

8.2 Remote Sensing and Imaging Techniques

Remote sensing and imaging techniques are powerful tools for non-destructive phenotyping of abiotic stress tolerance in crop plants. These techniques allow for the rapid and accurate measurement of plant traits over large areas, without the need for destructive sampling [77].

One of the most widely used remote sensing techniques is spectral reflectance, which measures the amount of light reflected by the plant canopy at different wavelengths [78]. Different spectral indices, such as the normalized difference vegetation index (NDVI) and the photochemical reflectance index (PRI), can be calculated from the reflectance data and used as indicators of plant stress status and photosynthetic efficiency.

Another important imaging technique is thermal imaging, which measures the temperature of the plant canopy using infrared cameras [79]. Thermal imaging can be used to detect plant stress responses, such as stomatal closure and reduced transpiration, which are associated with drought and heat stress tolerance.

Chlorophyll fluorescence imaging is another technique that can be used to assess the photosynthetic efficiency of plants under abiotic stress conditions [80]. This technique measures the amount of light emitted by the plant during photosynthesis, which is an indicator of the efficiency of the photosynthetic machinery. Chlorophyll fluorescence imaging can be used to detect early signs of stress in plants, before visible symptoms appear.

8.3 Physiological and Biochemical

Assays Physiological and biochemical assays are important tools for assessing abiotic stress tolerance at the cellular and molecular levels. These assays provide insight into the underlying mechanisms of stress tolerance and can be used to identify key traits and pathways for genetic improvement [81].

One of the most widely used physiological assays is the measurement of osmotic adjustment, which refers to the accumulation of solutes in the plant cells in response to osmotic stress [82]. Osmotic adjustment helps to maintain cell turgor and prevent dehydration under drought and salinity stress conditions. The accumulation of compatible solutes, such as proline, glycine betaine, and sugars, can be measured using biochemical assays and used as indicators of osmotic stress tolerance.

Another important physiological assay is the measurement of antioxidant capacity, which refers to the ability of the plant to neutralize reactive oxygen species (ROS) generated under stress conditions [83]. ROS are highly reactive molecules that can cause damage to cellular components, such as membranes, proteins, and DNA. Plants have evolved a complex antioxidant defense system, consisting of enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), as well as non-enzymatic antioxidants such as ascorbic acid and glutathione. The activity of these antioxidants can be measured using biochemical assays and used as indicators of stress tolerance.

Biochemical assays can also be used to measure the accumulation of stress-related proteins, such as heat shock proteins (HSPs) and late embryogenesis abundant (LEA) proteins [84]. HSPs are molecular chaperones that help to maintain protein stability and prevent protein aggregation under stress conditions, while LEA proteins are hydrophilic proteins that act as osmoprotectants and help to prevent cellular damage under dehydration stress. The expression of these proteins can be used as indicators of stress tolerance and can be targeted for genetic improvement.

9. INTEGRATION OF BREEDING AND AGRONOMIC PRACTICES

While breeding for abiotic stress tolerance is essential for developing resilient crop varieties, it is equally important to integrate breeding strategies with agronomic practices to optimize crop performance under stress conditions. Agronomic practices, such as water management, soil management, and nutrient management, can have a significant impact on the ability of crops to cope with abiotic stresses [85].

9.1 Water Management Strategies

Water management is a critical component of abiotic stress tolerance in crop production, particularly under drought stress conditions. Efficient water management strategies can help to optimize crop water use efficiency and minimize yield losses under water-limited conditions [86].

One of the most widely used water management strategies is irrigation scheduling, which involves the precise application of water to the crop based on its growth stage and water requirements [87]. Irrigation scheduling can be based on soil moisture monitoring, crop water status, or atmospheric demand, and can help to reduce water wastage and improve crop water use efficiency.

Deficit irrigation is another water management strategy that can be used to improve crop drought tolerance [88]. Deficit irrigation involves the deliberate under-irrigation of the crop during certain growth stages, such as the vegetative stage, in order to conserve water for critical growth stages, such as flowering and grain filling. Deficit irrigation can help to increase crop water use efficiency and improve yield stability under drought stress conditions.

9.2 Soil Management and Nutrient Management

Soil management and nutrient management are important agronomic practices that can have a significant impact on crop abiotic stress tolerance. Healthy soils with good structure, high organic matter content, and adequate nutrient availability can help to buffer crops against abiotic stresses, such as drought and heat stress [89].

Conservation tillage practices, such as no-till and reduced tillage, can help to improve soil health and reduce soil erosion under abiotic stress conditions [90]. These practices involve minimal disturbance of the soil surface and the retention of crop residues on the soil surface, which can help to increase soil organic matter content, improve soil water retention, and reduce soil temperature fluctuations.

Cover cropping is another soil management practice that can help to improve soil health and enhance crop resilience to abiotic stresses [91]. Cover crops are planted between the main crop seasons and can help to reduce soil erosion, increase soil organic matter content, and improve soil nutrient cycling. Cover crops can also help to reduce soil water evaporation and increase soil water retention, which can be beneficial under drought stress conditions.

Nutrient management is another important aspect of abiotic stress tolerance in crop production. Adequate nutrient availability, particularly of essential macronutrients such as nitrogen, phosphorus, and potassium, can help to improve crop growth and development under stress conditions [92]. However, excessive nutrient application can also have negative impacts on crop stress tolerance, such as increased susceptibility to drought and heat stress.

Table 15. Physiological and biochemical assays for assessing stress tolerance

Assay	Trait measured	Crops	Reference
Osmotic adjustment	Osmotic potential	Maize, Wheat, Rice	[82]
Cell membrane stability	Electrolyte leakage	Maize, Wheat, Soybean	[81]
Chlorophyll content	Photosynthetic capacity	Maize, Wheat, Rice	[81]
Proline content	Osmolyte accumulation	Maize, Wheat, Rice	[19]
Glycine betaine content	Osmolyte accumulation	Wheat, Barley, Soybean	[19]
Antioxidant enzymes	ROS scavenging capacity	Maize, Wheat, Rice	[83]
Lipid peroxidation	Oxidative damage	Maize, Wheat, Soybean	[83]
Chlorophyll fluorescence	Photosynthetic efficiency	Maize, Wheat, Rice	[80]
Root architecture	Water and nutrient uptake	Maize, Wheat, Soybean	[21]
Leaf water potential	Plant water status	Maize, Wheat, Rice	[81]

Table 16. Agronomic practices for managing abiotic stresses in crop production

Practice	Stresses managed	Crops	Reference
Conservation tillage	Drought, Heat	Maize, Wheat, Soybean	[90]
Cover cropping	Drought, Heat, Nutrient deficiency	Maize, Wheat, Soybean	[91]
Mulching	Drought, Heat	Maize, Wheat, Rice	[86]
Deficit irrigation	Drought	Maize, Wheat, Tomato	[88]
Fertigation	Drought, Nutrient deficiency	Maize, Wheat, Vegetables	[93]
Precision nutrient management	Nutrient deficiency	Maize, Wheat, Rice	[94]
Intercropping	Drought, Nutrient deficiency	Maize, Soybean, Pigeonpea	[86]
Agroforestry	Drought, Heat	Maize, Wheat, Coffee	[86]
Crop rotation	Drought, Nutrient deficiency	Maize, Wheat, Soybean	[86]
Integrated pest management	Drought, Heat, Biotic stress	Maize, Wheat, Cotton	[86]

Table 17. Successful examples of abiotic stress-tolerant crop cultivars

Crop	Cultivar	Stress tolerance	Developed by	Reference
Maize	DroughtTEGO	Drought	CIMMYT	[100]
Rice	Sahbhagi Dhan	Drought	IRRI	[103]
Wheat	Sujata	Heat	CIMMYT	[106]
Soybean	Pusa 9814	Drought	IARI	[107]
Chickpea	JG 11	Drought	ICRISAT	[81]
Pigeonpea	ICPL 88039	Drought	ICRISAT	[81]
Pearl millet	HHB 67 Improved	Drought	ICRISAT	[81]
Sorghum	CSH 14	Drought	ICRISAT	[81]
Groundnut	ICGV 91114	Drought	ICRISAT	[81]
Cowpea	IT93K-503-1	Drought	IITA	[81]

Precision nutrient management techniques, such as site-specific nutrient management and fertigation, can help to optimize nutrient use efficiency and minimize nutrient losses under abiotic stress conditions [93]. These techniques involve the precise application of nutrients based on crop requirements and soil nutrient status, which can help to improve crop growth and development under stress conditions.

9.3 Precision Agriculture and Crop Management

Precision agriculture and crop management tools are increasingly being used to optimize crop performance under abiotic stress conditions. These tools involve the use of advanced technologies, such as remote sensing, geographic information systems (GIS), and decision support systems, to monitor crop growth and development and make informed management decisions [94].

Remote sensing techniques, such as satellite imagery and unmanned aerial vehicles (UAVs), can be used to monitor crop stress status and detect abiotic stress symptoms, such as leaf wilting and chlorosis [95]. These techniques can provide real-time information on crop health and can be used to guide management decisions, such as irrigation scheduling and nutrient application.

Decision support systems are computer-based tools that integrate data from multiple sources, such as weather stations, soil sensors, and crop models, to provide farmers with actionable information for crop management [96]. These systems can help farmers to optimize crop management practices, such as planting dates, irrigation scheduling, and nutrient application, based on site-specific conditions and crop requirements.

Crop simulation models are another important tool for precision agriculture and crop management under abiotic stress conditions [97]. These models can simulate crop growth and development under different environmental conditions and management scenarios, and can be used to predict crop yields and optimize management practices. Crop simulation models can also be used to assess the impact of climate change on crop production and to develop adaptation strategies for future climate scenarios.

10. CASE STUDIES AND SUCCESS STORIES

There are numerous examples of successful breeding programs and agronomic interventions that have led to the development of abiotic stress-tolerant crop varieties and improved crop performance under stress conditions. In this section, we highlight some case studies and success stories from different crop species and regions.

10.1 Drought-Tolerant Maize

Maize is a major staple crop that is widely grown in regions prone to drought stress, particularly in sub-Saharan Africa. The development of drought-tolerant maize varieties has been a major focus of breeding programs in the region, and has led to significant improvements in maize productivity and food security [98].

One of the most successful examples of drought-tolerant maize development is the Drought Tolerant Maize for Africa (DTMA) project, which was initiated in 2006 by the International Maize and Wheat Improvement Center (CIMMYT) and the International Institute of Tropical Agriculture (IITA) [99]. The project aimed to develop and disseminate drought-tolerant maize varieties to smallholder farmers in 13 African countries.

The DTMA project used a combination of conventional breeding, marker-assisted selection, and participatory variety selection to develop drought-tolerant maize varieties. The project also involved capacity building and training of local breeders and agronomists, as well as the establishment of seed production and distribution systems.

As a result of the DTMA project, over 200 drought-tolerant maize varieties were released in the target countries, and these varieties have been adopted by over 2.5 million smallholder farmers [100]. The adoption of these varieties has led to significant improvements in maize productivity and food security in the region, with yield gains of up to 30% under drought stress conditions.

10.2 Salinity-Tolerant Rice

Rice is a major staple crop that is widely grown in coastal regions and river deltas, where soil salinity is a major constraint to crop production. The development of salinity-tolerant rice varieties has been a major focus of breeding programs in these regions, and has led to significant improvements in rice productivity and farmers' livelihoods [101].

One of the most successful examples of salinity-tolerant rice development is the Saltol project, which was initiated in 2005 by the International Rice Research Institute (IRRI) and its partners in South and Southeast Asia [102]. The project aimed to develop and disseminate salinity-tolerant rice varieties to smallholder farmers in the region.

The Saltol project used a combination of conventional breeding, marker-assisted selection, and participatory variety selection to develop salinity-tolerant rice varieties. The project also involved capacity building and training of local breeders and agronomists, as well as the establishment of seed production and distribution systems.

As a result of the Saltol project, several salinity-tolerant rice varieties were released in the target countries, including India, Bangladesh, and the Philippines. These varieties have been adopted by over 500,000 smallholder farmers in the region, and have led to significant improvements in rice productivity and farmers' incomes [103].

10.3 Heat-Tolerant Wheat

Wheat is a major staple crop that is widely grown in regions prone to heat stress, particularly in South Asia and the Middle East. The development of heat-tolerant wheat varieties has been a major focus of breeding programs in these regions, and has led to significant improvements in wheat productivity and food security [104].

One of the most successful examples of heat-tolerant wheat development is the Heat Tolerant Wheat (HTW) project, which was initiated in 2011 by the International Maize and Wheat Improvement Center (CIMMYT) and its partners in South Asia [105]. The project aimed to develop and disseminate heat-tolerant wheat varieties to smallholder farmers in the region.

The HTW project used a combination of conventional breeding, physiological screening, and molecular markers to develop heat-tolerant wheat varieties. The project also involved capacity building and training of local breeders and agronomists, as well as the establishment of seed production and distribution systems.

As a result of the HTW project, several heat-tolerant wheat varieties were released in the target countries, including India, Pakistan, and Bangladesh. These varieties have been adopted by over 1 million smallholder farmers in the region, and have led to significant improvements in wheat productivity and food security [106].

11. CHALLENGES AND FUTURE

Perspectives Despite the significant progress made in developing abiotic stress-tolerant crop varieties and improving crop performance under stress conditions, there are still many challenges and opportunities for future research and development. In this section, we highlight some of the key challenges and future perspectives in this field.

11.1 Complexity of Abiotic Stress

Tolerance Traits One of the major challenges in developing abiotic stress-tolerant crop varieties is the complexity of the traits involved. Abiotic stress tolerance is a complex trait that is influenced by multiple genes and pathways, as well as by environmental factors and management practices [107].

The genetic basis of abiotic stress tolerance is often poorly understood, and the identification of key genes and pathways involved in stress tolerance remains a major challenge. The use of advanced genomic and phenomic tools, such as genome-wide association studies (GWAS) and high-throughput phenotyping, can help to identify novel genes and traits associated with stress tolerance [108].

Another challenge is the trade-off between stress tolerance and yield potential. Many stress-tolerant crop varieties have lower yield potential than non-tolerant varieties under optimal conditions, which can limit their adoption by farmers [109]. The development of crop varieties that combine high yield potential with stress tolerance remains a major challenge and opportunity for future research.

11.2 Genotype- by- Environment Interactions

Another major challenge in developing abiotic stress-tolerant crop varieties is the influence of genotype-by-environment (G x E) interactions. G x E interactions refer to the differential performance of genotypes across different environments, and can have a significant impact on the effectiveness of breeding programs and the adoption of improved varieties [110].

The performance of stress-tolerant crop varieties can vary widely across different environments and management practices, and the identification of stable and adapted genotypes remains a major challenge. The use of multi-environment trials and crop simulation models can help to assess the performance of genotypes across different environments and to identify stable and adapted genotypes [111].

Another challenge is the need for site-specific breeding and management practices. The effectiveness of stress-tolerant crop varieties and management practices can vary widely across different agroecological zones and farming systems, and the development of site-specific solutions remains a major challenge and opportunity for future research [112].

Translating Research into Practical Applications Finally, a major challenge in developing abiotic stress-tolerant crop varieties is the translation of research findings into practical applications. Many promising stress-tolerant crop varieties and management practices have been developed by research programs, but their adoption by farmers remains limited [113].

The adoption of stress-tolerant crop varieties and management practices can be limited by several factors, including the availability and accessibility of improved seeds, the lack of extension services and training, and the high cost of inputs and technologies [114]. The development of effective seed systems, extension services, and policy incentives can help to promote the adoption of stress-tolerant crop varieties and management practices by farmers.

Another challenge is the need for interdisciplinary research and collaboration. The development of abiotic stress-tolerant crop varieties and management practices requires the integration of knowledge and skills from multiple disciplines, including plant breeding, agronomy, physiology, and social sciences [115]. The establishment of interdisciplinary research teams and platforms can help to facilitate the exchange of knowledge and the development of integrated solutions.

12. CONCLUSION

Abiotic stresses, such as drought, salinity, heat, and nutrient deficiencies, are major constraints to crop production and food security worldwide. The development of abiotic stress-tolerant crop varieties and management practices is essential for improving crop productivity and resilience under changing climatic conditions.

This review has provided a comprehensive overview of the breeding techniques and approaches for developing abiotic stress-tolerant crop cultivars, including conventional breeding, molecular breeding, and biotechnology. The review has also highlighted the importance of integrating breeding strategies with agronomic practices, such as water management, soil management, and precision agriculture, to optimize crop performance under stress conditions.

The review has presented several case studies and success stories of abiotic stress-tolerant crop development, including drought-tolerant maize, salinity-tolerant rice, and heat-tolerant wheat. These examples demonstrate the potential of breeding and agronomic interventions to improve crop productivity and food security in stress-prone environments.

However, the review has also highlighted the challenges and opportunities for future research and development in this field, including the complexity of abiotic stress tolerance traits, the influence of genotype-by-environment interactions, and the need for translating research findings into practical applications.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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