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Review

Recent Advancements in Mitigating Abiotic Stresses in Crops

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Abstract: In recent years, the progressive escalation of climate change scenarios has emerged as a significant global concern. The threat to global food security posed by abiotic stresses such as drought, salinity, waterlogging, temperature stress (heat stress, freezing, and chilling), and high heavy metal accumulation is substantial. The implementation of any of these stresses on agricultural land induces modifications in the morphological, biochemical, and physiological processes of plants, leading to diminished rates of germination, growth, photosynthesis, respiration, hormone and enzyme activity disruption, heightened oxidative stress, and ultimately, a reduction in crop productivity. It is anticipated that the frequency of these stresses will progressively escalate in the future as a result of a rise in climate change events. Therefore, it is crucial to develop productive strategies to mitigate the adverse effects of these challenges on the agriculture industry and improve crop resilience and yield. Diverse strategies have been implemented, including the development of cultivars that are resistant to climate change through the application of both conventional and modern breeding techniques. An additional application of the prospective and emerging technology of speed breeding is the acceleration of tolerance cultivar development. Additionally, plant growth regulators, osmoprotectants, nutrient and water management, planting time, seed priming, microbial seed treatment, and arbuscular mycorrhiza are regarded as effective methods for mitigating abiotic stresses. The application of biochar, kaolin, chitosan, superabsorbent, yeast extract, and seaweed extract are examples of promising and environmentally benign agronomic techniques that have been shown to mitigate the effects of abiotic stresses on crops; however, their exact mechanisms are still not yet fully understood. Hence, collaboration among researchers should be intensified to fully elucidate the mechanisms involved in the action of the emerging technologies. This review provides a comprehensive and current compilation of scientific information on emerging and current trends, along with innovative strategies to enhance agricultural productivity under abiotic stress conditions.

Keywords: biostimulant; management strategies; plants; tolerance; emerging strategies

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1. Introduction

Global agricultural output has been substantially adversely impacted by the emergence of climate change. Drought, salinity, waterlogging, temperature stress (heat stress, freezing, and chilling), and heavy metal accumulation are all consequences of climate change; as a result, crops become susceptible to additional stresses, including pests and diseases. Abiotic stress possesses significant effects on plants at every stage of their life cycle especially during plant growth and development [1]. More than 50% of production loss is attributed to the diverse array of stresses that affect 91% of the world's cropland [2]. The impact of abiotic stress on plants manifests in alterations to their morphological, physiological, and biochemical processes (Figure 1); however, the specific effects of abiotic stress vary by crop, stress type, and exposure duration [3].

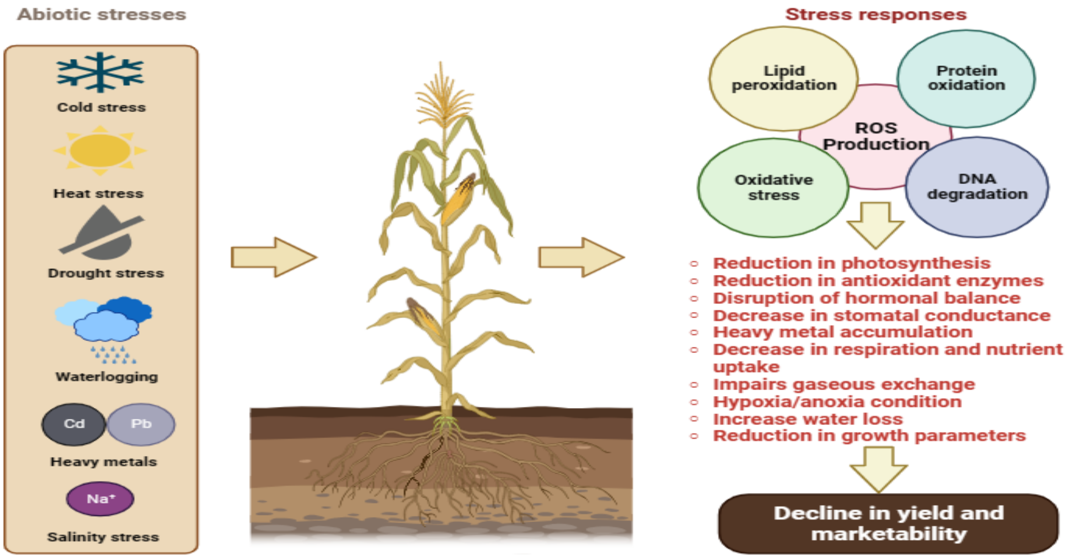

Figure 1. Plant response to abiotic stresses. This image was created using BioRender (https://biorender.com/, accessed on 19 December 2023).

Although the global climate change process is ongoing, it has significantly accelerated over the last century. The accumulation of greenhouse gases due to anthropogenic activities has led to global warming, contributing to an increase in the global temperature [4] by 0.9 °C since the 19th century [5]. Likewise, intense solar radiation during the day, promoting processes like evapotranspiration, causes an increase in the temperature. It is estimated that at the end of the 21st century, the world temperature will increase by 4.5 °C [6], making it a major threat to agricultural productivity. By 2050, it is predicted that 45% of the world's maize-producing regions will probably experience an annual mean episode of five days at maximum temperatures of more than 35 °C during the reproductive stage. This is significant because the commercial yield of maize crops can be reduced by 3–13% with just a 1 °C increase in mean seasonal temperature [7]. The exponential surge in global temperature has resulted in a rise in climate change events such as waterlogging, drought, erratic rainfall patterns, a decline in glaciers, strong typhoons and hurricanes, changes to animal habitats, the movement of plant habitats northward, and other extreme events [5]. As climate change bites harder, the occurrence of abiotic stress events is expected to increase, resulting in reduced agricultural yields.

Abiotic stresses severely hamper the economic and yield quality of numerous crops by modifying the physiological, biochemical, and molecular pathways and processes [8]. Based on studies both in model plants and other plants, responses to abiotic stresses are quite similar in most cases including the dehydration of the cell, stomatal closure, osmotic stress, the disruption of photosynthesis activity, the accumulation of reactive oxygen species (ROS), the inhibition of protective enzymatic functions, and the modification of gene expression, consequently bringing about reduced growth rates and nutritional quality [6,8]. Plants grown in saline soil and contaminated areas tend to accumulate sodium ions and heavy metals resulting in reduced growth and development and yield decline. Due to the inability of plants to move from one place to another, under extreme conditions, the plant responds to these stresses by modifying their metabolic networks to perform critical functions thus bringing about reduced productivity [9]. About 10–17% yield decline is reported as a result of high temperatures that occur at various stages of the plant life cycle [10]. In recent years, the total yields of legume crops such as chickpea, soybean, and mungbean declined by approximately 60 and 70%, respectively, due to cold stress [11]. It was reported that 10 to 40% of yield is lost due to heat and cold stress [12]. Furthermore, 5–50% of yield declines are caused by salinity [12]. The economic implications of climate change incidence have also been widely reported. For instance, global warming has resulted in significant financial losses of about US$125 billion [13].

To address the projected increase in food demand for the estimated global population of 9 to 10 billion people by 2050 and to improve food security, various strategies have been implemented to mitigate and improve crop performance under abiotic stress. These strategies include different breeding techniques (conventional and modern) [14], agronomic practices, seed priming and microbial seed treatment, microorganism inoculation, and grafting, as well as the use of plant growth regulators and osmoprotectants [15,16]. In recent times, cost-effective and environmentally friendly emerging/novel strategies, like the application of biochar, yeast extract, and seaweed extract, as well as the use of agri-nanotechnology, have also been implemented to enhance abiotic stress tolerance in crops [17,18]. While many studies have shown the promising potential and roles of biostimulants to reduce abiotic stresses, enhance quality, and increase yield, the underlying mechanisms of biostimulant–plant interactions at morphological, physiological, and molecular levels to overcome stress adversities remain unclear. This review provides a comprehensive and current compilation of scientific information on emerging and current trends, along with innovative strategies and the underlying mechanisms of action mediated by a wide range of emerging technologies during critical climate change events.

2. Management Strategies of Abiotic Stress

To alleviate the impact of abiotic stresses on plants and improve plant productivity, various management strategies have been implemented, ranging from breeding approaches, including conventional, molecular, and genetic engineering, and most recently, speed breeding techniques, to agronomical approaches such as nutrient management (Figure 2).

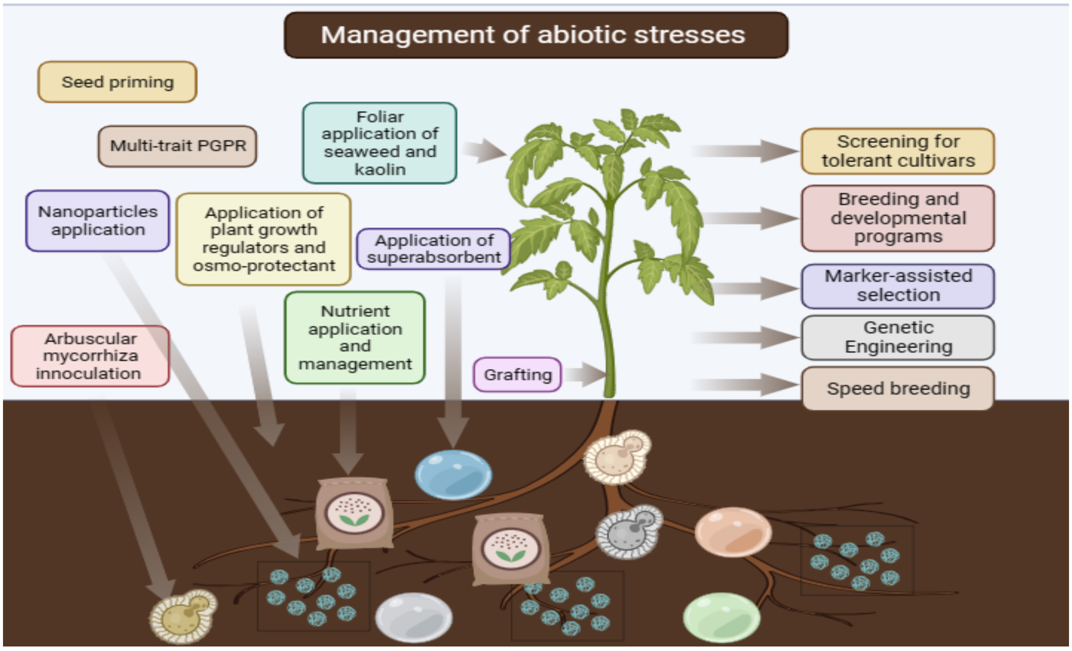

Figure 2. Overview of the management strategies of abiotic stresses. The image was created using BioRender (https://biorender.com/, accessed on 19 December 2023).

2.1. Breeding Approach

2.1.1. Conventional Breeding

Conventional breeding is considered an ancient, effective, and powerful approach to improving crop tolerance against abiotic stresses. The general stages of conventional breeding include variability creation, selection, evaluation, and cultivar release. In the past, a lot of work has been undertaken to increase plant yield and quality via conventional breeding; however, there has not been much research on increasing crops' resilience to abiotic stresses. Probably, this is attributed to plant breeders' primarily focusing on increasing crop output and quality rather than stress tolerance [19]. Nevertheless, plant breeders have been conducting a variety of breeding programmes over the past century, carefully utilising crop genetic variation at the intra-specific, inter-specific, and inter-generic levels to generate tolerant lines and cultivars [19]. Various conventional breeding methods, such as pedigree selection, recurrent selection, backcrossing, hybridization, and induced mutation, have been implemented by scientists to screen and identify cultivars under abiotic stresses (Table 1). It has been established that in various cereal crops, including wheat, rice, maize, sorghum, and legume crops, the mass screening and selection of cultivars for beneficial features under drought and salinity can increase yields [5]. Through the screening of different rice accessions under flooding stress, Indian accessions FR13A and FR43B and some Sri Lankan varieties such as Kurkaruppan, Goda Heenati, and Avalu were identified as having tolerance against waterlogging [20]. The screening of 380 cultivars of soybean led to the identification of eight lines that showed a tolerant phenotype under waterlogging [21]. Furthermore, several salt-tolerant rice genotypes, such as CSR10, CSR13, and CSR27, have been generated via conventional breeding techniques [22]. KRL1-4, a promising salt-tolerant genotype, was developed in Northern India via the crossing of Kharchia 65 and WL711 [23]. This genotype showed improved yield performance under saline soil in Northern India; however, it recorded low yield output when grown in Pakistan because of heavier soils and waterlogging events [24].

An induced mutation is regarded as another conventional breeding method that is successful in producing enhanced agronomic qualities, including increased grain production, with the major advantage of generating new gene alleles that are not present in the gene pool. This approach has been used to produce new mutant lines that are tolerant to a wide range of abiotic stresses. Pham et al. [25] recently identified a mutant tomato (HT7) that showed improved traits such as an increased number of fruits, total pollen number, and viability under heat stress compared with the control. Improved traits were associated with higher heat-related gene expressions, such as heat shock transcription factor (*SlHsfA1b*) and heat shock protein. This approach has also been used by the Nuclear Institute for Agriculture and Biology (NIAB), Faisalabad, Pakistan, to enhance rice mutant (*NIAB Rice-1* and *PSR 1-84*) tolerance to salinity stress and to increase yield. Major crops, including wheat, rice, barley, cotton, peanuts, and beans, have been enhanced through the application of induced mutations [26]. Despite the benefits of conventional breeding, the primary drawback faced by plant breeders is the relatively low level of genetic variation present in the gene pool of the majority of crop species. Other obstacles encountered using this approach include the fact that it takes a lot of time and is labor-intensive; unwanted genes are frequently transferred along with desired traits; and reproductive obstacles prevent the transfer of advantageous alleles from interspecific and intergeneric sources [26].

Table 1. List of Cultivars Developed Using Conventional Breeding.

Abiotic Stresses	Crops	Tolerant Cultivars	Selection Method	Country	References
Salinity	Tomato	Edkway	Natural selection	Egypt	[27]
	Barley	Golden Promise	Induced mutation	Scotland	[26]
	Alfalfa	AZ Germ Salt 1	Back crossing selection	USA	[27]
	Rice	Jiabuyu	Recurrent selection	China	[28]
	Rice	(CSR-1), Dasal (CSR-2), and Getu (CSR-3)	Pure line selection	India	[29]

Table 1. *Cont.*

Abiotic Stresses	Crops	Tolerant Cultivars	Selection Method	Country	References
Heat stress	Tomato	L72	Hybridization		[30]
	Cowpea		Pedigree backcross		[31]
	Tomato	Saladette	Selection	USA	[31]
Waterlogging	Soybean	NN1138-2, M8206, and ZXD	Selection		[32]
Cold stress	Alfalfa		Recurrent selection		[33]
Heavy metal	Rice		Induced mutation	Japan	[34]
	Wheat	Strongfield	Selection	Canada	[35]
Drought	Rice	Tarom Mahalli	Induced mutation	Iran	[14]
	Cotton	BH-167	Pedigree method	Pakistan	[36]
	Rice	Jiabuyu	Recurrent selection	China	[28]
	Rice	MR219-9 and MR219-4	Induced mutation	Malaysia	[14]

2.1.2. Grafting

Grafting is an ancient technique used in plant science to enhance the production of crops, especially vegetables. Grafting is the process of replacing the root system of a desired cultivar that is vulnerable to one or multiple stresses using a vigorous plant. The new root system is known as rootstock, while the scion is the upper part of the desired cultivar [37]. This technique has been utilized to improve endogenous hormone synthesis, nutrient uptake, tolerance against abiotic stress, and water use efficiency, and to minimize the impact of heavy metals on plants [38,39]. A study demonstrated an increase in eggplant yield grown under elevated temperature conditions when grafted onto heat-tolerant eggplant rootstock [40]. Generally, under heat stress scenarios, rootstocks tolerant to heat stress promote antioxidant production by lowering reactive oxygen species production, enhancing the rate of photosynthesis, protecting the integrity of the chloroplast membrane, and decreasing photo-oxidative damage [41]. Furthermore, a reduction in the total phenol content was observed in the grafted plant compared with the non-grafted plant, which subsequently helped to enhance the development of the shoot as well as biomass accumulation [42]. Grafting alleviates salinity stress in plants by minimizing the excess uptake of sodium ions in the soil [43]. In addition, grafted tomatoes demonstrated an enhanced tolerance to waterlogging with a significant increase in yield compared with non-grafted ones [44]. Recent findings conducted by [45] showed that grafted cucumber exhibited tolerance against drought stress by enhancing the growth traits, chlorophyll content, and malondialdehyde content compared with the non-grafted control. Interestingly, current scientific advancements have paved the way and made it easy to monitor the transmission of genetic material and signal transduction routes from the root to the shoot and vice versa in grafting union using omics approaches, such as genomic and proteomic approaches [46]. For instance, a study conducted by Muneer et al. [47] demonstrated that the graft interface protects the plants against heat by altering their proteomic and physiological responses to generate new cellular homeostasis and maintain several proteins for cellular defence: photosynthetic proteins, ion binding/transport proteins, and protein synthesis under diverse temperatures.

2.1.3. QTL Mapping and Marker-Assisted Breeding

Quantitative trait loci (QTL) mapping via the use of genetic markers has become essential in the enhancement of stress tolerance due to the intricacy of abiotic stress tolerance and the challenge of phenotypic selection. Since abiotic stresses such as heat and drought are controlled by multiple QTL, mapping is a quick way to find and identify the genes responsible for abiotic stress tolerance in crops. There are several stages involved in identifying QTL that regulate traits for abiotic stress: (i) identifying populations where the relevant traits associated with the particular abiotic stress are found; (ii) identifying polymorphic markers; (iii) polymorphic marker-based genotyping of mapping populations; (iv) accurate phenotyping based on traits associated with abiotic stress tolerance; and

(v) mapping QTL using phenotypic and genotypic data [48]. In QTL mapping, the most commonly employed segregating populations include full-sib F_1, F_2, doubled-haploid lines (DHLs), backcross 1 (BC_1), recombinant inbred lines (RILs), and near-isogenic lines (NILs) [48]. In summary, a large number of QTL linked to abiotic stress tolerance have successfully been mapped (Table 2). In a recent study, a recombinant inbred line mapping population was developed from a cross between Otis and Golden Promise grown under irrigated and rainfed conditions in the field and genotyped using a single nucleotide polymorphisms array. From the investigation, twenty-three QTL (eleven for seed weight, eight for shoot dry weight, and four for protein content) were detected across several barley chromosomes, which can be used to improve drought tolerance [49]. La Borde et al. [50] recently discovered novel QTL in sorghum associated with chilling tolerance at germination and early seedling stages.

Marker-assisted selection (MAS) is a useful approach that can be used to introduce desired traits into selected cultivars. It is a DNA-based marker approach utilized by plant scientists for three main reasons: to trace the desired alleles as dominant or recessive through generations in order to accumulate favourable alleles; to select the desired individuals using the complete genome or a portion of the allelic composition from segregated breeding lines; and to successfully integrate the desired alleles in selected cultivars by disrupting the unwanted linkage loci [14]. The MAS approach is simpler, faster, eco-friendly, more accurate, less expensive, and saves time for developing durable cultivars. Due to the complexity of abiotic stress tolerance and the influence of environmental factors, the selection and improvement of abiotic tolerance via conventional breeding alone are highly discouraged. Hence, the development of long-term abiotic stress tolerance cultivars can be achieved through the application of MAS [15]. After the identification of closely linked markers connected with the desired traits, this strategy is relatively quick and affordable for genetic improvement. Many studies have successfully utilized MAS to improve crops' tolerance to different abiotic stresses such as drought, salinity, and waterlogging in rice [51], heavy metals in rice [52], drought and heat stress in rice [53], drought in wheat [54], and heat stress in chilli and rice [55]. Recently, Mohd Ikmal et al. [56] reported success in the introduction of *Sub1* into the background of UKM91 (with drought yield QTL $qDTY_{3.1}$). The resultant lines performed better under both stressed and non-stressed conditions, with grain yield advantages of up to 1713 kg/ha and 1028 kg/ha over UKM91, respectively. Numerous studies have successfully identified QTL associated with cold tolerance, but most of these QTL have not been integrated for genotype improvement under chilling temperatures. Hence, the validation of QTL in multiple environments and populations and the introgression of these QTL to enhance crop tolerance should be prioritized in future studies.

Table 2. List of QTL identified for different abiotic stresses.

Abiotic Stresses	Crop	Population	QTL	Traits	References
Waterlogging	Soybeans	Benning × PI 416937	*qFTS-1*, *qSR-5.1*	Flooding tolerance scores and survival rates	[57]
	Rice	Indra × AC39416A	*qAG3.1*, *qSF10.1*	Anaerobic germination	[58]
	Wheat	Yangmai 16 × Zhongmai 895	*QWTC.caas-4AL*	Confer tolerance	[59]
Drought	Maize	SNJ201126 × HKI161	*qCH1–1*, *qCW2–1*	Cob weight, cob height	[60]
	Horsegram	HPKM249 × HPK4	*qRL01*, *qRL02*, *QCHL01*, *QPRO01*	Root length, chlorophyll, proline	[61]
	Chickpea	Pusa 362 × SBD 377	*qYLD7.1*, *qRWC1.1*	Yield, relative water content	[62]
	Tomato	Advanced generation	*Flw1.1* and *FW2.2*	Time to flower and fruit weight	[63]

Table 2. *Cont.*

Abiotic Stresses	Crop	Population	QTL	Traits	References
	Bean	Portillo × Red Hawk	*DF3.2*, *DF11.1*	Days to flowering	[64]
	Barley	TX9425 × Franklin	*QRMO.TxFr.2H*, *QPC-D.TxFr.3H*	Relative water content and proline	[65]
	Common bean	BAT 881 × G21212	*Yd4.1*	Yield components	[66]
	Rice	Lvhan 1 × Aixian 1	*qPH10.1*, *qEPN6.1*, *qPL9.1*, *qTGW2.1*, *qTGW6.1*, *qTGW8.1*, *qLL7.1 qLW7.1*, *qLA7.1*	Plant height, effective panicles number, panicle length, thousand-grain weight, leaf length, leaf width, and leaf area (LA)	[67]
	Groundnut	TAG 24 × ICGV 86031	*qDW-A05.2*, *qISC-A04.1*, *qNB-A07.1*, *qTR-A09.1*	Total dry matter, canopy conductance, number of branches, transpiration rate	[68]
Salinity	Chickpea	ICCV 10 × DCP 92	*qPHC5.2*, *qYPPS6.1*, *q100SWS3.1*	Plant height and yield traits	[69]
	Barley	TX9425 × Franklin	*QPC-S.TxFr.3H*, *QST.TxFr.7H*	Proline, salt tolerance	[65]
	Rice	R29 × Pokkali	*qSIS1*, *qRSH12*	Salt injury score, height	[70]
	Sorghum	Shihong 137 × L-Tian	*qTB6*, *qSFW9*, *qJW9*,	total biomass, stem fresh weight, juice weight	[71]
	Tomato	Advanced generation	*Flw1.1* and *FW2.2*	Time to flower and fruit weight	[63]
	Indian mustard	CS52 × RH30	*QBYP8.1*, *QSP4.1*, *QPB4.1*, *QSS4.1*, *QSS4.2*, *QSYP4.1*, *QMI8.1*	Yield per plant, siliquae per plant, primary branches, seed per silique, seed yield per plant, and membrane injury	[72]
	Cucumber	CG104 × CG37	*qST6.2*	Salt tolerance	[73]
	Jute	J009 × GFG	*qJST-1*, *qJST-2*	Salt tolerance	[74]
Heat stress	Chickpea	DCP 92-3 × ICCV 92944	*CaDFI_LS6.1*, *CaDPI_LS7.2*, *CaCHL_NS4.3*	Days to flowering, chlorophyll, and yield traits	[75]
	Tomato	LA1698 × LA2093	*qHII-1-1*	Heat injury index	[76]
	Cotton	MNH-886 × MNH-814	*qFSHa1*, *qNOB1*	Sympodial node height, Number of bolls	[77]
	Cucumber	99,281 × 931	*qHT1.1*	Heat tolerance	[78]
	Bread wheat	Germplasm	*QTL.16*	Thousand kernel weight	[79]
	Bottle gourd.	L1 (P17) × L6 (P23)	*qHT2.1*	Relative electrical conductivity	[80]
Cold stress	Rice	Natural population	*qSR2–1*, *qSR3–4*, *qSR3–5*	Seedling survival rate	[81]
	Alfalfa	3010 × CW 1010	*dbr1*, *dft1*	Cold tolerance and biomass ratio	[82]
	Peanut	DF12 × Huayu 44	*qRGRB09*	Cold tolerance	[83]
Heavy metal	Rice	WTR1 × Hao-an-nong	*qRChlo1*	Chlorophyll content	[84]
	Soybean	AC Hime × Westag-97	*Cda1*	Low Cd concentration	[85]
	Cabbage	Y177 × Y195	*Zn100SDB6*	Shoot dry biomass	[86]
	Maize	Huang-C × Xu178	*qLAV1* and *qSAC1*	Kernel	[87]

2.1.4. Genetic Engineering of Abiotic Stress Tolerance

In the present decade, the implementation of genetic engineering techniques has become a more popular and alternative tool to enhance crop tolerance to a wide range of environmental stresses with a minimum yield penalty. Transgenic plants have undergone genetic modification through the direct insertion of desired genes into a plant cell [19]. Several techniques, such as agrobacterium-mediated and particle bombardment techniques, are commonly employed to directly deliver desired traits into the cell genome [88]. This approach is fast and less time-consuming for improving plant traits compared with conventional breeding methods. The implementation of genetic engineering techniques has led to the modification of gene expression and production of targeted genes, enzymes, and proteins and has consequently brought about improved tolerance to abiotic stresses in a wide range of crops [16]. Many studies have reported increased tolerance in genetically engineered plants under abiotic stresses (Table 3). The overexpression of a novel cold-responsive transcription factor *LcFIN1* cloned from sheep grass in Arabidopsis enhanced tolerance under chilling temperature conditions [89]. The overexpression of metal resistance protein 1 (*MTP1*), cloned from ryegrass, enhanced transgenic rice tolerance to zinc and cadmium [90]. An increased survival rate (74–79%) and accumulation of proline and soluble sugar were observed in transgenic rice after zinc finger protein *OsZFP252* was overexpressed [14]. The overexpression of peroxisomal *BADH* in transgenic rice resulted in reduced sodium ion and chloride ion accumulation and improved ion selectivity by the accumulation of higher potassium ions under salinity stress [26]. Enhanced heat tolerance was observed in transgenic tomatoes by preventing photosystem II from oxidative stress due to the overexpression of *HSP21* [91]. Transformed *E. coli*, yeast, and *Arabidopsis* with *RcHsp17.8*, cloned from *Rosa chinensis*, demonstrated tolerance to a wide range of stresses [22]. Despite the benefits associated with the application of genetic engineering techniques, the acceptability of genetically engineered crops among the public is still low due to potential health risks associated with their consumption. For instance, a study to create genetically modified peas by adding a bean protein that provided weevil resistance was shelved after it was discovered that the genetically modified peas triggered lung allergies in mice [92]. In conclusion, the transgenic technique is a promising and fast approach that has been used to improve genetically engineered crops under multiple stresses successfully. Nonetheless, most of the transgenic plants need to be tested in the field to evaluate their performance under natural conditions.

Table 3. Enhancing crop tolerance to abiotic stresses through engineering genes.

Transgenic Crop	Abiotic Stresses	Gene and Its Source	Traits Improved	References
Tobacco	Salinity	*bet A* from *Escherichia coli*	Enhanced biomass	[26]
Arabidopsis and tobacco	Salinity, drought, and cold stress	*GmbZIP1* from soybean	Enhanced tolerance to multiple stresses	[22]
Rice	Heavy metal	*MTH1745* from thermophilic archaea	Improved photosynthesis and conferred mercury tolerance	[93]
Potato	Salinity	*pyrroline-5-carboxylate synthetase (P5CS)* gene from Arabidopsis	Increased proline content and tuber production	[94]
Tomato	Heat stress	*StGLP* from yeast	Improved tolerance to gradual heat stress	[95]
Tall fescue	Salinity	*AtNHX1* from Arabidopsis	Increased shoot and root dry weight	[19]
Arabidopsis	Salinity and drought	*TaMYB2A* from wheat	Enhanced tolerance to drought and salinity	[22]
Rice	Waterlogging, salinity, and drought	*OsARD1* from rice	Increased ethylene synthesis and conferred tolerance to submergence, drought, salt, and osmotic stresses	[96]

Table 3. *Cont.*

Transgenic Crop	Abiotic Stresses	Gene and Its Source	Traits Improved	References
Potato	Cold stress	*Δ12-desaturase* gene from cyanobacteria	Improved tolerance by reducing malondialdehyde content	[94]
Tobacco	Cold stress	*TaMYC2* from caucasian clover	Increased production of antioxidant enzymes	[89]
Arabidopsis	Heat stress	*TaHsfA6f* from wheat	Enhanced heat tolerance and abscisic acid (ABA) accumulation	[97]
Medicago truncatula	Cold stress	*MtDREB1C/MtCBF3* from *Medicago truncatula*	Inhibited growth of the shoot and enhanced cold tolerance	[98]
Alfalfa	Heavy metal	*ATP sulfurylase* gene from Arabidopsis	Improved tolerance to heavy metal	[99]
Tomato	Cold stress	*SiFBA5* from Snow Lotus	Enhanced photosynthetic efficiency and tolerance to cold stress	[100]
Potato	Drought	*BADH transgene* from spinach	Enhanced fresh weight	[94]
Medicago truncatula	Drought	*MtP5CS* from *Medicago truncatula*	Increased proline production and conferred tolerance	[98]

2.1.5. Genome Editing

Apart from the transgenic method, genome editing is considered an emerging technique for improving plant traits via the gain or loss of gene function, or a multiplex genome-editing strategy. Out of the various gene-editing tools available, CRISPR-associated Cas protein (CRISPR-Cas9) systems are widely employed by researchers to improve plant performance under multiple stresses. A wide range of crop species (such as Arabidopsis, tobacco, and rice) have been gene-edited for different agronomic traits and improved abiotic stress tolerance using CRISPR-Cas9 [101]. A recent study used CRISPR-Cas9 to enhance rice cold tolerance as well as yield traits by simultaneously editing three genes: *OsPIN5b* (a panicle length gene), *GS3* (a grain size gene), and *OsMYB30* (a cold tolerance gene). The resultant mutant showed increased panicle length, enlarged grain size, and increased cold tolerance, respectively [102]. Knocking out the *SIAGL6* gene in tomatoes with the aid of CRISPR-Cas9-mediated genome editing confers heat tolerance as well as enhanced fruit setting [103]. With the aid of the CRISPR-Cas9 system, a gene associated with salt and drought tolerance in the indica mega rice cultivar "MTU1010" was mutated. The resultant mutant plant showed reduced stomatal activity, wider leaves, and improved leaf water preservation under stress conditions [104]. Based on the recent progress made so far, CRISPR tools can be regarded as a promising technique to generate new germplasm for breeding programs as well as develop new cultivars with improved traits under abiotic stresses.

2.1.6. Speed Breeding: A Speedy Approach to Develop Crop Resilience to Abiotic Stress

In the past and even up to the present era, conventional breeding has been implemented to improve crop yield, quality, and tolerance to diverse biotic and abiotic stresses, which has gained popularity among plant breeders. However, most of these traditional techniques require a lot of manpower, and it takes a lot of time (10–15 years) from the first crossing to variety release. Thus, researchers are creating a new methodology to speed up the breeding process by minimizing the amount of time needed to create new lines, which gives rise to a new technology known as "speed breeding" [105]. Speed breeding is a fascinating and emerging breeding technique that hastens the rate of plant growth from crossing to variety release. Speed breeding also aids in increasing the number of plant cycles per year. NASA initially used this technique to grow wheat in space by prolonging the light supply at the optimum temperature. This led to significantly accelerated growth as well as enhanced plant growth and photosynthesis rates. Since then, this technology has been successfully employed on our planet to grow crops [106]. This technique is conducted in a controlled environment with artificial LED lights with a wavelength of 400–700 nm and a photoperiod of 22 h and 2 h of darkness [105]. It has been employed for the rapid production of many crops. For example, crops such as chickpea, barley, durum wheat, spring wheat, amaranth, and pea were grown six times a year, while canola and groundnut completed four growing cycles in a year [107,108] (Figure 3). With lentils, a prolonged photoperiod, plant growth regulator treatment, and immature seed cultivation led to the production of up to eight generations per year. Similarly, up to six generations per year of lentils were obtained through continuous light supply (20 h light–4 h dark) and immature seed cultivation [109]. Furthermore, the use of an embryo rescue approach has been successfully employed by plant breeders to reduce the breeding cycle of sunflowers [110].

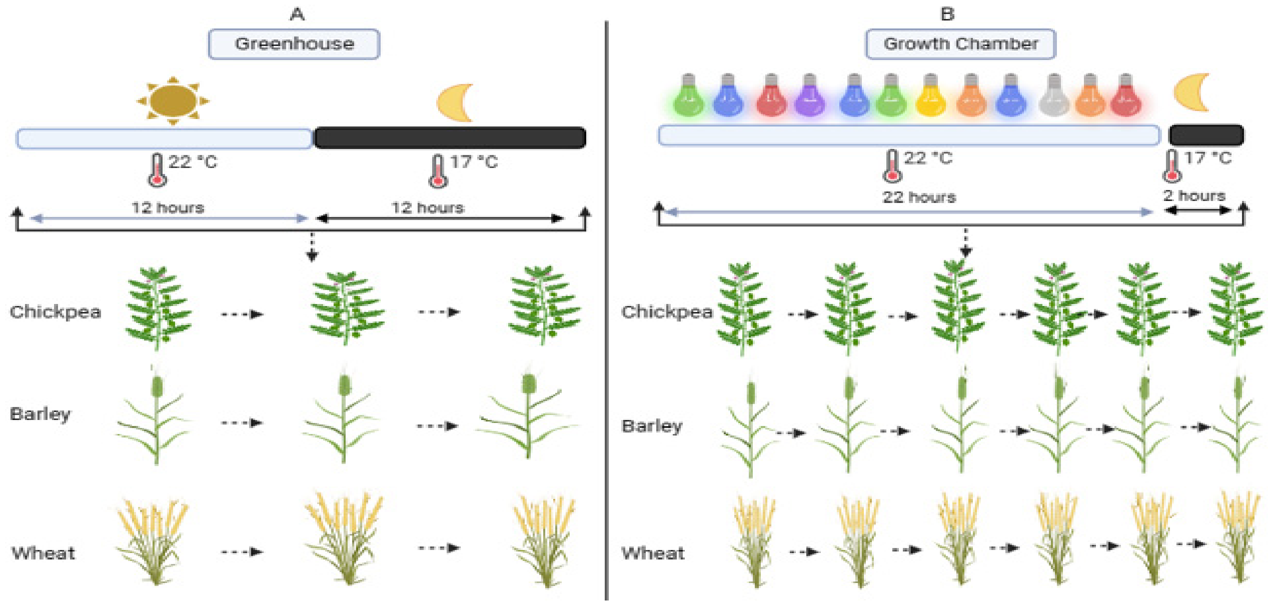

Figure 3. Advantages of speed breeding (22 h artificial light, 2 h dark) over conventional breeding (12 h sunlight, 12 h dark). (**A**) Conventional breeding; (**B**) Speed breeding.

Speed breeding technology has been integrated into various selection techniques, such as single plant selection, single seed descent, marker-assisted selection, and clonal selection, to reduce the breeding process, maximize resource utilization, and accelerate the release of high-yielding tolerance cultivars to multiple abiotic stresses [111]. The incorporation of speed breeding in MAS has been employed to enhance multiple disease resistance in barley [112], fire blight in apples [110], and confer salinity tolerance in rice [113]. Speed breeding has also been used to develop a wheat cultivar tolerant to drought, and up to five generations of stay-green inbred lines have been produced in 18 months. Additionally, over 40,000 molecular markers were found during the investigation, which helped identify unique QTL responsible for stay-green traits [114]. This technique, coupled with CRISPR-Cas9 and MAS, has been used to develop elite hybrid lines [110]. With the aid of speed breeding, "YNU31-2-4" (a new salt tolerance cultivar) was successfully produced. This was carried out by using single nucleotide polymorphisms to insert the genes, then speed breeding to fast-track the breeding cycle with 14 h of light and 10 h of darkness from the germination to the vegetative stages, and then 10 h of light and 14 h of darkness were applied to start the reproductive stages. To shorten the time before seed maturity, the tillers were cut off, and an embryo rescue technique was applied, allowing the researchers to obtain four to five generations of rice annually [106]. Despite the numerous benefits associated with this technology, drawbacks such as a shortage of personnel skilled in the methodology, the availability of suitable equipment, and limited funding to support the research (such as setting up a standard controlled environment) may affect the acceptability of this technology, particularly in developing nations with limited power supplies [111]. In the future, however, the utilization of speed breeding will enhance our knowledge about plant responses to abiotic stresses and the mechanisms involved. It will also aid in accelerating the release of more high-yielding tolerance genotypes through the integration of omics, biotechnological, MAS, and conventional breeding techniques [115] and serve as a long-term solution, improving sustainable and precision agriculture and increasing farmer income.

2.2. Seed Priming Techniques

In the current era, various strategies have been adopted to effectively inhibit the impact of abiotic stresses on plants, starting from the seedling until harvest. Seed priming is regarded as one of the most suitable, least expensive, and effective methods to alleviate the impact of abiotic stresses, especially during the seedling phase, which is generally vulnerable. This method enhances seedling germination and morpho-physiological and biochemical traits under abiotic stresses [116]. This pre-sowing strategy aims to prepare the seed for radicle protrusion without causing radicle emergence during the process by starting the germination process in the seed's metabolic component. Compared with non-primed seeds, primed seeds have higher germination rates and more uniformity because their germination process is more efficient [117]. Seed priming is a three-step procedure that begins with immersing seeds for a stipulated time in the selected priming agents. In the second stage (known as the activation phase), several metabolic activities at the cellular level are activated, including protein synthesis and other protective enzymes, as well as new mitochondria formation. In the last stage (rehydration phase), priming induces various processes such as cell division, nucleic acid synthesis, and Adenosine triphosphate to increase cellular energy [118].

This technique affects the soluble sugar and starch concentration of germinated seeds and the activities of different enzymes involved in the process [119]. Various seed priming techniques, such as hydropriming, osmopriming, biopriming, and molecular priming, have effectively been used in different crops to mitigate abiotic stresses and enhance seedling growth and establishment (Table 4). The effectiveness of these priming techniques depends on the type of plant and a wide range of environmental factors [120]. Melatonin and nanoparticles are new emerging agents used for seed priming and are considered effective. The use of melatonin as a priming agent confers heat tolerance in Arabidopsis and induces heat shock proteins. During heavy metal stress, a seed primed with melatonin inhibits oxidative damage induced by ROS by enhancing antioxidant enzymes [121]. Seed priming with nanoparticles has been reported to alleviate drought in wheat by upregulating the antioxidant enzymes [122]. Though the use of nanoparticles is a promising tool to increase plant productivity under diverse conditions, its usage must be optimized to avoid further ecosystem damage and ensure safe agricultural produce.

Table 4. Improving crop tolerance using various seed priming approaches.

Abiotic Stress	Crop	Priming Technique	Impacts	References
Heavy metal	Pigeon pea	Phytohormones priming	Increased germination speed index, germination percentage, and tolerance to cadmium	[116]
	Garden cress	Phytohormone priming	Improved seed germination, seedling emergence and tolerance index and reduced phytotoxicity.	[123]
	Mustard	Phytohormone priming	Improved shoot emergence and decreased accumulation of heavy metal	[124]
	Maize	Nanoparticle priming	Reduced uptake of toxins and improved photosynthesis pigments and plant ultra-cellular structures	[125]

Table 4. *Cont.*

Abiotic Stress	Crop	Priming Technique	Impacts	References
Salinity	Maize and wheat	Biopriming	Improved physiological and morphological traits	[120]
	Rice	Phytohormone priming	Reduced sodium ions accumulation and increased potassium concentration	[126]
	Capsicum	Nanoparticle priming	Increased enlargement of roots and promoted salt tolerance	[122]
	Rapeseed	Hydropriming	Increased germination percentage	[118]
	Sweet pepper	Osmopriming	Conferred tolerance due to enhanced biosynthesis of plastidial pigments	[118]
Drought	Plants	Molecular priming	Induced tolerance against oxidative stress	[117]
	Rye seed	Hydropriming	Stimulated antioxidant enzymes production	[127]
	Soybean	Hydropriming	Enhanced germination and seed yield	[128]
	Caraway	Osmopriming	Increased germination and fresh and dry weights of the plumule in the seeds	[127]
Waterlogging	Rice	Phytohormone priming	Increased α-Amylase activity, sucrose, glucose, and fructose	[116]
	Rice	Chemical and hormonal priming	Improved tolerance to waterlogging	[119]
	Okra	Chemical priming	Induced aerenchyma development resulting in okra survival	[129]
Heat stress	Tall fescue	Phytohormone priming	Induced heat-responsive genes	[121]
	Maize	Phytohormone priming	Increased photosynthetic pigment, membrane stability index, relative water content, growth rate, grain yield, harvest index, and grain protein	[130]
	Yarrow	Heat priming	Improved photosynthesis and stomatal conductance	[131]
	Arabidopsis	Thermopriming	Modified energy pathway and enhanced branched-chain amino acids production	[132]
Cold stress	Canola	Thermopriming	Improved germination	[26]
	Rapeseed	Phytohormones and hydropriming	Improved photosynthesis, stomatal conductance, transpiration rate, and antioxidant enzymes	[133]
Chilling stress	Maize	Phytohormone priming	Enhanced germination, antioxidant enzyme, starch metabolism, and malondialdehyde content	[134]
Salinity and drought	Chickpea	Osmopriming	Suppressed stress effect	[116]

Seed Treatment with Microbes

The treatment of seeds with biological agents such as fungi and bacteria has been identified as another way to ameliorate the impact of abiotic stresses and enhance resistance in plants. For instance, treating tomato seeds with *Trichoderma* enhanced their germination and uniformity, compared with the control, under osmotic, salt, or suboptimal temperature conditions [135]. Under heat stress conditions, the treatment of seeds with *Bacillus* spp. and *Azospirillum* spp. increased tolerance levels by lowering ROS accumulations [16]. The improved germination and growth of wheat seedlings treated with *B. subtilis 10-4* were observed under limited water circumstances, and its negative effect was remarkably mitigated [136]. The seedlings of canola treated with *Bacillus subtilis* (bacterium), *Macrophomina* *phaseolina* (fungus), or a combination of both improved the rates of germination under salinity conditions [135]. The germination index and seedling growth of *Glycine max* were significantly enhanced under cold stress due to the inoculation of their seeds with *Bacillus megaterium*, *Trichoderma longibrachiatum*, and *Trichoderma simmonsii* [137]. Extensive research is still required to fully understand the role of biological agents in the alleviation of abiotic stresses and the underlying mechanisms involved.

2.3. Plant Growth Regulators and Osmoprotectants

The utilization of plant growth regulators and osmoprotectants, including polyols, glycine betaine (GB), mannitol, salicylic acid (SA), and many others, has been shown to alleviate several environmental stresses in different crops during production by enhancing the antioxidant enzymes and osmotic adjustment [5,15] (Table 5). Under water-deficit conditions, using abscisic acid, uniconazole, brassinolide, and jasmonic acid exogenously increased plant productivity [117]. It has also been demonstrated that salinity stress was alleviated in crops due to the application of gibberellic acid, zeatin, and ethephon [138]. The application of salicylic acid exogenously enhanced pea growth traits and biomass under high temperatures [46]. In addition, heat tolerance was elevated in tomato seedlings due to the exogenous application of ascorbic acid at 0.5 mM, which scavenged reactive oxygen species and increased ascorbic acid content, proline, and photosynthetic pigment [139]. Heavy metal stress, particularly copper stress, was ameliorated in wheat and enhanced yield due to the application of proline [140]. The foliar application of trehalose had a favorable impact on photosynthetic components, osmolyte synthesis, and ion contents of tomatoes under salinity. It also increased the expression and activity of antioxidant enzymes and decreased reactive oxygen species (ROS) compared with tomato plants that were not treated [141]. Recently, new plant-growth regulator-stimulating compounds have been identified and shown to improve plant tolerance to abiotic stresses, including strigolactones and melatonin. Under heat stress, thiourea confers tolerance to camelina by upregulating gas exchange and water relations [142]. Improved abiotic stress tolerance was demonstrated in plants by regulating the stomatal guard cell and the number of stomata on the leaf surface after exogenous strigolactone treatment [136].

Table 5. List of plant growth regulators and osmoprotectants used to enhance plant abiotic stress tolerance.

Abiotic Stresses	Plant Growth Regulators and Osmoprotectants	Crop	Mechanism	References
Salinity	5-Aminolevulinic acid	Cotton	Enhanced seedling germination	[26]
	Proline	Wheat	Enhanced hormones accumulation and reduced malondialdehyde	[23]
	Thiamin	Sunflower	Enhanced chlorophyll content, biomass, and leaf relative water content	[26]
	Indole acetic acid	Wheat	Reduced oxidative stress	[88]
	Brassinosteroid	Wheat	Increased yield	[23]
Drought	Melatonin	Wheat	Enhanced seedling vigour and tolerance	[138]
	Abscisic Acid	Rice	Increased antioxidant enzymes, proline, and soluble sugar content	[117]
	Gibberellic acid	Faba bean	Improved relative water content, cell membrane stability, and nutrient status	[143]
	Salicylic acid	Sunflower	Enhanced yield traits and quality	[144]

Table 5. *Cont.*

Abiotic Stresses	Plant Growth Regulators and Osmoprotectants	Crop	Mechanism	References
Waterlogging	Gibberellic acid	Soybean	Improved flooding tolerance	[21]
	Cytokinin and gibberellic acid	Mungbean	Enhanced growth and biomass, photosynthesis pigments and proline, and total soluble sugars	[145]
	6-Benzyladenine	Maize	Suppressed the effect of stress on grain yield	[146]
	Salicylic acid and kinetin	Soybean	Increased antioxidant enzymes activities and the glyoxalase system	[147]
Heat stress	24- epibrassinolide	Mustard	Induced heat tolerance	[16]
	Trehalose	Maize	Reduced the accumulation of malondialdehyde and enhanced cell integrity	[144]
	Indole-3-acetic acid	Rice	Improved yield	[148]
	Proline	Okra	Enhanced antioxidant enzymes activities and growth traits	[149]
Heavy metal	Gibberellic acid	Lupin plants	Improved amylase and catalase activities	[150]
	Salicylic acid gibberellic acid and triacontanol	Menthol mint	Reduced cadmium accumulation in the leaves and upregulated proline and antioxidant enzymes	[151]
	24-epibrassinolide	Mustard	Reduced heavy metal accumulation and enhanced growth rate	[150]
Cold stress	Brassinosteroids	Tomato	Improved growth by reducing oxidative stress	[152]
	Auxin	Pea	Reduced conjugated polyamines and increased proline content	[153]
	Abscisic acid	Banana	Maintained cell membrane stability by reducing ion leakage and lipid peroxidation	[154]
	Strigolactones	Mung bean	Reduced phenolic contents and enhanced water status and proline content	[155]

Melatonin: An Emerging Plant Growth Regulator

Melatonin (N-acetyl-5-methoxytryptamine) is a tryptophan derivative identified in 1995 in plants. Melatonin is found in different parts of the plant, including roots, leaves, flower buds, and petals. Melatonin biosynthesis mostly takes place in the mitochondria and chloroplasts [156]. Several factors can stimulate the production of melatonin in plants, such as light, dramatic temperature changes, and UV-B radiation. In plants, melatonin biosynthesis occurs via two pathways. The first pathway involves the conversion of tryptophan by tryptophan decarboxylase into tryptamine in the cytoplasm, then tryptamine 5-hydroxylase catalyses it into serotonin. Serotonin N-acetyltransferase (SNAT)/arylalkyl amine N-acetyltransferase (AANAT) turns serotonin into N-acetyl serotonin. N-acetyl-serotonin methyltransferase (ASMT)/hydroxyindole-O-methyltransferase (HIOMT) converts N-acetyl serotonin to melatonin. This pathway usually occurs under normal conditions [157–159]. In the second pathway, serotonin converts into 5-methoxy-tryptamine by HIOMT, then SNAT converts 5-methoxy-tryptamine into melatonin. This pathway usually occurs under extreme conditions [157–159]. The role of melatonin in mammals' physiological processes has been fully studied, while its role in plants is still being investigated. Melatonin has been suggested to play a role in several plant developmental processes, such as seed germination, the regulation of plant growth, and fruit ripening, among other factors [140]. Apart from these functions, the application of melatonin has recently been reported to play a crucial role in alleviating the impact of abiotic stress (drought, heat stress, salinity, and heavy metals) on crops by safeguarding the plant from oxidative stress and damage, regulating plant growth and development, and stress signaling pathways. Furthermore, it modifies gene expression, controls hormone balance, and enhances plant physiological adaptation, making it an eco-friendly approach to combating abiotic stress during crop production [160].

The application of melatonin has been demonstrated to improve crop performance under abiotic stress, such as tomatoes under salinity, maize under heat stress, cucumber under cold stress [161], and tomatoes under heavy metals, by reducing the production of reactive oxygen species and improving the accumulation of antioxidant enzymes [160]. The use of melatonin exogenously was found to enhance the alfalfa plant's tolerance to waterlogging significantly [161]. The interplay between melatonin and other plant growth phytohormones, such as auxin, cytokinin, gibberellins, abscisic acid, ethylene, jasmonic acid, and salicylic acid, has been reported [140]. The treatment of plants with melatonin ameliorates the suppression of flowering induced by drought by stimulating the biosynthesis of gibberellic acid. Improved tolerance under water stress conditions can be associated with positive crosstalk between melatonin and abscisic acid, which regulate stomatal closure [156]. Moreover, researchers have suggested that the application of melatonin that brings about the enhancement of alfalfa performance under waterlogging events could be attributed to the interplay with or by directly modulating the metabolic pathways of polyamines and ethylene [161]. Additionally, melatonin decreases the accumulation of abscisic acid in plants and enhances the expression of cold-responsive genes, thereby significantly improving cold tolerance [162]. Melatonin helps protect against oxidative stress by interacting with jasmonic acid and suppressing the expression of LOX- related genes [159]. Although studies have demonstrated the ability of melatonin to mitigate abiotic stress, nevertheless, multiple field trials should be conducted in arid regions where these natural environmental challenges are prevalent in order to examine the potential of melatonin under abiotic stresses effectively.

2.4. Inoculation of Arbuscular Mycorrhiza (AMF)

Crops are treated with microbial plant biostimulants (MPBs) to improve growth and productivity by facilitating the uptake of various nutrients and their utilization. A wide range of MPBs, such as mycorrhizal and non-mycorrhizal fungi, bacterial endosymbionts, and plant growth-promoting rhizobacteria (PGPR), are applied either directly or indirectly to stimulate crop productivity under non-stressed and stressed circumstances [163]. The use of arbuscular mycorrhiza (AMF) has been widely recognized and established as a strategy, among many others, to alleviate abiotic stress encountered in crop production. Arbuscular mycorrhiza are common microorganisms that have a mutualistic relationship with the roots of most terrestrial plants. AMF fungi enhance and help facilitate growth and development as well as plant establishment via an increase in water relations and nutrients. They help to boost immobile nutrient absorption and uptake. Additionally, they also help enhance soil structure and alleviate environmental stresses in the plant [164]. A previous study on crops such as rice has shown that AM formation can help enhance drought resistance in the plant by inhibiting the production of malondialdehyde and oxidative damage, increasing the activities of antioxidant enzymes such as glutathione and soluble sugar accumulation in the plant, enhancing the plant biomass and photosynthetic efficiency, and improving the roots' hydraulic conductivity [165,166]. Higher root cell water permeability coupled with enhanced root hydraulic properties could determine the different root-to-shoot ABA signaling networks under water stress, which disrupt the stomata function or bring about a decrease in the rate of transpiration, subsequently leading to the improved photosynthesis and metabolism of carbohydrates in crops [167]. With the aid of a glycoprotein known as glomalin, AMF is able to bind heavy metals from the rhizosphere, resulting in enhancing plant tolerance [168]. It has been found that inoculation with AMF improves soybean tolerance to heat stress by increasing seed production, chlorophyll content, and plant development indices when compared with the control (without AMF) [169]. The application of *Poncirus trifoliata* (L.) Raf. and *Rhizoglomus intraradices* enhanced the concentration of abscisic acid, indole-3-acetic acid, and methyl jasmonate in the root, resulting in improved growth traits under salinity conditions [170]. AMF symbiosis has been utilized in genetic engineering to upregulate the expression of certain genes, which are responsible for improving drought tolerance levels and enhancing the water-use efficiency of the plant [171]. Numerous studies have demonstrated that the crosstalk between plant growth-promoting rhizobacteria and AMF treatment increases plant growth rates and crop yields under stress conditions by preserving hormonal and nutritional balances, solubilizing essential plant nutrients, and producing plant growth regulators [172]

2.5. Agronomical Approach

2.5.1. Cultural Practices

The implementation of sustainable management through agronomical or cultural farm practices has been demonstrated to ameliorate abiotic stresses. For instance, proper spacing (row to row: 20 cm and plant to plant: 15 cm and more) improved rice tolerance during waterlogging [119]. Saline soil is reclaimed using various strategies, such as leaching excess sodium, deep ploughing to mix calcareous subsoil into topsoil, and applying acidifying minerals like gypsum and pyrite. Leaching is an effective method that works well on saline soil [138]. The proper shading of a plant under extreme temperature conditions helps to protect and improve plant productivity. A recent study by Formisano et al. [173] demonstrated that lettuce grown under shaded conditions during high temperatures showed improved yield compared with the unshaded control. Moreover, planting at the appropriate time is considered another factor that has a major impact on the yield. Different studies have reported maximum plant yields due to early sowing, while reduced yields have also been attributed to delays in sowing [16]. The implementation of proper cutting management is crucial to enhancing the photosynthesis rate and root carbohydrate reserves, resulting in an increased survival rate of plants during the winter period [89].

Efficient and adequate irrigation management is also another critical factor that can help minimize the impact of abiotic stresses on plants. Drought stress impact was alleviated in plants due to improved irrigation in water management, such as ridge-furrow planting systems being used in combination with plastic film mulching, and the enhanced uptake of water and nutrients [88]. The use of the most efficient irrigation method, for example, the drip irrigation method, delivers water directly to the roots of the plant, decreasing the loss of water through evaporation. Moreover, planting crops that are suitable for the region's climate is another way to obtain more crops per drop. Plant varieties that are native to semi-arid and arid areas are more drought- and heat-tolerant than those selected from irrigated areas [5]. During the winter, the proper management of irrigation is crucial to prevent increased cold stress in plants. A high moisture content in the soil during the winter causes the heaving effect. An increased heaving effect exposes the plant to cold stress by destroying the crown bud and small roots, consequently inhibiting moisture and nutrient uptake. Hence, appropriate irrigation management is required [89]. High soil moisture helps to reduce the availability of heavy metals in the soil [174]. The use of misting, sprinkling, and overhead watering can reduce the water vapour pressure deficit and tissue temperature during heat stress. The use of straw, an organic mulch with a low density, can help dissipate heat and reduce surface radiation by reflecting light [15]. It has been demonstrated that sprinkler irrigation or ridge and furrow systems can lessen waterlogging problems. Growing plants on ridges helps to keep their roots out of wet regions, and furrows allow fields to drain properly. It has been noted that implementing raised-bed planting systems with furrow irrigation and conservation agriculture can also lessen crop lodging [119].

2.5.2. Nutrient Management

Low crop productivity is usually encountered under abiotic stresses coupled with a lack of or deficient nutrient availability. An inadequate supply of macronutrients (N, P, K, Ca, etc.) and micronutrients (B, Zn, Fe, Cu, Si, etc.) during crop production has a significant impact on the growth performance of a plant, as well as the ability of the plant to withstand climate-induced stress (drought, heat, heavy metals, salinity, and submergence) [175]. According to reports, almost 60% of soils globally lack sufficient nutrients, which affect plant output [16]. Hence, it is important to provide plants with a balanced and adequate nutrient supply of macronutrients (N, P, K, Ca, etc.) and micronutrients (B, Zn, Fe, Cu, Si, etc.) for plant structure stability and essential physiological processes. The exogenous use of macro- and micronutrients such as selenium (Se), boron (B), manganese (Mn), nitrogen (N), potassium (K), silicon (Si), sulfur (S), magnesium (Mg), and calcium (Ca) has been proven to confer tolerance to plants under abiotic stresses by regulating the stomatal and upregulation of physiological and metabolic processes [142], subsequently improving crop growth and development, and ultimately economic yield.

Studies have indicated that Si is critical in alleviating abiotic stress such as waterlogging, heat, drought, and cold by improving the cell walls of culms, hulls, leaves, and roots [119]. Under heat stress, applying Si enhanced cucumbers' photosynthesis rates, decreased water loss, and increased yields [176]. Under heavy metals, the use of Si decreased electrolytic leakage and malondialdehyde in cotton [177]. Applying phosphorus and nitrogen before flooding incidence helped to improve initial seedling vigor and the concentration of shoot carbohydrates in rice. Moreover, it also helped to enhance plant growth and development after waterlogging events [119]. Molybdenum has been well documented to improve plants' resistance to abiotic stressors such as salt, low temperatures, and water stress [178]. The application of S conferred heat tolerance in canola by enhancing the photosynthesis rate and stomatal conductance, subsequently increasing yield [142]. Selenium has been widely used to alleviate abiotic stresses in plants by delaying senescence, enhancing photosynthesis and antioxidant enzymes, reducing oxidative stress, and thereby promoting growth and productivity [88]. The crosstalk between these nutrients, when applied, can confer plant tolerance. For instance, the interplay between K and Ca improves plant tolerance to drought, salinity, and cold stress by enhancing plant molecular and bio-physiological traits [175].

2.6. Emerging Strategies

2.6.1. Biochar Application

Biochar is a substance that is rich in carbon and has remarkable resistance to decomposition. It is mainly generated via the pyrolysis (thermal degradation) of biomass, particularly agricultural leftovers, in a closed furnace with limited oxygen supply [179]. Because of its fine-grained and incredibly porous charcoal, it can help retain water and nutrients in the soil, increase biodiversity in the soil, and reduce deforestation [172] (Figure 4). The addition of biochar has been shown to mitigate the impact of abiotic stresses (heat, drought, heavy metals, and salinity) and also improve yield [46] (Table 6). Biochar has the ability to enhance drought-stressed soil by reducing ionic and osmotic toxicity and increasing water availability. The activity of antioxidant enzymes is significantly impacted by the presence of biochar. Biochar improves water use efficiency, water bioavailability, and crop nutrient uptake by boosting growth and drought resistance [172]. Due to its greater cation exchange capacity, biochar emits Ca and Mg on its surface, which helps to decrease the presence of heavy metals in the soil [180]. Adding biochar to soil has positive impacts on soil parameters that support biological nitrogen fixation, pathogen control, and the reduction of nitrate leaching and nitrous oxide emission for the rehabilitation of contaminated soil. Also, applying biochar at different rates significantly increases the enzymatic activity of saline soil [181] and also helps to recover saline soil [182]. Research on the role of biochar in alleviating heat and cold stress is scanty and requires more attention due to the increasing air temperature globally.

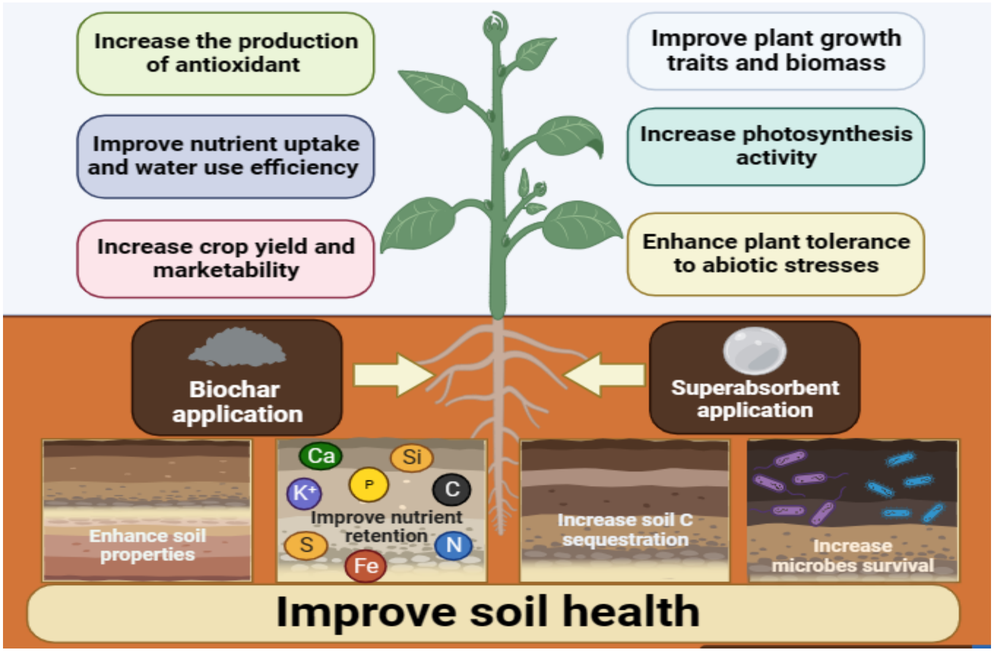

Figure 4. Role of biochar and superabsorbent under abiotic stresses.

Table 6. The role of biochar application in improving plants under abiotic stresses.

Abiotic Stresses	Crop	Biochar Dosage	Impact	References
Drought	Barley	1%	Enhanced growth of root and shoot	[181]
	Cabbage	10%	Improved rate of photosynthesis, nutrient uptake, and growth traits	[182]
	Tomato	5%	Promoted seedling growth	[183]
	Coffee	8 t/ha	Improved photosynthesis	[184]
Heavy metal	Wheat	5%	Increased growth and plant dry weight	[180]
	Squash	4%	Reduced heavy uptake by roots and shoot	[185]
	Sunflower	50%	Enhanced biomass and decreased heavy metal accumulation	[180]
Heat stress	Rice	40 g/kg	Improved uptake and assimilation of nitrogen and transport of proteins and enhanced root traits	[186]
	Rice	300 g	Enhanced pollen germination rate, anther dehiscence, and pollen fertility	[187]
	Thymus	5%	Improved growth traits, leaf chlorophyll, and photosynthetic rates	[188]
Salinity	Beans	10% and 20%	Increased growth of root and shoot	[181]
	Eggplant	5%	Improved photosynthesis activities and reduced leaf temperature and electrolyte leakage.	[179]
	Maize	5%	Increased proline content and decreased sodium content	[182]
	Wheat	2%	Improved root and shoot length, leaf water potential, and osmotic potential	[189]
Waterlogging	Soybean	0.1%	Enhanced growth traits	[190]
	Salix psammophila	3%	Promoted cadmium and zinc accumulation in the plant	[191]
Cold stress	Rice	10%	Enhanced tolerance	[192]

2.6.2. Kaolin

Kaolin is a mineral clay that dissolves readily in water, and when sprayed on plants, it forms a protective particle film. It has been used to reduce the impact of abiotic stresses (heat, drought) under greenhouse conditions by lowering the temperature of the canopy, minimizing the effects of water stress, and reflecting solar energy off the leaf surface [193]. However, the impact of kaolin application on crops has not been fully understood. However, some studies have reported the positive results of kaolin application under stress conditions (Figure 5). A recent study by Hamdy et al. [194] demonstrated that kaolin application greatly enhanced the leaf area, photosynthesis activities, leaf carotenoids, and yield in mango, and reduced sunburn caused by high temperatures. In a very high concentration, kaolin reduces the leaf content of antioxidants such as total phenolic, total flavonoid, and other enzyme activities. Generally, kaolin application (5% and 7.5%) reduced the detrimental effects of drought stress and enhanced the quality of walnut kernels by increasing chlorophyll content and gas exchange, and lowering leaf temperature [195]. Tomato's water potential was enhanced under salinity conditions due to the application of kaolin [196]. The use of kaolin is considered a promising, eco-friendly, and suitable alternative to alleviate abiotic stresses in plants. More research is needed to fully understand the effect of kaolin on crops under abiotic stresses and the underlying mechanisms.

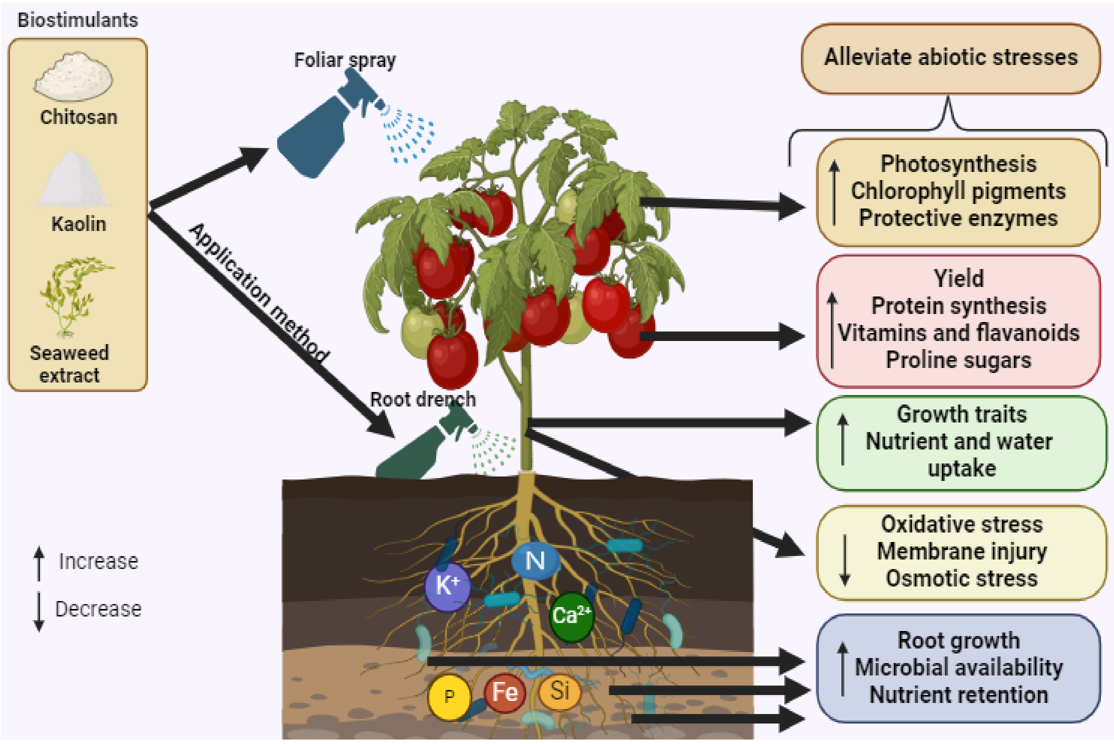

Figure 5. Role of biostimulants under abiotic stresses.

2.6.3. Superabsorbent: A Novel Soil Conditioner

Superabsorbent (such as hydrogel) is a cross-linked hydrophilic water-soluble polymer that has the ability to absorb excessive amounts of water (up to 100 times its original) without being dissolved and release the water in response to mechanical stress conditions [197]. Apart from its water retention ability, hydrogel itself has become an effective adsorbent for extracting heavy metal ions from wastewater due to its three-dimensional network structure and diverse functional groups [198]. Superabsorbent (SAP) has been used in various industries, including pharmaceuticals and agriculture. In agriculture, superabsorbents have been used for diverse purposes, including enhancing seed germination rates, plant growth and development, and soil physicochemical properties, improving soil water and nutrient retention, decreasing water run-off and erosion, and improving overall crop productivity [197] (Figure 4). In the present decade, superabsorbent is used as a buffer to neutralize the impact of abiotic stresses (drought, salinity, heat, and heavy metals) encountered by plants during agricultural production. The amendment of soil with SAP has been demonstrated to increase the biomass, growth, leaf surface area, and yield of soybeans under limited water conditions [199]. The use of SAP in combination with organic manure has been reported to increase plant growth and production under water stress conditions. For example, rabbit dung and SAP increased eggplant growth and output at a 35% irrigation rate [199].

Apart from drought, SAP has been reported to play a significant role in alleviating salinity and heavy metals. Under saline conditions, SAP application improved nutrient contents (nitrogen and phosphorus) and growth traits, as well as nutrient availability, while decreasing the electrolyte leakage, soil electrical conductivity, nitrate, and proline content [200]. Improved salinity tolerance encountered in plants during stress can be associated with reduced SAP swelling due to the support of anionic electrostatic repulsion. These studies have shown that using SAP can ameliorate the impact of salinity stress on plants. However, detailed and comprehensive knowledge of how SAPs mediate improvements in salinity tolerance at the molecular level is needed [200]. The application of SAP also improved the biomass of eucalyptus (*Eucalyptus globulus* Labill.) to 9.17%, 8.39%, and 18.02% under salinity, drought, and combined stress, respectively [201]. The amendment of soil with SAP decreases the number of heavy metals in plants by replenishing the ionic balance within the soil environment. A reduction in the bioavailability of heavy metal by SAP can be attributed to the presence of high-density metal-chelating groups in the gel, which can effectively bind to the heavy metal and hence reduce the numbers of heavy metals in the soil environment [200]. In a recent study by Du et al. [198], the use of biochar-based composite hydrogel was reported to enhance tolerance to Cadmium stress in tobacco by improving the photosynthesis rate and antioxidant activities while decreasing malondialdehyde (MDA) content and leaf cell death. Superabsorbents also play a significant role in enhancing plant traits under low fertility conditions, as indicated by Ostrand et al. [201]. Based on our knowledge, no studies on using SAP to alleviate heat stress have been reported. Since there is a direct relationship between heat stress and drought, full irrigation implementation and proper management practices are vital to improving plant yield under heat conditions. However, this may not be possible due to the continuous diminishing of freshwater required for agriculture. We suggested that the SAP application under heat stress conditions could help mitigate and improve plant metrics by making water available to plants during critical heat regimes. However, this hypothesis must be tested in a greenhouse to ascertain this claim.

2.6.4. Seaweed Extract

Seaweed is regarded as an emerging and promising biostimulant. Seaweeds (also known as macroalgae) are multicellular marine algae that form a vital part of marine coastal ecosystems. Based on their pigmentation, seaweeds are primarily divided into three main groups: phaeophyta (brown), rhodophyta (red), and chlorophyta (green) [202]. Seaweed contains different beneficial compounds, including phytohormones, macro- and micronutrients, proteins and (bioactive) peptides, polysaccharides, pigments, and phenolic compounds [17,202]. Seaweed is frequently used in agriculture and horticulture to feed animals, as a food source, in industrial raw materials, for medicinal and botanical applications, in soil fertilization, and as extracts to stimulate plant development [17]. In the face of climate change, recent research has implicated seaweed extract biostimulants in mitigating the impact of climate change on crops. Several reports have shown that seaweed extract has successfully stimulated plant growth and survival under diverse abiotic stresses (Table 7, Figure 5). A recent report demonstrated that the application of seaweed extract (*Ascophyllum nodosum* and *Sargassum* spp.) as a spray improved barley tolerance to cold stress by enhancing winter hardiness capacity, root growth traits, proline, the accumulation of non-structural carbohydrates, and osmotic adjustment [203].

Under limited water conditions, the foliar application of seaweed extract promotes the growth of sugarcane, stalk yield, enzymatic and physiological processes, sugar production, and enhanced tolerance. Similarly, brown algae extract (*A. nodosum*) has been reported to enhance antioxidant enzyme production and the cellular accumulation of defense metabolites [204]. Another seaweed extract (*Padina gymnospora*) was reported to alleviate salinity stress in tomatoes by increasing the total chlorophyll content, photosynthesis rate, stomatal conductance, and accumulation of antioxidant enzymes, consequently enhancing fresh weight and fruit yield [205]. The foliar application of seaweed extract (3 mL/L and 5 mL/L) stimulated the growth and yield traits in *Brassica juncea* under temperature stress and reduced the membrane injury percentage [206]. A recent study has demonstrated that the use of seaweed extract in combination with arbuscular mycorrhiza (AMF) inoculation improved the postharvest yield quality of pepper under salinity conditions [207]. Seaweed extract has also been implicated in demonstrating high antifungal activities. For instance, Lotfi et al. [208] reported that hexane, chloroform, acetone, and methanol extracts of seaweed (*Ulva fasciata*, *Ulva lactuca*, and *Cladophora sericea*) demonstrated high antifungal activities against *Macrophomina phaseolina* (Tassi) Goid. and *Fusarium oxysporum* by inhibiting the growth of mycelial. Furthermore, the use of seaweed extract (*Gracilariopsis persica*) at 1000 µL completely inhibited the growth of mycelial in four important plant pathogenic fungi, including *Botrytis cinerea*, *Aspergillus niger*, *Penicillium expansum*, and *Pyricularia oryzae* [209]. Though the application of seaweed extract has been shown to improve plant tolerance to multiple abiotic stresses, the molecular, metabolic, and physiological mechanisms underlying seaweed's mode of action are still not fully understood and need to be investigated. Furthermore, comprehensive information on the optimum rates of seaweed needed for maximum plant growth as well as the extent of its effectiveness should be investigated. Moreover, as shown in the latest study, the application of seaweed extract in combination with other biostimulants should be considered.

Table 7. Improving crop performance under abiotic stresses using seaweed extract.

Abiotic Stresses	Seaweed Extract	Plant under Study	Impacts	References
Salinity	Seaweed extract	Bell pepper	Improved leaf relative water content, leaf greenness, and membrane stability index	[207]
	Ulva fasciata, *Cystoseira compressa*, *Laurencia obtuse*	Cowpea and Maize	Increased biomass and conferred tolerance	[210]
	Ascophyllum nodosum	Tomato	Increased root to shoot ratio and yield	[211]
Cold stress	*A. nodosum*	Arabidopsis	Downregulated chlorophyll degradation genes and improved chlorophyll content	[212]
	A. nodosum	Tobacco	Upregulated freezing tolerance genes	[213]
	Brown-seaweed extract	Tomato	Increased accumulation of proline, polyphenols, flavonoids, tannins, and carotenoid contents	[214]
Drought	*Fucus spiralis*, *Ulva lactuca*, *Laminaria ochroleuca*	Fababean	Enhanced soluble sugars accumulation and relative water content and reduced malondialdehyde	[215]
	Ascophyllum nodosum	Soybean	Expressed stress-responsive genes and antioxidant enzymes	[216]
	Ascophyllum nodosum	Arabidopsis	Downregulated stress-responsive negative growth regulator	[217]
	Ecklonia maxima	Chicory plants	Enhanced physiological traits (relative water content, water use efficiency, chlorophyll content, nutrient uptake)	[218]
Heat stress	*Ascophyllum nodosum*	Spinach	Improved germination percentage and germination speed, and reduced hydrogen peroxide and malondialdehyde content	[219]
	Seaweed extract	Bentgrass	Enhanced tolerance	[220]

2.6.5. Higher Plant Extract

Higher plant extracts are also used as potential alternatives to chemical fertilizers in alleviating abiotic stresses by regulating physiological processes and enhancing productivity in crops. Various parts of these plants, including the seeds, roots, stems, leaves, bark, and flowers, are used [221]. The plants used for biostimulants are rich in phytohormones, antioxidants, minerals, amino acids, and many other bioactive compounds with nutritional and growth-promoting potential [222]. Their mechanism of action involves releasing phosphorus (P) from soils, triggering the metabolism of nitrogen (N), promoting root growth, regulating hormones, and enhancing soil microbial activity [223]. Previous reports have demonstrated that using plant extract has improved a number of physiological processes, such as photosynthesis, nutrient uptake and utilization, water use efficiency, the production of hormones (cytokinins, gibberellins, and auxins), germination; reduced senescence, resulting in enhanced plant production, yield, post-harvest quality, and the shelf life of agricultural commodities [223]; and increased tolerance to a wide range of abiotic stresses (Table 8). The application of *Moringa oleifera* leaf extract exogenously improved tolerance to heavy metal stress and enhanced germination, growth, chlorophyll content, and phenolic accumulation in maize [224]. Under salinity stress, the application of cypress leaf extract activated the expression of stress-inducible antioxidation-related genes and enhanced photosynthesis in zucchini seedlings [225]. Similarly, *Moringa oleifera* leaf aqueous extract application enhanced linseed traits such as plant height, tiller production, leaf chlorophyll pigments, phenolics content, sugar content, seed yield, and fiber quality under water stress conditions [226]. Based on previous positive results, the use of natural extracts can be regarded as a promising and nature-friendly approach to mitigating a wide range of abiotic stresses in plants. Apart from abiotic tolerance, plant extracts have demonstrated high antifungal effects. A recent study by Besrukow et al. [227] reported that the application of a novel ligninsulfonate-based grape cane extract, alone and in combination with a copper-based agent, significantly decreased the grapevine's downy mildew disease severity and showed high antifungal effects.

Table 8. The role of higher plant extract under abiotic stresses.

Abiotic Stresses	Plant Extract	Extract Type	Method of Application	Plant under Study	Impacts	References
Salinity	Sorghum	Whole plant	Seed priming	Camelina	Increased growth traits (emergence percentage, root length, shoot length, biomass, α-amylase activity, chlorophyll content, antioxidant enzymes activity)	[228]
	Maize	Grain	Soaking and foliar	Bean	Improved relative water content, proline, photosynthesis, ascorbic acid, and mineral nutrients	[229]
	Rosmarinus officinalis and *Artemisia herba-alba*	Leaf	Seed priming	Maize	Enhanced germination percentage, germination indexes, and photosynthesis pigments	[223]
	Foeniculum vulgare and *Ammi visnaga*	Seed	Foliar spray	Cowpea	Improved osmoprotectants content and antioxidant enzymes	[230]
	Mangosteen	Pericarp	Soaking	Mungbean	Enhanced growth and yield traits and conferred tolerance	[231]

Table 8. *Cont.*

Abiotic Stresses	Plant Extract	Extract Type	Method of Application	Plant under Study	Impacts	References
Drought	Carrot	Root	Seed priming	Bean	Enhanced chlorophyll content and photosynthesis	[232]
	Moringa oleifera	Leaf	Foliar	Soybean and Maize	Increased growth traits (leaf area, plant height, and biomass production)	[222]
	Moringa oleifera	Leaf	Foliar	Petunia plants	Scavenged ROS and increased the accumulation of phenol compounds and total soluble sugars	[233]
	Moringa oleifera	Seed	Foliar	Cancer bush	Enhanced growth and yield traits, water use efficiency, leaf photosynthetic pigments, and antioxidant enzymes	[234]
	Basil	Leaf	Foliar	*Eucalyptus citriodora*	Improved the accumulation of essential oil fresh leaves	[235]
Heat stress	Sorghum and *Moringa oleifera*	Whole plant and leaf	Foliar	Wheat	Enhanced yield traits (spike length, number of grains per spike, and 1000-grain weight)	[236]
	Moringa oleifera	Leaf	Foliar	Quinoa	Enhanced leaf chlorophyll and antioxidants enzymes	[237]
	Moringa oleifera	Leaf	Foliar	Maize	Enhanced chlorophyll content and reduced chlorophyll-to-carotenoids ratio	[238]
Heavy metal	Ginger	Whole plant	Mixed with soil	Maize	Increased accumulation of antioxidant enzymes	[239]
	Moringa oleifera	Leaf	Foliar	Bean	Enhanced photosynthesis, proline, and relative water content	[222]
	Sonchus oleraceus	Grain	Priming	Wheat	Increased growth traits, photosynthetic efficiency, and yield	[240]
UV-radiation	*Lawsonia inermis* L.	Leaf	Foliar	Soybean	Enhance crop performance	[241]
Cold stress	*Moringa oleifera*	Leaf	Foliar	Moringa	Improved morpho-physiological traits (number of branches, leaves, chlorophyll, and phenolic contents)	[242]

2.6.6. Yeast Extract

Since ancient times, yeast has been employed in a wide range of processes, including fermentation, the food industry (producing biomass and alcoholic beverages), the production of several metabolic items (enzymes, vitamins, capsular polysaccharides, carotenoids, polyhydric alcohols, lipids, glycolipids, citric acid, ethanol, and carbon dioxide), agriculture, research, and medicine [17]. In agriculture, it is considered a natural, eco-friendly, and safe source of biofertilizer that can stimulate plant growth and development as well as yields. Yeast contains vital elements including vitamins B1, B2, and B12, pyridoxine, thiamine, riboflavin, and cytokines, among other minerals. Yeast contains essential hormones, including cytokinins that can promote the production of proteins and nucleic acids, as well as cell division and elongation, and enhance the amount of mineral nutrients [243]. The inoculation of yeast promotes the soil's physical and chemical properties, such as water retention and nutrient availability, and also enhances osmotic adjustment by improving compatible solutes in the cells of seedling roots [244]. Active yeast extracts have been shown to improve crop tolerance to a wide range of abiotic stresses and productions (Figure 5). The inoculation of *Cryptococcus* sp., a cadmium-tolerant yeast with plant growth capabilities, showed a drastic reduction in the heavy metal content in soils and improved the shoot biomass of *Sedum plumbizincicola* without alteration in the soil microbial community [245]. Under salinity conditions, the application of yeast extracts at different rates improved the growth, physiological, anatomical, and yield traits of lupine cultivars compared with the control [246]. At high stress levels (100 and 150 mM NaCl), yeast inoculation confers salinity tolerance in lettuce by enhancing the growth traits; however, some physiological traits such as proline, sugar, and chlorophyll contents were reduced. This indicates that foliar application can help confer tolerance to salinity stress and serves as a good source of improving nutrients in stressed plants via the leaves [247].

The role of yeast extracts under drought, heat, and cold stress has been documented. Alzandi and Naguib [248] demonstrated that the application of yeast activates soil enzymes, prevents nutrient leaching, enhances the accumulation of osmolytes and antioxidant enzymes, reduces lipid peroxidation, and confers drought tolerance in corn. Under cold stress, tomato vegetative and yield traits as well as fruit quality traits (total sugars, vitamin C, carotenoids, and lycopene content) were enhanced due to the foliar application of yeast extract [249]. Pea seeds treated with yeast extract showed a significant increase in growth traits, yield traits, photosynthesis pigments, total soluble sugars, and indole acetic acid (IAA) content under heat stress conditions [250]. Though the inoculation of yeast extract has come with numerous benefits, its application has some physiological implications for crops, as highlighted by Babaousmail et al. [247] and Monteiro et al. [17] in lettuce and vines, respectively. Although the physiological cost may vary from one plant to another and from one cultivar to another, more research should be conducted on a wide range of crops and their cultivars to determine which plant is best suited to using yeast extract without physiological damage. Apart from this, the use of yeast extract in combination with other biostimulants may also be a viable option to offset these problems. The positive interplay between yeast and other biostimulants has been found to alleviate abiotic stresses in crops with improved physiological responses. For instance, the combined use of chitosan and yeast at 300 mM and 8 g/L, respectively, led to significant improvements in the plant height, chlorophyll content, relative water content, ascorbic acid levels, antioxidant enzymes, and reduction in electrolyte leakage and levels of malondialdehyde and hydrogen peroxide in the garlic plant under drought conditions [243]. Furthermore, the addition of AMF (1%) and yeast extract (2%) improves the growth and yield traits of wheat under salinity conditions [244]. Finally, the combined application of yeast extract and glycine betaine at 9 g/L and 5 mM, respectively, improves physiological traits such as chlorophyll content, as well as the peroxidase and catalase activity of tomatoes under cold stress compared with individual usage. This result indicates that the application of both yeast extract and other biostimulants has no physiological cost implications for plants [249]. Further studies are required to determine optimum yeast extracts as well as gain more insight into the mechanism of this biostimulant in alleviating abiotic stresses in different crops.

2.6.7. Chitosan

Chitosan is a linear polysaccharide present in shrimp, fungi, insect exoskeletons, crab shells, and algae. Chitosan is a non-toxic, biodegradable, and biocompatible substance that helps mitigate the negative impacts of abiotic stressors via the stress transfer pathway through secondary signaling. Furthermore, chitosan plays a key role in the upregulation of many defensive genes in the crop's pathogenesis-related genes (glucanase and chitinase) [251], thereby conferring tolerance to plants. For example, the application of 200 ppm of chitosan was demonstrated to elevate heat tolerance in cucumbers by maintaining the osmotic balance and cell turgor pressure. Soil amendment with chitosan enhanced leaf photosynthesis, leaf biomass, gas exchange, and chlorophyll fluorescence in lettuce [252]. Chitosan application reduced damage caused by cold stress in cucumber seedlings [253]. The application of chitosan and biochar was reported to improve wheat's biochemical, physiological, anatomical, and morphological traits under drought stress [254]. Applying chitosan exogenously reduced oxidative stress in peas under heavy metal conditions [255].

Recently, the application of chitosan nanoparticles and other elements such as selenium and copper to alleviate abiotic stresses has gained more attention from researchers. Scientists have even indicated that the use of bulk chitosan may be less effective than chitosan-based metallic nanoparticles in anti-pathogenic and plant growth-promoting activities [256]. The foliar application of chitosan nanoparticles enhanced the fresh weight and biomass of 14 and 41% of banana plants under cold stress [257]. A recent study by Aazami et al. [251] demonstrated that the application of the treatment of grape plants with chitosan-salicylic acid nanocomposite enhanced the total antioxidant enzymes, chlorophyll fluorescence parameters, carotenoids, and proline contents under salinity conditions. The study indicated that using chitosan-salicylic acid nanocomposite can be a suitable alternative and eco-friendly approach to improving plant productivity under stressful conditions. This research demonstrated that the crosstalk between chitosan and other biostimulants can be beneficial in enhancing plant tolerance and productivity under stress conditions. The application of foliar nanochitosan nitrogen, phosphorus, and potassium fertilizer on wheat plants improved the harvest, crop index, and yield compared with the control [256]. Research on using chitosan (alone or in combination with other compounds) to alleviate heat stress is scarce. Thus, more research is needed in this aspect. However, some studies have suggested that abscisic acid (ABA) could trigger heat shock-related genes, such as *ABF3*, which may improve heat tolerance [258].

2.6.8. The Use of Nanotechnology

Nanotechnology is regarded as a new field that can be utilized to ensure plants' resilience to environmental pressures, boost productivity, and address current issues pertaining to the food system and food security. In agriculture, nanotechnology can be utilized in different forms, which include nanosensors, nanofertilizers, nanoherbicides/nanopesticides, and nanoremediators [3]. The use of nanotechnology in the form of nanosensors can be helpful in practicing precision agriculture, causing overall change in the food chain via the use of various technologies to determine soil moisture levels and soil nutrient status and levels in plants. Furthermore, these nanotools can provide information on the best sowing and harvesting times as well as an appropriate time for agrochemical applications [88]. No doubt, farmers having this information at their disposal will improve sustainable agriculture practices across the world. The application of nanoparticles can also take the form of nanofertilizers and nanopesticides to improve crop growth and development as well as yield under stressed and non-stressed conditions. The use of nanoparticles to alleviate various types of environmental stresses has been widely reported [259]. Nanoparticles penetrate the plant cell to improve the plant's uptake of water by regulating osmotic imbalance. At the seedling phase, nanomaterials enter the tissues of the seeds via intercellular spaces or form new pores, mainly by inducing aquaporin production and genes associated with several processes such as cell divisions [43]. Several types of nanoparticles, such as silicon nanoparticles (Si-NPs) and zinc oxide (ZnO-NPs), have been utilized to ameliorate the effects of abiotic stresses such as drought, chilling stress, salinity, and heavy metal toxicity in plants by improving their morpho-physiological and biochemical traits, including chlorophyll, proline, relative water contents, and carotenoids [117].

The use of biogenic nanoparticles (BioNPs) enhanced wheat tolerance to cold stress by increasing antioxidant enzyme production and reducing ROS [260]. Similarly, titanium dioxide (TiO2-NPs) enhanced chickpea tolerance to cold stress by improving photosynthesis activities using transcriptional regulation [261]. Under salinity stress, seed priming with manganese-NPs enhanced pepper seedling tolerance by modifying molecular mechanisms. These NPs can help protect the plant from ionic stress by reducing the concentration of salt ions in the cells [259]. The application of TiO_2 NPs to soil helps to reduce cadmium toxicity in soybeans and improve the physiological parameters and photosynthetic rate [3]. The application of 2 ppm of silver nanoparticles was reported to improve soybean growth under waterlogging conditions. A further study on the proteome profile showed a reduction in proteins related to fermentation and glyoxalase II 3, which normally increase under flooding conditions [260]. Under drought stress conditions, the foliar application of metal-oxide nanoparticles, such as titanium dioxide (TiO_2), ZnO, and iron oxide (Fe_3O_4), improved plant resilience to drought stress by stimulating the plant's physiological and metabolic processes [261]. However, the use of nanotechnology has been receiving much attention from researchers due to its ability to increase plant productivity in stressed and non-stressed plants. However, more research is needed to understand how NPs work at the molecular and genomic levels. The environmental implications of these particles should be assessed carefully to avoid the deposition of residue in water and other areas. Consequently, it is necessary to determine the optimized number and size of nanoparticles required for production. Furthermore, more studies are required to determine the presence of any nanoparticles in the plant after production to avoid negative effects on consumer health.

3. Conclusions and Future Prospect

Abiotic stresses affect the plant's morphological, biochemical, and physiological mechanisms, resulting in reduced germination, growth, photosynthesis rates, modifications in gene expression, disruptions of hormone and enzyme activities, increased oxidative stress, and declines in yields. Crops display diverse physiological, morphological, biochemical, and molecular responses under stress conditions. Understanding these changes is critical and essential to helping scientists mitigate abiotic stresses as well as develop climate-resilience cultivars. To a greater extent, the mechanisms involved in these processes have been fully understood. However, several field evaluations are still required to better understand the mechanisms associated with nutrient uptake under a wide range of abiotic stresses. Various breeding techniques have been employed to improve plant resilience under stressful conditions. There is a need to screen more germplasm under natural conditions to identify more tolerance accessions under different stresses that can be used for breeding programs. To avoid the loss of genetic resources through natural problems, genetic erosion, and climate change effects, the identified genetic resources should be conserved properly via both in situ (seed storage, gene bank storage, botanical garden, pollen, and DNA storage) and ex situ (on-farm, field farm, natural parks, gene sanctuary, and biodiversity hotspots) conservation methods.

In addition to conventional breeding methods, the introduction of QTL mapping, marker-assisted breeding, genetic engineering, and speed breeding techniques has improved the ability of plants to withstand abiotic stress issues. These advancements have also deepened our knowledge of the mechanisms involved in crop tolerance to abiotic stress. Furthermore, these new techniques can be used to generate new germplasm for breeding programs as well as develop new cultivars with improved traits under abiotic stresses. Nevertheless, there are other unresolved questions that require comprehensive investigation. These include assessing the adaptability of the generated genotypes with identified QTL in various environments to ascertain their efficacy in the natural environment. These will enhance our understanding of the genotype through environmental interactions and allow us to identify genotype-specific environments. Furthermore, genetically engineered crops should also be subjected to stringent screening in the natural environment. More research should focus on the integration of speed breeding with other breeding approaches to accelerate the release of more high-yielding tolerance genotypes. The application of nanomaterials, osmoprotectants, plant growth regulators, grafting, and nutrient management has been useful in enhancing plant tolerance under abiotic stresses. Emerging agronomical approaches (biochar, kaolin, chitosan, use of superabsorbents, and seaweed extract) look promising and have been demonstrated to counteract the effects of abiotic stresses on crops, though their mechanisms still remain unclear, and more clarity is required. Interdisciplinary crosstalk via international collaboration, conferences, publications, and data sharing is required to enable researchers to integrate knowledge and skills from several disciplines to obtain a better and thorough an understanding of the problems, resulting in comprehensive solutions.

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