

Abiotic stress enhancement tools for improving crop tolerance

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Abstract

Abiotic stresses create an unfavourable environment for plant growth, increasing the possibilities of low yield and associated economic loss. Several steps have been taken to address this problem. During the last twenty years, techniques of genetic engineering/transgenic breeding have made significant advances in gene manipulation for inciting desirable traits in transgenic plants. Transgenic techniques allow us to identify potential genes, transcription factors (TFs), and miRNAs, engaged in certain processes in plants, allowing us to gain a comprehensive understanding of the processes at molecular and physiological levels which determine plant resilience and production. The reliability and specificity of this approach ensure that future plant enhancements will be a huge success. As a result, transgenic breeding has been determined to be a viable strategy for improving crop abiotic stress tolerance. The approach of CRISPR/Cas gene-editing technique to create stress-tolerant plant variants is gaining popularity right now. The researchers like this user-friendly technology because of its versatility. In the gene-editing process, the DNA sequence "CRISPR" and the endonuclease "Cas" collaborate under the supervision of specific guide RNA. In a variety of plant species, the CRISPR/Cas system is being utilized. In the majority of situations, Cas9 is employed. Various reports have surfaced which demonstrate the utilization of CRISPR/Cas9 technology to improve the abiotic stress tolerance of plants. Therefore, this review aimed to review the promising and effective applications of transgenic plant breeding for enhancing environmental stress tolerance and crop productivity, as well as its recent developments.

Keywords: abiotic stress; CRISPR; miRNAs; transcription factors; transgenic plants

Introduction

Extensive increases in several environmental stresses, exhibit a remarkable effect on crop productivity (Seleiman and Kheir, 2018; Seleiman *et al.*, 2020; 2021a; 2021b). Because of the current loss in the agricultural area, water scarcity, global warming, and climate change, it is approximated that crop productivity will decrease further in the future (Arora, 2019; Usman *et al.*, 2020). Abiotic stresses have a negative impact on crop development and yield (Seleiman, 2019). There are various kinds of abiotic stresses like drought, salinity, temperature stress, excessive water, heavy metal stress, and UV stress. Reduction in agricultural production has been noticed in the past few decades because of the decreased agricultural land area due to increased population and environmental stresses (Arora, 2019; Usman *et al.*, 2020). Thus, novel approaches in the agricultural sector like the application of new techniques and continuous agricultural innovation are critical.

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To satisfy the growing need for food and counteract the negative impacts of abiotic stress on crop yield, it is essential to generate transgenic lines with increased tolerance to a broad range of abiotic stresses (Pandey *et al.*, 2017; Noman *et al.*, 2017). Conventional breeding approaches were utilized for genetic variability developing from intergeneric or interspecific hybridizations and diverse germplasms to stimulate cellular and tissue culture level mutations to make the plant more resilient to abiotic stresses. But there are various restrictions with these approaches (Dita *et al.*, 2006). To introduce new plants much time is needed, and various undesired genes can be moved alongside desired genes, due to the intricate stress reactions and their performance, there is a modest yield improvement under stress conditions, and there is no assurance of getting a specific gene association among millions of crosses (Muehlbauer *et al.*, 2006). The ability of gene identification and functional genomics in plants to govern a specific feature has altered dramatically as a result of recent biotechnology breakthroughs (Choudhary *et al.*, 2012). Plant engineering and genetic manipulation strategies for abiotic stress resistance (Mushtaq *et al.*, 2019) rely on gene expression, which is primarily concerned with regulatory and signalling networks that control genes encoding stress-resistant proteins and enzymes for functional metabolite synthesis (Caño-Delgado *et al.*, 2004; Noman *et al.*, 2017). Therefore, the focus of this review is on the promising and effective applications of transgenic plant breeding for enhancing environmental stress tolerance and crop productivity, as well as its recent developments.

Abiotic stress control via transgenic approach

Abiotic stresses like salinity (Al-Ashkar *et al.*, 2019; Al-Ashkar *et al.*, 2020; Seleiman *et al.*, 2020; Taha *et al.*, 2020;), heat, and drought (Batool *et al.*, 2020; Roy *et al.*, 2021) are leading environmental cues which affect crop productivity of crops (Mukhtar *et al.*, 2020; Elshayb *et al.*, 2022). The use of traditional plant breeding methods is not much established in augmenting environmental stress so far. This could be because of the traits being regulated by several genes located at a quantitative trait locus (QTL). For impeding harmful impacts of numerous environmental conditions, it is required to verify the possible genes or QTLs (gene networks) linked to extensive tolerance to different abiotic stresses. These abiotic stresses negatively impact plant growth and yield by modifying vegetative and reproductive growth and development phases. Plants undergo a range of physiological, biochemical, and molecular changes which are prompted by the abiotic stresses which impair the cellular machinery (Rai *et al.*, 2011). These modifications comprise disorganization of cellular osmotic equilibrium which leads to deteriorated homeostasis, disposition of ions, and oxidative damage denaturing the intrinsic proteins of plants. The response of plants to various abiotic stresses occurs through various processes that stimulate the cell signalling, transcriptional controls, and generation of stress-tolerant proteins, antioxidants, and osmolytes which sustain homeostasis and restore damaged integral proteins. Usually, stress-sensitive plants which are not able to produce such compounds under stress conditions become subjected to several stresses that obstruct their growth. Several genes have been recognized in several plants/organisms, which encode stress-defending compounds and can be directed for genetic transformation into susceptible genotypes. These genes have been grouped into three classes as (a) osmolytes such as mannitol, glycine betaine, proline, and heat shock protein-coding genes, (b) genes accountable uptake of ion and water and transport like aquaporins and ion transporter, and (c) genes modulating transcriptional controls and signal transduction processes, like *MAPK* and *DREBI*.

Nanotechnology for abiotic stress tolerance

Abiotic stresses have an adverse impact on plant growth and productivity. Because of the increasing negative impacts of abiotic stresses, researchers have great interest to rationalize the impact of abiotic stresses and enhance crop yield. According to FAO reports, by 2050 there will be an addition of 2.3 billion people

worldwide and to feed such an enormous population, there is a considerable challenge for plant researchers to enhance crop production to 70% of towards world agriculture. Hence there is an urgent need to recognize novel research areas to curb technological obstacles in tackling yield blockade, resource use efficiency, and development of environmentally accepted technology. Nanobiotechnology is becoming a promising area in mitigating the impacts linked with abiotic and biotic stress to acquire a sustainable future for agriculture globally. Nanoparticles are synthesized from metal or metal oxide by different modes i.e, physical, chemical, and biological. Due to their smaller size, nanoparticles have gained some special properties which have opened new approaches in the agriculture sector. These particles are assessed for their possible function in plant development and protection from various stresses. Still, there is a long way to develop technology to attain sustainable agriculture (Saxena *et al.*, 2016) (Figure 1).

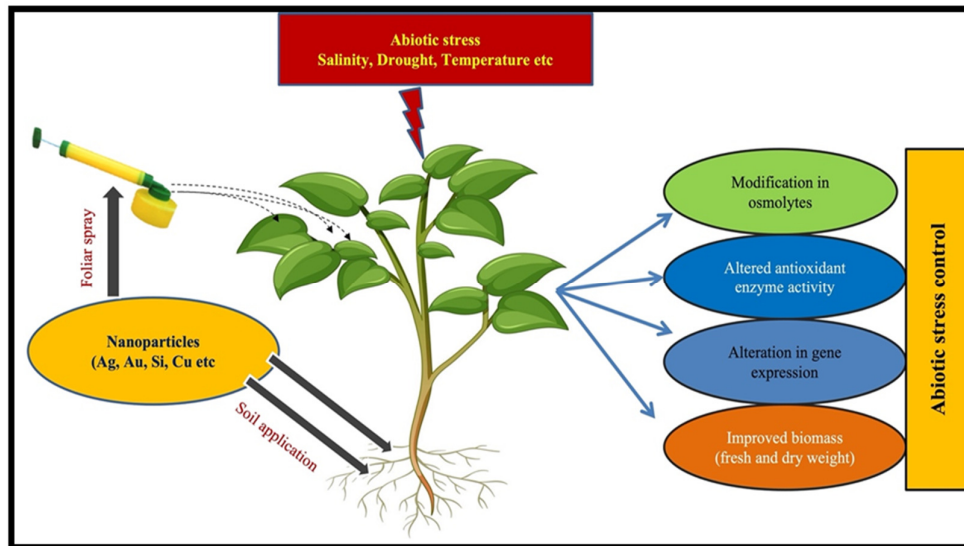


Figure 1. depicts the physiological, biochemical, and molecular basis of abiotic stress tolerance in plants under the treatment of different nanoparticles

The agricultural application of nanoparticles can increase production sustainably and productively there by adding to the agriculture reliability (Fincheira *et al.*, 2020). In agricultural fields Nanotechnology has been utilized to screen the quantity of water, nutrient availability, and plant stress caused by environmental and biotic factors (Singh and Singh, 2019). In *Cucumis sativus* L., increased growth and productivity were observed due to improved nutrient uptake by the supplementation of silicon dioxide (SiO₂) nanoparticles in presence of drought and salinity stress (Alsaedi *et al.*, 2019). In presence of salt stress, the application of Ag nanoparticles amended the germination rate, shoot and root length, and fresh and dry mass of seedlings which led to alleviated development of *Lathyrus sativus* L. (grass pea) (Hojjat, 2019). In soybean (*Glycine max* L.) plants application of SiO₂ nanoparticles immobilized and inactivated the mercury thereby reducing the adverse impact of mercury (Li *et al.*, 2020). Supplementation of various levels of silica nanoparticles enhanced plant resilience to water deficit conditions in hawthorns (*Crataegus* sp.), hawthorn seedlings physiological and biochemical reactions vary in response to contrasting levels of silica nanoparticles during various stages of drought (Ashkavand *et al.*, 2015). It was demonstrated that silica nanoparticles had a positive impact on photosynthesis attributes. It was revealed that silica nanoparticles and fertilizer demonstrated a pronounced impact on the physiological and morphological characteristics of basil under salinity stress (Kalteh *et al.*, 2018).

Apart from the above effects, nanoparticles, due to their unusual attributes, have the potential to promptly transfer DNA particles inside cells of plants to modify their metabolic functioning, being able to

easily penetrate in plant cells (Giraldo *et al.*, 2014). The genotoxic impacts brought about by salinity in *Solanum lycopersicum* L. were overcome by the supplementation of zinc oxide (ZnO) by alteration of cytosine methylation (Haliloglu *et al.*, 2020). Currently, genome editing approaches are currently widely adopted perspectives for the crop enhancement program (Tiwari and Lata, 2019; Bhat *et al.*, 2020; Ansari *et al.*, 2020), as a result, a group of scientists has merged this method with nanotechnology and created a method for characterization of plant genome of plant species by employing carbon nanotubes and CRISPR-cas9 gene-editing methods which leads to enhanced protein expression level (Demirer *et al.*, 2019), indicating that in future genome editing along with the use of nanoparticles may induce enhancement of several plant attributes including yield, quality, and stress resistance.

Application of Biotechnology in Abiotic Stress Tolerance

Various biotechnological techniques like molecular breeding and genetic engineering in plants propose certain alternatives for procuring enhanced and genome-edited plants in a brief period (Mishra *et al.*, 2017). Genetic engineering might repress reproductive hurdle in several plant species (Noman *et al.*, 2019). Transgenic breeding effectively enhanced yield via genetic alterations and improvements, with a small breeding phase (Gantait and Mondal, 2018). As advancement in the physiology of plants increased, understanding of complications in stress-resilient procedures and their association with various attributes, selection regulation employing genomic techniques will lead to recognition of quantitative trait loci (QTL) and genes associated with attributes (Young, 1996). Recognition of potential genes accountable for stress resilience in plants is necessary for creating transgenic plants with increased stress resistance (Muehlbauer *et al.*, 2006).

Over the last two decades, plant engineering approaches for environmental stress resistance were extensively investigated. Scientists examined gene expression which was possibly associated with plant defence signalling pathways that coded proteins involved in abiotic stress tolerance. Currently, several achievements have been attained to enhance plant stress tolerance by genetic transformations (Noman *et al.*, 2019); moreover, the complicated genetic procedures for abiotic stress tolerance make the work complex (Mishra *et al.*, 2017). Thus, there should be a combination of plant biotechnology and conventional breeding and physiology.

Quantitative Trait Loci (QTL)

In abiotic stress resilience, Quantitative trait loci (QTL) mapping turned out as remarkable approach in plant breeding and is an excellent procedure for exploring genetically complex systems (Shen *et al.*, 2018). Under various abiotic stress conditions, improved crop yield was attained via the use of QTL, which regulated explicit agronomic attributes and physiological mechanisms for increased crop yield. Corresponding to their constancy and reaction to several environmental stresses QTL can be classified as “adaptive and constitutive” (Collins *et al.*, 2008). The later ones are common in environments, while adaptive QTL occurs environmental conditions, like QTL that are expressed in presence of high or low temperature, specifying the role of QTL in regulating temperature stresses (Shen *et al.*, 2018).

In rice (*Oryza sativa* L.) plants growing under salinity stress, several QTL were distinguished to regulate fundamental attributes in plants. In these plants meta-analysis of QTLs which regulate early-stage salt resilience was carried out by employing QTL data from numerous studies. 11 meta-QTLs for three attributes of little intervals were located on chromosomes 1 and 2 with the use of a consensus map. Upon analyzing 56 various genotypes and breeding lines, six salt-resistant genotypes (Bharathy, I Kung Ban 4-2 Mutant, Langmanbi, Fatehpur 3, CT-329, and IARI 5823) were described. A study of meta-QTL regions unveiled various prospect genes consociated with salinity resilient traits (Islam *et al.*, 2019). Genetic studies and QTL mapping in cucumber were conducted for thermo-tolerance utilizing recombinant inbred line (RILs; HR) population and a doubled haploid (DH; HP) population which were deduced from heat-sensitive (65G) and

tolerant (02245) parents. Upon inheritance investigation, it was proposed that multiple genes in cucumber (*Cucumis sativus* L.) seedlings influence both short-term extreme and long-term mild heat tolerance. Six QTLs for heat tolerance were observed which include *qHT3.1*, *qHT3.2*, *qHT3.3*, *qHT4.1*, *qHT4.2*, and *qHT6.1*. Amongst these, *qHT3.2* was frequently observed thrice in HR and HP at various conditions, which interpreted phenotypic variations. The 481.2 kb region harboured 79 genes, nine of which might be taking part in heat stress reactions (Dong *et al.*, 2020). In triticale, freezing resilience is a major attribute that leads to its winter hardiness. QTL and molecular markers related to cold resistance in winter triticale were identified by Wasek *et al.* (2021). They recognized three coherent QTL for various fluorescence parameters with complex interval mapping (CIM) and single-marker analysis (SMA). The first locus *Qfr.bm-7A.1* justified the observed 9% disparity of both leakages of ions and plants recovery after freezing. The chief locus *Qchl.bm-5A.1* was noticed for chlorophyll fluorescence traits that accounted for 19.6% of phenotypic dissimilarity. Co-location of QTL on chromosomes 7A.1, 4R, and 5R, clearly defined physiological and genetic link of the plant survival after freezing with the capability of exerting favourable photochemical activity of the photosystem II and fixing the integrity of cell membranes. Genes present in observed QTL were those which encode BTR1-like protein, transmembrane helix proteins like potassium channel, and phosphoric ester hydrolase concerned with osmotic stress response and proteins which regulate expression of the gene, chloroplast RNA processing, and pyrimidine salvage pathway (Wasek *et al.*, 2021). QTL linked with attributes like seed germination and early plant growth were studied in wheat (*Triticum aestivum* L.) cultivars, 'Pasban 90' (salt-tolerant), and 'Frontana' (salt susceptible) using recombinant inbred lines. Composite interval mapping (CIM) was employed for analyzing QTL for various traits and in this analysis total 44 QTLs were distinguished. 26 Eleven main QTLs were present in 1B, 2B, 3B, 5B, 6B, and 7B chromosomes of the mapping population under salinity stress conditions. The results divulged that QTLs play an important part in salinity resistance at the early seedling growth stage (Batool *et al.*, 2018). It has been deduced that conventional QTL mapping, QTL-sequencing, can quickly distinguish candidate genes, thereby altering the breeding methods and enhancing the breeding efficacy (Sharma *et al.*, 2017). Through functional genomic strategies, QTL can be an excellent tool for translational genomics and the generation of quantitative characteristics in some plants (Adhikari *et al.*, 2019; Wen *et al.*, 2019). These studies established the essentiality of QTL identification and therefore proposed a novel and unique marker with huge potential to ameliorate abiotic stress resistance and crop production.

miRNAs in abiotic stress resistance

MicroRNAs are small about 22-24 nucleotide, non-coding regulatory RNAs which are required in sequence-specific composite regulatory mechanisms of gene silencing in plants. miRNAs are also involved in modulating abiotic stress resistance in plants. Defence responses in plants during biotic or abiotic stresses are arbitrated by alterations in both genes and miRNAs expression levels which are then implicated in regulating stress response and tolerance in plants. Several pieces of evidence have proposed the remarkable contribution of high-throughput sequencing technologies towards the recognition and functional description of various miRNAs in plants. Recently it has been revealed that primary miRNA transcripts (pri-miRNAs) code for regulatory peptides, which play a role in amending numerous agronomic attributes (Jatan and Lata, 2019).

With the utilization of a recent machine learning pattern, it was depicted that miRNA169, miRNA159, miRNA396, and miRNA393 have the most important function in plant reaction to water deficit conditions, salt stress, and temperature stress respectively (Vakilian, 2020). In maize, impact of miRNAs on its biochemical pathways was ascertained and several new miRNAs were discovered which increased the amelioration of drought stress. microRNAs modulate their target gene expression by their up-regulation or down-regulation which affects metabolic reactions of maize to drought conditions (Upadhyay *et al.*, 2019). It was found that miRNA393 was vigorously up-regulated by dehydration, freezing, high salt, and ABA administration in several plants (Zhang, 2015). In drought-stressed *Arabidopsis*, miR169 was down-regulated, and its target nuclear factor YA5 (NF-YA5) was remarkably stimulated when subjected to drought stress (Nadarajah and Kumar,

2019). Plants overexpressing miRNA169a- were susceptible to drought, in comparison to wild plants, whilst the miRNA169a-targeted NF-YA5-overexpression enhanced drought stress resistance in plants (Ni *et al.*, 2013). Similarly, in *Arabidopsis thaliana*, *GmNF-YA3* gene, a target of miR169, remarkably increased drought stress resilience in these plants (Zhang *et al.*, 2011). In guava, 40 potential microRNAs which belonged to 19 families were differentiated. These differentiated miRNA precursors constituted stable stem-loop structures and demonstrated high sequence conservation among various plant species. Under salinity stress distinctive expression pattern of seven selected guava miRNAs (*pgu-miR156f-5p*, *pgu-miR160c-5p*, *pgu-miR162-3p*, *pgu-miR164b-5p*, *pgu-miR166t*, *pgu-miR167a-5p*, and *pgu-miR390b-5p*) were recorded and among these *pgu-miR162-3p*, *pgu-miR164b-5p* and *pgu-miR166t* were most affected ones. A total of 49 putative target transcripts of the differentiated guava miRNAs in this work were discovered to be involved in metabolic pathways, cellular development, and stress response signalling using the psRNA Target tool (Sharma *et al.*, 2020). In cotton extreme sequencing was done to unravel significant roles of miRNAs in reaction to salinity and drought (Xie *et al.*, 2015). Wang *et al.* (2016) classified the range of temperature stress-responsive miRNAs and their targets in cotton by using deep sequencing. In Cd stressed Brassica napus 44 known miRNAs (belonging to 27 families) and 103 new miRNAs were recognized. An intense investigation of miRNA expression description revealed 39 distinctively expressed miRNAs between control and Cd-stressed plants. The functions of matching target genes were found in transcription factor modulation, biotic stress reaction, ion homeostasis, and secondary metabolism, among other processes. These results indicated the role of miRNAs in the modulation of TFs and said processes in response to Cd stress in Brassica napus (Jian *et al.*, 2018) (Figure 2).

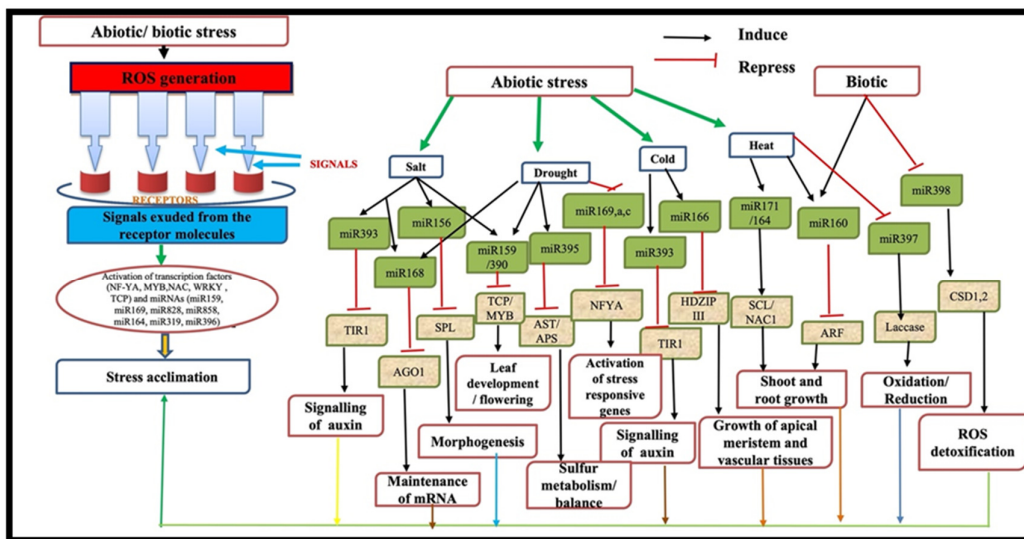


Figure 2. Interaction between different miRNAs and TFs and their regulatory pathways in response to different stresses

CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats)/Cas9 and Abiotic stress tolerance

Various environmental stresses restrain crop yield around the globe (Pandey *et al.*, 2017). Several traditional methods have been used to enhance crop production, but those methods are now becoming restrained because of the decrease in genetic resources of plants and those methods are very time consuming (Gantait and Mondal, 2018). There is an urgent demand for effective crop enhancement programmes with new genome editing approaches, like CRISPR-Cas9 (Tang *et al.*, 2017), that is quick, swift, and precise in getting genome-edited plants.

CRISPR-Cas9 system is a structured genome engineering tool, that is effectively implemented in several organisms like bacteria, animals, and plants (Sander *et al.*, 2014). Because of its effectiveness in specific gene editing via targeted traits, CRISPR-Cas9 system can be employed in crop increment, and this will open numerous approaches concerning this. CRISPR/Cas9-mediated genome editing for the generation of diverse abiotic stress resilient crops is depicted in Figure 3 as a step-by-step process.

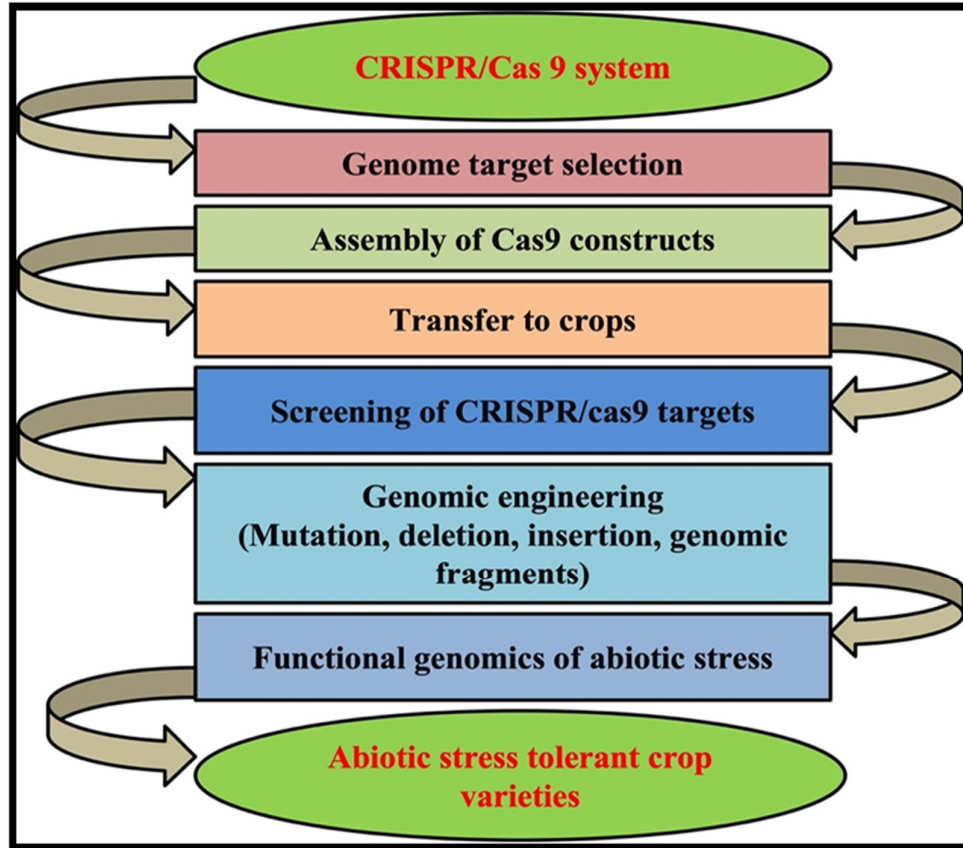


Figure 3. Step-by-step presentation of CRISPR/Cas9 mediated genome editing for the development of different abiotic stress resistance varieties of crops

CRISPR/Cas9 has also been utilized in plants like wheat, maize (*Zea mays* L.), tomato (*Solanum lycopersicum* L.), soybean (*Glycine max* L.), and sorghum (*Sorghum bicolor* L.) besides its utilization in model plants (Osakabe and Osakabe, 2017). CRISPR/Cas9-interceded editing technique in tomato to develop its long shelf life was employed through targeted mutagenesis and gene replacement (Yu *et al.*, 2017), through complex genome-editing to increase lycopene content (Li *et al.*, 2018) and through concomitant editing of miR482b and miR482c for increased tolerance to *phytophthora infestans* (Hong *et al.*, 2020). Likewise, in soybean, plant height and internode length were modulated with the use of CRISPR/Cas9 editing approach and it was also utilized to regulate the flowering time of the plants (Cheng *et al.*, 2019; Li *et al.*, 2020). Apart from this, the utilization of this technique to enhance abiotic stress-resilience in plants has evoked the curiosity of several researchers. The multiplex of genes is engaged in environmental stress reactions modulating metabolism, signalling, and regulatory pathways of plants. CRISPR/Cas9 system can target single or multiple genes to enhance plant potentiality to stress resistance. Point mutations, insertions or deletions or

transcriptional modulations might be produced for the target-based gene-editing via CRISPR/Cas9 system (Jain, 2015). Important things which need to be taken into consideration in this system for enhancing environmental stress tolerance in plants are the designation of the desired promoter for cas9 expression, guide RNA outline, formation of novel alleles for abiotic stress-reactive genes, and the development appropriate gene delivery system (Osakabe and Osakabe, 2017). In *Arabidopsis* a genetic character, ABRE1 was utilized for enhancing water deficit tolerance since abscisic acid-responsive element-binding protein 1/ABRE binding factor 2 (ABRE1/ABF2) are involved in modulating the drought stress reactions (Roca Paixão *et al.*, 2019). In this study, CRISPR/Cas9 genome-editing was employed for stimulation of endogenous ABRE1 promoter and in this study inactive Cas9 (dCas9) was combined with HAT or histone acetyltransferase. Utilization of CRISPR/dCas9^{HAT} in *Arabidopsis thaliana* exhibited an ameliorated tolerance against drought stress by positively regulating ABRE1 (Roca Paixão *et al.*, 2019). With CRISPR/Cas9 technology, Alfatih *et al.* (2020) developed rice *PARAQUAT TOLERANCE 3* knockout mutants (*OsPQT3*). These mutants exhibited higher resilience to salt and oxidative stresses (Alfatih *et al.*, 2020). To enhance drought stress resistance in *Arabidopsis* CRISPR/Cas9 was employed to establish novel alleles of OST2 (playing an effective role in stomatal movement), by the co-expression of Cas9 and GFP (green fluorescent protein) for enhancing tolerance against drought (Osakabe *et al.*, 2016). These authors employed truncated guide RNA (tru-guide RNA) for site-specific alterations not causing any off-target impacts. The modified stress responses in *Arabidopsis* through a high expression of OST2 in germline cells propose an increased inheritable stress-resilience in the plant (Osakabe *et al.*, 2016). CRISPR/cas9 stimulated ARGOS8 variations in maize resulting in improved grain yield of the plants under drought stress (Shi *et al.*, 2016). All these studies showed the capability of CRISPR/cas9 system to produce crop plants that are resistant to drought stress by developing new allelic variations. CRISPR/cas9 approach has also been employed to decrease the metal toxicity of plants. With CRISPR/Cas9 system, a group of researchers successfully developed rice plants with less cesium by disabling K⁺ transporter OsHAK1 (Nieves-Cordones *et al.*, 2017). Similarly, a rice plant with less cadmium was developed by knocking out the metal transporter gene OsNramp5 (Tang *et al.*, 2017). Additionally, rice plants resistant to herbicide were developed through CRISPR/Cas9 interceded homologous recombination of acetolactate synthase (ALS). Research is advancing for utilizing CRISPR/Cas9 genome-editing technique to surpass problems occurring via various abiotic stress conditions. In Table 1, some selected studies for a better understanding of the role of biotechnology in abiotic stress tolerance in plants are presented. While the elevation of different abiotic stresses with different techniques on plant is shown in Table 2.

Transcription Factors linked with abiotic stress

Crop plants are negatively impacted by a diverse environmental stress that have a pronounced effect on crop production. Plants have developed advanced approaches, and genes encoding transcription factors (TFs), which are prime modulators of stress-receptive genes which are eminent prospects for crop enhancement. Examples associated with recent works comprise TF gene regulation and overexpression perspectives in plants to increase stress resilience. But there is still a lot to learn regarding various plant TFs. Of more than 80 TF families, only a few have been extensively studied for their role in abiotic as well as biotic stress reactions and among these, some of the important TFs are NAC, MYB, WRKY, bZIP, and ERF/DREB (Baillo *et al.*, 2019).

When plant cells perceive abiotic stress via receptors or sensors, ROS levels increase, resulting in cell oxidative damage and, finally, cell death. ROSs have recently been recognized as important second messengers in complicated signalling networks of abiotic stress reactions in plants. As a result, controlling ROS signalling and homeostasis is an essential technique for improving stress resistance in plants under adverse environmental conditions (You and Chan, 2015). TFs play a key function downstream of ROS signalling pathways as the main modulatory proteins taking part in abiotic stress responses. During abiotic stress reactions in plants,

members of the MYB, bHLH, WRKY, bZIP, and NAC families have been shown to play essential roles in modulating ROS signal transduction.

Table 1. Some selected studies for a better understanding of the role of biotechnology in abiotic stress tolerance in plants

Biotechnological approaches	Type	Species	Function	References
Transcription Factors (TFs)	NAC	<i>Oryza sativa</i> L.	Drought stress tolerance	Shim <i>et al.</i> , 2018
		<i>Triticumaestivum</i> L.	Dehydration tolerance	Chen <i>et al.</i> , 2018
		<i>Pyrusbetulifolia</i> L.	Chilling and drought stress resistance	Jin <i>et al.</i> , 2017
		<i>Tamarix hispida</i> L.	Tolerance to salinity and osmotic stress	He <i>et al.</i> , 2019
	MYB	<i>Solanum lycopersicum</i> L.	Heat stress tolerance	Meng <i>et al.</i> , 2015
		<i>Oryza sativa</i> L.	Heat and salinity stress tolerance	Deeba <i>et al.</i> , 2017
		<i>Zea mays</i> L.	High temperature and drought stress tolerance	Casaretto <i>et al.</i> , 2016
		<i>Arabidopsis thaliana</i> (L.) Heynh.	Heat and drought stress tolerance	Zhao <i>et al.</i> , 2017
		<i>Nicotiana tabacum</i> L.	Cold stress tolerance	Xing <i>et al.</i> , 2019
		<i>Arabidopsis thaliana</i> (L.) Heynh.	Drought tolerance	Yu <i>et al.</i> , 2016
		<i>Oryza sativa</i> L.	Drought tolerance	Fávero <i>et al.</i> , 2018
		<i>Oryza sativa</i> L.	Cold and salt stress tolerance	Yang <i>et al.</i> , 2012
	WRKY	<i>Triticumaestivum</i> L.	Drought and oxidative stress tolerance	Wei <i>et al.</i> , 2017
		<i>Arabidopsis thaliana</i> (L.) Heynh.	Heat stress tolerance	Li <i>et al.</i> , 2011
		<i>Triticum aestivum</i> L.	Drought stress tolerance	He <i>et al.</i> , 2016
		<i>Triticum aestivum</i> L.	Heat stress tolerance	Wang <i>et al.</i> , 2017
QTL	<i>Arabidopsis thaliana</i> (L.) Heynh.	Resistance to waterlogging	Raineri <i>et al.</i> , 2015	
	<i>Oryza sativa</i> L.	Salt tolerance	Kobayashi <i>et al.</i> , 2017	
	<i>Hordeum vulgare</i> L.	Salt stress tolerance	Han <i>et al.</i> , 2018	
	<i>Triticum aestivum</i> L.	Salt stress tolerance	Batool <i>et al.</i> , 2018	
	<i>Oryza sativa</i> L.	Salt stress tolerance	Islam <i>et al.</i> , 2019	
	<i>Cucumis sativus</i> L.	High-temperature stress tolerance	Dong <i>et al.</i> , 2020	
MicroRNAs	<i>Triticum aestivum</i> L.	Freezing tolerance	Wąsek <i>et al.</i> , 2021	
	<i>miR396b</i>	<i>Arabidopsis thaliana</i> (L.) Heynh.	Cold tolerance	Zhang <i>et al.</i> , 2016
	<i>miR319</i>	<i>Oryza sativa</i> L.	Cold tolerance	Liu <i>et al.</i> , 2017
	<i>miR393a</i>	<i>Agrostis stolonifera</i> L.	Salt tolerance, drought tolerance, heat tolerance	Zhao <i>et al.</i> , 2018
	<i>miR172a</i>	<i>Glycine max</i> (L.) Merr.	Salt stress tolerance	Pan <i>et al.</i> , 2016
	<i>miRNA169a</i>	<i>Arabidopsis thaliana</i> (L.) Heynh.	Drought stress tolerance	Ni <i>et al.</i> , 2013
	<i>miR169</i>	<i>Solanum lycopersicum</i> L.	Drought stress tolerance	Rao <i>et al.</i> , 2020
<i>Osa-miR319</i>	<i>Oryza sativa</i> L.	Cold stress tolerance	Sun <i>et al.</i> , 2020	

Table 2. Elevation of different abiotic stresses with various techniques used

Abiotic stress tool	Abiotic stress	Plant species	Reference
Biotechnological approach	Salt stress	<i>Hordeum spontaneum</i> L.	Kuang <i>et al.</i> , 2019
	Cold and drought stress	<i>Camellia sinensis</i> L.	Wang <i>et al.</i> , 2016
	Salt stress	<i>Gossypium hirsutum</i> L.	Gao <i>et al.</i> , 2016
	Drought and salinity stress	<i>Gossypium hirsutum</i> L.	Liang <i>et al.</i> , 2016
	Salt stress	<i>Paulownia fortune</i> L.	Fan <i>et al.</i> , 2016
	Salt stress	<i>Glycine max</i> L.	Pan <i>et al.</i> , 2016
	Salt stress	<i>Populus cathayana</i> L.	Qiu <i>et al.</i> , 2021
	Salt stress	<i>Oryza sativa</i> L.	Ai <i>et al.</i> , 2021
	Drought stress	<i>Arabidopsis thaliana</i> L.	Roca Paixão <i>et al.</i> , 2019
	Salt stress	<i>Oryza sativa</i> L.	Farhat <i>et al.</i> , 2019
	Drought stress	<i>Phaseolus vulgaris</i> L.	Dramadri <i>et al.</i> , 2019
	Salt stress	<i>Solanum lycopersicum</i> L.	Tran <i>et al.</i> , 2021
	Drought stress	<i>Triticum aestivum</i> L.	Shi <i>et al.</i> , 2018
	Drought stress	<i>Perennial ryegrass</i> L.	Hang <i>et al.</i> , 2021
	Salt stress	<i>Arabidopsis thaliana</i> L.	Denver <i>et al.</i> , 2019
	Drought stress	<i>Arachis hypogaea</i> L.	Kiranmai <i>et al.</i> , 2018
Nanobiotechnological approach	Drought stress	<i>Triticum aestivum</i> L.	Ikram <i>et al.</i> , 2020
	Salt stress	<i>Fragaria × ananassa</i>	Avestan <i>et al.</i> , 2019
	Drought stress	<i>Zea mays</i> L.	Karvar <i>et al.</i> , 2022
	Drought stress	<i>Solanum melongena</i> L.	Semida <i>et al.</i> , 2021
	Salt stress	<i>Trachyspermum ammi</i> L.	Abdoli <i>et al.</i> , 2020
	Salt stress	<i>Solanum lycopersicum</i> L.	Almutairi <i>et al.</i> , 2016
Genetic approach	Drought and heat stress	<i>Triticum aestivum</i> L.	El-Esawi <i>et al.</i> , 2019
	Drought stress	<i>Glycine max</i> L.	Ning <i>et al.</i> , 2017
	Drought stress	<i>Ipomoea batatas</i> [L.] Lam	Zhang <i>et al.</i> , 2019
	Salt stress	<i>Transgenic chrysanthemum</i> L.	Liang <i>et al.</i> , 2017
	Drought and Salt Stress	<i>Gossypium Hirsutum</i> L.	Salisu <i>et al.</i> , 2021
	Salt stress	<i>Arabidopsis thaliana</i> L.	Zhao <i>et al.</i> , 2019
	Salt and drought stress	<i>Arachis hypogaea</i> L.	Banavath <i>et al.</i> , 2018
	Drought stress	<i>Oryza sativa</i> L.	Takeuchi <i>et al.</i> , 2016
Drought and salt stress	<i>Agrostis stolonifera</i> L.	Takeuchi <i>et al.</i> , 2016	

NAC TFs

NAC is a category of TFs which plays a part in growth modulation of plants and is related to abiotic stress, morphogenesis, and metabolism. In a study conducted on Celery (*Apium graveolens* L.), a total of 111 putative NAC TFs were ascertained based on the celery transcriptome and genome database. These 111 NAC TFs were classified into 18 subfamilies based on their NAC domain. Real-time quantitative PCR (RT-qPCR) depicted that few *AgNAC* genes were distinctively expressed in presence of extreme environmental conditions (heat, cold, drought, and salt). It was observed that *AgNAC63* (ortholog of *ANAC072/RD26*) was stimulated by heat, cold, and salt conditions. From this study, it was concluded that *AgNAC* TFs might be involved in celery stress resistance (Duan *et al.*, 2020). In drought-stressed peanut plants, 132 *AhNACs* were described by the genomic study of the plants and were grouped into eight subgroups (I–VIII) based on their association with *Arabidopsis* NAC proteins. Transcriptomics exhibited several *AhNAC* genes that countered the water deficit and abscisic acid (ABA) stresses. Additionally, 20 of them were chosen in response to PEG and ABA application and were assessed by quantitative real-time polymerase chain reaction. Results depicted these genes

remarkably retaliated to water deficit and ABA in roots and/or leaves. The work was useful in directing the useful depiction and enhanced drought-resilient germplasms in peanuts (Li *et al.*, 2021). Heterologous overexpression of *Arabidopsis ANAC042/AtJUB1* in tomato (*S. lycopersicum*) and *Arabidopsis* enhanced abiotic stress resilience in these plants (Alshareef *et al.*, 2019). In wheat, it was revealed that *TaNAC47* gene is stimulated by low temperature, salinity, water deficiency, and ABA, depending on distinctive levels of expression. Overexpression of *TaNAC47* in transgenic *Arabidopsis* resulted in ABA vulnerability and increased resistance to above-mentioned stresses. *TaNAC47* overexpression also caused various metabolic alterations, because of the stimulation of downstream genes such as *AtRD29A*, *AtRD29B*, and *AtP5CS1*; the alterations might have facilitated the transgenic plants to curb the stress. ONAC5/6/9 and ONAC10, four rice NAC genes, were found to be overexpressed in a study, that led to enhanced drought resistance and decreased grain loss in presence of drought (Chung *et al.*, 2018). These researchers deduced that ONACs function as the cellular constituent that modulate several target genes which might change root structure for drought resistance (Chung *et al.*, 2018).

The MYB TFs

The MYB family is an extensive and diversified class of transcription factors in eukaryotes. The proteins belonging to this family are largely linked to protein-protein association, DNA attaching and regulatory activity control of proteins (Roy *et al.*, 2016). A number of MYB proteins have been described in modulating different cellular processes like stress responses and cell morphogenesis in various crop species (Ambawat *et al.*, 2013). Several MYB TFs are noticed to have remarkable function in modulating the temperature stress of temperature several plants. In tomatoes, overexpression of *LeAN2* enhanced plant resilience to high-temperature conditions via the higher activity of antioxidants (non-enzymatic) and decreased ROS accumulation (Meng *et al.*, 2015). It was also revealed that overexpression of *OsMYB1* gene enhances the resilience of rice plants to heat and salt stresses (Deeba *et al.*, 2017). Whilst *OsMYB55* in maize was effectual in improving high temperature and dehydration tolerance through increased growth of plants (Casaretto *et al.*, 2016). Six MYB genes were identified in wheat which were associated with heat stress and among them *TaMYB80* was effectual in imparting tolerance against high temperature and water deficit conditions in transgenic *Arabidopsis* (Zhao *et al.*, 2017). Likewise, *PbrMYB5* from *Pyrusbetulafolia* conferred resistance against cold stress by regulating the ascorbic acid synthesis in tobacco (Xing *et al.*, 2019).

WRKY TFs

WRKY is one of the most distinguished groups of a plant being TFs and in plants, it influences the various developmental, physiological, and metabolic processes (Raineri *et al.*, 2015). Recently it has been observed that WRKY proteins take part in several environmental stresses in numerous plants (Chen *et al.*, 2017; Qin *et al.*, 2015). Like in *Arabidopsis*, WRKY46, WRKY54, and WRKY70 were observed to function with BES1 TF to elevate brassinosteroid (BR)-modulated plant development, however, it contrastively modulated water deficiency tolerance (Raineri *et al.*, 2015). In *Arabidopsis*, salt stress stimulated *WRKY71* has been found to induce flowering in plants, hence, facilitating the early completion of the life cycle of the plants to avoid salt stress (Yu *et al.*, 2018). In addition to this, varied expression of maize *ZmWRKY17* in salt-stressed *Arabidopsis* led to decreased ABA susceptibility which was exhibited by thriving green cotyledons and long roots—concerning exogenously applied ABA however enhanced plant susceptibility to salt stress (Cai *et al.*, 2017). In rice, *OsWRKY30* and *OsWRKY47* have been revealed to bestow drought resistance. Concurrently, *OsWRKY71* acts as a promising modulator of cold stress resistance by modulating downstream target gene expression, such as *OsTGFR* and *WSI76* (Kim *et al.*, 2016). *TaWRKY146* from wheat showed a remarkable

expression in wheat seedlings after osmotic stress and manifested dehydration resilience to transgenic Arabidopsis by promoting closure of stomatal (Ma *et al.*, 2017).

Conclusions

Abiotic stresses pose a significant threat to crop productivity around the world, and their impact is expected to worsen in the future. Plant reactions to abiotic stressors are mediated by extremely complicated signalling networks, necessitating a multi-pronged effort to identify the genes involved and untangle the reaction for practical use. Plant abiotic stress has been an important topic for researchers in the last two decades, prompting the identification of candidate genes and transcriptional factors as well as the use of diverse biotechnological techniques. To combat abiotic challenges such as temperatures, drought stress, and metal stress, numerous transcription factors (NAC, ARF, MYB, SOC, MAPK, CBFs, and so on) have been found. MiRNAs have been discovered to play a role plant development, and stress responses in recent studies. Identification of miRNAs taking part in plant life processes and stress responses has been sped up because of better sequencing and bioinformatics technologies. In recent years, several *in silico* methods and databases have been of great assistance in identifying miRNAs implicated in plant development, and stress reactions, as well as predicting their target gene networks. For speedy deployment and adoption of the technique in the field, genome-edited crops using CRISPR/Cas9 must be deemed BE (bioengineered) crops. We believe that use of CRISPR/Cas9 approach in a variety of plant species could usher in a second green revolution, ensuring that need for need and nutritional security are satisfied for the world's growing population. As previously said, the world population is quickly expanding, and this has a negative impact on the environment. We can boost crop yield to fulfil the demand for food by employing genome editing technologies. We should exploit this chance to boost crop output and save the lives of millions of people who are starving due to lack of food globally, particularly in developing countries.

Authors' Contributions

The author read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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