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REVIEW ARTICLE

Modern biotechnological approaches to enhance plant responses to abiotic stresses

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Abstract

Abiotic and biotic stresses are major global challenges that reduce plant productivity, quality and sustainability worldwide. These stresses threaten global food security as the human population continues to grow. These stresses threaten global food supply in the current era of increasing population. Stresses negatively affect the normal growth and development of plants. They are mainly divided into 2 groups: abiotic and biotic stress. In particular, abiotic stresses lead to impaired growth and development of plants, disruption of the photosynthesis process and water regime. High temperatures lead to protein denaturation and decreased enzyme activity, while low temperatures lead to membrane damage. Abiotic stressors are one of the primary elements influencing the growth and production of major agricultural income crops. Environmental elements that cause physiological and biochemical pain in plants include salinity, drought, low temperature, heavy metals and chemical pollution. This article examines biotechnological approaches that use modern genetic engineering technologies such as RNA interference (RNAi) and CRISPR/Cas9 systems to improve plant resilience to abiotic stressors. RNAi plays a crucial role in activating plant defence mechanisms by modulating the expression of stress-responsive genes, whereas CRISPR/Cas9 technology allows for the creation of new, stress-tolerant types by introducing precise alterations in the genome. These biotechnologies have significant potential to develop stable, high-yielding and stress-resilient crops. Overall, this review summarizes recent advances in RNAi and CRISPR/Cas9 technologies for improving plant resilience to abiotic stresses.

Keywords: abiotic stress; biotechnology; drought; genetic engineering; heavy metals; low temperature; salinity

Introduction

Global climate change and anthropogenic activities are increasing plant exposure to abiotic stresses. The growing world population is leading to an increase in demand for food products. Developing stress-resistant crop varieties is a pressing global priority (1). Abiotic factors are usually understood as water scarcity, sudden changes in temperature, salinity, heavy metals and other inorganic stress factors (2). Stresses lead to a significant decrease in plant productivity and disruption of physiological processes (3). Although there are natural adaptation mechanisms to ensure plant resistance to abiotic stresses, they are not systematic and permanent. Thus, modern biotechnological approaches are essential to develop stress -resistant plants.

Emerging technologies in genetic engineering and molecular biology, such as RNA interference (RNAi) and CRISPR/Cas9, are creating opportunities for the generation of stress-tolerant genotypes in plants (4, 5). While the RNAi mechanism allows for the suppression or blocking of the expression of specific genes through microRNAs, CRISPR/Cas9 allows for the precise and efficient editing of DNA.

This article reviews the effects of abiotic stresses on plants, the key genes responsible for them, phytochrome genes and studies on the creation of stress-tolerant plants using RNAi and CRISPR/Cas9 technologies. The main objective is to evaluate the effectiveness and future potential of these modern biotechnological methods tools.

Abiotic factors and their effects on plants

Abiotic factors affect plant growth as a result of environmental stresses caused by non-living factors: drought, temperature changes, salinity, heavy metals, ultraviolet light (UV) and carbon dioxide (CO_2) changes. Such stresses impair plant growth and development, reduce photosynthetic efficiency and ultimately lower yields (Fig. 1).

Drought

Plants under drought stress experience a decrease in transpiration rate and carbon assimilation due to the closure of small pores on the surface of their leaves, i.e. stomata, which are important for photosynthesis, transpiration and gas exchange processes. This results in the production of reactive oxygen species (ROS).

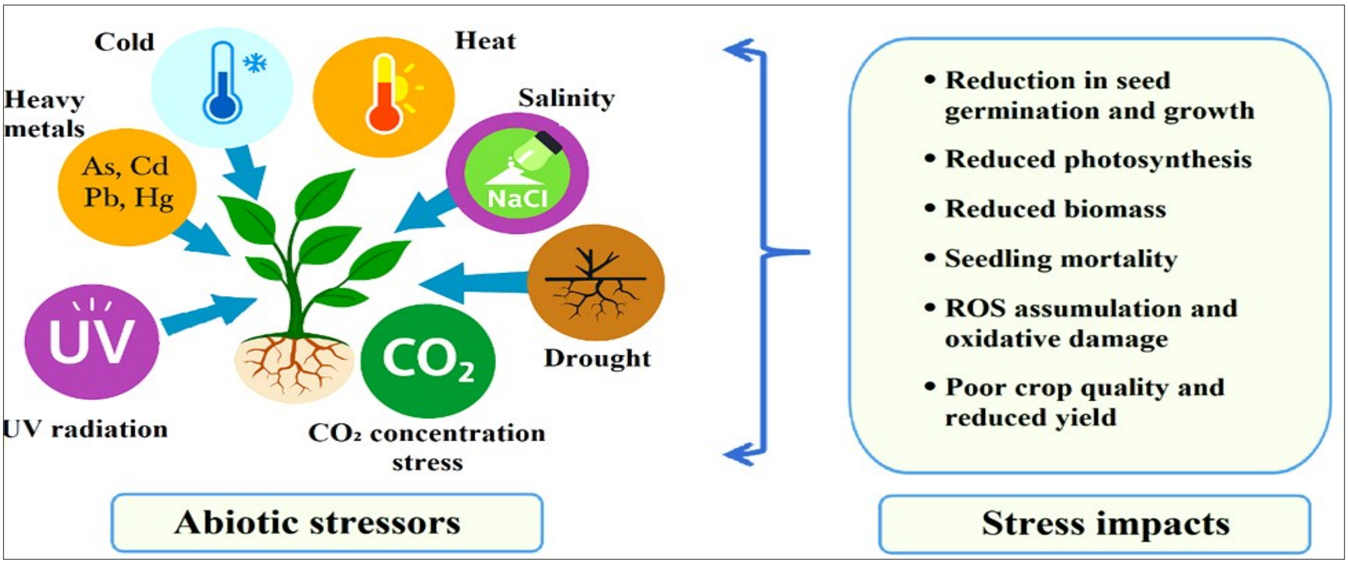

Fig. 1. Impact of abiotic stresses on plant growth and development.

Antioxidant systems such as superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX), which protect proteins, lipids and deoxyribonucleic acid (DNA) from oxidation, increase in efficiency (6). The abscisic acid (ABA) hormone, mitogen-activated protein kinase (MAPK) and calcium ions (Ca^{2+}) pathways are the main ones involved in signal transduction, while osmotic stabilizers such as proline and glycine-betaine help to maintain growth.

High and low temperature (temperature stress)

High temperatures impair photosynthetic efficiency by disrupting enzyme activity and thylakoid membrane stability. Stomata opening is controlled by hormonal and temperature-dependent signalling pathways that affect plant productivity. Cell membrane fluidity decreases under low temperature and the activation of ROS-related stress mechanisms increases as a result of *AFP* (antifreeze protein) aggregation. Transcription factors such as dehydration response element binding factor (DREB) and WRKY play a key role in this stress response (7).

Salt stress

There are 2 main types of salt stress: osmotic stress (substances or effects related to osmotic pressure) and ionic stress, which disrupts Na^+/K^+ balance. These conditions increase ROS production and impair membrane integrity and photosynthetic activity. The activity of the signalling pathways the salt overly sensitive (SOS), calcium-dependent protein kinase (CDPK), MAPK and ABA is accelerated. Osmotic substances such as proline, glycine-betaine and trehalose help maintain a stable water content in the cell (8). Sodium (Na^+) and potassium (K^+) ions transporters - HKT1, SOS1 and NHX1 -function to ensure ion homeostasis. Signalling pathways such as the wall associated-kinase (WAK) and the receptor-like kinase (RLK) also play a key role in overcoming cell wall and endoplasmic reticulum stress (9). The antioxidant mechanisms of plants, including SOD, CAT, APX and flavonoids, protect the cell from ROS-related damage (6).

Heavy metals

In plants, heavy metals enter the cell through the roots from the soil and through the green parts from the atmosphere. This accelerates ROS formation, leading to oxidative damage of membranes, proteins and DNA. NAC and WRKY transcription factors are actively involved in the signalling pathways. Organic substances such as polyamines and phytochelatin, which are involved in combating the effects of heavy metals, isolate and protect important cell structures from damage. Detoxification mechanisms are an active area of ongoing research.

Ultraviolet radiation and CO_2 concentration

UV radiation induces CPD (cyclobutane pyrimidine dimer) in DNA damage or mutation, DNA-repair mechanisms (this is a natural biological process in which a cell detects and corrects damaged or erroneous DNA molecules) and antioxidants are activated. WRKY transcription factors play an active role in the management of UV stress. CO_2 is essential for photosynthesis and increasing it can speed up the process of photosynthesis and also affect plant responses to climate-related stresses. In plants, light (including UV radiation) signals involving phytochromes regulate active response mechanisms under conditions of abiotic stress.

Natural adaptation mechanisms of plants

The role of hormones (ABA, ethylene, jasmonate)

Plant hormones play a key role in natural adaptation mechanisms. In particular, abscisic acid is a key regulatory hormone in adaptation to stresses such as drought, salinity and low temperature. ABA regulates seed dormancy during adverse weather conditions and prevents the spread of disease and helps plants conserve water by closing stomata. Under various stress conditions, ABA, which is synthesized from β-carotene by the enzyme 9-cis-epoxycarotenoid dioxygenase (NCED), enhances the activity of antioxidant enzymes (CAT, SOD, APX) and ensures the efficiency of the photosynthetic apparatus (10). Ethylene maintains physiological balance under drought and salinity stress conditions. It activates defense responses against toxic substances resulting from salinity stress by ensuring the stability of the ethylene overproducer 2 (ETO2) and ethylene Insensitive 2 (EIN2) signaling. Jasmonates (JA) are involved in the signalling pathway involving Ca^{2+}, ROS and nitric oxide (NO), as well as phosphorylase and potassium channels, which affect stomatal closure under water stress conditions. There is a coordinated interaction between JA and ABA, which work together to regulate stomatal closure and the expression of stress-responsive genes, such as Responsive to dehydration 22 (RD22) gene (11).

Signalling pathways (MAPK, Ca^{2+} signalling)

The MAPK (Mitogen-Activated Protein Kinases) cascade is one of the main signalling pathways that mediate the plant's stress response. MAPK3 and MAPK6 kinases are involved in responses to drought, salinity and temperature stresses, including the research model *Arabidopsis thaliana* and crops such as tobacco and rice. Stress-activated signalling pathways regulate downstream transcription factors, with WRKY and DREB genes controlled via MAPK cascades rather than as direct targets. (12). Ca^{2+} signalling is involved in rapid and secondary messengers in plant cells to external stress. Temperature, salinity, or drought stress increases the concentration of Ca^{2+} inside plant cells. This in turn activates other signalling pathways through Ca^{2}-dependent kinases (CDPKs) and CaM (calmodulin) (13). Ca^{2+} signals are not only a signal receptor system, but also a "Ca^{2+} code" that encodes the type of stress (aspects of amplitude, duration, repetition). Studies in Arabidopsis roots have shown that Ca^{2+} pulses activate gene expression in response to a certain level of winter stress (MEKK1-MKK2-MAPK cascade) (14). MAPK and Ca^{2+} signalling is interconnected and Ca^{2+} activity can also activate MAPK cascades. For example, ABA induces rapid Ca^{2+} signalling under stress conditions and affects stomatal closure and gene expression through MAPK cascades. Thus, there is a close relationship between Ca^{2+} signalling and the MAPK cascade (15).

Photomorphogenesis and stress response coordination through phytochromes

Phytochromes are used by plants to detect temperature and other stress factors in accordance with the light environment. Plants activate physiological processes in response to stress by receiving light signals. Phytochrome genes, *PhyA, PhyB, PhyC, PhyD* and *PhyE,* play an important role in the reception of light signals and adaptation to environmental factors in plants. Phytochromes control plant development, flowering, seed germination and responses to stress factors (16). *PhyA* is primarily responsive to far-red light and is synthesized in the dark and rapidly degraded in light (17).

The expression level of *PhyA* can change depending on solar radiation and mechanical stresses (18). *PhyB* mainly senses red light and is involved in the regulation of photoperiodism, phototropism, and elongation. It also balances stress responses as a result of its combined effect with jasmonic acid and abscisic acid. *PhyB* is actively involved in sensing high-temperature stress. At high temperatures, the active form is converted to a passive state. This results in an effect on photomorphogenesis and stomatal opening. In the presence of ultraviolet-B radiation and oxidative stress, the defence system is activated through hormones such as jasmonic acid and salicylic acid. (19). *PhyC* does not function alone, but forms a heterodimer with *PhyB* and participates in the transmission of light signals (20). *PhyC* works together with *PhyB* in stress responses. The expression level of *PhyC* can change in response to changes in photoperiod and environment.

PhyC, in conjunction with *PhyB*, is involved in regulating the timing of flowering and temperature sensitivity of plants, as well as their response to light (21). *PhyD* also exhibits similar properties to *PhyB*, being mainly sensitive to red light. It has functional similarities to *PhyB* in photomorphogenesis and light-stress responses. It is involved in the adaptation of plant development to external environmental influences. The fact that *PhyB* can enhance the sensitivity to ER-stress (Endoplasmic Reticulum stress response) under the influence of red light naturally indicates that *PhyD* and *PhyB* perform the same function (22). Recent studies have investigated the role of *PhyB* and *PhyC* in overcoming HIL (High-intensity light) stress (23). *PhyE* also works in coordination with *PhyB* and *PhyD*. Due to its sensitivity to red light, it is involved in photomorphogenetic processes (24). *PhyE*, together with *PhyB* and *PhyD*, participates in light and temperature responses (25).

Genes responsible for abiotic stresses

Plants harbour diverse stress-responsive genes that regulate adaptation mechanisms. Also, their functions activate defence mechanisms against stress and control the reception of signals and reactions to these signals. In particular, the *DREB, NAC, WRKY, HKT1, SOS1, NHX1* and late embryogenesis abundant (*LEA*) genes are present in almost all evolutionarily developed plants (Table 1).

Plants have transcription factors involved in stress responses. In particular, *DREB, NAC* and *WRKY* genes are active transcription factors. These genes are involved in the regulation of various signaling pathways. In particular, they control the response to stress in the cell and are actively involved in enhancing tolerance. Many scientists have conducted studies on *DREB, NAC* and *WRKY* genes in plants such as *Arabidopsis thaliana, Oryza sativa, Zea mays, Triticum aestivum, Glycine max, Vitis vinifera, Solanum tuberosum* and *Solanum lycopersicum* (Table 2).

Enhancing stress tolerance using RNA interference (RNAi) technology

RNA interference (RNAi) technology allows the control of the activity of specific genes plants. It is a natural molecular mechanism that controls gene expression at the post-transcriptional stage. In RNAi technology, the expression of a targeted gene is silenced or attenuated by specifically targeted small interfering RNAs (siRNA, miRNA).

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Table 1. Key genes involved in plant responses to abiotic stresses

Gene name	Gene category	Main task	Types of active stress	References
DREB	Transcription factor (TF)	Activates stress-related genes through DRE/CRT motifs	Cold, drought, salinity	(26)
NAC	Transcription factor (TF)	Controls the expression of many genes that respond to stress	Drought, salinity, high temperature	(27)
WRKY	Transcription factor (TF)	Coordinates stress, immune and hormone signals	Drought, salinity, infections	(28)
HKT1	Na^+ transporter (membrane protein)	Na^+ limits transport and maintains the K^+/Na^+ balance	Salinity	(29)
SOS1	Na^+/H^+ antiporter	Provides salt tolerance by removing Na^+ ions from the cell	Salinity	(30)
NHX1	Vacuoles are Na^+/H^+ antiporters	Storage of Na^+ in the vacuole, stabilization of osmotic pressure	Salinity, drought	(31)
LEA	Reserve protein (Late Embryogenesis Abundant)	Protects against water loss and keeps proteins and membranes stable	Drought, low temperature	(32)

Table 2. Studies on DREB, NAC and WRKY transcription factors in abiotic stress responses

Gene	Plant type	Genes	Type of stress	References
DREB	*A. thaliana*	*AtDREB1A, AtDREB2A*	Drought, low temperature, salinity	(33-35)
	O. sativa	*OsDREB1A, OsDREB1G*	Low temperature, drought, salinity	(36-38)
	Z. mays	*ZmDREB2A*	Drought, high temperature	(39, 40)
	T. aestivum	*TaDREB*	Osmotic stress	(41)
	G. max	*GmDREB1/A, GmDREB1B;1, GmDREB1A;2*	Low temperature, high temperature, drought, salinity	(42, 43)
	V. vinifera	*VvDREB2A VviDREBA1- , VviDREBA1-6 VviDREBA1-7*	Drought, low temperature	(44-46)
	S. tuberosum	*StDREB StDREB1*	Salinity, drought	(47-49)
	S. lycopersicum	*SlDREB*	Drought, low temperature, high temperature, salinity	(50, 51)
NAC	*A. thaliana*	*AtNAC*	Salinity	(52, 53)
	O. sativa	*OsNAC OsNAC3*	Drought, salinity	(54, 55)
	Z. mays	*ZmNAC55*	Drought	(56)
	T. aestivum	*TaNAC29*	Salinity, drought	(57)
	G. max	*GmNAC085*	Salinity	(58)
	V. vinifera	*VvNAC17*	Salinity, low temperature, drought	(59)
	S. tuberosum	*StNAC053*	Salinity, drought	(60)
	S. lycopersicum	*SlNAC3*	Salinity, drought	(61)
WRKY	*A. thaliana*	*AtWRKY25 AtWRKY33*	Salinity	(62)
	O. sativa	*OsWRKY11*	Drought, high temperature, pathogen	(63)
	Z. mays	*ZmWRKY40*	Drought, salinity, high temperature	(64)
	T. aestivum	*TaWRKY1 TaWRKY33*	Drought, high temperature	(65)
	G. max	*GmWRKY12*	Drought, salinity	(66)
	V. vinifera	*VvWRKY28*	Low temperature, salinity	(67)
	S. tuberosum	*StWRKY*	Drought, salinity, high temperature	(68)
	S. lycopersicum	*SlWRKY3*	Drought, salinity	(69)

This method is actively used in research processes and agrobiotechnology (70). Commercial applications of RNA interference include the development of virus-resistant papaya and apple with reduced browning (71).

In particular, RNA interference enables targeted regulation of genes involved in plant responses to abiotic stress, such as heat shock protein (*HSP*) genes (72, 73). Studies have been conducted on obtaining plants that are resistant to factors such as drought, salinity and low temperatures (Table 3).

Increasing stress tolerance using CRISPR/Cas9 technology

CRISPR/Cas9 technology can be used to increase the tolerance of plants to drought, salinity, low and high temperatures. This technology reliably and effectively edits the genes that respond to stress in plants. In this case, closing the plant's evaporative pores (stomata) reduces gas exchange and consequently the rate of photosynthesis, limits water loss and can activate antioxidant defenses to combat stress (84). In recent years, many scientists have achieved positive results using CRISPR/Cas9 technology in adapting plants to drought, salinity and high and low temperature changes (Table 4).

Comparative analysis of RNAi and CRISPR/Cas9 technologies

Both (RNAi and CRISPR/Cas9) technologies are used to make plants more resistant to biotic and abiotic stresses (drought, salinity, low and high temperatures). RNAi works by reducing gene expression, resulting in a temporary downregulation/silencing of gene activity. CRISPR/Cas9 technology, on the other hand, can change the function of genes for a long time by editing the genome.

The effect of RNAi is temporary and limited to a decrease in gene expression. CRISPR/Cas9, on the other hand, shows that it works effectively for a long time through changes in the genome. RNA interference is suitable for reducing or silencing gene expression, while CRISPR technology makes stable and precise changes (93). By using RNAi and CRISPR/Cas9 technologies together, it is possible to reduce the level of gene activity and precisely change the genome structure. As a result, it creates new opportunities to increase stress tolerance in plants.

Table 3. Studies on the role of RNAi in enhancing plant tolerance to abiotic stresses

Type of stress	Plant type	Studied gene	Result	References
Salinity	*A. thaliana*	*Ath-miR393a*	Increased resistance to salinity stress	(74)
	O. sativa	*Osa-miR319*	Increased resistance to salinity stress	(75)
	S. lycopersicum	*SlARF2-RNAi*	Increased resistance to salinity and drought stress	(76)
Drought	*A. thaliana*	Regulation of TIR1/AFB2 receptors by *miR393*	Under drought and osmotic stress conditions, miR393 inhibited lateral root growth by disrupting *TIR1/AFB2* genes	(77)
	O. sativa	*miRNA (amiRNA/STTM), (miR169g, miR393, miR402)*	The signaling pathways related to yield maintenance and stress tolerance through the regulation of these miRNAs under drought stress have been studied	(78)
	Z. mays	*ZmmiR408a*	miR408a knockout lines showed increased proline content and decreased MDA. *AGO/DCL/RDR* gene expression dynamically changed during drought	(79)
	S. tuberosum	*StmiR169a*	NF-YA3 expression increased by *miR169a* knockdown (RNAi) under drought stress	(80)
Low temperature	*V. vinifera*	*Vvi-miRNAs*	*44 DEM miRNAs* were identified, which regulated TFs such as AP2, MYB, bZIP	(81)
	T. aestivum	*CBF/ICE/COR* signaling genes	Mechanisms of cold adaptation through the ICE CBF COR pathway have been studied	(82)
	S. tuberosum	*miR5125, miR10881 ABF, GA3ox* target genes	Under cold stress conditions, the expression of these miRNAs controls genes associated with cold tolerance	(83)

Table 4. Studies on abiotic stresses using CRISPR/Cas9 in plant species

Type of stress	Plant type	Studied gene	Result	References
Salinity	*A. thaliana*	*AtWRKY3, AtWRKY4*	Increased sensitivity to salinity stress	(85)
	O. sativa	*OsRR22*	Increased tolerance to salinity	(86)
	S. tuberosum	*StDREB2, AtDREB1A*	Increased osmo protective response in response to salinity stress	(87)
Drought	*O. sativa*	*SRL1, SRL2*	Leaf folding enhances drought tolerance by activating ROS scavenging mechanisms	(88)
	Z. mays	*ZmDREB*	Drought stress studies have been done	(89)
	G. max	*GmHdz4*	Root development, osmolyte accumulation and activation of the antioxidant defense system were observed	(90)
Low temperature	*O. sativa*	*OsMYB30*	Knock-out results in increased cold tolerance, improved yield and stability	(91)
	S. tuberosum	*StInvVac, StPPO2*	*InvVac/PPO2* genes were edited to improve quality during low temperature storage	(92)

Conclusion

Abiotic stresses such as drought, salinity, low and high temperatures are serious threats to plants, significantly reducing their growth and yield. The role of biotechnology in overcoming these problems is invaluable. In particular, it is possible to increase the stress tolerance of plants through CRISPR/Cas9 and RNAi technologies. These methods increase plant resistance to stresses by silencing genes through RNAi or by knocking out, altering, or inserting sequences with CRISPR. RNAi and CRISPR/Cas9 technologies play an important role in the creation of new varieties through the genetic engineering of plants. RNAi technology reduces the sensitivity of plants to stress by reducing gene expression. It is necessary to examine how genetic engineering affects plant ecological stability, identify new genes that influence stress tolerance, and continue developing improved methods. Environmental, economic, and social factors must also be considered to broaden the use of biotechnological approaches.

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Authors' contributions

FIB and KAU planned, drafted and revised the manuscript. BKR, AAB, ANA, SAA, HNY, NRR, SOK and MSA participated in literature collection and manuscript editing. ZTB edited and approved the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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