

ABIOTIC STRESS, PLANT RESPONSE AND INDUCTION OF ITS TOLERANCE IN PLANTS: AN OVERVIEW

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Article Received on
16 November 2020,

Revised on 06 Dec. 2020,
Accepted on 27 Dec. 2020

DOI: 10.20959/wjpr20211-19530

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ABSTRACT

The global population is increasing day-by-day, simultaneously; crop production needs to increase proportionately. Environmental stress also known as abiotic stress conditions such as drought, heat, salinity, cold, or pathogen infection can have a devastating impact on plant growth and yield under field conditions. Mechanisms that protect against abiotic stress are essential for plant survival, for growth and productivity, is particularly very important for agriculture. Whereas, increase crop production being restricted due to abiotic and biotic stresses, abiotic stresses adversely affect crop growth and development, leading to crop loss globally and thereby causing a huge amount of economic loss as well. Since last many years, advancement

and modern developments in plant physiology, genetics and molecular biology improve our understanding in plant responses to abiotic stress condition. Plants can overcome environmental stresses either by chemical priming or by activating molecular networks including signal transduction, stress perception, metabolite production, and expressions of specific stress-related genes. Regulation of functional genes and increase stress tolerance of plants can be enhance by chemical priming agents as well as genetic engineering. This review summarizes the major abiotic stress, its response on plants and major achievements in molecular approaches that can potentially enhance and induce the abiotic stress tolerance in plants.

KEYWORDS: Abiotic stress, tolerance, molecular approach, chemical priming, plant responses.

INTRODUCTION

Owing to their sessile life style, plants are continuously exposed to a broad range of environmental stresses. There are two types of stress 1. Biotic stress 2. Abiotic stress. Former one is the type of stress that occur as a result of damage done to plants by biological agents such as bacteria, fungi, virus, parasites, harmful insects as well as cultivated native plants. While, abiotic stress which is the negative impact of non- living factors on the plants such as drought, salinity, heat, cold, chilling, freezing, nutrient, high candlepower, ozone (O₃) and anaerobic stresses.^[1-6] Abiotic stress, as a natural part of every ecosystem affects plants in a variety of ways. It's been estimated that crops attain only about 25% of their potential yield due to the detrimental effects of environmental stress.^[7] The abiotic stresses are location specific, exhibiting variation in frequency, intensity and duration. It can produce at any stage of plant growth and development according to environmental conditions, thus showing the dynamic nature of crop plants and their productivity. To make sure plant survival and improve production efficiency, different strategies are developed to reinforce plant stress resistance. Abiotic stresses generally stimulate overproduction of reactive oxygen species (ROS) leading extensive cellular damage and inhibition of important physiological processes in crops. To survive under this unwanted conditions, plants have better fight mechanism that was evolved intricate mechanisms, which allowing maximum responses that enable to overcome the stress. These can be in the form of osmotic stress, malfunction of ion distribution and plant cell homeostasis. The growth rate and productivity is affected by a response caused by group of genes by changing their expression patterns. The abiotic stress response mechanisms in crop plants can be study by identifying of responsive genes against abiotic stress. The abiotic stresses occurring in plants are summarized in Table 1 and figure 1.

Salinity

Salinity in soil or water is one of the major abiotic stresses that reduce plant growth & productivity worldwide. It is categorized by an excessive concentration of soluble salts in growing media, causes significant crop damage.^[8] The problem is constantly rising because of accretion of salt-affected soil day by day which is triggered by various environmental and anthropogenic influences.^[9,10] Another reason for salinization is poor water quality that is used for irrigation. The first symptoms from the associated with saline stress are displayed in

the roots by suffering an osmotic stress associated with the accumulation of phycotoxic ions. Salinity invites oxidative stress through a series of actions. It triggers stomatal closure, leading decreases CO₂ availability for carbon fixation in the leaves, unmasking chloroplasts to extreme excitation energy which in turn rise the generation of reactive oxygen species (ROS) such as superoxide (O₂•-), hydrogen peroxide (H₂O₂), hydroxyl radical (OH•) and singlet oxygen (1O₂) (11-14) that initiate programmed cell death^[16-18] Salinity impairs the imbibition of seeds due to lower osmotic potential^[19] which alters the activity of enzymes associated with nucleic acid metabolism^[20] and protein metabolism^[21, 22] leading hormonal imbalance^[23] and lessens the utilization of seed reserves^[24,25] thus reduces seed germination. Salt stress is also believed to damage the ultrastructure of cell, tissue and organs^[26,27] that hinder the germination processes. Salinity adversely exhibits its effect on plants in several ways, it could be primarily by high salt concentration in soil, which strongly interferes with the water absorption capacity of plant roots and decline to drastic level making plant more vulnerable. The salt stress also exhibits its adverse effect on plant growth and yield by creating ionic toxicity, which is perhaps, due to an increased cellular concentration of salt within the plants.^[28,8]

Drought

Drought stress is the most serious threat to world food security. Drought stress causes different negative effects on plant growth and total yield by drought such as:

1. Decreased leaves absorption of photosynthetic active radiation.
2. Reduced radiation-use efficiency.
3. Minimized harvest index

Drought tolerance can be defined as the ability to grow, flower and display economic yield under sub-optimal water supply. Its magnitude and severity depend on several factors which include, frequency of drought occurrence, rainfall pattern, water holding capacity of soil etc, making it unpredictable to assess the magnitude of drought. Plant water relationship has a major impact on vital plant functions, cellular processes and adaptive responses in plants under abiotic stress i.e., drought and salt. Under limited water stress, photosynthesis is effectively reduced. The quick stomatal closure in order to preserve the moisture is one of the initial strategies of plants to mitigate the adverse effect of stress. This reduces stomatal conductance and reduces CO₂ exchange into the leaves. The increase in drought conditions,

accumulation of salts and ions in the upper layers of the soil around the root cause osmotic stress and ion toxicity.

Heat

Stress by high temperature (HT) is a major environmental stress that limits plant growth, metabolism, and productivity worldwide. Numerous biochemical reactions involved in Plant growth and its development which are sensitive to temperature. Their responses to HT vary with the degree and duration of HT and the plant type. Plant growth, development, physiological processes, and yield become multifarious, and often adverse, alterations.^[29] One of the major effect of high temperature stress is the excess production of reactive oxygen species (ROS), that is the main cause of oxidative stress. High temperature can change metabolism in plants, particularly by producing compatible solutes which are building blocks of proteins and cellular structures, regulates turgidity by osmotic maintenance, and modify the antioxidant system.^[30-32] At the molecular level, changes in gene expression involved in direct protective mechanism of HT stress.^[29,30] These genes responsible for the expression of osmoprotectants, detoxifying enzymes, transporters, and regulatory proteins. Heat stress may cause damaging functions in plants such as scorching and sunburns of leaves and twigs, branches and stems, leaf senescence and abscission, shoot and root growth inhibition, fruit discoloration and damage [Min Y., *et al* 2016].

Cold: Cold is another important environmental stress affecting plant growth and crop productivity, Chilling (low temperatures above 00 C) and freezing (temperatures below 00 C inducing extracellular ice formation) limit and affect the crop losses (Xin and Browse, 2000).

Waterlogging

This is a serious problem, which showed its effect on crop growth and yield in areas with less rain. The main cause of damage under waterlogging is oxygen deprivation, which affect nutrient and water uptake, so the plants show wilting even when surrounded by excess of water. Aerobic mode to anaerobic mode shifted by lack of oxygen. Although all higher plants require access to free water, excess water in the root environment of land plants can be injurious or even lethal because it blocks the transfer of oxygen and other gases between the soil and the atmosphere. Growth is greatly inhibited in the deficiency (hypoxia) or complete absence of oxygen. This blocks the ion transport systems that normally create the gradient in water potential across the root endodermis.

MINERAL TOXICITY

Aluminum toxicity

Optimum growth and productivity and even cultivation of most of plants is severely restricted within the soil with the elevated levels of Aluminum (Al). It's the third most abundant element on the earth's crust. Al toxicity mainly targets root apex, leading to inhibited root growth and performance (Roy and Mandal, 2005a). In plants with genetic resistance to Al toxicity, the Al-exclusion and uptake from root tips are found to be correlated to their increased capacity to release organic acids like acid which chelates Al^{3+} outside the cell wall. (Delhaize *et al.*, 2007).

Cadmium toxicity

Cadmium (Cd) may be a strongly phytotoxic heavy metal in an increasing environmental problem worldwide. It's one among the foremost dangerous metal thanks to its high mobility and little concentration at which it effects on the plants being to seem. It's released in to the environment by power plant, heating systems, metal working industries, or urban traffic. It's recognized as a particularly significant pollutant thanks to its high toxicity and enormous solubility in water (Pinto *et al.*, 2004). Cd toxicity is that the highest within the acidic environment and reduces because the soil pH, redox potential, and other physiochemical parameters. The effect Cd salt on the expansion of seedlings was weaker in loamy soil and stronger in sandy soil.

In future it's predicted that water scarcity will increase and ultimately intensity of abiotic stresses will increase. Hence there's an urgency to develop crop varieties that are resilient to abiotic stresses to make sure food security and safety in coming years. A plant's first line of defense against abiotic stress is in its roots. The probabilities of surviving stressful conditions are going to be high if the soil holding the plant is healthy and biologically diverse. Approaches for engineering and breeding stress-resistant crops supported chemicals and intensive studies that link genetics, genomics, physiology, and agronomics will advance our knowledge of stress resistance.

Approaches for inducing abiotic stress tolerance

Plants have evolved various general defense mechanisms to counteract different types of abiotic stresses which can be stress avoidance response or stress tolerance response. But it is more convenient approach to engineer the stress tolerant trait into the sensitive species. However, the fact is that stress tolerance is a quantitative trait (controlled by many genes)

which involves a highly complicated molecular mechanism. A number of approaches, like chemical priming, marker-assisted breeding, Quantitative Trait Loci (QTL) mapping, genetic engineering, association mapping and the recent omics approaches have been used to incorporate the stress tolerance trait into the desired cultivars. These approaches are briefly discussed in the following sections. (figure 2)

1. Chemical Priming

Priming refers to a technique in which plants are treated with chemical agents to protect them against environmental effects. Many types of molecules, such as reactive oxygen-nitrogen-sulfur species^[30,31], hormones^[32], and synthetic compounds^[37], are potential plant protectants utilized for reducing the effects of abiotic stresses (Table 1) Another type of priming agent is naturally occurring metabolites, including hormones and vitamins. The priming function of these compounds is applied through an indirect mechanism, such as through osmoprotection [e.g., trehalose^[38]], or even via direct antioxidant properties [e.g., glutathiol^[39]]. Chemical priming is a potential approach in plant stress physiology and management because chemical priming agents effectively prepares plants against various abiotic stresses. Therefore, the searches for effective priming agents as well as the combination effect of those agents against multiple stresses on the mode of action and on the crop yield have been considered in further research for the application in crop stress management. Few Compounds that are potential plant protectants utilized for reducing the effects of abiotic stresses (Table 2)

2. Plant Breeding

Plant breeding enables the incorporation of stress resistance genes from a tolerant variety into the desired sensitive cultivar through sexual hybridization. Plant breeders generally rely on genetic variation in wild varieties as a source of stress tolerance genes. For example, *Triticum dicoccoides* and *Hordeum spontaneum*, the wild relatives of wheat and barley, have been extensively used for introgressing salt and drought tolerance traits into durum wheat and barley cultivars.^[39]

3. Genetic Engineering

Another approach is genetic engineering which involves the introduction of one or more specific genes into the desired cultivar. Lot of efforts worldwide have been made to develop abiotic stress tolerant crops through the application of recombinant DNA technology, employing a spectrum of different gene, encoding osmoprotectants, ion channel proteins, molecular chaperons and other stress-related functional proteins. In comparison to other

genes, biosynthetic accumulation of glycine betaine, proline and other osmoprotectant genes, in several transgenic crop plants, have shown some improvement in abiotic stress tolerance.^[40] For example: improved stress tolerance was demonstrated by transgenic tomatoes expressing mannitol-1-phosphate dehydrogenase gene^[41]; potato expressing non-specific lipid transfer protein-1 (StnsLTP1)^[42]; chili pepper expressing tobacco osmotin gene^[43]; sweet potato overexpressing betaine aldehyde dehydrogenase gene.^[44]

The transgenic approach also allows scientists to study and validate the mechanism governing stress tolerance by over-expressing the gene into a model plant species and to monitor the phenotypical and biochemical changes before and after a specific abiotic stress treatment.^[45,46] One of the most promising and practical approaches for development of new stress tolerant varieties is genetic engineering. Through the use of transgenic technology, one can produce plants with desired traits such as tolerance to various abiotic stresses that includes water stress (flood and drought), temperature stress (high and low), and salt stress more precisely.

The genes implicated in abiotic stresses are broadly classified in two groups. Proteins that act directly. For example, osmoprotectants, detoxifying enzymes, late embryogenesis abundant (LEA) proteins and molecular chaperones.

1. Proteins involved in regulating stress responsive genes. For example, transcription factors.
2. QTL approach:

Quantitative trait loci (QTLs) are stretches of DNA that are closely linked to the genes that underlie the trait in question. QTLs can be molecularly identified (for example, with PCR) to help map regions of the genome that contain genes involved in specifying a quantitative trait.

A set of genetic markers must be developed for the species in question and then to identify the marker that is significantly more likely to co-occur with the trait through statistical association. Analysis generally reveals regions of DNA that are very close to the genes in question rather than finding the specific gene in question. When a QTL is found, often it is not the actual gene underlying the phenotypic trait, but rather a region of DNA that is closely linked with the gene. Where such linkage occurs, the marker locus and the QTL will co-segregate.

5. OMICS APPROACHES

5.1 Genomics

Since the molecular mechanism of stress tolerance is complex, it requires information at the whole genome level to understand it effectively. The discovery of novel genes, determination of their expression patterns in response to abiotic stress, and an improved understanding of their roles in stress adaptation will provide the basis of effective engineering strategies leading to greater stress tolerance. It allows large scale gene function analysis with high throughput technology and incorporates interaction of gene products at cellular and organism level,^[47,48] Functional genomics allows large-scale gene function analysis with high throughput technology and incorporates interaction of gene products at cellular and organism level show in table 3.

5.2 Metabolomics

The study of stress biology in plants and other organisms by identifying different compounds such as by-products of stress metabolism, stress signal transduction molecules or molecules that are part of the acclimation response of plants. The metabolome represents the complete set of metabolites in a biological cell, tissue, organ, organisms, which are the end products of cellular process. Some of the metabolites that have been involved in the plant responses to stress are listed in Table 4.

5.3 Proteomics

The adaptation of plants to biotic or abiotic stress conditions is mediated through deep changes in gene expression which result in changes in composition of plant transcriptome, proteome, and metabolome. Proteins not only include enzymes catalyzing changes in metabolite levels, but also include components of transcription and translation machinery. Plant transcription factors linked to plant stress responses, such as responses to ultraviolet light, wounding, anaerobic stress, and pathogens. Proteomics involved in plant responses to stress shown in Table 5.

Table 1.^[49]

Stress	Consequences	Plant response
Heat stress	High temperature leads to evaporation and have deficit in water. There is a increase in turn of enzymes which leads to plant death.	Efficient protein repair and have general protein stability support survival and temperature can lead to accumulation.
Chilling and cold stress	Biochemical reaction are at slowest rate photosynthesis proceeds fixation of CO ₂ , leading to oxygen radical damage. Freezing leading to ice crystal formation that disrupt cell membrane.	Ceasation of growth in adaptable species overcome by change in metabolism. Ice crystal formation prevented by osmolight accumulation and there is a synthesis of hydrophilic proteins.
Drought	Inability to water transport to leaves which leads to decline in photosynthesis.	Leaf rolling and other adaptation. stoma closure reduces evaporative transpiration induced by ABA. Accumulation of metabolids, having lower internal water and water attracting.
Flooding	Generate microaerobic and anoxic condition interfering with mitochondrial respiration.	Development of cavities in roots that facilitate exchange of ethylene and oxygen between root and shoot i.e, aerenchyma.
Toxicity: Aluminum	Al toxicity mainly target roots apex, resulting in inhibited root growth and function.	In plants with genetic resistance to Al toxicity, the Al- exclusion and uptake from root tips have been found to be correlated to their increased capacity to release organic acids such as citric acid which chelates Al ³⁺ outside the plasma membrane. (Delhaize et al., 2007).
Cadmium	It has high mobility and small concentration at which it effects on the plants being to appear.	Cd toxicity is the highest in the acidic environment and decreases as the soil pH, redox potential, and other physiochemical parameters. The effect Cd salt on the growth of seedlings was weaker in loamy soil and stronger in sandy soil.
Heavy metal	Excess of detoxification reaction Leads to storage or insufficient capacity exceeds.	Excess of metal ions may be countered by export or vascular deposition but metal ion may generate oxygen radicals.
Highlight stress	Excess light can lead to increased production of highly reactive intermediates and by products that can potentially cause photo-oxidative damage and inhibit photosynthesis.	Exposure of a plant to light exceeding what is utilized in photochemistry leads to inactivation of photosynthetic functions and the production of reactive oxygen species (ROS). The effects of these ROS can be the oxidation of lipids, proteins, and enzymes necessary for the proper functioning of the chloroplast and the cell as a whole.

Table 2:

Sr. no.	Compounds	Stress response	References
1	Allantoxin	Salt stress	[50]
2	ROS	Biotic and abiotic stress	[51]
3	H ₂ O ₂	Drought, heat, chilling and salinity	[52,53]
4	Sodium nitroprusside	UV-B radiation and salinity	[54, 55]
5	H ₂ S	Abiotic stress	[56]
6	NaHS	Heat stress	[57,58]
7	Glutathione	Oxidative stress	[59]
8	Polyamine	Drought and salinity	[60]
9	Melatonin	Salt and chilling	[61-63]
10	Glycinbetaine	Salinity and drought	[64, 65]
11	5-aminolevulinic acid	Chilling and flooding	[66]
12	Salicylic acid	Oxidative stress	[67]
13	Ascorbic acid	Oxidative stress	[68]
14	Strobilurin	Abiotic stress	[69]
15	NOSH- aspirin	Abiotic stress	[63]
16	Paclobutrazol	Drought, cold, UV-B radiation, high temperature, and flooding	[70,71]
17	Benzyl aminopurine	Salt stress	[72]
18	Calcium chloride	Flooding	[73]
19	Ketoconazole	Drought	[74]
20	Triadimefon	Salinity	[75]

Table3.

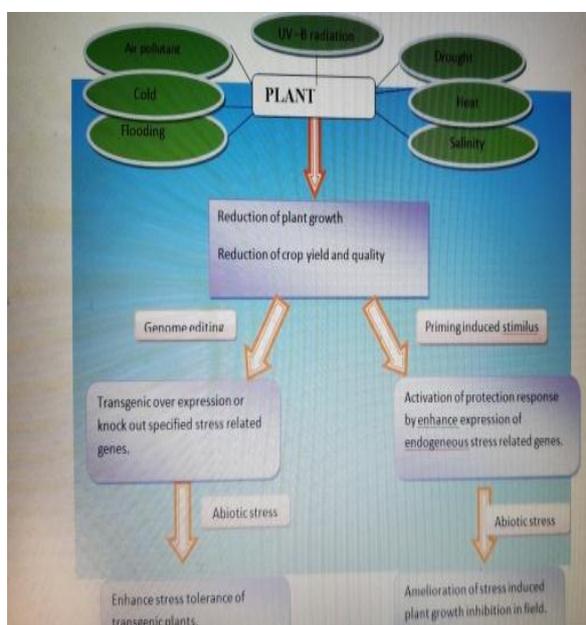
Sr. no.	Genes	Stress	References
1.	MAPK	Abiotic	[76]
2.	MPK3,MPK4andMPK6	Abiotic stress (pathogens)and oxidative stress	[76,77]
3.	CBF/DREB families(CBF1,CBF2,DREB2A)	Drought,cold,salinity	[78-80]
4.	bZIPs family(e.g.,ABF1,ABF2)	Drought,temperature,salinity	[81-89]
5.	WRKY family (AtWRKY2,AtWRKY6,AtWRKY18)	Pathogens, wounding, salinity, temperature, drought, oxidative stress	[90]
6.	ATAF	drought,salinity,cold,pathogens	[91]
7.	HVA1	Salinity and drought	[92]
8.	14.3.3genefamily(GF14b,GF14c)	Salinity,drought,fungal	[93]

Table 4.

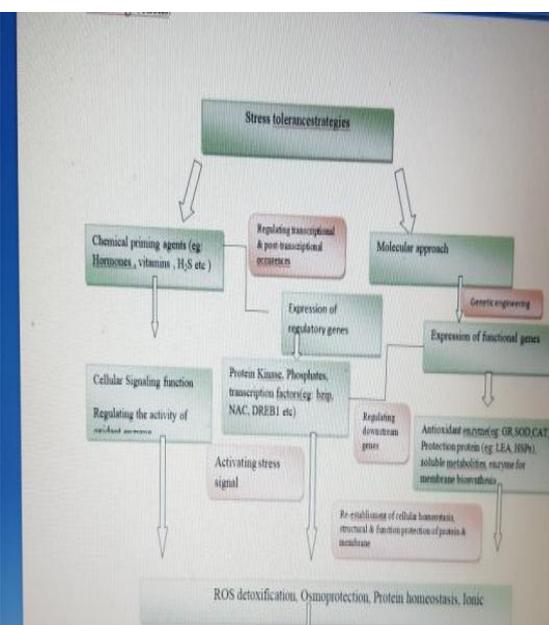
Sr. no.	Genes	Stress	Reference
1.	Abscisic acid, jasmonic acid, salicylic acid, polyamines, and others	Drought, cold, salinity	[94, 95]
2.	Proline, glycine-betaine, and other compatible osmolytes	Environmental stresses: drought, salinity, osmotic.	[96-98]
3.	ROS,malondialdehyde	Abiotic stresses	[94, 95,99]
4.	Phytochelatin and metallothioneins	Heavy metal intoxication	[100, 101]
5.	Terpenes	Toxins and pathogens	[102]
6.	Unsaturatedfattyacids	Environmental stresses	[103]

Table 5.

Family	Gene	Inducibleby	References	Function
Bzip	ABFY ABF2 ABF3 ABF4	Cold Salt,drought Salt Drought,salt,cold	[104]	It has been found that bZIP play important role in plant growth and stress responses such as seed maturation, diseases resistance and drought resistance.
MYC	AtMYC2	Drought,salt	[105]	MYC proteins function as regulators in regulating plant seed production, root elongation, leaf senescence, and stamen development. They also regulate plant secondary metabolism and are actively involved in hormone-mediated plant growth.
MYB	AtMYB2 AtMYB4 AtMYB6 AtMYB7 AtMYB44 MYB15	Drought, salt Salt, ethylene, JA Salt, ethylene, JA Salt, ethylene, JA Salt, ethylene, JA Drought, salt, cold	[106-108]	Function as in cell –cycle control, hormone signalling, secondary metabolism, meristem formation cellular morphogenesis. These has been found to involve in plant salt stress response.
NAC	ATAF1 AtNAC2 AtNAC019 AtNAC055 SNAC1 SNAC2	Drought Salt Drought, salt Drought, salt Cold, drought, salt Cold, drought, salt	[109-113]	Function as positive or negative regulators of plant immunity ti biotrophic, hemibiotrophic or necrotrophic pathogens, as, modulators of hypersensitive responses & stomal immunity or as virulence targets of pathogen effectors.
WRKY	OsWRKY45 GmWRKY21 GmWRKY54 GmWRKY13 NbWRKY		[114,115,116]	It acts as a activators or repressors in ABA signaling.



(Fig:1)



(Fig:2)

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