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Oxidative Stress and Approaches to Enhance Abiotic Stress Tolerance in Plants.

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ABSTRACT

Plants are plastic and totipotent and can tolerate stress to an extent with the aid of various metabolites synthesized in them. Severe biotic and abiotic stresses can ultimately lead to oxidative stress in plants due to the formation of reactive oxygen species. Trials on improving tolerance to such stresses are attempted by crop scientists for attaining food security.
Keywords: stress, biotic, abiotic, reactive oxygen species, tolerance.

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INTRODUCTION

Abiotic stress caused due to drought, flood, salinity and cold drastically affects the metabolism and growth of plants. World's arable lands exposed to these abiotic stress conditions have seen a major decline in the global food production [1]. Hence, considerable losses to agricultural production worldwide have been reported [2]. These stress factors can lead to several changes in development, productivity and even impair the chances of plant survival. Such drastic changes enhance the accumulation of secondary metabolites [3]. They can reduce biosynthetic capacity of plants and eventually cause various changes on plant metabolism like oxidative stress. Several reactive oxygen species (ROS) are continuously produced as byproducts in metabolic reactions such as photosynthesis, photorespiration and respiration [4]. A variety of responses are exhibited by plants to abiotic stresses that facilitate them to tolerate and withstand unfavorable conditions [5].

Oxidative Stress

Oxidative stress can be defined as a change in balance between pro-oxidative and anti-oxidative reactions, favouring the former, caused by various abiotic and biotic factors such as light, drought, hyperoxia, xenobiotics, toxins, pathogen infection, ageing of plants, metal ions, pollutants and high salinity [6]. Oxygen deprivation stress is characterized by three different levels: anoxia, transient hypoxia and reoxygenation. In both hypoxia and reoxygenation ROS is produced.

Free radical can be defined as any species that contains one or more unpaired valence electrons or an open electron shell [7]. ROS is a cumulative term that encompasses both oxygen radicals like superoxide, peroxyl, hydroxyl and hydroperoxyl radicals and certain non-radical or molecular oxidizing agents like hydrogen peroxide, hypo chloric acid, singlet oxygen and ozone, that can be easily transformed into radicals [8]. Numerous abiotic stresses lead to the overproduction of ROS in plants which are exceptionally reactive and toxic. They cause damage to proteins, lipids, carbohydrates and DNA [9]. The increased steady state ROS levels induce oxidative damage in cellular components. If oxidative stress exceeds a limit, the homeostasis is disturbed which in turn leads to apoptosis or cell death and necrosis. Oxidative stress is usually induced by oxidant factors. This may also be accompanied by various endogenous and exogenous factors such as drought conditions [10].

According to Barsotz, aging of leaves, fruit ripening and flower maturation, either directly or indirectly is related to oxidative stress. He observed increased lipid peroxidation in senescing carnation petal cells in which senescence time was delayed by anti-oxidants. It was reported that oxidative stress also played a major role in aging of stored seeds. However, the major damage caused to the seeds by oxidative stress was seen during the initial stages of seed germination and the intensity of damage increased over time during storage [6].

Oxidative stress is associated with various diseases in plants. During pathological conditions enzymatic deficiencies eventually lead to oxidative stress. This usually occurs due to mutations in genes coding for anti-oxidants also known as genetic polymorphisms. Antioxidants and many related enzymes are potential targets of oxidative modifications which may define the destiny of the cell as well as worsen diseases [11].

Source of Reactive Oxygen Species

Reactive oxygen species were considered only to be the harmful by-products of aerobic metabolism, previously. However, it has now become probable that plants actively generate ROS as signaling molecules to control processes such as apoptosis, abiotic stress responses, pathogen defense and systemic signaling. Current advancements including microarray studies and the development of mutants with modified ROS-scavenging mechanisms provide new insights into how the steady-state level of ROS is regulated in plant cells [12].

There are many potential sources of ROS in plants. Some are reactions associated with regular metabolism, such as respiration and photosynthesis [13]. Some also belong to pathways augmented during abiotic stresses like photorespiration by glycolate oxidase in peroxisomes. However, recent studies state that different sources of ROS have been recognized in plants, including NADPH oxidases, amine oxidases

and cell-wall-bound peroxidases. These are tightly regulated and aid in the production of ROS during programmed cell death (PCD) and pathogen defense [14][15].

Superoxide Radical

In plant cells, another important source of superoxide radical (O_2^-) are chloroplasts where the concentration is very high (300 mol.m^{-3} or above) [16]. These ROS radicals react with compounds that contain double bonds like that of iron-sulfur cluster of proteins. Superoxide radicals are generated in several photo-oxidation reactions, much like as seen in Mehler and electron transport chain reactions in chloroplast and mitochondria. Superoxide dismutase enzymes or SODs are the main scavenging systems for $O2^-$ [17]. It has been observed that drought conditions lead to generation of $O2^-$ in wheat (*Triticum vulgare*) chloroplasts because of disruption in photo systems, making them leaky [18].

Hydrogen peroxide

Superoxide radicals are basically moderately active and are soon converted into hydrogen peroxide by SOD. Overproduction of H_2O_2 in the plant cells leads to the occurrence of oxidative stress. Hydrogen peroxide may result in inactivation of enzymes by oxidation of their thiol groups [9]. They are involved in oxidation of proteins and react with superoxide radical in iron catalyzed reactions to form hydroxyl radical. The reactive hydroxyl radical removes electrons from any molecule in its path, changing that molecule into a free radical and so causing a chain reaction. Naturally H_2O_2 is more destructive to DNA than hydroxyl radical as the lower reactivity of hydrogen peroxide affords enough time for the molecule to travel into the nucleus of the cell, successively causing disorder on macromolecules such as DNA [13]. The emergence of H_2O_2 from O_2^- decomposition and the oxygen uptake in chloroplasts is significantly determined by the production of O_2^- [19].

Hydroxyl radical

Hydroxyl radicals are generated by sequential monovalent reduction of di-oxygen (O_2) in cell metabolism, and are principally accountable for the cytotoxic properties of oxygen in plants [20]. OH radicals are produced by ultra violet photolysis of hydrogen peroxide. They are very reactive and harm most macromolecules, including DNA, proteins and lipids. Most plants when subjected to water stress generate •OH in the Fenton-type Haber Weiss reactions [21]. These OH radicals are chiefly responsible for arbitrating oxygen toxicity *in vivo*. They can potentially react with all biological molecules such as proteins, lipids and DNA. Due to the absence of any enzymatic mechanism for the elimination of this highly reactive ROS, overproduction of •OH radical eventually leads to cell death [9].

Singlet oxygen

Abiotic stresses lead to closing of stomata which results in low accumulation of intercellular CO_2 in the chloroplast. This favors the formation of singlet oxygen ($^1O_2$) [22]. $^1O_2$ directly oxidizes protein, polyunsaturated fatty acids, and DNA. They are formed during the processes of photo-inhibition and photosystem II electron transfer reactions occurring in chloroplasts. They are extremely reactive, toxic to cells and can be involved in the signaling of programmed cell death. It has been shown that cercosporin, a toxin of the soya bean - 'Cercospora' pathogen produces singlet oxygen in a photosynthesized reaction and thus leads to oxidative stress by production of ROS [23]. The major scavenging systems for singlet oxygen are carotenoids and α-tocopherols [24].

Effects of ROS on Macromolecules

Increased levels of ROS can cause injury to biomolecules such as lipids, proteins and DNA. These reactions can change intrinsic membrane properties like ion transport, fluidity, loss of enzyme activity, inhibition of protein synthesis and DNA damage, which subsequently results in apoptosis.

Lipids

When ROS level goes beyond the threshold level, enhanced lipid peroxidation takes place in both cellular and organelle membranes. This, consequently, affects regular cellular functioning. Lipid peroxidation

aggravates the oxidative stress by production of lipid-derived radicals that can react with and disrupt proteins and DNA [25]. Two common sites of ROS attack on the phospholipid molecules are the unsaturated double bonds between two carbon atoms and the ester linkage as well as between glycerol and fatty acid. The polyunsaturated fatty acids (PUFAs) present in membrane phospholipids are particularly susceptible to attack by ROS. Peroxidation of polyunsaturated fatty acid can lead to chain breakage, leading to an increase in membrane fluidity and permeability [26].

Proteins

Direct alteration of proteins is associated with modulation of its activity through carbonylation, nitrosylation, disulphide bond formation, and glutathionylation. Proteins can also be altered indirectly by breaking down products of fatty acid peroxidation [27]. As a result of excessive ROS production, fragmentation of the peptide chain, site-specific amino acid modification, aggregation of cross-linked reaction products and altered electric charge, an increased sensitivity of proteins to proteolysis occur. Injury to tissues due to oxidative stress usually indicates higher concentrations of carbonylated proteins which is an extensively used marker for protein oxidation [28]. Several research works have revealed that after a certain degree further damage leads to extensive cross-linked and aggregated products, which are not only mediocre substrates for degradation, but can also confine proteases to degenerate other oxidized proteins [29]. ROS prompts signal transduction events, like mitogen-activated protein kinase cascades, evoking specific cellular responses. The impact of these molecules on cellular processes is interceded by both the continuation of their production and their improvement by scavenging enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). The location, amplitude, and duration of production of these molecules determine the specificity of the rapid responses they direct [30].

DNA

ROS exerts genotoxic effects in the DNA of plants, damaging them in the process as a consequence of exposure to abiotic stresses [31]. ROS is capable of inducing damage to almost all cellular macromolecules including DNA which includes base deletion, pyrimidine dimer formation, cross-links, strand breaks and base modifications, such as alkylation and oxidation [32]. Decreased protein synthesis, cellular membrane destruction and damage to photosynthetic proteins, result from DNA damage, which affect growth and development of the entire organism [33].

Antioxidants Involved In Scavenging Free Radicals

The cellular processes for scavenging ROS and toxic organic radicals include ascorbate, carotenoids, glutathione, tocopherol, alkaloids, polyphenols etc. Enzymatic antioxidants including superoxide dismutase (SOD), catalase, peroxidase and glutathione reductase detoxify either by destroying toxic compounds or by regenerating antioxidants involving reducing power. Manganese superoxide dismutase (MnSOD), catalase (CAT), and glutathione peroxidase (GPX-1) are the major enzymes that work together in order to detoxify free radicals [34].

Antioxidants inhibit the formation of ROS by scavenging them, by binding transition metal ions and by intercepting the formation of hydroxyl ions. Scavenging can also be done by decomposition of lipid hydroperoxides or by combination of both the processes [35].

Types of antioxidants and their roles in plants

Cells have developed an elaborate system of enzymatic and non-enzymatic antioxidants that help to scavenge primordially generated ROS. Different enzymes which are involved in ROS-scavenging have been genetically engineered, over expressed or down-regulated [36].

Extensive research has shown essential roles of signaling in the regulation of photosynthesis with antioxidants such as ascorbate and glutathione [37]. Manipulation of the antioxidant network has repeatedly indicated that, reduction of discrete antioxidant components has an adverse effect on photosynthesis. Depletion of either catalase (CAT) or cytosolic ascorbate peroxidase (APX) has a broad negative impact.

Tobacco plants that are short in both CAT and cytosolic APX showed a less noticeable phenotype than the parent lines [38].

Enzymatic antioxidants

Superoxide dismutase (SOD)

Superoxide dismutase provides the first line of defense against the toxic levels of ROS. The SODs are involved in a dismutation reaction that involves catalyzing the reduction of hydrogen peroxide. This decreases the risk of hydroxyl (OH) formation through the metal catalyzed Haber Weiss-type reaction [39]. A chimeric gene encoding chloroplast localized Cu/Zu SOD of transgenic tobacco plant (*Nicotiana tabacum*) was showed to protect photosynthetic leaves from oxidative stress caused by exposure to severe light intensity and low temperature [40].

Catalases (CAT)

Catalases are tetramers by nature. The have heme containing enzymes with the capacity to dismutate the H_2O_2 into H_2O and O_2 and is crucial for ROS detoxification during stressed conditions [41]. Catalases have the highest turnover rates amongst all enzymes. Around 6 million molecules of H_2O_2 are converted to H_2O and O_2 per minute by one molecule of catalase. Catalases are also crucial in the removal of H_2O_2 that peroxisomes generate by oxidases. These are involved in β-oxidation of fatty acids, catabolism of purines and photo-respiration. The isozymes of catalases have been studied widely in higher plants [42], like in *Helianthus vulgare* and *Helianthus annus* cotyledons and around 12 isozymes have been studied in Brassica species. Three isoforms of maize (CAT1, CAT2 and CAT3), found on different chromosomes are expressed differentially and are independently controlled. CAT1 andCAT2 are found localized in peroxisomes while CAT3 is found in mitochondria. CAT isozymes have been shown to react differentially to light [43].

Ascorbate Peroxidase (APX)

Ascorbate peroxidase plays the most significant role in scavenging ROS, and protecting lower plant cells such as Euglena and other organisms. APX is involved in H_2O_2 scavenging in water-water and the ascorbate-glutathione (ASH-GSH) cycles and utilizes ASH as the electron donor. The APX family constitutes of five different isoforms such as thylakoid and glyoxisome membrane forms as well as chloroplast, stromal soluble form and cytosolic forms [44].

Non enzymatic antioxidants

Ascorbic acid (Vitamin C)

Ascorbic acid is the most abundant, dominant water soluble antioxidant that prevents or minimizes the losses caused by ROS in plants [45]. Plant mitochondria not only synthesizes ASH by L-galactono-g-lactone dehydrogenase but also plays a role in the restoration of ascorbate (ASH) from its oxidized forms. ASH is considered as a prevailing ROS scavenger because of its ability to donate electrons in a number of enzymatic and non-enzymatic reactions. It can provide protection to membranes by directly scavenging the O_2 and OH radicals and by regenerating α-tocopherol from tocopheroxyl radical [46].

α-Tocopherols (Vitamin E)

α-Tocopherol is formed from homogentisate and phytylpyrophosphate in chloroplasts. Homogentisate originates from tyrosine formed by the plastidic shikimate pathway [47]. Tocopherols, are lipid soluble antioxidants found in biomembranes. Tocopherols help avert the chain propagation step in lipid autooxidation making it an effective free radical trap. Apart from that, it has been assessed that one molecule of α-tocopherol can scavenge up to 120 $^1O_2$ molecules by resonance energy transfer. In response to environmental constraints, the level of α-tocopherol changes differentially which depends on the extent of the stresses [48].

Table 1

Serial No.	SOURCE	HOST	GENE	FUNCTION	EFFECT	REFERENCE
1.	*Medicago sativa*	MsNHX1(*Medicago sativa* Na$^+$/H$^+$ antiporter)	*Arabidopsis thaliana*	Promotes better seed germination under salt stress	Transformation results suggested that the MsNHX1 product plays a crucial role in salt tolerance of the alfalfa, and its transcript expression is possibly partially regulated through ABA-dependent signaling pathway.	Sen Gupta *et al.* (1993). [54]
2.	*Vigna aconitifolia*	p5cs (pyrroline-5-carboxylate synthetase)	*Nicotiana tabacum*	Improves drought tolerance	*Overexpression of Pyrroline-5-Carboxylate Synthetase increased proline production and conferred osmotolerance in tobacco.*	Kavi Kishor *et al.* (1995). [55]
3.	*Escherichia coli*	MtD (mannitol phosphate dehydrogenase)	*Arabidopsis thaliana*	Enhances seed germination under salinity stress	*Increased plant height, fresh weight and improved seed germination under salt stress.*	J.C. Thomas, et al. (1998). [56]
4.	*Arthrobacter*	Choline oxidase	*Oryza sativa*	Enhances tolerance to cold induced stress response	Transgenic rice plants with COD targeted either to chloroplasts or to the cytosol, demonstrated enhanced tolerance to salt or cold induced photo inhibition.	Alia *et al.* (1998). [57]
5.	*Escherichia coli*	Choline dehydrogenase	*Nicotiana tabacum*	Enhances tolerance to salt stress	Transformation of tobacco with the gene for CDH enriched tolerance to salt at high levels of NaCl in terms of growth yield and observable injury to leaves.	Alia *et al.* (1998). [57]
6.	*Hordeum vulgare*	Superoxide dismutase	*Nicotiana tabacum*	Promotes photosynthesis during chilling	Transgenic tobacco over expressing chloroplastic Cu/Zn SOD showed enhanced tolerance to oxidative stress in the presence of high intensity light and low temperature.	Wangxia *et al.* (2003). [58]
7.	*Nicotiana plumbaginifolia*	AtZEP (zeaxanthin epoxidase gene)	*Arabidopsis thaliana*	Improves tolerance to drought and salinity stress	*The transfer of AtZEP showed that increased drought stress tolerance was attributed to increased leaf and lateral root development and increased survival.*	Schwartz *et al.* (2003). [59]
8.	*Hordeum vulgare*	HVA1 (high voltage activated gene 1)	*Oryza sativa*	Improves dehydration tolerance	*HVA1 proteins helped in better performance of transgenic rice plants by protecting cell membrane from injury under drought stress.*	Chandra *et al.* (2004). [60]
9.	*Arabidopsis thaliana*	ERA1/(early retinoic acid) farnesyl-transferase	*Brassica napus*	Increases tolerance to water stress and better yields	Transgenic canola showed enhanced ABA sensitivity and significant decrease of water transpiration and stomatal conductance under drought stress.	Wang *et al.* (2005). [61]
10.	*Ipomoea batatas*	Spinach betaine aldehyde	*Arabidopsis thaliana*	BADH converts betaine	The expression of	Sakamoto *et al.* (2005).

		dehydrogenase	(Cultivar Sushu-2)	aldehyde to glycine betaine that enhances oxidative stress tolerance	the *SoBADH* gene augmented BADH activity and GB synthesis in these transgenic sweet potato plants, which subsequently amended their tolerance to several abiotic stresses by initiation or activation of ROS scavenging and the amassing of proline.	[62]
11.	*Oryza sativa*	DREB2 (Dehydration Responsive Element Binding Factor-2)	*Arabidopsis thaliana*	Increases tolerance for drought, high salinity and cold	The active form of DREB2 transactivated target stress-inducible genes and enhanced drought tolerance in transgenic Arabidopsis.	Shinozaki *et al.* (2007). [63]
12.	*Apium graveolens*	M6PR (mannose-6-phosphate reductase)	*Arabidopsis thaliana*	Improves salt tolerance exceptionally	*Not only improved salt tolerance but also increased growth-dry weight, more leaves and specific leaf weight.*	Sickler *et al.* (2007). [64]
13.	*Solanum lycopersicum*	NCED(9-cis-epoxycarotenoid dioxygenase)	*Arabidopsis thaliana*	A key enzyme in ABA (Absicisic Acid) biosynthesis	It was demonstrated that overexpression of the gene NCED led to increased drought tolerance in Arabidopsis and also resulted in ABA biosynthesis.	Shinozaki *et al.* (2007). [63]
14.	*Oryza sativa*	SnRK-2 Protein kinase.(serine threonine kinase)	*Arabidopsis thaliana*	Activated by drought and salinity stress and is involved in stomatal closure	A family of serine –threonine protein kinases (SRK2C) also functions in transgenic plants to improve stress tolerance. Many of the downstream genes it affects are stress inducible.	Shinozaki *et al.* (2007). [63]
15.	*Arabidopsis thaliana*	RD26 gene (responsive to dessication-26) encoding a NAC transcription factor	*Oryza sativa*	Expression of the RD26 NAC transcription factor gene is induced by high salinity, drought, ABA(abscissic acid), and JA(jasmonic acid) treatments. RD26 protein is localized in the nucleus and has transcriptional activity.	It was observed that ABA- and stress-inducible genes were up-regulated in the RD26-overexpressing transgenic plant.	Shinozaki *et al.* (2007). [63]
16.	*Arthrobacter globiformis*	CodA (choline oxidase)	*Arabidopsis thaliana*	Enhances tolerance to high temperature during imbibition and germination of seeds, and during growth of young seedlings	Transformation of Arabidopsis with the *codA* gene from *A. globiformis* resulted in the accumulation of glycine betaine in various organs of transformed plants that enhanced heat tolerance in plants.	Bao-Yan *et al.* (2008). [65]
17.	*Beta vulgaris*	Betaine dehydrogenase	*Nicotiana tabacum*	Betaine acts as an osmoprotectant by stabilizing both the quaternary structure of	Transgenic tobacco lines accumulating glycine betaine exhibited enhanced tolerance to salt stress as demonstrated by	Bao-Yan *et al.* (2008). [65]

				proteins and the highly ordered assembly of membranes against the adversarial effects of high salinity and extreme temperatures. BADH converts betaine aldehyde to glycine betaine.	biomass production of greenhouse-grown intact plants.	
18.	*Arabidopsis thaliana*	AtMYB41 (*Arabidopsis thaliana* myb domain protein 41) - over expressed.	*Arabidopsis thaliana*	Improves drought resistance	*Transgenic expression of AtMYB41, which encodes an R2R3-MYB transcription factor, expressed at high levels in response to drought, and salt treatments.*	Cominelli *et al.* (2008). [66]
19.	*Oryza sativa*	OsDREB1 (*Oryza sativa* dehydration responsive element binding factor-1)	*Arabidopsis thaliana*	Improves drought and chilling tolerance, stress responsive gene expression and stress tolerance	OsDREB1 transformed Arabidopsis showed stress responsive gene expression leading to enhanced tolerance to oxidative stress response.	Weijuan. *et al.* (2012). [67]
20.	*RFOs(Raffinose family Oligosaccharides)*	Galactinol synthase	*Arabidopsis thaliana*	Improves drought tolerance	*AtGolS2*-expressing transgenic plants displayed significantly enhanced drought tolerance, with increased expression of *AtGolS2*.	Weijuan, *et al.* (2012). [67]

Flavonoids

Flavonoids are usually found in leaves, floral parts and pollens. They serve as ROS scavengers by locating and neutralizing radicals before they can damage the cell and hence are important for plants growing under adverse environmental conditions. Flavonoids inhibit a wide array of kinases that replace key steps of growth and differentiation in eukaryotic cells [49]. Their ability to act as antioxidants depends on the reduction potentials of their radicals and accessibility of the radicals [50].

Antioxidant enzyme activity may be strictly depressed during the midday hours, as strong light could result in severe excess-light stress, especially when plants are simultaneously faced with other stresses, such as high temperature and drought. The increase in zeaxanthin as an outcome of high light and drought stress [51] holds back ROS generation through the thermal dissipation of surplus energy via nonphotochemical quenching and antioxidant activity in thylakoid membranes [52]. The comparative significance of key constituents of the antioxidant machinery, such as antioxidant enzymes, ascorbic acid, carotenoids and flavonoids, may strongly depend upon their subcellular and temporal distribution.

Molecular Approaches to Combat Abiotic Stresses

Since plant efficiency is significantly influenced by environmental stresses, tolerance to such factors can be attained by the transfer of genes encoding protective proteins or enzymes from other organisms or by overexpression of the endogenous genes. Strategic methodologies are presently being examined and engineered to alter the rate of scavenging by ROS [53]. Given below in the table (Table 1.) is a list of genes that have been transferred into plants to study their effects towards improvement of abiotic stresses.

CONCLUSION

Abiotic stresses on plants are becoming more unpredictable with the change in climatic patterns. Introducing tolerance towards multiple stresses in domesticated plants is necessary to meet the demand of the increasing human population. Though research can help in alleviating the problem, it cannot give mankind a permanent solution unless our earth gets environmentally protected.

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