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Abiotic Stress Tolerance in Plants: Insights into the Functions of Glutathione Peroxidases

Susmita Samal, Nirjhar Dasgupta *

[a] *Department of Biotechnology, Techno India University, EM-4, EM-4/1, EM Block, Sector V, Bidhannagar, Kolkata, West Bengal – 700091(IN)*

Abstract

Years of evolution and numerous adaptations have developed plants to be a unique eukaryotic multicellular organism which is independent in nature. One of such miraculous features of plant is its inbuilt defense mechanism which had protected itself from any extreme condition. Unfortunately, we human and our action had over exploited every natural resource to such an extent that the "Mother Earth" which gave us life, are undergoing drastic changes hampering its actual ambience. One of the most recent concerning issues that had made scientist distressed is the rapid change of climatic condition of nature, which therefore followed by increase in rate of abiotic stress. Due to this increase abiotic stresses, high rate of ROS production takes place in plant which create an imbalance in its homeostasis. Reactive Oxygen Species (ROS) are highly reactive and toxic which effects the biosynthesis of chlorophyll, photosynthetic capacity, and carbohydrate, protein, lipid, and antioxidant enzyme activities. ROS is the byproduct of cellular metabolism of plant cell which triggers the stress signal transduction activating the defense mechanism, that is synthesis of antioxidants which maintains the level of this reactive species. The activity of several types of enzymatic and non-enzymatic antioxidant has greatly contributed on the defense mechanism of plants helping it to withstand the adverse condition of the environment. In this article, we will be assessing the process of how the plants physiological and biochemical changes take play on exposure to these abiotic stresses and how antioxidant in cell combat these changes for plant to survive.

***Keywords**:* ROS, Plant Abiotic Stress Physiology, GPX, Antioxidant defense mechanism, RNS, Lipid Peroxidation

1. INTRODUCTION

Plant belonging to kingdom Plantae are eukaryotic organism, having an autotrophic mode of nutrient. It undergoes the process of photosynthesis in which CO2 and water are combined in the presence of sunlight trapped by Mg2+ containing green pigment, known as chlorophyll in order to synthesize its energy from inorganic compound [1]. According to the above mention fact it proves that plants are self-dependent in synthesizing their own food, it is also self-sufficient in facing and adapting itself according to the adverse environmental condition occurred due to naturally or man-made to certain extent. The adverse environmental conditions also known as environmental stress occurring mainly due to sudden climatic changes which is consequences of sessile human lifestyle. When environmental stress occurs due to biotic factor then it is known as biotic stress and when occurs due to abiotic factor it is known as abiotic stress. Abiotic stress has now become one of the most extensive studies for researchers and its effect on plants and mainly on field crops [2]. It's various type such as radiation UV A and UV B, water (drought and flood), salinity, temperature (high and low), chemical factors (heavy metal and pH), nutrient (deficiency and excess), light (high and low) intensity, gaseous

* Corresponding author. Tel.: (+91) 98307 64523; e-mail: **dr.nirjhardg@gmail.com** .

pollutant (ozone, sulfuric gas), mechanical factor and anaerobic has garnered quite a lot attention of researchers [2,6]. This leads to the discovery of all type of coping mechanism adapted by the plants to deal these stresses and to sustain normal growth under such condition. Sometimes combination of these stresses brings unique cellular level modification that cannot be expected from individual stressors [6]. These modification results in biochemical and physiological changes in plant, generating certain secondary metabolites which induces stress signals which then help the plant to produce stress signaling pathways in response to it. These pathways help to maintain homeostasis and acclimating itself to the modified conditions. These changes are also expressed in their genes [5], inherited by their progeny hence evolving in order to survive in these adverse changes. Major of this abiotic stress researches are done in laboratory, under controlled conditions which may vary with the condition that actually occurs in the field [3]. Environmental stress has become a concerning issue among scientist due to its detrimental effect on crop productivity and its development, majorly to meet the demands of enhanced food requirement (Table 1).

Table 1: Abiotic Stress Types and Their Effects on Plants

Abiotic Stress	**Key Effects**
Drought	Reduced cell division, smaller leaf size, nutrient uptake hindrance, water loss.
Salinity	Ion toxicity, disrupted photosynthesis, membrane disorders, oxidative stress.
Temperature	Delayed or early flowering, reproductive phase disruptions.
Heavy Metals	ROS overproduction, biomolecule inactivation, oxidative stress.

As by the word “abiotic” we understand something that is not obtain from living organism. Abiotic factors are physical rather than biological. Abiotic factors in environment are all the natural resources such as sunlight, water, temperature, soil, wind, humidity etc. Human’s overexploitation of these natural resources had lead to the drastic changes in natural course of natural resources resulting extreme conditions known as “stress” or more specifically “abiotic stress”. Plant getting exposed to such abiotic stresses have independently developed its coping mechanism by making changes in its cellular metabolism.

Plants exposed to abiotic stress are found to have an increase in amount of ROS (Reactive Oxygen Species) which are highly reactive and toxic, affecting the biosynthesis of chlorophyll, photosynthetic process, and carbohydrate, protein, lipid and antioxidant enzyme activities [8]. Plant use molecular oxygen for its cellular metabolism. Reactive Oxygen species also known as ROS are the byproduct of mitochondrial oxidative phosphorylation and also by cellular response to xenobiotics, cytokines, and bacterial invasion. Reactive oxygen species such as superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical (HO•), are of radical and non-radical oxygen species formed by the partial reduction of oxygen [34] in sites such as chlorophyll, mitochondria both are double membraned subcellular organelles [40] and Peroxisomes is single membraned subcellular organelles [41]. This increase in accumulation of ROS in cell disturb the homeostasis and ion distribution [40,42] which increases the oxidative stress in plant [34]. ROS-mediated oxidative stress causes damage of nucleic acids, proteins, and lipids involves in carcinogenesis [35], neurodegeneration [36,37], atherosclerosis [34], diabetes [38], and aging [39]. So plants are fully evolved to regulate all this overwhelming production of ROS and to thereby reduces the toxic effect of high ROS by the production of antioxidants. Antioxidants are biomolecules that reduces, repairs or prevent the effect by inhibiting the oxidation of oxygen species present in ROS (e.g. O_2^-, H_2O_2, OH^-, O_2) [4]. They are first line of defense against the harmful effects caused by free radicals [33,43,44,45]. Plant antioxidants have an important role in plant development and has a wide range of mechanism and function [40]. Plant antioxidant detoxify in three major ways i) antioxidants that forage produced ROS ii) antioxidant that inhibit ROS production iii) antioxidant that cures or alters the damage caused by ROS [7]. It does not completely eradicate oxidants

but rather maintains an optimum level [46]. Antioxidant defense system comprises of two types :-
i)Enzymatic antioxidant
ii) non-enzymatic antioxidant (Table 2).

Table 2: Antioxidant Defense Mechanisms in Plants

Antioxidant Type	Key Enzymes	Function
Enzymatic Antioxidants	SOD, CAT, GPX, APX	Neutralizes ROS by converting them to non-toxic forms.
Non-Enzymatic Antioxidants	Ascorbic acid, Glutathione, Phenolic compounds, Flavonoids	Maintains redox balance, scavenges ROS.

- → **Enzymatic antioxidant** - superoxide dismutase (SOD), catalase (CAT), peroxidases (POX), glutathione peroxidase (GPX), glutathione reductase (GR), glutathione S-transferases (GST), ascorbate peroxidase (APX), monodehydroascorbate reductase (MD-HAR) and dehydroascorbate reductase (DHAR) [47-49].
- → **Non-enzymatic antioxidant** - ascorbic acid (AA), glutathione (GSH), phenolic compounds, alkaloids, flavonoids, carotenoids, free amino acids and α-tocopherols [47-49].

As this work primary focuses on **GLUTATHIONE PEROXIDASE** which falls under the category of PEROXIDASE enzyme, so we will be discussing about the PEROXIDASE enzymes.

2. PEROXIDASE(POX):-

Peroxidase is a hydrogen peroxide (H_2O_2) decomposing enzyme accompanying oxidation of various phenolic and non-phenolic substrates. Its application as an industrial enzyme for medicinal, immunological, biotechnological aspect, bioremediation, textile etc.[68] Its various use makes it one of the primary enzyme

Table 3: Characteristics of Peroxidase Enzymes

Peroxidase Type	Function	Examples
Heme Peroxidase	Catalyzes H2O2 decomposition; innate immunity.	Myeloperoxidase (MPO), Eosinophil Peroxidase (EPO).
Non-Heme Peroxidase	Reduces hydroperoxides and detoxifies lipid peroxides.	Thiol Peroxidase, Alkylhydroperoxidase.
Class III Plant-Specific	Oxidoreduction of H2O2; stress response.	Cytochrome c Peroxidase, Ascorbate Peroxidase.

Peroxidase is categorized into two types:
A) Heme peroxidase B) Non-Heme peroxidase [68]

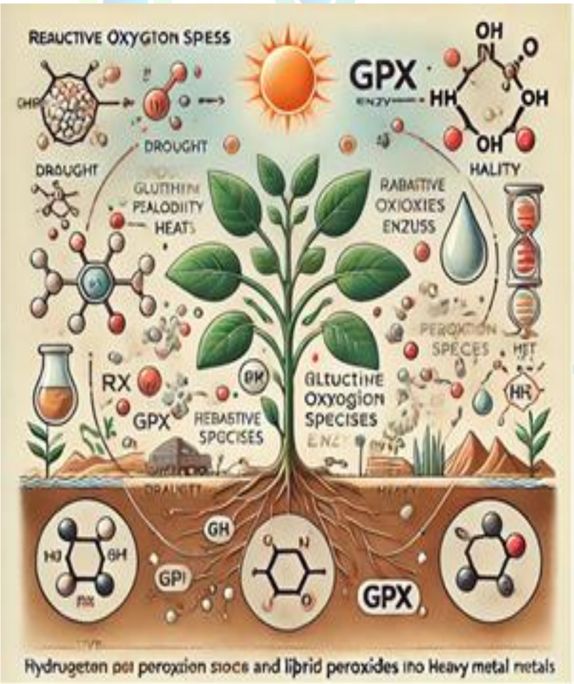
A) Heme peroxidase is further divided into two:
1) Peroxidase-Cyclooxygenase Superfamily (PCOXS) – is animal specific peroxidase and takes part in innate immunity, defense mechanism etc. E.g.- Myeloperoxidase (MPO), Eosinophil peroxidase (EPO), Lactoperoxidase (LPO), Thyroid peroxidase (TPO)
2) Peroxidase-Catalase Superfamily (PCATS) – is a plant specific peroxidase which is further subdivided into following three classes [53] :-
   - ➢ Class I plant peroxidase – involves intracellular enzymes in plants, bacteria and yeast such as
     - o Cytochrome c peroxidase {EC 1.11.1.5}
     - o Bacterial catalase-peroxidase {EC 1.11.1.6}
     - o Ascorbate peroxidase {EC 1.11.1.11}
   - ➢ Class II plant peroxidase – extracellular peroxidase from fungi such as
     - o Lignin peroxidase {EC 1.11.1.14}
     - o Mn^{2+}-dependent peroxidase {EC 1.11.1.13}

- Class III plant peroxidase – Peroxidases {EC 1.11.1.7}

B) Non-Heme peroxidase is further divided into:

1) Thiol Peroxidase
2) Halo-Peroxidase
3) Alkylhydroperoxidase
4) NADH peroxidase

Peroxidases enzyme (POX) {EC number 1.11.1.7} is a Class III plant-specific peroxidase whose function is to catalyze oxidoreduction of H_2O_2. It is usually stable at high temperature and its activity is determined by using simple chromogenic reactions, which makes it an ideal enzyme for study of protein structure, enzyme reaction and enzyme functions for any practical application [51] such as immunoassays, diagnostic assays and industrial enzymatic reaction [50]. Peroxidase is a heme-containing glycoprotein which encode a large multigene family in plant [51].



In spite of GLUTAHTHIONE PEROXIDASE {EC 1.11.1.9} falls under the animal peroxidase super-family, it is noticed that its activity is found in plants and various other cDNAs encoding its homologs [52,56,57]. So, focusing on actual topic of this review paper that is GLUTATHIONE PEROXIDASE, here we will be discussing about its characteristic and its tolerance against certain abiotic stress.

2.1. <u>GLUTATHIONE PEROXIDASE:-</u>

Thiol peroxidase is a non-heme peroxidase which includes thioredoxin peroxidases or peroxiredoxins (Prxs) and Glutathione peroxidases (GPXs). On the basis of their amino acid sequence, substrate specificities, and subcellular localization, GPX is divided into five classes [69]. Glutathione peroxidase is chief compound in gluthathione-ascorbate cycle which reduce H_2O_2 by oxidizing reduced glutathione (GSH) to disulfide form (GSSH) [70,71]. A conserved catalytic cysteine near the N-terminus of these protein is known as peroxidatic cysteine (Cys_p-S^-) whose function is to reduce hydroperoxides and peroxynitrites. First the Cys- residue is transformed into a sulfenic acid (CysP-SOH) when exposed to peroxides. The main difference between the different classes is the mechanism of regeneration of the CysP-SOH, which can be reduced directly (1-Cys mechanism) or by involving a second, so called resolving Cys residue (CysR-SH), which condenses with the sulfenic acid to form a disulfide (2-Cys catalytic cycle). The 2-Cys disulfide is reduced by thioredoxin – a low-molecular weight protein with two vicinal Cys residue – or by glutathione (reduced form GSH, -glu-cys-gly) [54,55]. As said before GPX is found in mammalian cell, but noticed its activity in plant cell [56,57] and has function such as detoxifying lipid hydroperoxides and other reactive molecules in different species undergoing several stress[59-63]. Plant GPX gene showing homology with animal GPX gene ((GPx4/PHGPX enzyme) are isolated from plant[54]. Plant GPXs are found to be in monomeric form [64] except for the poplar GPX5, which showed an unique dimerization pattern mainly depending on hydrophobic contacts and was able to interact with Cd2+ ions [65]. Glutathione are considered as actual thioredoxin peroxidase [66]. Studies suggest that plant GPX is considered to be more effective in reducing peroxides different from H_2O_2 such as organic hydroperoxides and lipid peroxides [67].

Table 4: GPX Activity under Different Abiotic Stresses

Abiotic Stress	Observed GPX Activity
Drought	High activity in guard cells, decreased glutathione pool in rice seedlings, negligible activity in barley root tips.
Salinity	GPX activity correlates with maintaining homeostasis in chickpea and mangroves, high activity observed in GPX3 rice plants.
Temperature	Moderate heat stress increases GPX activity in apple leaves; activity peaks at 4 hours under high temperatures.
Heavy Metals	Increased GPX activity under Cd and Hg stress; negligible activity for Co exposure.

As for now we have a thorough knowledge about the enzyme Glutathione peroxidase (Table 4), hence we will be discussing about how different abiotic stress affecting the environment and how GPX is able combat those abiotic stresses:

Drought stress – Crops exposed to severe climatic condition, had affected its growth and development, which then hinders the productivity of plants [13,15,17]. Drought stress is considered one of most detrimental environmental stress than any other stress [14,15]. Reduction in rainfall with higher transpiration rate leads to agricultural drought [13]. Lack of water in soil, results in reduced rate of cell division, expansion of leaf size, stem elongation and root proliferation and deficiency of certain nutrients [15,18]. Water deficiency enhances abscisic acid (ABA) biosynthesis, reducing stomatal conductance to minimize transpirational losses [15,19]. ABA signaling pathway is activated by the drought stress response[5,72]. Studies of chemical genetics and protein-interaction recognizes the PYR/ PYL/RCAR, START domain proteins as receptors for ABA[73,74].

In *Arabidopsis thaliana*, studies suggest that Glutathione peroxidase 3(ATGPX3) shows excess water loss, high sensitivity to H O and excess accumulation in guard cell [69]. In rice seedling grown for 20 days when exposed to drought stress hand shown a 20-38% decrease in glutathione concentration from total glutathione pool [75]. In barley root tip, negligible GPX activity is found against drought stress [76].

Salinity stress – Soil salinity is a worldwide problem affecting approximately 20% of cultivating land, reducing growth and development of plant in field [21,22], becoming one of serious limiting factor for agricultural basis [8]. Soil with high salinity contains high concentration of soluble salt and exchangeable sodium on surface [8,23] ,which then affects the root system of the plant[8]. Salinity not only affects the roots in plant it also affects in many other ways such as the alternation metabolic processes, membrane disorders, irregular cell division, reduction in photosynthetic activity, protein synthesis, increase in plant toxicity and enzymatic disorder [8,24]. Plants undergoing salinity stress takes up excess amount of Na^+ and Cl^- ions, hence increasing accumulation of ion in tissues of plant, leading to oxidative stress [8,25]. Such accumulation result in increased toxicity effecting by inhibiting protein formation, photosynthesis and susceptible enzymes [8,25]. Plant mechanism to respond such stresses Na^+/K^+ homeostasis and Na^+ exclusion [26]. Excessive accumulation of Na^+ and Cl^- in plants results in overproduction of ROS [24].

In barley root tip, no activity of GPX is visible [76]. When chickpea (*Cicer arietinum*) cultivation is taken place with different level of saline water, there is increase hydrogen peroxide and lipid peroxidation, treatment with Glutathione resulted in decrease level of hydrogen peroxide and lipid peroxidation, thereby maintaining homeostasis [77]. GPX3s rice plants are shown to be sensitive towards salinity stress, presences of GPX3 helps to withstand the stress [78]. While working with mangroves, scientists had found a direct correlation between the concentration of Peroxidase enzyme and Salinity [80, 81]. They found out that for majority of the mangrove plant species the concentration of peroxidase increased along the salinity gradient up to a certain threshold level, beyond which it declined showing the inability of the plant to sustain any further salinity.

Temperature stress – Among many abiotic factor, optimum temperature is one of the crucial factors that helps to sustain life on earth. Extreme heat and cold temperatures have awful influence on all stages of plant growth and development but mainly on its reproductive stages [8]. According to the Intergovernmental Panel on Climate Change (IPCC), growth of plant will be challenged with warmer environment as the average surface temperature will increase 2.0–4.5°C by the end of this century [8,27]. Temperature stress could be categorized in to different type one is heat stress and cold stress. Although both kind of stress equally hampers plant physiology and biochemical mechanism. Heat stress sometime stimulates early flowering hence causing the start of reproduction process before time similarly the cold stress causes delay of flowering delaying the formation of seeds. Temperature stress sometime asynchronizes the maturation of male and female part [33].

In barley root tip, no activity of GPX on temperature stress [76]. When 2-year-old apple (*Malus domestica* Borkh) exposed at 40°C for 0-8hr, GPX activity was highest until 4 hr after that starting decreasing [79].

Heavy metal stress – In this present era, with growing industrialization and technology has led to release of toxic heavy metal elements such as Iron, Arsenate, Cadmium, Chromium, Lead, Copper, Mercury and Aluminum in environment has created global threat for all human beings [8]. This metal when found in trace amount are useful to life [8,28] but when accumulated in excessive amounts in plant causes reducing fertility and other damaging impact on it [29,30,31]. This chemicals through industrial effluent gets in contact with the soil, accumulates in it and then toxicating the soil. Increase in quantity of heavy metal in cellular level causes damage in mechanisms of plant, one of the most common ones is overproduction of ROS (reactive oxygen species) causing oxidative stress. Other harmful effects such as inactivation of biomolecules by displacing essential metal ions or obstructing functional groups [8,33]

In barley root tips – Cd-induced inhibits growth of root with increased activity of GPX, slight increase is observed when treated with Pb, Ni, and Zn, strong increase when treated with Hg and Cu and no activity when treated with Co[76].

3. DISCUSSION

Different type of abiotic stress and their detrimental effects on plants development and their productivity is the major concerning issue for researchers. When exposed to certain abiotic stress, plants response against those stresses are quite complex signalling pathways [8]. Plant has evolved various methods for sustaining under this constant physiological stress. The significant increase in the ROS (Reactive Oxygen Species) and RNS (Reactive Nitrogen Species) during the various abiotic stresses impose severe threat towards the survivability of these habitats. ROS and RNS can cause severe damage in cells by lipid Peroxidation, Oxidation of proteins and DNA, ultimately causing death of the cell (Parida et al., 2004). Antioxidant enzymes are one of the major defense mechanisms for plants to counter the detrimental effects of the reactive species generated in them (Dasgupta et al., 2012). Many scientific approaches had been discovered for proper genetic expression studies of such genes which helped them to determine and come up with all the mechanisms that have been helping plants from eons to protect themselves from such stresses. The fact that how antioxidant enzymes acting as a first line of defense and maintaining homeostasis of ROS in plant had proven a boon to us. Further researches and studies providing us with more new information and with their every achievement we are moving one step forward towards the insight of how we can protect more plants by inducing this mechanism in order to survive in the worsening situation of environment which we might face in future.

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