Middle East Journal of Applied Sciences
Volume: 14 | Issue: 02| April – June | 2024

EISSN: 2706 -7947 ISSN: 2077- 4613
DOI: 10.36632/mejas/2024.14.2.15
Journal homepage: www.curresweb.com
Pages: 205-221

Enhancement of Plant Tolerance to Oxidative Stress Injury by Exogenous Application of Hydrogen Peroxide: A Review

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Received: 25 Feb. 2024 **Accepted:** 05 April 2024 **Published:** 20 April 2024

ABSTRACT

Under oxidative stress, there are excess production of reactive oxygen species (ROS) e.g Singlet oxygen ($O^{\bullet}_2$), Super oxide (O^{-}_2), Hydrogen peroxide (H_2O_2) and Hydroxyl radical (OH^{-}). These reactive radicals almostly damage all cell components such as membrane lipids, photosynthetic pigments and chloroplasts, enzymes and nucleic acids. In spite of H_2O_2 is a strong oxidizing agent under stresses, its high levels damage plant photosynthesis and cause poorly developed plants and initiate programmed cell death. In contrast, H_2O_2 at low concentration is considered as a stress signal, keeping reactive oxygen species under control, limiting endogenous H_2O_2 concentration to enhance plant tolerance under stress. At low concentration acts also as a promotor and a key regulator in a broad range of physiological and biochemical processes in plants under various stresses. H_2O_2 at low concentration would enhance the production of enzymatic activity e.g super oxide dismutase (SOD), catalase (CAT), guaiacole peroxidase (POD), ascorbate peroxidase (APX), glutathione reductase (GR)) and non enzymatic antioxidants e.g carotenoids, ascorbic acid (ASA), glutathione (GSH), α-tocopherol (Vit E), proline, total phenols, soluble sugars and some minerals) which cause marked decrease in the oxidative damage represented by lipid peroxidation (MDA) and electrolyte leakage of plant cells to finally improve growth, yield and fruit quality.

Keywords: Stress, Hydrogen peroxide, Lipid peroxidation, Electrolyte leakage, yield, ROS.

Introduction

Stress in general reduced plant growth, development and yield due to the over production of free radicals or reactive oxygen species (ROS) which damage various macromolecules and cellular structures (Apel and Hirt, 2004), that beside photosynthetic, cellular membrane, apparatus, nucleic acids and enzymes activity and leading to programed cell death (Lukatkin, 2003; Liu *et al.,* 2010; Goud and Kachole, 2011). These ROS, such as singlet oxygen, hydrogen peroxide, superoxide and hydroxyl ions, resulting in oxidative damage at the cellular level (Hung *et al.,* 2005; Goud and Kachole, 2011). these ROS may play two very different roles: exacerbating cells injury or signaling the activation of defense mechanisms (Yi *et al.,* 2014). ROS in low concentrations act as signaling molecules mediating a variety of physiological responses, including stomatal movement and gene expression (Yi *et al.,* 2014). Whereas over production of ROS damage almost all cell components including membrane lipids, chloroplasts, pigments, enzymes and nucleic acids (Liu *et al.,* 2010; Goud and Kachole, 2011). However, plant species have evolved various mechanisms to cope with environmental stresses. In order to overcome stress induced damage, plants may up-regulate various scavenging mechanisms like enzymatic antioxidant activities (superoxide dismutase, peroxidase, catalase and glutathione reductase) (Noctor and Foyor, 1998; Abd El-Motty and Orabi, 2013) and non-enzymatic metabolites e.g., ascorbic acid(Orabi , 2004; Ahmad *et al.,* 2013; Orabi and mekki, 2008) and osmoprotectants (Mekki and Orabi, 2007; Ahmad *et al.,* 2013) and polyamines (Orabi *et al.,*2016,2017[a], 2020[a,b]).Toxic potential effects of ROS lead to induce protein oxidation, DNA damage, lipid peroxidation of membranes represented by malondialdehyde MDA and electrolyte leakage contents (Orabi, 2004; Orabi and Mekki, 2008; Ahmed

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et al., 2010; kassab *et al.,* 2012; Abd El Hamid *et al.,* 2016; Abd El-Razek *et al.,* 2019; Orabi *et al.,* 2021,2022) and destruction of pigments (Hussein and Orabi, 2008; Hussein *et al.,* 2009; Mekki *et al.,* 2010). Redox changes of plants result in modification or induction of various physiological and bio-chemical processes through enzymatic and non enzymatic antioxidant capacity (Orabi, 2004; Orabi *et al.,* 2017[a,b,c], 2018[a,b,c]). ROS and antioxidants regulatory networks act to reprogramming transcriptome that including the set of all RNA molecules, proteome including all proteins expressed by genome and metabolome such as metabolic intermediates, hormones and other signaling molecules etc. (Foyer and Noctor, 2009). For induction of acquired tolerance and alleviation of oxidative stress there are various strategies to cope with environmental stresses such as the use of antioxidants or signal molecules such as H_2O_2 (Orabi and Abo Hussein, 2019) and sometimes the use of biofertilizers for enhancing stimulatory effects in plants (Ahmed *et al.,* 2009; Mohamed *et al.,* 2023).

Hydrogen peroxide (H_2O_2) is recognized as being in the forefront of transcription independent signal molecules in one line with CA2+ and ATP (Cordeiro and Jacinto, 2013; van der Vliet and Janssen-Heinmger, 2014), it diffuses through cells and tissues as a messenger to initiate cellular effects and serves fundamental regulatory functions in metabolism beyond its role as damage signal (sies, 2014). To support spatiotemporal organization of key processes it serves as a key molecule in the third principle of the redox code that known as "Redox sensing" through activation/deactivation cycles of H_2O_2 production linked to the NAD and NADP systems (Jones and Sies, 2015). H2O2 has no net charge (Halliwell, 2006). Beside his larger half-life than that of the superoxide anion radical, therefore hydrogen peroxide is more likely to be a long-distance signaling molecule than superoxide (Vranova *et al.,* 2002).

H_2O_2 is used as plant growth promoting chemical and is widely being used by farmer in small-scale and large-scale farming. Where, it has been regarded as a signalling molecule and regulator of the expression of some genes in cells (Quan *et al.,* 2008). It also reported that H2O2 have regulatory effects on plant growth, development and quality of fruit, where H_2O_2 acts as a promotor agent, H_2O_2 application might promote cell division (Hameed *et al.,* 2004) and secondary wall formation (Abass and Mohamed, 2011), it takes part in reinforcement of plant cell wall (lignification, cross-linking of cell wall structural proteins), phytoalexin production and resistance enhancement (Quan *et al.,* 2008). Promoting the expiration of the flower related gene (zhou *et al.,* 2012). fruit production Through solving initial bud drop problems e.g in wax apple fruit (syzygium samarangense) (Khandaker *et al.,* 2012). H_2O_2 treatments promoted early ripening of kyoho berries and 300mmol/L H_2O_2 was the most effective treatment, where it ripened berries 20 days earlier than the untreated fruits (Guo *et al.,* 2019). Hydrogen peroxide can be used as a sanitizing treatment on fresh-cut pineapple stored at 5°C as there is no significant differences in microbial counts, physiochemical values and sensory attributes were observed between samples left untreated or treated with 1 or 3% of H_2O_2, Meanwhile, fresh-cut pineapple treated with 3% H2O2 had the highest lightness value and maintained flesh firmness better than 1% H2O2 (Aida *et al.,* 2011). H_2O_2 occurs through various paths in plant cells (NADPH oxidase, lipid peroxidation, and photosynthetic electron transport chain) after that, it can diffuse rapidly across the cell membrane (Rojkind *et al.,* 2002). NADPH oxidases is a particularly relevant source of H_2O_2 due to their sole function seems to be the Tightly-regulated production of superoxide/H2O2 (Brandes *et al.,* 2014). Hydrogen peroxide is present in virtually all aerobic organisms, it is a non-radical oxidant and it is recognized to play important roles in cellular physiology (Jones and sies, 2015). H_2O_2 plays dual roles in plant cells at low and normal concentrations (one to five mmol/g FW) since it acts as a messenger molecule involved in adaptive signaling and in triggering tolerance against various abiotic stresses. Meanwhile, at high concentrations, (H_2O_2 above seven mmol/g FW), the tissues would suffer from cell death orchestrates the programmed cell death (Cheeseman, 2006).

Cellular sources and generation of hydrogen peroxide (H_2O_2):

One- or two- electron reduction were identified as sources of H_2O_2. NADPH oxidases and the mitochondrial respiratory chain are the major enzymatic generators for H_2O_2, beside considerable number of oxidases (Bedard *et al.,* 2007; Lassègue *et al.,* 2012). In a complex chain of events O_2 In aerobic organisms is considered to be the final electron acceptor for mitochondrial cytochrome oxidase resulted in the formation of high-energy phosphates needed for multiple cellular functions. In this process, O_2 undergoes a four-electron reduction to form H_2O_2. A side-product of mitochondrial oxidative phosphorylation is the accumulation of reactive oxygen species (ROS) such as H_2O_2 , which

is more stable, less reactive , H_2O_2 is converted to the dangerous •OH, via the so-called Fenton reaction, in the presence of Fe2+ or Cu+ (Roj Kind *et al.,* 2002). Brandes *et al.,*(2014) reported that the particularly relevant source of H_2O_2 is NADPH oxidases because their sole function seems to be the tightly-regulated production of superoxide H_2O_2 . Production of H_2O_2 is balanced by the action of antioxidant enzymatic systems, such as catalase, glutathione peroxidases, and peroxiredoxins, that remove H_2O_2 very rapidly (Sies, 2017; Flohé, 2016). The amount of ROS formed is not negligible due to the high amount of O_2 consumed by aerobic organisms. Indeed, approximately 2–4% of oxygen consumed in mitochondria is converted to the superoxide ion by iron-sulfur proteins. Thus, to maintain homeostasis, accumulation of excess ROS is prevented by multiple enzymatic and non-enzymatic systems that receive the generic name of 'host antioxidant defense systems (Roj Kind *et al.,* 2002).

H_2O_2 is considered to be as being in the forefront of transcription-independent signal molecules, in one line with Ca2+ and ATP (Cordeiro and Jacinto, 2013; van der Vliet and Janssen-Heininger, 2014). H_2O_2 diffuses through cells and tissues to initiate immediate cellular effects, such as cell shape changes, initiation of proliferation and recruitment of immune cells. It became clear that H_2O_2 serves fundamental regulatory functions in metabolism beyond the role as damage signal (Sies, 2014). The term "oxidative eustress" (Sarsour *et al.,* 2014; Niki, 2016) which denotes physiological oxidative stress, may serve in the distinction from excessive load, "oxidative distress", causing oxidative damage (Aschbacher *et al.,* 2013; Ursini *et al.,* 2016).

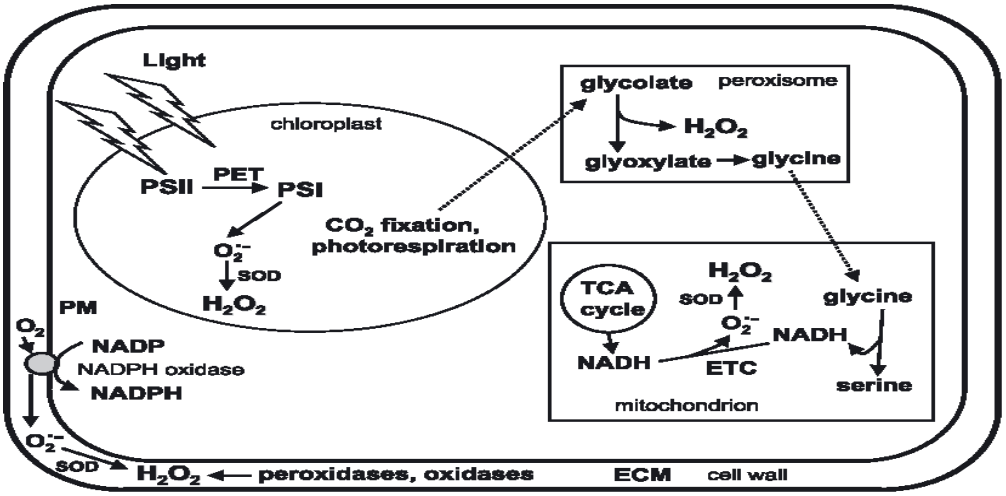

Fig. 1: Illustrates the major H_2O_2 generators: one-or two-electron reduction, NADPH oxidases and the mitochondrial respiratory chain and considerable number of oxidases.

It is worthy to mention that two general mechanisms responsible for H_2O_2 generation: (i) by enzymatic or chemical dismutation of superoxide ions and (ii) by the action of certain oxidases via a two-electron reduction of oxygen. Also, H_2O_2 directly generated through the enzymes that include the following peroxisomal oxidases: glycolate, Damino, ureate, L-*a*-hydroxyacid and fatty-acyl-CoA oxidases. H_2O_2 is generated also by monoamino oxidase (Raimondi *et al.,* 2000; Vindis *et al.,* 2000,2001) and lysyl oxidase (Li *et al.,* 2000). Cell wall hydration in leaves allows cell wall extension through structural alteration. While, relaxing the cell wall stretches the plasma membrane, which promotes opening of Ca2+ channels. This resulting increases in cytoplasmic calcium affects growth by inhibiting P-ATPases and also activates NADPH-oxidase, that promotes secretion of superoxide into the cell wall, which further converted into H_2O_2 (Kalve *et al.,* 2014).

Hydrogen peroxide as a signaling molecule in plant tolerance

Unfavourable or un suitable environmental conditions include salinity, drought mechanical damage, herbicides, UV radiation, low/high temperature, flooding, high speed wind, nutrient loss and anaerobic conditions limiting growth, development and crop productivity (Kumar *et al.,* 2012). The inevitable leakage of electrons onto O_2 is the way to form ROS from the electron transport activities of chloroplasts, mitochondria, and plasma membranes or as a byproduct of various metabolic pathways

found in different cellular compartments. Firstly the stress signal is perceived by the receptors present on the plant cells membranes. After that the signal information is transduced downstream resulting in the activation of various stress responsive genes (Tuteja and Sopory, 2008).

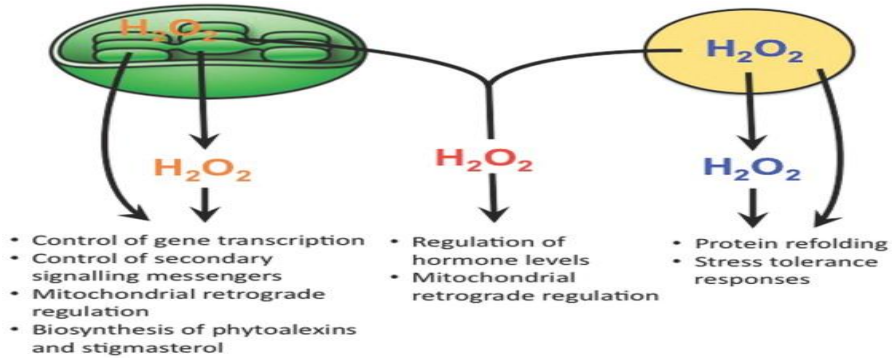

Fig. 2: Illustrates the physiochemical properties of H_2O_2 to serve as messenger carrying a redox signal to be involved in multiple physiological and biochemical processes.

H_2O_2 acts as a key regulator in a broad range of physiological processes including photosynthesis (Noctor and Foyer, 1998). Application of H_2O_2 at low concentrations signals the induction of defense responses in plants against oxidative stresses (Prasad *et al.,* 1994). Slesak *et al.,*(2007) suggested that H_2O_2 plays a crucial role as a signalling molecule in various physiological processes, including photosynthesis, respiration, translocation and transpiration. H_2O_2 production increased due to the case of NADPH oxidase activation, the steady-state approximation can calculate the transient formed during signaling events, there are dynamics of H_2O_2 where the very fast elimination of H_2O_2 by antioxidants systems occurs much quicker than the transient responses formed during signaling events (Antunes and Brito, 2017). H_2O_2 is maintained at normal level through a series of antioxidant enzymes and acts as a second messenger, it coordinates with other important signal molecules to protect plants from stresses and triggering stress tolerance (Noctor and Foyer, 1998). Hydrogen peroxide settles to a near steady-state as a result of continuous formation and elimination.

Regulation pathways occurs by the reaction of H_2O_2 with proteins harboring redox sensitive moieties, (Antunes and Brito, 2017) the proteins act as key players when they denominated redox switches in the biochemichal pathways regutation including protein phosphatases, Kinases or transcription factors (Marinho *et al.,* 2014). There are chemically, thiol proteins redox-controlled switches and metal switches (Go and Jones, 2013; Lee and Helmann, 2006; Santos *et al.,* 2016), when H_2O_2 was at low concentration only the most reactive switches will sense H_2O_2, in the same time the less reactive switches will sense high concentrations of H_2O_2. In other meaning the change in H_2O_2 concentrations will determines the change in the oxidation state of redox switch leading to a regulation of a downstream pathway and tranducing the information encoded in the H_2O_2 concentration profile along a signaling cascade (Antunes and Brito, 2017).

H_2O_2 is a vital cellular component, it has various functions in the development, metabolism and homeostasis of aerobic organisms. It acts to regulate basic processes, such as acclimation, defense and development. Beside acts as a translocating second messenger triggering Ca2+ fluxes, protein modifications and gene expression (Bienert *et al.,* 2006). Due to the physiochemical properties of H_2O_2, it is capable of serving as messenger to carry a redox signal from the site of its generation to a target site. Regulation of redox signaling occurs via control of single enzymatic activity or at the transcriptional level (Forman *et al.,* 2010). H2O2 is well suited for redox sensing and redox signaling (Marinho *et al.,* 2014; sies, 2017). H_2O_2 has the ability to diffuse away from the site of its generation to reach a certain distance to the more reactive target, whereas highly reactive oxidants such as the hydroxyl radical can not (Sies *et al.,* 2017), the latter is more harmful radical treats quickly with cell membrane causing lipid peroxidation and electrolyte leakage of cells and finally death therefore was the need for H_2O_2 detoxification before the dangerous hydroxyl radical (OH^-) would be occurred (Orabi *et al.,* 2004).

Detoxification of hydrogen peroxide (H2O2) via the antioxidant capacities

The antioxidant capacities include the antioxidant defense mechanisms (Enzymatic and non Enzymatic). An antioxidant is considered to be a molecule capable to slow or prevent the oxidation of other molecules. Oxidation is a process of a chemical reaction that transfers electrons from a substance to an oxidizing agent. Oxidation reactions can lead to production of free radicals, which start chain reactions that damage cells and tissues. Antioxidants terminate these chain reactions by removing free radical intermediates, and inhibit other oxidation reactions by being oxidized themselves. Antioxidative system including spontaneously reactive antioxidants and enzymatically catalyzed reaction aids the cells in displacing the harmful reactive oxygen species (ROS). When this neutral equilibrium is disrupted (the accumulation of ROS exceeds the capacity of defense mechanisms) due to multiple abiotic or biotic stress factors, the cell is then called under oxidative stress (Caverzan *et al.,* 2012).

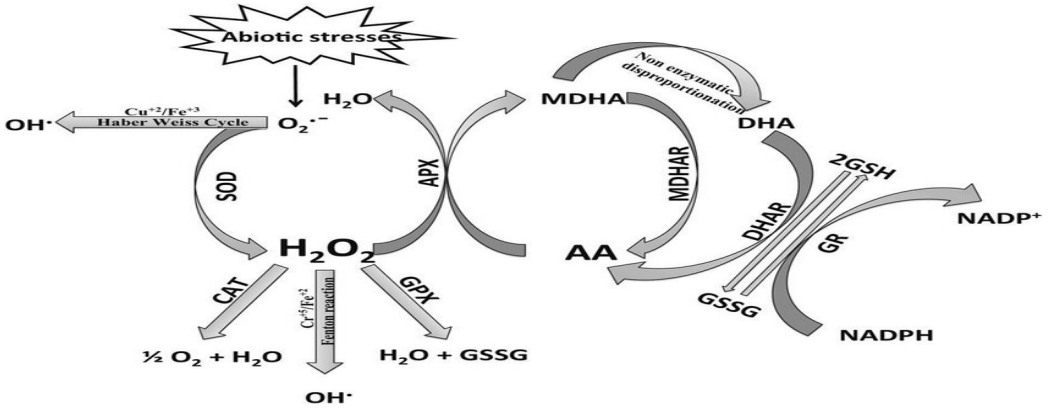

Fig. 3: Illustrates the detoxification of H_2O_2 via defense mechanisms (non-enzymatic antioxidants and antioxidant enzyme activities)

The antioxidant capacities

1- Defense mechanisms Non-enzymatic antioxidants

Ascorbate

Ascorbate fulfills many key functions in biology of plants. It is the most abundant low molecular weight antioxidant in the plant cell, it can participate in the regulation of mitosis and cell expansion (Noctor and Foyer, 1998). Ascorbate is also considered to be a substrate for key enzymatic reactions, such as the production of ethylene (McGarvey and Christoffersen, 1992). Orabi (2004) reported that ASA treatments on cucumber plant grown under cold stress gave the best results in growth characters, yield, activities and specific activities of SOD, CAT, POX, GR and APX enzymes, proline, soluble sugars, soluble protein with the lower levels of lipid peroxidation and electrolyte leakage for its protective role in plants. Orabi and Mekki (2008) stated that application of ASA on Suger beet plant grown under salt stress led to great increments in all growth characters and root yield beside enhancement of APX & GR activities to ascertain its role in ASA-GSH cycle. the most important reducing substrate In plant cells for the removal of H_2O_2 is AsA (Del Río *et al.,* 2006; Wu *et al.,* 2007) it could react with H_2O_2, O2•− and 1O2 to maintain the reduced state of the α-tocopherol. It may be involved in zeaxanthin synthesis to prevent oxidative damage in plants (Conklin *et al.,* 1996).

Glutathione

Glutathione (GSH) is very abundant in plants, it is the major non-protein thiol in plants, it has important functions including scavenging of the reactive ROS, heavy metal detoxification, transport and storage of sulfur, control of cell redox status, progression of the cell cycle, and protection of protein thiol groups, detoxification of xenobiotics beside it's role in gene activation and plant protection against oxidative stress injury (May *et al.,* 1998; Noctor and Foyer, 1998; Orabi, 2004; Orabi *et al.,* 2017[c],2021). The synthesis of GSH In the leaves occurs in the chloroplasts and cytosol (Noctor and Foyer, 1998). GSH is a substrate for glutathione reductase and glutathione peroxidase enzymes. Orabi, (2004) and Orabi *et al.,* (2017[c],2021) revealed that glutathione treatment increased glutathione

reductase enzyme activity in cucumber, Zea mays and faba bean plants under cold, salinity stress and water regime condition to maintain plant protection.

Carotenoids

It is a lipophilic and lipid soluble antioxidant and protects the photosynthetic apparatus against photo inhibitory injury by singlet oxygen (102) produced by the excited triplet state of chlorophyll. Carotenoids protect the photo systems when reacts with lipid peroxidation to terminate chain reactions (Burton and Ingold, 1984) it has the ability to deactivate 102 and quench the excited triplet state of chlorophyll, to indirectly reducing the formation of 102 species (Foyer and Harbinson, 1994). It was revealed that zeaxanthin is involved in the de-excitation of excess energy via nonradioactive dissipation in the pigment bed (Demmig-Adams and Adams, 1996). The primarily physical mechanism of Carotenoids is to "quench" singlet oxygen, where the excess energy of singlet oxygen is transferred to the carotenoid's electron-rich structure. This added energy has the ability to excite the carotenoid into a "triplet" state (3Car*), and then relaxes into its ground state (1Car) by losing the extra energy as heat. Orabi and Abdelhamid (2016) realized an increase in the carotenoids content of faba bean plants grown under salinity stress to participate in plant tolerance and decrease MDA production. Orabi *et al.,*(2017[b]) found also considered increase in carotenoid content with H_2O_2 treatments on cucumber grown under cold condition to maintain plant protection and lower level of H_2O_2, MDA and electrolyte leakage.

Tocopherols

Tocopherols (vitamin E) are synthesized and localized in plastids and accumulated to different degrees in all tissues, seeds generally containing the highest levels (Sheppard *et al.,* 1993). Tocopherols have a function as recyclable chain reaction terminators of polyunsaturated fatty acid (PUFA) radicals produced by lipid oxidation (Girotti, 1998). Tocopherols scavenge lipid peroxy radicals and yield a tocopheroxyl radical that can be recycled back to the corresponding tocopherol by reacting with other antioxidants or ascorbate (Liebler, 1993). Tocopherol levels increase in photosynthetic plant tissues and have the ability to protect plants in response to a variety of abiotic stresses (Munne´-Bosch and Alegre, 2002; Orabi and Abdelhamid, 2016; Orabi *et al.,* 2017[b],2018[c]).

Phenolic Compounds and Flavonoids

Phenolics are mainly synthetized from cinnamic acid. L phenylalanine ammonia-lyase (PAL) enzyme (EC 4.3.1.5), acts to produce cinnamic acid which form phenolic compounds. Phenolics act as diverse secondary metabolites (flavonoids, tannins, hydroxycinnamate esters and lignin) exist in plant tissues (Grace and Logan, 2000; Abd El-Motty and Orabi, 2013). Flavonoids are secondary metabolites of plants and have polyphenolic structure. They are formed by the polypropanoid pathway and the startup component is phenylalanine molecule. Phenolics and flavonoids are more effective than other antioxidants like Vitamin C, E and carotenoids (Dai and Mumper, 2010). The antioxidant activity of phenolic compounds may be exerted in different ways such as, they may directly scavenge some reactive species including hydroxyl, peroxyl and super oxide radicals, act as chain breaking antioxidants, they may suppress lipid peroxidation recycling other antioxidants such as α-tocopherol, in some cases they may bind pro-oxidant metals such as iron and copper to prevent free radicals formation from these pro-oxidants while simultaneously maintaining their capacity to scavenge free radicals (Halliwell, 2007). Some phenolics are related to the increase in the activity of antioxidant enzymes and induction of the synthesis of antioxidant proteins (Chung *et al.,* 2006).

Thioredoxins

Thirodoxins are a family of small proteins (approximately 12 kDa) that undergo NADPH-dependent reduction by thioredoxin reductase leading to reduce oxidized cysteine groups on proteins and act as hydrogen donors and determine the oxidation state of protein thiols (Rojkind *et al.,* 2002).

Transition metal-binding proteins

ceruloplasmin, metallothionein, ferritin, transferrin and lactoferrin are well known as metallo proteins and has critical role in metal homeostasis and act as storage reservoirs and/or chaperones for essential trace metals, such as copper and iron. During the acute-phase response and under oxidative stress conditions. To amelioration of the deleterious effects of ROS, by these proteins through

sequestering the redox-active metals iron and copper, leading to minimizing their capacity to catalyze ROS production via the Fenton reaction (Young and Woodside, 2001).

The antioxidant capacities

2. Defense mechanisms Antioxidant enzymes

Antioxidant enzymes are considered to be a sequence of ROS- scavenging or detoxification steps is neded to avoid the conversion of one reactive species into a second, more dangerous one. Superoxide dismutase (SOD) converts the superoxide radicals to H_2O_2. The latter is scavenged by catalase and/or guaiacol peroxidase in peroxisomes and ascorbate peroxidase in the chloroplast and cytosol (Perl-Treves and Perl, 2002). Glutathione reductase helps in regeneration of ascorbate through the ascorbate-glutathione cycle.

Catalase

Catalase (CAT, 1.11.1.6) reacts efficiently with H_2O_2 to form H_2O and molecular oxygen and with H+ donors (methanol, ethanol, formic acid, phenols) with peroxidase activity. CAT enzyme is important in the removal of hydrogen peroxide generated in peroxisomes by oxidases involved in ß-oxidation of fatty acids, the glyoxylate cycle (photorespiration) and purine catabolism. All forms of the enzyme are tetramers in excess of 220,000 molecular weights. Cat-1 and cat-2 are localized in peroxisomes and the cytosol, whereas cat3 present in mitochondria. Stress conditions which decrease protein turnover rate, such as salinity, heat extremes lead to the depletion of catalase activity (Hertwig *et al.,* 1992). CAT activity may be significant in plants for protection and tolerance against the oxidative components of adverse environmental stresses.

Guaiacol peroxidase

Many isoenzymes of (GPOX, 1.11.1.7) exist in plant tissues found in vacuoles, the cell wall, and the cytosol (Asada, 1992). GPOX participates in many important biosynthetic processes, such as lignification of cell wall, degradation of IAA, biosynthesis of ethylene, wound healing, and defense against biotic and abiotic stresses (Kobayashi *et al.,*1996). GPOX is effective quencher of reactive intermediary forms of O_2 and peroxy radicals under stressful conditions (Vangronsveld and Clijsters, 1994). Orabi *et al.,*(2015) discovered that the greater protection of cold-sensitive tomato cultivar from cold induced reduction in lipid peroxidation (MDA) and electrolyte leakage contents to attain plant tolerance with the increase in the guaiacol peroxidase (POX) activity. Moreover Orabi and Abdelhamide (2016) concluded that greater protection of salt-sensitive faba bean plants from salt-induced oxidative damage and reduction in MDA content were parallel to the increase in POX activity.

AsA-GSH Cycle Enzymes

The AsA–GSH cycle has a major protective role against ROS under normal or stress conditions exists in chloroplasts, cytosol, mitochondria, peroxisomes and apoplasts. The cycle contains four enzymes (APX, MDHAR, DHAR and GR) beside, ASA, GSH and NADPH acting to detoxify the ROS (H_2O_2) through many reactions to regenerate AsA and GSH. APX catalyses the reduction of H_2O_2 to H_2O with the simultaneous production of monodehydroascorbate (MDHA), which is converted to AsA by the action of NADPH-dependent MDHAR or disproportionates nonenzymatically to AsA and dehydroascorbate (DHA) (Asada, 1992). Where DHA undergoes irreversible hydrolysis to 2, 3-diketogulonic acid or form AsA by DHAR, GSH has a role as a reductant (Chen *et al.,* 2003). This results in the generation of GSSG, which is regenerated to GSH by GR.

Ascorbate Peroxidase

Ascorbate Peroxidase (APX, 1.11.1.11) is considerd to be the first H2O2 scavenging enzyme in the ASA-GSH cycle for cells protection in higher plants (Asada, 1994). APXs enzymes involved in scavenging H_2O_2 in water-water and AsA-GSH cycles using the antioxidant AsA as the substrate, to catalyz the transfer of electrons from AsA to H_2O_2 and production of DHA and water (Pang and Wang, 2010) .The enhancement of APX activity in plants under different environmental conditions will be attained (Orabi, 2004; Abd El-Motty and Orabi, 2013; Hasanuzzaman and Fujita, 2011; Orabi *et al.,* 2017[c],2021).

Glutathione reductase

Glutathione reductase (GR, 1.6.4.2) is considered to be a potential enzyme in the AsA-GSH cycle for plant protection against stress. GR activity confers oxidative stress tolerance where it alters the redox state of important components of the ETC. It catalyses the NADPH-dependent reduction of disulphide bond of GSSG and maintains the GSH pool (Chalapathi Rao and Reddy, 2008). Thus GR also maintains a high ratio of GSH/GSSG in plant cells, through catalyzing the reduction of GSH. GR has a crucial role to maintain plant tolerance under different stresses by maintaining the antioxidant machinery of the cell (Orabi *et al.,* 2017[c]), lowering MDA and electrolyte leakage contents, and stress tolerance (Orabi, 2004; Hossain *et al.,* 2011; Hasanuzzaman *et al.,* 2011; Orabi *et al.,* 2021). These antioxidant systems in successful plants prevent oxidation of cellular components which could lead to the death of plant cells or poorly development plants.

Glutathione peroxidase

GPXs (EC 1.11.1.19) act to catalyze the oxidation of glutathione at the expense of H_2O_2 or other hydroxyl peroxides. The activity of GPXs is dependent on the availability of reduced glutathione, beside activity of glutathione reductase and *g*-glutamyl cysteine synthase, the rate-limiting enzyme for reduced glutathione (GSH) synthesis (Holben and Smith, 1999). The distribution of glutathione reductase is similar to that of GPX (Gibson *et al.,* 1985).

Physiological and biochemical roles of hydrogen peroxide (H_2O_2) under abiotic stress

Many researchers have shown that H2O2 acts as a second messenger in response to heat, cold, drought and salt stress in plants (Prasad *et al.,* 1994; Li *et al.,* 2011). Application of H_2O_2 at low concentrations has been shown to induce stress tolerance in plants by increasing some metabolite and phytohormone levels as well as decreasing MDA and endogenous H_2O_2 concentration in plants (Liu *et al.,* 2010; Abass and Mohamed, 2011; Terzi *et al.,* 2014).

H_2O_2 can serve as a second messenger leading to stress elimination in signal transduction pathways. H_2O_2 could trigger the activation of antioxidants in plants to alleviate the oxidative damage and improve physiological attributes of the plant under stress (He *et al.,* 2009). Liu *et al.* (2010) mentioned that H_2O_2 treatments induced POD activity in cucumber leaves. Moreover, exogenous H_2O_2 under various biotic and abiotic stresses may induce oxidative stress tolerance by enhancing the activities of POD and PPO (Goud and Kachole, 2011). H_2O_2 improved osmotic stress resistance of two cucumber varieties by activating antioxidant system (Liu *et al.,* 2010). Available informations suggest that H_2O_2 directly regulates the expression of numerous genes involved in plant defense and the related pathways such as antioxidant enzymes, defense proteins and transcription factors (Hung *et al.,* 2005). Hence, H_2O_2 signaling functions importantly in plant growth and development and defense against environmental stresses. H_2O_2 pretreatment could improve, oxidative stress and multiple stresses (Chen *et al.,* 2009).

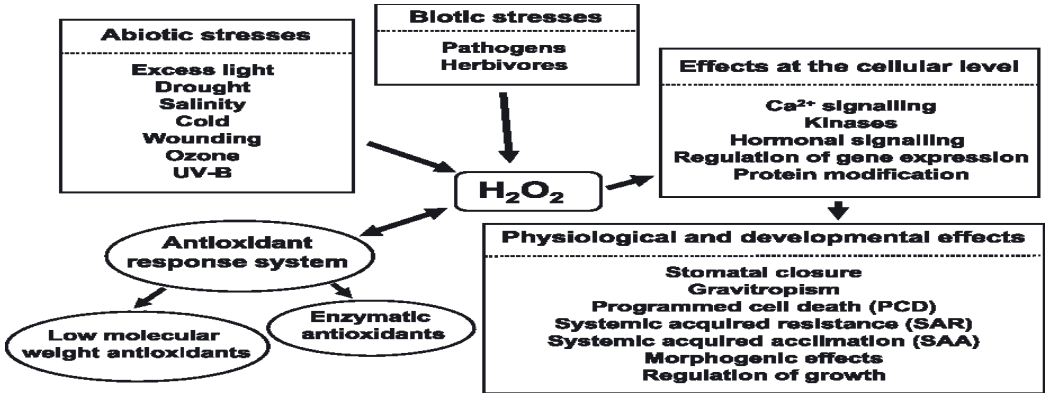

Fig. 4: Illustrates the different morphological, physiological and biochemical roles of H_2O_2 under various abiotic stresses (salt stress, drought stress and extreme temperatures).

Role of H_2O_2 under salt stress

H_2O_2 at low concentration acts as a signal molecule, H2O2 alleviates water uptake-reductive effect in case of salt stress (Chien and Lin, 1994) and involved in acclimatory signaling molecule triggering tolerance against salt stress (De Azevedo Neto *et al.,* 2005; Li *et al.,* 2011; Wang *et al.,* 2013). Likely, addition of H_2O_2 to the nutrient solution induces salt tolerance by enhanced activities of antioxidants and reduced peroxidation of membrane lipids in leaves and roots of maize as an acclimation response (De Azevedo Neto *et al.,* 2005). It protects photosynthetic machinery from salt induced ROS (Xiao *et al.,* 2001). In chickpea leaves, the carotenoids were measured and effective elevation over control was observed under salinity stress (Mishra *et al.,* 2009). Goldani *et al.,* (2012) showed that foliar application of H_2O_2 can improve oregano shoot and root dry weight and alleviate adverse effects of salinity. H_2O_2 in two concentrations (50&100nM) promote defense system in plants under salt stress and improve growth and photo synthetic ability of plants. Beside reduction in the severity of salt stress through the reduction in Na^+ and Cl^- content to maintain lower Na^+/K^+ ratio as compared to that in salt stressed plants and the increase in proline content and N assimilation and improve growth and photosynthetic ability of plants (Ascfaque *et al.,* 2014). H_2O_2 treatments increased photosynthetic pigments might through proline which act as antioxidant (Liheng *et al.,* 2009; Ashfaque *et al.,* 2014; Orabi and Sadak, 2015).

De Azevedo Neto *et al.* (2005) revealed that addition of H_2O_2 to the nutrient solution induced salt tolerance by enhanced activities of antioxidants and reduced peroxidation of membrane lipids in leaves and roots of maize. Under salt stress H_2O_2 treatment (0.5 mM) increased SOD and CAT enzymes activity in OAK (Xu *et al.,* 2009), H_2O_2 treatment decreased MDA content and increased SOD, POD, CAT and APX in salt stressed wheat (Li *et al.,* 2011) H_2O_2 treatment prevents the increase of oxidative stress by enhancing the production of enzymatic and non-enzymatic antioxidants under salt stress to quench the ROS and decrease lipid peroxidation or MDA content (Li *et al.,* 2011; Talukdar, 2012). H_2O_2 treatments (0.05mM, 0.1mM) resulted in more significant increases in total soluble sugars (Guzel and Terzi, 2013; Orabi and Sadak,2015) as osmoprotectants which correlated with the acquisition of plant tolerance (Hoekstra and Buitink, 2001). Exogenous application of 100mM H_2O_2 greatly increased nitrate reductase activity under salinity (Ashfaque *et al.,* 2014). Where it is a primary enzyme in nitrate assimilation pathway and a limiting factor in growth and development of plants (Yang *et al.,* 2009). Orabi and Sadak, (2015) stated that H_2O_2 treatments (50 µM, 100 µM) greatly increased the activity of SOD,CAT,APX,POX and PPO enzymes either under saline or non saline conditions. H_2O_2 treatment led to obvious reduction of H_2O_2 in plat tissues (Liheng *et al.,* 2009; Wang *et al.,* 2013; Orabi and Sadak, 2015). Under salt stress MDA and EL are indicators for membrane damage (Katsuhara *et al.,* 2005).

Role of H_2O_2 under drought stress

Abiotic stress, such as drought, will increase the production of ROS in the plant. Under drought stress H_2O_2 enhanced the drought resistance of wheat (Luna *et al.,* 2004). He *et al.,* (2009) revealed that H_2O_2 pretreatment enhanced the photosynthetic rate in wheat seedlings under drought conditions and could greatly alleviate the deleterious effects of drought on the membrane integrity and stability in the wheat seedlings through reducing membrane damage rate and MDA content. H_2O_2 under drought stress or normal condition increased both IAA and GA3 contents (Abass and Mohamed, 2011). Some antioxidant enzymes such as APX, CAT, POX, SOD were induced by H_2O_2 treatment in Arabidopsis plant and reed callus (Davletova *et al.,* 2005; Wang *et al.,* 2008[a,b]). H_2O_2 scavenging and MDA decrements provide evidence that H_2O_2 treatments with low concentration could greatly overcome the deleterious effects of drought on the membrane integrity and stability in the wheat seedlings (Santhy *et al.,* 2014). In general H_2O_2 pretreatment alleviate ROS accumulation and oxidative damage under drought stress (Abass and Mohamed, 2011). Application of H_2O_2 either with 1.0 or 2.0mM increased dry matter of canola shoots, root and yield while lipid peroxidation in canola plant decreased continuously as the concentration of H_2O_2 increased from 1.0mM up to 2.0mM under water regime (Orabi *et al.,* 2018[a]) i.e H_2O_2 can help plants to resist drought stress induced by prolonging periods between irrigation of canola plants, on the other hand total phenols, ASA and GSH concentrations in canola seeds were reversely responded which increased with the 2.0mM rather than with 0.1mM applied H_2O_2. Also APX, CAT and PPO enzymes reached its higher values with 2.0mM H_2O_2 where drought tolerance enhancement was realized in canola plants by exogenous application of H_2O_2.

Role of H_2O_2 under high temperature

Tolerance enhancement to heat stress is a major challenge in many C_3 crops given the threat of global warming. H_2O_2 is regulatory molecule in altering many criteria responsible for enhancing the tolerance capacity (Kumar *et al.,* 2012). H_2O_2 was found to induce small heat shock proteins in tomato, rice and wheat (Schoffl *et al.,* 1998; Kumar *et al.,* 2012; Sadak and Orabi, 2015). H_2O_2 treated potato nodal explants were found to be resistant to high temperature (Lopez-Delgado *et al.,* 1998). Kim and Portis (2004) investigated that H_2O_2 is a side reaction of oxygenation of Rubisco and that this side reaction occurs more frequently at higher temperatures. Where Rubisco is the most abundant protein on earth, catalyzes both photosynthetic carbon fixation and photorespiratory oxygen incorporation in plants. Soliman *et al.,*(2011) reported that heat tolerance is associated with tolerance to oxidative stress and the difference in sensitivity is due to the accumulation of H_2O_2 rather than tolerance to H_2O_2. H_2O_2 is one of the signaling molecules against abiotic stresses acts as regulatory molecules in altering various criteria related to enhancing the thermo tolerance capacity Where exogenous application of H_2O_2 resulted in an increases in the intra cellular accumulation of H_2O_2 which increase the antioxidant enzymes activity and influence the expression of stress associated genes like HSPS under heat stress and it affects the osmolyte accumulation in the cells as proline by altering the expression of pathway associated genes (Kumar *et al.,* 2012).

Role of H_2O_2 under low temperature

Hameed *et al.,* (2004) mentioned that exogenous application of H_2O_2 gave more vigorous root system in wheat and that increased nitrogen uptake where the latter led to better growth and yield (Liao *et al.,* 2004). Accumulation of proline content under cold stress was increased by the application of H_2O_2 and reversed the deleterious effects of cold stress (Yang *et al.,* 2009; Guzel and Terzi, 2013). Treatment with H_2O_2 at low concentrations (0.5& 1.0mM) led to a significant positive effect on plant growth, growth regulators (IAA, ABA, and GA3), antioxidant enzymes (CAT, POX, PPO) and antioxidant activity (DPPH scavenging) beside fruit yield and fruit quality and significant decreases in MDA and EL values in the two tomato cultivars relative to control plants under cold conditions (Orabi *et al.,* 2015). 1mM H_2O_2 was the most effective treatment rather than 2mM as it gave the highest increases in different studied growth parameters (plant height, number of leaves per plant and dry weights of leaves or stems of cucumber under cold condition, Moreover all H_2O_2 (0.5mM and 1.0mM) treatments caused significant increases in yield of cucumber relative to control plants grown under cold condition (Orabi *et al.,* 2017[b]). Furthermore, in case of post-harvest Cherry-tomato and mango fruits during cold storage at 2˚c induce a lower rate of chilling injury, lower H_2O_2 and MDA contents and higher chroma value as compared to the control (Zhao *et al.,* 2010). Moreover, Gehan *et al.,*(2016) studied the effect of all safe post-harvest treatments (hot water 50˚c, SA, $Cacl_2$ and H_2O_2) on banana fruit under cold storage at 10˚c where in general all treatments enhanced characteristics like firmness, decreased weight loss, peel color changing and chilling injury resistant.

In conclusion, Hydrogen peroxide scavenging activities in response to low temperature or stress in general (biotic or abiotic) enhanced H_2O_2 at minor concerations ascertained the occurrence of an oxidative stress that catalyzes the production of reactive oxygen species (ROS) from which is H_2O_2, resulting in several damages represented by the accumulation of MDA content as a final product of lipid peroxidation and consequently leakage of electrolytes of the essential elements out the cells. Therefore the over production of H_2O_2 under stressful conditions are overcomed by enzymatic and non enzymatic antioxidants beside protectants to enhance stress tolerance.

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