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Oxidative stress in plants and its management with antioxidants systems

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ملخص

تتعرض النباتات باستمرار لظروف بيئية قاسية، مثل الجفاف والملوحة والبرد والمعادن الثقيلة والأشعة فوق البنفسجية وغيرها. ونتيجة لذلك، تتغير حالة الأكسدة والاختزال في الخلية النباتية نتيجة للإنتاج المفرط لجزيئات الأكسجين التفاعلية. ومع ذلك، من المعروف أن التخليق الحيوي لهذه الجزيئات السامة للنباتات يلعب دورًا رئيسيًا في حياة الخلية النباتية وموتها وبالتالي، يمكن أن تكون ضارة ومفيدة للكائن النباتي وتحتوي الخلية الحية على ترسانة من مضادات الأكسدة الإنزيمية وغير الإنزيمية لتحديد هذه الجذور الحرة بشكل دائم؛ حيث تعمل هذه المضادات على حبس جزيئات الأكسجين التفاعلية هذه لتكوين مركبات مستقرة تساعد على تخفيف الأضرار الناجمة عن الإجهاد التأكسدي.

الكلمات المفتاحية: جزيئات الأكسجين التفاعلية، الإجهاد التأكسدي.

Abstract

Plants are constantly subjected to extreme environmental conditions such as: drought, salinity, cold, heavy metals, UV irradiation etc. As a result, the redox status of the plant cell is altered by the excessive production of reactive oxygen species. However, it is known that the biosynthesis of these phytotoxic molecules play a major role in plant cell life and death. Thus, they can be both harmful and beneficial to the plant organism. The living cell has an arsenal of enzymatic and non-enzymatic antioxidants to permanently neutralize these free radicals; these antioxidants can act by trapping reactive oxygen species to form stable compounds which help to mitigate the oxidative stress-induced damage.

Keywords: Reactive Oxygen Species; oxidative stress.

Résumé

Les plantes sont constamment soumises à des conditions environnementales extrêmes telles que la sécheresse, la salinité, le froid, les métaux lourds, les rayons UV, etc. Par conséquent, l'état redox de la cellule végétale est altéré par la production excessive d'espèces réactives d'oxygène. Or, il est connu que la biosynthèse de ces molécules phytotoxiques joue un rôle majeur dans la vie et la mort de la cellule végétale. Ainsi, elles peuvent être à la fois nocives et bénéfiques pour l'organisme végétal. La cellule vivante dispose d'un arsenal d'antioxydants enzymatiques et non enzymatiques pour neutraliser durablement ces radicaux libres ; ces antioxydants peuvent agir en piégeant ces espèces réactives de l'oxygène pour former des composés stables qui contribuent à atténuer les dommages induits par le stress oxydatif.

Mots clés: espèces réactives d'oxygène ; stress oxydatif

1. Introduction

The particularity of plants lies in the fact that they are producers of oxygen, a molecule that is both vital and harmful. A free radical is oxygen containing molecule that has one or more unpaired electrons, making it highly reactive with other molecules.

Oxidative stress is defined by an imbalance between increased levels of Reactive Oxygen Species (ROS) and low activity of antioxidant mechanisms; thus the delicate balance between ROS generation and ROS scavenging is disturbed by the different types of stress factors like salinity, drought, extreme temperatures, heavy metals, pollution, high irradiance, pathogen infection, etc (Figure 1). The survival of the plants therefore depends on many important factors such as changes in growth conditions, severity and duration of stress conditions and the capacity of the plants to quickly adapt to changing energy equation (Miller et al., 2010).

Indeed, water stress can induce oxidative stress resulting from an imbalance between the production of reactive oxygen species (ROS) and antioxidant defense systems. At low concentrations, ROS act as promoters of plant growth and development. At high concentrations, they cause senescence and cell death (Deng et al., 2012). Thus, the intensity of stress is determined by the level of ROS found at the cellular level (Liu and Zhang, 2004). Moreover,

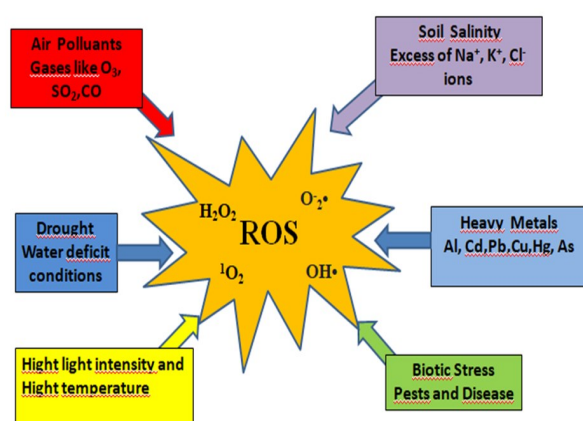


Figure 1. Various causes responsible for the generation of ROS (Das and Roychoudhury, 2014).

several authors have shown that these ROS play an important role in the defense system against pathogens (Bolwell et al., 2002) and allow lignification and the triggering of other processes such as programmed cell death (Teichmann, 2001). They can also play the role of a signal molecule and alert the cell to the presence of environmental stress (Maksymiec, 2007).

2. Molecular damage caused by free radicals

2.1. Lipid Peroxidation

Lipid peroxidation is the most destructive process of the structure and functions of cellular and sub-cellular membranes. In addition, the products formed during lipid peroxidation are themselves mutagenic. Lipid peroxidation, which mainly concerns polyunsaturated fatty acids (PUFAs), occurs in three steps (Figure 2):

a. Initiation: it consists of the free radical tearing off a hydrogen atom from a methylene group ($-\text{CH}_2-$) adjacent to two double bonds.

b. Propagation: it begins when an O_2 molecule attacks the polyunsaturated fatty acid radical ($\text{L}\cdot$) to form a peroxy radical ($\text{LOO}\cdot$). ($\text{L}\cdot$) reacts with another PUFA (LH), and generates the formation of a lipid hydroperoxide (LOOH) and a new lipid radical ($\text{L}\cdot$) thus ensuring the propagation of the peroxidation process.

c. Termination: consists of the recombination of two radicals to form more or less stable compounds. During this phase, the hydroperoxide (LOOH) can be decomposed into other reactive species such as the alkoxyl radical ($\text{LO}\cdot$), aldehydes (malondialdehyde), acids and alkanes (ethane, ethylene, pentane).

2.2. Protein oxidation

Oxidation can be direct, occurring at the level of the side chain of amino acids, or by the fixation of aldehydes resulting from lipid peroxidation on the amino acids, thus forming adducts. Oxidized proteins

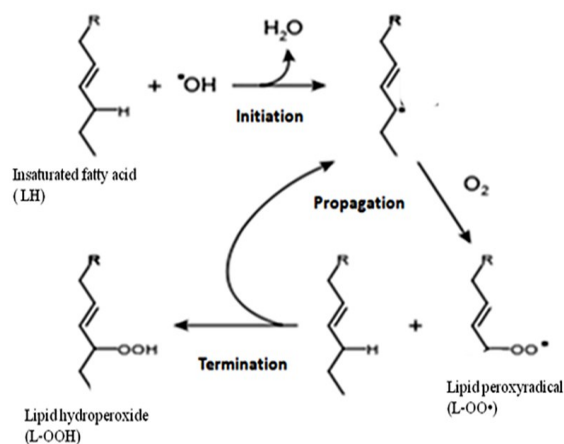


Figure 2. Schematic representation of lipids peroxidation. When a fatty acid (LH) is attacked by a free radical ($\text{OH}^\bullet$), a hydrogen atom is abstracted from the lipid. As a result, in the presence of oxygen (O_2), a lipid peroxy radical ($\text{L-OO}^\bullet$) and finally a lipid hydroperoxide (L-OOH) are formed.

become very hydrophobic (removal of ionizable amine groups or exteriorization of central hydrophobic zones, which will then form clusters in the cells). In all cases, protein oxidation is irreversible; the oxidized protein becomes more sensitive to the action of proteases and will be eliminated by the proteasome (multi-protein enzyme complex) (Obata et al. 2011).

2.3. Nucleic acids oxidation

DNA damage is mainly due to the hydroxyl radical $\text{OH}^\bullet$, which acts on purine or pyrimidine bases as well as on deoxyribose (Gill and Tuteja, 2010). These DNA damage result in cellular disturbances such as decreased protein synthesis, destruction of the cell membrane, and damage to photosynthetic proteins that will affect the growth and development of the plant (Figure 3). The DNA molecule, once damaged, cannot be replaced and must be repaired.

On the other hand, if the lesions persist due to the extent of the damage, errors in reading and synthesis of DNA, they can cause a point mutation in the genome, which will lead to apoptosis (Favier, 2003).

For example, under drought conditions ROS concentrations are elevated in several ways. First, the plant closes its stomata to avoid water loss from the leaf surface. This stomata closure leads to a decrease in photosynthetic activity in plants, causing a reduction in NADP^+ . Second, under drought conditions, there is an increase in the transfer of electrons to oxygen (O_2) during photosynthesis (Carvalho, 2008).

3. Cellular defense mechanisms against reactive oxygen species

Oxidative stress is controlled by endogenous antioxidant defense systems. Cellular antioxidants can be non-enzymatic or enzymatic (Table 1).

3.1. Enzymatic Antioxidants

These systems mainly include superoxide dismutases, catalases, ascorbate peroxidases, and glutathione peroxidases. Generally, the increase in the activities of enzymes involved in defense reactions appears to be linked to the species, the physiological conditions of the plant used, or the type of oxidative stress applied.

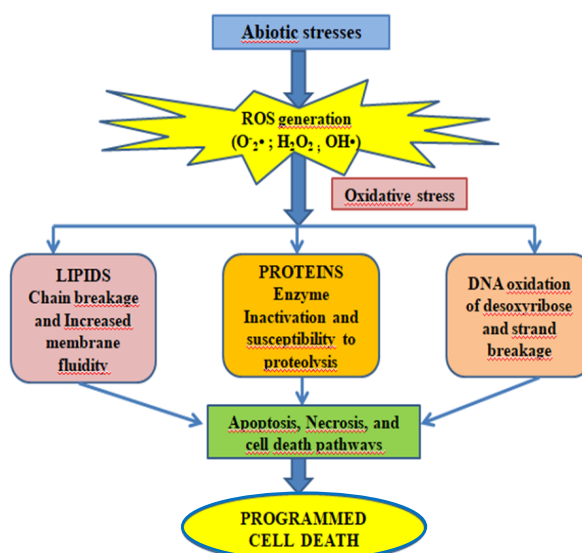


Figure 3. Systemic diagram showing correlation of high-temperature stress with signal transduction pathways and activation of defense pathway in response to ROS (Awasthi et al. 2015).

Table 1. List of all the enzymatic and non-enzymatic antioxidants along with their functions and cellular localization (Das and Roy-choudhury. 2014)

Enzymatic Antioxidants	Enzyme code	Reaction catalyzed	Subcellular location
Superoxide dismutase (SOD)	1.15.1.1	$O_2^- + O_2^- + 2H^+ \rightarrow H_2O_2 + O_2$	Peroxisomes, Mitochondria, Cytosol, and Chloroplast
Catalase (CAT)	1.11.1.6	$2H_2O_2 \rightarrow O_2 + 2H_2O$	Peroxisome and Mitochondria
Ascorbate peroxidase (APX)	1.11.1.11	$H_2O_2 + AA \rightarrow 2H_2O + DHA$	Peroxisomes, Mitochondria, Cytosol, and Chloroplast
Monodehydroascorbate reductase (MDHAR)	1.6.5.4	$2MDHA + NADH \rightarrow 2AA + NAD$	Mitochondria, Cytoplasm, and Chloroplast
Dehydroascorbate reductase (DHAR)	1.8.5.1	$DHA + 2GSH \rightarrow AA + GSSG$	Mitochondria, Cytoplasm, and Chloroplast
Glutathione reductase (GR)	1.6.4.2	$GSSG + NADPH \rightarrow 2GSH + NADP^+$	Mitochondria, Cytoplasm, and Chloroplast
Guaiacol peroxidase (GPX)	1.11.1.7	$H_2O_2 + DHA \rightarrow 2H_2O + GSSG$	Mitochondria, Cytoplasm, Chloroplast, and ER

Non-enzymatic Antioxidants	Function	Subcellular location
Ascorbic Acid (AA)	Detoxifies H_2O_2 via APX	Cytosol, Chloroplast, Mitochondria, Peroxisome, Vacuole, and Apoplast
Reduced Glutathione (GSH)	Acts as a detoxifying co-substrate for enzymes like peroxidases, GR, and GST	Cytosol, Chloroplast, Mitochondria, Peroxisome, Vacuole, and Apoplast
α -Tocopherol	Guards against and detoxifies products of membrane LPO	Mostly in membranes
Carotenoids	Quenches excess energy from the photosystems, LHCs	Chloroplasts and other non-green plastids
Flavonoids	Direct scavengers of H_2O_2 and $^1O_2$ and $OH^\bullet$	Vacuole
Proline	Efficient scavenger of $OH^\bullet$ and $^1O_2$ and prevent damages due to LPO	Mitochondria, Cytosol, and Chloroplast

3.1.1. Superoxide dismutase (SOD, EC 1.15.1.1)

They are part of a group of metalloproteins; SODs have been isolated and characterized in many organisms. The main known types are: One class of SOD that has Cu and Zn at the active site (Cu/Zn SOD), present in the cytosol and chloroplast of eukaryotic cells and in some prokaryotes; another class (Mn SOD), present in prokaryotes and in mitochondria; and another (Fe SOD), found in prokaryotes, algae, and in the chloroplasts of some higher plants. These metals change valence during the reaction through the loss of electrons associated with the reduction step (Moran et al., 2003).

3.1.2. Catalases (CAT, EC 1.11.1.6)

Catalases are tetrameric heme protein enzymes consisting of four polypeptide chains. They are located primarily in peroxisomes, but they are also found. They are involved in the elimination of H₂O₂ to produce water and O₂. According to Willekens et al. (1997), catalases play an important role in the antioxidant defense of plant cells under stress conditions. These enzymes are known to be among the most active, with exceptionally high turnover (Khalifa et al., 2011).

3.1.3. Guaiacol peroxidase (GPX, EC 1.11.1.7)

Several studies have shown that guaiacol peroxidase (GPX) is involved in numerous physiological processes such as plant development, senescence (Abdes et al., 1988), lignin biosynthesis (Kay and Basile, 1987), organogenesis via IAA degradation (Schneider and Wightman, 1974), and ethylene biosynthesis. GPX is involved in stress conditions (Albert and Anderson, 1987). It has a significant potential for eliminating reactive oxygen species.

3.1.4. Ascorbate peroxidase (APX, EC 1.11.1.11)

Plants possess several APX isoforms distributed in different subcellular compartments, including the chloroplast and cytosol. In the chloroplast, some isoforms are found in the stroma and others attached to the thylakoids. APX eliminates hydrogen peroxide by using ascorbate (vitamin C) as a co-substrate and by its oxidation (Halliwell, 2006). In addition to the binding site for ascorbate, they have

a second potential binding site for phenolic compounds. Their enzymatic activity is regulated by ascorbate availability and ROS concentrations, with a more oxidizing cellular environment resulting in overexpression of APX activity. Some isoforms are in fact regulated quantitatively and others qualitatively. The affinity of APX for H₂O₂ (μM) suggests that this enzyme is involved in fine regulation of ROS, particularly in a signal context (Mittler, 2002).

3.1.5. Glutathione peroxidase (GPX, EC 1.6.4.2)

They reduce hydrogen peroxide to water in the presence of glutathione. They are involved in the reduction of hydroperoxides including those of lipids (Eshdat et al., 1997). A family of glutathione peroxidase, phospholipid-hydroxyperoxide glutathione peroxidase, directly attacks hydroperoxides (Zhao et al. 2019).

3.2. Non Enzymatic Antioxidants

The accumulation of antioxidant molecules will protect antioxidant enzymes from damage caused by hydroxyl radicals (Deng et al., 2012).

3.2.1. Ascorbic Acid (Vitamin C)

Vitamin C is present in all plants and in all cellular compartments (apoplasm, cytosol, vacuoles and mitochondria) but is particularly abundant in the chloroplast. It plays many roles in the plant such as development, hormonal signaling, cell cycle activation and wall extension (Horemans et al., 2000). Ascorbate is a major antioxidant for the plant, capable of neutralizing reactive oxygen species (ROS). It reacts directly with several ROS such as OH•, H₂O₂ and O₂•. Ascorbate also participates indirectly in the enzymatic detoxification mechanisms of the plant through antioxidant enzymes such as ascorbate peroxidase (APX). (Shao et al., 2008).

3.2.2. α-tocopherols (Vitamin E)

Tocopherol is a soluble lipid antioxidant considered as a potential scavenger of ROS and oxygenated lipid radicals. The antioxidant action is manifested at the level of chloroplast membranes by trapping singlet oxygen ¹O₂. There are 4 isozymes of

tocopherol. Alpha-tocopherol has the most potent antioxidant activity due to the presence of 3 methyl groups in its molecular structure (Gill and Tuteja, 2010). Recent studies have shown that oxidative stress activates the genes responsible for tocopherol synthesis (Wu et al., 2007).

3.2.3. Glutathione

It is the most abundant thiol in living organisms and systems. It is a tripeptide (L-glutamylcysteinylglycine) constituting the largest reserve of non-protein thiols, found in all cellular compartments in either the reduced form (GSH) or the oxidized (disulfide) form (GSSG). It is considered a cellular redox buffer and can directly reduce oxidized substrates. Several studies have demonstrated its role in cellular defense mechanisms and adaptation to oxidative stress (Liu et al., 2007). Present in the cytosol and in almost all cellular organelles (chloroplasts, mitochondria, endoplasmic reticulum, and vacuoles), GSH participates in various biochemical functions (Foyer and Noctor, 2000). It serves as a substrate or cofactor for several biochemical reactions; it interacts with hormones and redox molecules and participates in the transduction of induced stress signals; GSH also plays an important role in the regeneration of ascorbic acid via the glutathione ascorbate cycle (Szalai et al., 2009).

3.2.4. Carotenoids

They are the essential components of the photosynthetic membrane. They play an important role in the assembly of photosystems, in light harvesting and in the photoprotection of photosystems (Havaux, 1998). Carotenoids, such as β -carotene, can exert a photoprotective action by attenuating excited chlorophyll molecules or by dissipating excess energy through the xanthophyll cycle (Demmig-Adams and Adams, 1993). Carotenoids also play a vital role in photoprotecting the photosynthetic machinery by direct removal of singlet oxygen (Collins, 2001). In plants, xanthophylls are also the precursors of abscisic acid, a phytohormone, which modulates developmental processes and the response to abiotic stresses.

3.2.5. Flavonoids

Flavonoids are secondary metabolites; they perform many functions like regulating cell growth, attracting pollinating insects, and protecting against biotic and abiotic stresses (De Luna et al., 2020). They are highly effective at removing free radicals and defending cells from peroxidation (Liu et al. 2014).

3.2.6. Phenolic compounds

The antioxidant properties of phenolic compounds are associated with their ability to form intramolecular hydrogen bonds between hydroxyl groups and phenolic radicals (Visioli et al. 1998b). The degree of antioxidant activity of phenolic compounds is correlated with the number of hydroxyl groups and their position on the ring, the ortho-diphenolic situation giving them a strong antioxidant activity (Tripoli et al., 2005).

4. Conclusions and perspectives

Oxidative stress appears to be a ubiquitous mechanism in which numerous physiological reactions reveal a free radical component. ROS have been considered toxic byproducts naturally occurring from biochemical reactions of cellular metabolism. During biotic or abiotic stress, these toxic molecules cause oxidative stress that can lead to disruption of homeostasis and cell death. The damage caused to cells induces programmed cell death. Plant cells are equipped with an arsenal of enzymatic and non-enzymatic antioxidant systems that destroy ROS to maintain a balance conducive to cell survival and plant growth in stressful environments.

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