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Reactive Oxygen Species: Boon or Bane

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ABSTRACT: Reactive oxygen species are unavoidable consequences of aerobic metabolism which is generated mainly in cellular chloroplast, mitochondria, peroxisome and apoplastic space. ROS are double edged sword of plant life as it not only modifies cellular components and causes cell death but under defined window of ROS concentration it also regulate various plant growth and developmental processes such as cell wall synthesis, pathogen defence, plant senescence, plant cell death and stomatal behaviour. Plant is surfeited with strong enzymatic and non-enzymatic ROS scavenging mechanism which maintains ROS homeostasis in cell and avoid unavoidable toxicity. ROS is constantly produced at baseline levels under favourable settings. They are unable to cause damage, however, since they are scavenged by several antioxidant processes. Stress factors such as salt, drought, harsh temperatures, heavy metals, pollution, high irradiance, pathogen infection, and others disrupt the delicate balance between ROS formation and ROS scavenging. According to estimates, only 1–2 percent of the O_2 consumed by plant tissues results in the generation of ROS. Disturbance in the ROS homeostasis enforces plant to spend more energy in maintaining homeostasis results in compromise growth. Despite widespread interest, this field of study remains relatively unexplored, and our understanding of ROS signalling remains limited. Therefore a normal basal level of ROS level is required for maximal plant growth and development. Here we reviewed the good side of ROS-role of reactive species in plant growth and development; bad side- ROS led challenges imposed on plant.

Keywords: Reactive oxygen species, stomatal behavior, ROS scavenging mechanism.

INTRODUCTION

With the introduction of molecular oxygen by photosynthetic organisms that emit O_2 directly into the atmosphere, reactive oxygen species became an essential component of aerobic life (Taverne *et al*., 2018). Since the advent of oxidising atmosphere in the course of evolution, organism adapted to use molecular dioxygen (O_2) as terminal electron acceptor for generating energy. As reduction of dioxygen into water (H_2O) require high amount of activation energy, process is endergonic and thermodynamically unfavourable. Living organism adopted an alternative strategy in which it undergoes consecutive mono-electron reduction process resulting into several highly reactive intermediate oxygen species. These intermediates of oxidative metabolism called as reactive oxygen species (ROS) which can donate electron to various biomolecules. In ground state molecular dioxygen molecule is relatively stable and unreactive due to parallel spin of the electrons in the outer two uncompleted p*2p orbitals. Mono-electron reduction of dioxygen lead to production of highly reactive superoxide free radicle. High reactivity is attributed by unpaired electron in the one of the outer incomplete molecular orbital. It has a half-life of 1-4µs and reacts very rapidly with biomolecules in proximity, could diffuse to short migration distance of only about 30 nm. Further superoxide radicle undergoes mono-electron reduction to produce a negatively charged peroxide radicle which accept two protons from the biological medium and converted into hydrogen peroxide. Hydrogen peroxide is a relatively stable with a half-life of >1ms, being an uncharged molecule it can cross the plasma membrane. H_2O_2 undergoes fentonrection where a heterolytic fission results in production of hydroxyl radical and negatively charges hydroxyl ion in presence of ferrous ion (Fe^{2+}) (Demidchik *et al*., 2015). Singlet molecular oxygen species are generated by non-photochemical quenching in chloroplast which differs in orientation of electron in the outer empty molecular orbital. It has half-life of 1-4µs and can react with lipid, proteins and guanosine residue of DNA. ROS damages the lipid bilayer membrane and causes lipid peroxidation, which inactivates membrane-bound protein receptors and increases tissue permeability (Biney *et al.*, 2019).

Table 1: Types of reactive oxygen species and their feature.

ROS	$t_{1/2}$	Migration distance	Mode of action	Remarks
Superoxide ($O_2^{\bullet-}$)	1-4µs	30nm	• Reacts with Fe–S proteins • Dismutates to H_2O_2	• ETC chain of photosynthesis and respiration, • Instable & Inability to diffuse PM
Hydroxyl radical (OH•)	1	1nm	• Extremely reactive withal all biomolecules including DNA, RNA, lipids, and proteins	• Most Reactive ROS, poor diffusion • Act as H_2O_2 sensor
Hydrogen peroxide (H_2O_2)	>1ms	>1µm	• Reacts with Cys and Met residues. • Reacts with Heme proteins & DNA.	• Relatively stable, poor oxidant, high diffusion potential. • Best suited for signalling molecule
Singlet oxygen ($^1O_2$)	1–4 µs	30nm	• Oxidizes lipids, proteins (Trp, His, and Cysresidues), and Guanosine of DNA	• Generated due to excitation energy, react with molecule in proximity

Abiotic stressors, such as drought, heat, cold, salinity, and light, have a detrimental impact on plant growth, reproduction, and survival, affecting agricultural crop productivity and yield (Gupta *et al*., 2020; Lamers *et al*., 2020). A substantial overlap between ROS response and abiotic stress-induced networks can be attributed to a burst of ROS generation, which occurs in cells in response to various abiotic stimuli (Fichman and Mittler 2020).

Site of ROS Production. Major site of ROS generation in plant is electron transport of chloroplast and mitochondria along with monooxygenases and oxidases present in peroxisome, glyoxisome, apoplastic space between cell wall and plasma membrane.

Chloroplast. Photosystem I and Photosystem II are major site of ROS production in chloroplast. Under high light condition, when phylloquinone undergoes over reduction, electron from pheophytin is transferred to molecular oxygen to produce superoxide ion (Asada, 2006). Non-photochemical quenching of both pigment system lead to production of singlet oxygen (Fischer *et al*., 2013). Besides this Fe-S containing proteins of PSI and PSII are prone to oxidation under high light condition. In Pigment system I, electrons are transferred to molecular oxygen and superoxide radical (Mehler reaction) is generated which is dismutated by Superoxide dismutase and converted into water through various antioxidant enzyme (Borisova *et al*., 2012). Reactive oxygen species generated through mehler reaction protect photosynthetic electron transport chain from over reduction and provide an efficient mechanism of protection. Thus ROS generation seems a strategy for plant survival in high light condition (Foyer and Shigeoka, 2011).

Mitochondria. Mitochondria is major site of ROS production in animal but possess significant potential to contribute in plant system too. Complex I (NADH: UQ dehydrogenase) and ubisemiquinone in complex III can transfer electrons to molecular oxygen (Blokhina and Fagerstedt, 2010). Role of non-proton pumping external and internal NADH dehydrogenases in ROS generation is still unclear. A membrane protein Alternate oxidase dissipates excess energy and prevent over reduction of component of electron transport chain by accepting electrons directly from ubiquinone. Overexpression of Alternate oxidase lowers down the accumulation level of ROS in mitochondria (Clifton *et al*., 2006; Cvetkovska *et al*., 2013). An uncoupling protein which diminish the proton gradient across the membrane prevent over reduction of ETC of mitochondria. These Uncoupling proteins are activated by free fatty acids and lowers down the accumulation of ROS.

Apoplast

In addition to chloroplast and mitochondria, apoplastic space between cell wall and plasma membrane also contribute to the ROS accumulation in cell. NADPH oxidase, Oxalate oxidase and Class III peroxidases are major site of ROS production in apoplast. Apart from this various amino acid oxidases such as polyamine oxidase, diamine oxidase oxidises polyamines like putrescine, cadaverine, spermidine and spermine led to production of H_2O_2 (Blomster *et al*., 2011). ROS produced in apoplastic space transfers electron to monolignols and initiate polymerization event for lignin biosynthesis. Rboh (Respiratory burst of oxidase homolog) is regulated by cytosolic Ca^{2+} and associated proteins (Bindschedler *et al*., 2006).

Oxidases of photorespiration (Glycolate oxidase) and nucleotide catabolism such as urate oxidase contribute to the metabolic ROS level in peroxisomes. A specialised peroxisome involved in lipid metabolism in plant also harbour oxidases which generate ROS.

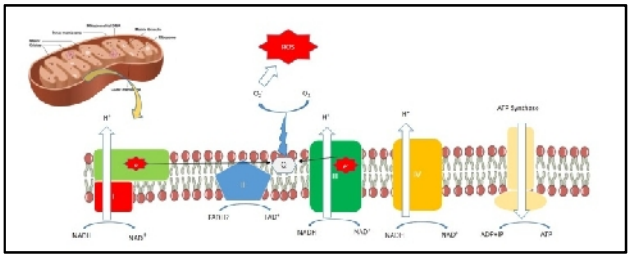

Fig. 1. ROS production in mitochondria.

ROS: Bane for Plant. Phospholipids of plasma membrane and glactolipids of chloroplast are rich in polyunsaturated fatty acids such as linoleic (18:2) and linolenic acid (18:3). These PUFA are highly susceptible and reacts with singlet oxygen and hydroxyl radical results in production of complex mixture of hydroperoxides, aldehydes, hydroxyl and keto fatty acids (Fry, 1998; Mueller, 2004). Aldehydes and their degradative product such as 4-hydroxy-2-nonenal (HNE) conjugates with DNA and proteins (Farmer and Mueller, 2013). Aldehyde accumulation in mitochondria causes cytoplasmic male sterility in maize because a maize restorer gene of CMS encodes for aldehyde dehydrogenase (Liu *et al*., 2001). Some oxidised product of PUFA act as secondary messenger which modify enzymes activity either directly or indirectly. Peroxidation of membrane lipid induces membrane leakiness and causes secondary damage to proteins (Halliwell *et al*., 2006).

Protein oxidation via covalent interaction is caused by reactive oxygen species or consequences of oxidative stress (Lerner *et al*., 2017). Protein oxidation in response to ROS accumulation is wide spread and often used as marker. Most of the protein modifications are irreversible but modifications to thiol containing amino acids are reversible in some cases and being extensively utilised by plant to modulate signalling pathway in plant (Ghezzi and Bonetto, 2003). Cystein reacts with singlet oxygen and hydroxyl radical to form disulphide bond and futher oxidation convert it into sulfenic (R-SOH) and sulfinic acid (RSO2H). Methionine oxidation to methionine sulfoxide is also a reversible modifications (Biteau *et al.,* 2003). Carbonylation of Arg, His, Lys, Pro, Thr and Trp has also been reported under abiotic stress.

Component of DNA especially nucleotides are susceptible to attack by singlet oxygen and hydroxyl radical. It attacks guanine and hydroxylate to form 8-Hydroxyguanine (Wiseman and Halliwell, 1996). Mitochondria and chloroplast possess multiple copies of DNA with no histone protein, thus susceptible to ROS generated damage, this could be the one of probable reason for multiple copies of genome as both organelle are hot site of ROS production (Thorslund *et al*., 2002).

Hydroxyl radical reacts with sugars and polyols, accumulation of mannitol in stressed cell removes hydroxyl radical and prevents further damage to essential cellular components (Shen *et al*., 1997). Cell wall polysaccharides of plants are susceptible to hydroxyl radical mediated damage. Cell wall peroxidases generate hydroxyl radicle strategically for loosen the complex polysaccharide network during cell extension and elongation process (Fry *et al*., 1998). Auxin hormone involved in cell elongation promotes apoplastic ROS generation. ROS mediate oxidation of sugars produces formic acid (Isbell *et al*., 1973).

A Strong Antioxidant System: To maintain ROS homeostasis. Plant has evolved with strong antioxidant machinery to avoid the unavoidable toxicity of reactive oxygen species and it maintains homeostasis under normal plant growth and development. These antioxidant machinery composed of non-enzymatic and enzymatic components present in different subcellular organelle.

Non-enzymatic antioxidants

It includes ascorbic acid, reduced glutathione, tocopherol, carotenoids, flavonoids and proline. Ascorbic acid is low molecular weight water soluble antioxidant, act as co-substrate for ascorbate peroxidase. Glutathione is low molecular weight thiol tri-peptide, act as co-substrate for glutathione peroxidase enzyme and widely distributed in subcellular organelle. A group of lipophilic antioxidants called tocopherol involved in non-photochemical quenching, it dissipates excess energy and protect PSII. Ubiquitously present carotenoid pigment scavenges singlet oxygen and reacts with lipid peroxidation products and terminate the chain reaction (Foyer and Noctor, 2011). It dissipates excess excitation energy as heat and prevent production of generation of singlet oxygen. Proline act as a lipid peroxidation inhibitor and scavenges hydroxyl radical and singlet oxygen. Flavonoid act as scavenger of ROS generated and provide protection from UV rays.

Antioxidant enzymes. Enzymatic antioxidants include Superoxide dismutase (SOD), Catalase (CAT), Ascorbate peroxidase (APX), Monodehydroascorbate reductase (MDHAR), Dehydroascorbate reductase (DHAR) and Glutathione reductase (GR). Superoxide dismutase is a member of metalloenzyme family, ubiquitously present in all aerobic organism and act as first line of defence against ROS-induced damages (Liang *et al*., 2013). SOD dismutate superoxide radical into O_2 and H_2O_2 and prevent production of more reactive hydroxyl ions by Haber-Weiss reaction. Based on metal cofactor associated with protein, it has been classified into three classes, Fe-SOD, present in chloroplast; Mn-SOD commonly observed in mitochondria and peroxisomes; Cu/Zn-SOD often present in cytosol, peroxisomes and chloroplast (Racchi *et al*., 2001; Alscher *et al*., 2002). Catalase is a heme containing enzyme which reduces hydrogen peroxide into water and O_2. It has very high affinity for H_2O_2 than organic peroxide radical (Das and Roychoudhary 2014) and catalyses reaction with very high turnover rate. Interestingly its only antioxidant enzyme which does not utilize cellular reducing equivalent for reaction. It is most abundant in peroxisome where β-oxidation fatty acid leads to production of H_2O_2 (Mittler 2002; Foyer and Noctor, 2003). Ascorbate-Glutathione cycle regenerate ascorbate utilized by ascorbate peroxidase (APX) enzyme through set of three enzyme MDHAR, DHAR and GR. Monodehydroascorbate reductase reduces monodehydroascorbate into ascorbate with the help of metabolic reducing equivalent NAD(P)H. Dehydroascorbate resulted from a non-enzymatic conversion of monodehydroascorbate, undergoes glutathione dependent reduction by DHAR to

regenerate ascorbate. Oxidised glutathione is reduced to glutathione by GR where reduction utilises metabolic NAD(P)H.

Reactive Oxygen species: Boon for plant existence. During the course of aerobic evolution plant has evolved with very strong ROS scavenging mechanism to evade the unavoidable toxicity of reactive oxygen species which helps in maintaining a balance (Foyer and Noctor, 2013). Many of the earlier finding, which was thought to be due to the direct modification of cellular component by reactive oxygen species being reported as a regulated processes. Various plant growth and development processes such as root development, plant cell death and senescence and stomatal movement are strictly regulated by ROS. Role of ROS in signal perception, transduction and direct modulation of effector proteins are now being reported widely in various plant.

ROS as a redox regulator/modulator. Reactive oxygen species like H_2O_2 can directly oxidise thiol containing proteins such as peroxiredoxin (PRX) and thioredoxin (TRX), upon oxidation these intramolecular and intermolecular sulphide linkages are regenerated by redox transmitters. Thiol oxidation of protein induces conformational change in proteins which can change the specificity or modulate affinity for a protein (Dietz *et al*., 2008). These induced changes in response to reactive oxygen species is the major mode through which it modulate the proteins involved in signal transduction pathway (Konig *et al*., 2012). Receptor like Kinases (RLKs) are large family of protein present in plasma membrane characterised by N-terminal extracellular domain and a C-terminal cytosolic kinase domain. RLKs perceive the apoplastic ROS level and act as communicator to interior of cells. Ligand binding to RLK can also trigger the Ca^{2+} dependent ROS production by activating RBOH or NADPH oxidase.

Role of ROS in Stomatal Closure. ABA induced activation of signalling cascade triggers the ROS generation through membrane protein NADPH oxidase (RBOH). ROS accumulation in cytosol of guard cell activate MAPK dependent signalling cascade which opens SLAC1 anion channel present on plasma membrane. Cytosolic calcium spiking in response to increased ROS level sets calcium dependent protein kinase cascade resulting in inhibition of potassium inward (K^+ inward) channel, activation of K+ outward channel and anion channel SLAC1 (Wang *et al*., 2015). The differential activation and repression of plasma membrane channels, ion pumps results into membrane depolarization and loss of turgor. H_2O_2 led rise in cytosolic Ca^{2+} concentration also modulate thiol based transcription factor such as HSF, WRKY, NPR1, Zats and up regulate abiotic stress associated gene.

ROS and Plant Cell Death. Paradoxically cell death is integral part of life. It is essential for maintenance of cell growth and development along with cell proliferation, growth as well as differentiation. Prominent role of ROS is being revealed in the induction, signalling and cellular death. Initially the spatio-temporal correlation with ROS accumulation cell death indicated its role in PCD. At least 158 genes are involved in regulation of spatio-temporal network of ROS production in Arabidopsis genome. Biphasic oxidative burst during hypersensitive response and ozone stress is best characterized example of ROS-derived PCD. Some of the hallmarks of PCD such as Cytochrome c release from mitochondria, DNA laddering and chromosome condensation has been observed prior to discrete cellular lesions (Lam *et al*., 2004). External application of antioxidants or transgenic plants with high level of antioxidant enzymes such as Superoxide dismutase, catalase and ascorbate peroxidase exhibit lower cellular lesion on both ROS derived and ozone-derived PCD. High and sustained accumulation of phytotoxic level of ROS in the cell leads to necrotic cell death but transient level may initiate various signal transduction pathway with significant cross talk with phytohormones such as Ethylene, Salicylic acid, jasmonate. Besides MAPK-driven phosphorylation cascade various posttranslational modifications such as protein oxidation, nitrosylation plays important role in ROS dependent cell death.

Root development. Root is a vital plant organ which enables uptake of nutrients and water and provide support within the soil for plant development. Root of plant can be divided longitudinally into three regions; a meristematic zone, an elongation zone and a maturation zone. Meristematic zone is characterised by high proliferation rate and little or no elongation. Cells in elongation zone undergoes rapid elongation without cell proliferation. Cells of maturation zone have completed elongation and destined to differentiation viz. root hair development, vascular tissue formation etc. (Mendrinna and Persson, 2015). Reactive oxygen species plays very crucial role in all aspects of root development. ROS homeostasis in root tip cells is maintained by peroxidases which is negatively regulated by a bHLH transcription factor UP BEAT1 (UPB1), *ubp1-1* mutant exhibit longer meristem whereas UPB1 overexpression lines shows shorter meristem in comparison to wild type (Tsukagoshi *et al*., 2010). Tips of root hair is in direct control of RBOH. In *rhd2* (Root hair defective 2) mutant of *Arabidopsis thaliana* shows short root hairs and stunted roots development due to defective Ca^{2+}. RHD2 encodes a RBOHC or NADPH oxidase protein, transfer electrons from NADPH to electron acceptor and generate reactive oxygen species which in turn regulate Ca^{2+} channels (Foreman *et. al*., 2003). ROS generated in apoplastic region transfer electrons to monolignols and induce free radical polymerization in lignin biosynthesis. Differential lignin deposition and secondary wall development has wider impact on the differentiation (Novo-Uzal *et al.*, 2013). ROS also affects cell division in apical meristem cells of root; roots treated with DNA double strand break inducer like zerocin leads to accumulation of H_2O_2, A transcription factor SOG1

was reportedly induced in response to double strand break in DNA directly regulate expression of a FMO1 gene encoding for a flavin-containing monooxygenase that oxidises molecular oxygen (Yoshiyama *et al*., 2019; Chen and Umeda 2015). *ROOT MERISTEM LESS1* (RML1) mutant fails to form an active root meristem, later investigation suggest that it encodes a protein involved in glutathione biosynthesis (Vernoux *et. al*., 2000). Glutathione level is a very important regulator for G1 to S cell cycle transition. H_2O_2 regulated SPINDLY (SPY) gene encodes for an O-linked N-acetyl glucosamine transferase, reportedly plays a critical role in cortex proliferation. ROS accumulation in response to abiotic stress and hormone absisic acid reduces root growth by altering auxin distribution which in turn regulate cell elongation, root gravitropism (Joo *et al.*, 2001) and other developmental processes. ABA regulated ABA *overlay sensitive 8* (*abo8*) gene encodes a P-type pentatricopeptide repeat domain protein which is involved in splicing of Mitochondrial NADH dehydrogenase subunit 4 (NAD4) and linked to ROS accumulation (Hong *et. al.*, 2013). These evidences confirms that ROS homeostasis is critical for complete development of root in plant.

CONCLUSION AND FUTURE SCOPE

In recent years, scientists have focused on the deteriorative effects of ROS/RNS and the mechanisms demonstrating the involvement of antioxidants in mitigating these free radicals. These free radicals are unavoidable because they are results of regular cell metabolism. Reactive oxygen species appears to be double edged sword of life. Plants are surfeited with strong ROS scavenging mechanism to avoid the toxic level of accumulation. A balance of ROS production and ROS scavenging is maintained in the cell. Plant strategically utilizes ROS for growth and development processes such as pathogen defence, programme cell death and stomatal behaviour under normal condition. However, under stress condition plant forced to spend more energy on ROS scavenging to maintain ROS homeostasis. Imbalance in ROS homeostasis leads to accumulation of ROS and thereby modification of cellular components. Although recent research insight into the ROS mediated plant developmental processes has solved many enigmatic questions such as plant cell death. Further insight into many processes including the signalling components of Reactive oxygen species mediated responses are required. This research will aid in understanding the physiology of plants when stressed, as well as the stress-relieving processes that are activated within plant cells. Breeders can generate such better varieties that can tolerate/resist stress by knowing the core process underlying this. Significant progress has been made in boosting stress tolerance in plants through the production of transgenic plants with improved antioxidant enzyme activity as a result of recent advances in molecular and genetic techniques. Nonetheless, over expression of genes producing antioxidant enzymes in transgenic plants improves abiotic stress tolerance and increases the antioxidant enzymes' capacity.

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