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## DECIPHERING THE MECHANISMS OF REACTIVE OXYGEN SPECIES GENERATION AND THEIR MULTIFACETED EFFECTS ON PLANT CELLULAR PROCESSES

**Vaishali Gangwar[1]*, Vijay Sharma[2], Mukul Kumar[3], C., M. Singh[4], Kammaludin[5] and Om Prakash[6]**

*Department of Crop Physiology[1], Department of Genetics and Plant Breeding[2,3.4,5], Department of Fruit Science[6]*
*Banda University of Agriculture and Technology, Banda, Uttar Pradesh (India) 210001*
*Email: vaishaligangwar2013@gmail.com*

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**Abstract:** Reactive Oxygen Species (ROS) play a significant role in plant development and cellular processes. ROS are molecules that are generated as by-products during various cellular reactions, including photosynthesis and respiration. While ROS are known to have harmful effects on plants in high concentrations, they are also essential signaling molecules that regulate many physiological processes in plants. ROS regulates plant development by controlling the balance between cell growth and death. For example, in roots, ROS promote cell elongation and differentiation, while in leaves, they regulate leaf size and shape. ROS also play a role in regulating the plant's response to environmental stressors, such as drought and salinity. In addition to regulating plant development, ROS also participate in various cellular processes, including hormone signalling, defence responses, and programmed cell death. ROS are involved in the synthesis and signalling of plant hormones, such as abscisic acid, which is critical in regulating plant responses to abiotic stress. ROS also play a role in the activation of defence responses, such as the synthesis of pathogenesis-related proteins and the induction of systemic acquired resistance. Furthermore, ROS are involved in programmed cell death, which is essential for plant growth and development, as well as for the defence against pathogens. In conclusion, ROS play a crucial role in plant development and cellular processes. While high levels of ROS can be harmful to plants, low levels of ROS are essential for regulating plant growth, development, and responses to environmental stressors. Understanding the role of ROS in plants is important for developing strategies to enhance plant growth and productivity in agricultural settings while also helping plants to cope with the challenges of changing environmental conditions.

**Keywords:** Cellular processes, Oxidative stress, Mitochondria, Developmental stages

## INTRODUCTION

Genotypic and environmental factors continuously influence and drive plant growth, development, and survival. Due to their sessile nature, plants have developed mechanisms that enable them to utilise their metabolism and grow in a variety of situations. One such mechanism is the incorporation of primary metabolic products into essential processes. One example of a metabolic product that controls plant growth and development is reactive oxygen species (ROS) (Foyer and Noctor, 2009; Mittler, 2017; Noctor *et al.*, 2017). Plants, like all living organisms, are exposed to a variety of stress factors, such as high light intensity, extreme temperatures, and pathogen infection. In response to these stress factors, plants have evolved a number of physiological and biochemical mechanisms to protect themselves from damage. One of these mechanisms involves the generation of reactive oxygen species (ROS), which are highly reactive molecules that can damage cellular components, but also play important roles in signalling and defenseresponses. Several cellular organelles, including mitochondria, peroxisomes, and chloroplasts, are restricted in plants in order to produce ROS. In addition to the previously described ROS production locations, environmental stress can also cause ROS to be produced in cell walls and plasma membranes, which contain peroxidases and amine oxidases, respectively. Singlet oxygen ($^1O_2$), hydrogen peroxide ($H_2O_2$), superoxide ($O^{2-}$) and hydroxyl radicals are some examples of ROS ($OH^-$). They display a range of physiological reactions, structural alterations, and macromolecule breakdown [Huang, 2019]. According to many studies, the formation of ROS is a fundamental sign of plant toxicity under abiotic stress. According to many studies, the formation of ROS is a fundamental sign of plant toxicity under abiotic stress. The level of

*Corresponding Author

phytotoxicity rises along with increase in ROS production. Plant development and metabolism are negatively impacted in such hazardous environments, which lowers agricultural output. Although ROS play a role in the cellular metabolism of plant cells, when they are produced in excess under stressful situations, they destroy numerous cellular components like proteins, lipids, nucleic acids, and carbohydrates through photooxidative damage [Raja, 2017]. In addition to the formation of ROS, their management is primarily accomplished by protective mechanisms, such as antioxidants, both enzymatic and non-enzymatic. Superoxide, in the enzymatic system, converts hydroxyl to hydrogen peroxide, which is then catalysed by peroxidase and catalase (CAT) to produce water and dioxygen. Low-molecular-mass antioxidants including glutathione, ascorbic acid, carotenoids, flavonoids, etc. mediate the non-enzymatic scavenging mechanism by attacking hydroxyl radicals and singlet oxygen. Plant cells experience oxidative stress when there is an imbalance between the generation and scavenging of ROS, which ultimately results in oxidative modification and cell death [Gechev, 2006]. ROS take part in various processes as a secondary messenger, such as cell division, differentiation, biotic and abiotic responses as the cells are maintained in a reduced state as a result of low ROS levels [Zeng, 2017]. As a result, ROS are essential for plant growth and development, and maintaining a threshold level is key. In addition to their destructive effects, ROS are also thought of as a signalling molecule that has a significant impact on plant growth and development, the expression of stress-responsive genes, and the induction of programmed cell death. Under stressful circumstances, it aids in the development of increased tolerance in a number of cellular systems (Mansoor, 2022).

Reactive oxygen species (ROS) are thought to be by-products of plant aerobic metabolism and are produced in a number of cellular compartments, including chloroplasts, mitochondria, and peroxisomes (Dietz *et al*., 2016; Sandalio and Romero-Puertas, 2015). In addition to causing irreversible DNA damage and cell death, ROS serve as significant signalling molecules that control how plants grow normally and react to stress. This shows that depending on varied levels of reactivity, sites of production, and the ability to cross biological membranes, ROS play a dual role in vivo (Miller G. *et al.*, 2010). Some fundamental biological processes, such as cellular proliferation and differentiation, require low ROS levels to progress (Tsukagoshi *et al.*, 2010; Zafra et al., 2010). Higher levels of ROS constitute a serious risk that could eventually result in DNA damage and improper timing of PCD (Xie *et al.*, 2014). Overall, ROS generation in plants can be both a boon and a bane depending on the circumstances. While moderate levels of ROS can play beneficial roles in plant growth and stress responses, excess ROS accumulation can lead to oxidative damage and cellular dysfunction. Therefore, maintaining redox homeostasis is critical for plant survival and stress adaptation.

**Types of ROS**

Phototrophs are essential for maintaining life on Earth because they transform solar light energy into metabolic energy. The cost of this is that they run the risk of suffering oxidative damages as a result of the many ROS, including $^1O_2$(singlet oxygen), $H_2O_2$(hydrogen peroxide), $O^{\bullet-}_2$ (superoxide radical), and $OH^{\bullet}$ (hydroxyl radical), which are produced as undesirable by-products. They are produced using just 1% to 2% of the total $O_2$ consumed by plants (Bhattacharjee, 2005). The various ROS members produced at various sites of plants are as follows:

***a) Superoxide Radical ($O^{\bullet-}_2$)***

Superoxide anion is a highly reactive free radical that is generated by the incomplete reduction of molecular oxygen. It is produced in the mitochondria during respiration, as well as in the chloroplasts during photosynthesis. Superoxide anion can react with other molecules to produce other ROS, such as hydrogen peroxide and hydroxyl radical. It can also react with nitric oxide to produce peroxynitrite, a highly reactive molecule that can damage cellular components (Halliwell, 2006).

***b) Singlet Oxygen ($^1O_2$)***

Singlet oxygen is a non-radical ROS that is generated by the interaction of excited chlorophyll molecules with molecular oxygen during photosynthesis. It can also be produced by other photosensitizers, such as porphyrins and flavins. Singlet oxygen is highly reactive and can damage cellular components, such as lipids and proteins. It can also act as a signaling molecule, modulating cellular processes such as gene expression and cell death (Krieger-Liszkay *et al.*, 2008).

***c) Hydrogen Peroxide ($H_2O_2$)***

Hydrogen peroxide is a non-radical ROS that is generated by the dismutation of superoxide anion. It is also produced by various enzymatic reactions, such as catalase and peroxidase. Hydrogen peroxide can diffuse across membranes and into cellular compartments, where it can oxidize cellular components and modulate cellular signaling pathways. At low concentrations, hydrogen peroxide can act as a signaling molecule, whereas at high concentrations, it can cause oxidative damage and cell death(Sharma *et al.*, 2012) (Peng *et al*., 2005)(Tanou *et al.*, 2009b).

***d) Hydroxyl Radical ($OH^{\bullet}$)***

Hydroxyl radical is a highly reactive free radical that is generated by the reaction of superoxide anion with hydrogen peroxide. It is considered to be one of the most reactive ROS and can damage cellular components, such as DNA, proteins, and lipids. Hydroxyl radical is not produced enzymatically but is instead generated by the Fenton and Haber-Weiss reactions, which involve the reaction of iron or

copper ions with hydrogen peroxide (Pinto *et al.*, 2003).

***e) Peroxyl radical (ROO•)***

Peroxyl radical is a free radical that is generated by the reaction of lipid radicals with molecular oxygen. It is highly reactive and can cause lipid peroxidation, a process that damages cellular membranes and can lead to cell death. Peroxyl radical is also involved in the generation of other ROS, such as hydroxyl radical and singlet oxygen. The peroxyl radical plays an important role in the oxidation of lipids, DNA damage, changes in the protein backbone, and the degradation of food.

***f) Alkoxy radical (RO•)***

Alkoxyl radicals are produced during lipid oxidative degradation or peroxidization without the aid of enzymes through the Fenton reaction, electron reductions, or the fusion of two peroxyl radicals. Alkyl radical oxidation may cause apoptosis and DNA changes. Alkoxyl radicals can damage DNA and trigger apoptosis since they are potent oxidizers (Kehrer, 2010).

**Sites of ROS production and ROS-scavenging**

Reactive oxygen species (ROS) are produced by several cellular processes, including photosynthesis, respiration, and oxidative metabolism. While ROS are essential for several physiological processes, their overproduction can lead to oxidative stress and damage to cellular components. Therefore, plants have developed an intricate system to regulate ROS levels and protect themselves from oxidative damage. ROS can be produced in multiple sites such as, in the mitochondria, plasma membranes, chloroplasts, endoplasmic reticulum, peroxisomes, and cell wall, both under normal and stressful conditions (Choudhury, 2013; Das, 2014). Different types of ROS and its site of production along with its functions, and the factors that elicit production are presented in Table 1.

**Table 1.** ROS site of production, functions, and the factors that elicit production (Choudhary, 2020; Sharma, 2012)

| S. no. | Site of production | ROS | Factors favoring ROS production | ROS function |
|---|---|---|---|---|
| 1. | Plasma membrane | Superoxide anion, hydrogen peroxide | Biotic stress, mechanical stress, high salinity, low temperature | Cell wall reinforcement, defence against pathogens, programmed cell death |
| 2. | Chloroplast | Singlet oxygen, superoxide anion, hydrogen peroxide | High light intensity, UV radiation, heat stress, high CO2, nutrient deficiency | Photosynthesis regulation, lipid peroxidation, signaling, programmed cell death |
| 3. | Mitochondria | Superoxide anion, hydrogen peroxide | High respiratory rate, oxidative phosphorylation uncoupling, nutrient deficiency | Energy production, apoptosis, signaling |
| 4. | Peroxisomes | Hydrogen peroxide, superoxide anion, hydroxyl radical | Fatty acid oxidation, photorespiration, abiotic stress | Detoxification, cell wall formation, signaling |
| 5. | Apoplast | Hydrogen peroxide, superoxide anion, singlet oxygen, hydroxyl radical | Biotic stress, abiotic stress, wounding, UV radiation, heavy metals | Defense against pathogens, programmed cell death, signaling |
| 6. | Endoplasmic reticulum | Hydrogen peroxide, superoxide anion | Protein folding stress, lipid biosynthesis, calcium homeostasis | Protein quality control, signaling |
| 7. | Vacuoles | Hydrogen peroxide | Metabolic processes, cellular waste management, programmed cell death | Cellular waste management, defense against pathogens, signaling |
| 8. | NADPH oxidases | Superoxide anion, hydrogen peroxide | Biotic stress, hormonal stimuli, high light intensity | Defense against pathogens, programmed cell death, signaling |

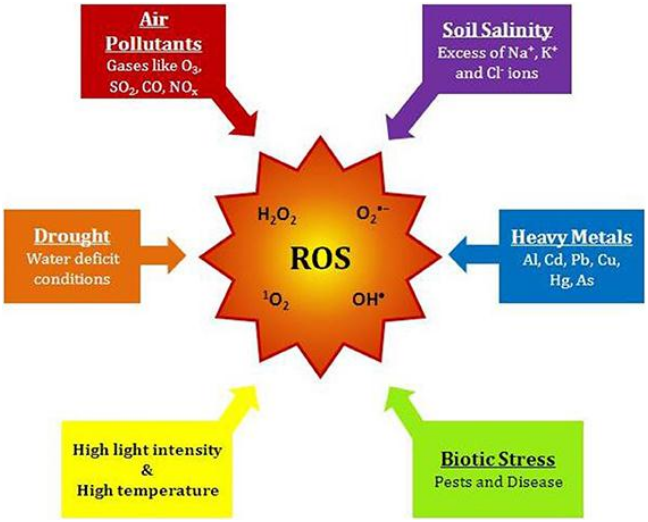


**Fig. 1.** Various causes responsible for the generation of ROS

**Role of ROS in plant development process**

ROS have been traditionally viewed as harmful molecules that cause oxidative damage to cellular components, such as lipids, proteins, and DNA, leading to cellular dysfunction and cell death. However, recent studies suggest that ROS also play important roles in plant signaling and defense responses, and that their accumulation can trigger adaptive responses to various stress conditions. Several studies have demonstrated the beneficial effects of ROS in plants. For example, ROS can act as signaling molecules to induce the expression of genes involved in stress responses, including defense genes, antioxidant genes, and genes related to stress tolerance (Mittler *et al*., 2011; Wrzaczek *et al*., 2013; Baxter *et al.,* 2014). ROS can also trigger the synthesis of secondary metabolites that can enhance plant defenses against pathogens or herbivores. The growth of the root apical meristem, shoot apical meristem, root hair cells, pollen tubes, leaves, and lateral roots are all processes in which ROS take an active part (Noctor *et al*., 2018, Mittler, 2017). For ROS to exert its regulatory activity, a careful balance between its production and scavenging must be maintained (de Pinto *et al.,* 2012; Sharma *et al*., 2012; Baxter *et al.,* 2014). Plants have developed the capacity to acquire a great degree of control over the toxicity of ROS, as evidenced by the applications of ROS as signalling molecules (Bhattacharjee, 2012; Mattila *et al*., 2015). ROS types and its cellular localization along with its role in developmental process are presented in Table 2.

**Table 2.** Source and type of ROS, cellular localization, and Role in Developmental Process

| Type of ROS | Sources | Cellular Localization | Role in Developmental Process |
|---|---|---|---|
| Superoxide | NADPH oxidases, mitochondria, peroxisomes | Cell wall, apoplast, cytoplasm, mitochondria, peroxisomes | Regulate cell proliferation and differentiation, stimulate cell wall synthesis and lignification |
| Hydrogen Peroxide | NADPH oxidases, peroxisomes | Cell wall, apoplast, cytoplasm, mitochondria, peroxisomes | Regulate root hair development, stomatal closure, programmed cell death, and response to biotic and abiotic stress |
| Singlet Oxygen | Photooxidation | Chloroplasts, mitochondria, peroxisomes | Regulate chloroplast biogenesis and photosynthesis, and plant growth |
| Hydroxyl Radical | Fenton reaction, photooxidation | Nucleus, cytoplasm, mitochondria, peroxisomes | Trigger programmed cell death, regulate plant growth and development |
| Peroxynitrite | Reaction of nitric oxide (NO) with superoxide radical (O2-•) | Nucleus, cytoplasm, mitochondria, peroxisomes | Modulate stomatal aperture, root growth, and plant response to biotic and abiotic stress |

Here are some of the roles of ROS in plant growth and development (Singh, 2016) are presented in Table 3a and 3b. The role of ROS can be broadly classified in 4 categories: -

a) ***Seed Germination:*** ROS are necessary for seed germination as they activate enzymes that help break down stored nutrients in the seed and initiate cell division. Studies have shown that ROS levels

increase during seed germination, and inhibiting ROS production in seeds leads to reduced germination rates (Bailly, 2004). ROS-mediated seed germination has been found to be regulated by multiple pathways, including gibberellin signalling, reactive nitrogen species, and ethylene signalling (Oracz, 2016).

**Table 3a.** ROS and its role in germination, development of root and leaf, and flowering process.

| ROS Type | Role in Seed Germination | Role in Root Development | Role in Leaf Development | Role in Flowering Process |
|---|---|---|---|---|
| Superoxide radical | Stimulates cell elongation and division, activates antioxidant defense systems | Involved in root hair elongation, cell elongation and differentiation, lateral root formation | Involved in chloroplast biogenesis, photosynthesis, and stomatal regulation | Promotes flowering through the activation of downstream genes such as FT and SOC1 |
| Hydrogen peroxide | Regulates seed dormancy, stimulates cell elongation and division, activates antioxidant defense systems | Stimulates root growth, regulates cell division and differentiation, involved in stress responses | Regulates stomatal closure, involved in senescence, programmed cell death, and stress responses | Regulates floral organ development, promotes the transition from vegetative to reproductive growth |
| Singlet oxygen | Causes oxidative damage to cellular components, regulates seed dormancy | Induces programmed cell death in roots under stress conditions | Involved in programmed cell death and regulation of photosynthesis | Regulates the expression of genes involved in flower development |
| Hydroxyl radical | Causes oxidative damage to cellular components, regulates seed dormancy | Involved in programmed cell death and regulation of root growth | Involved in programmed cell death and regulation of leaf growth | May play a role in floral senescence |
| Peroxynitrite | Causes oxidative damage to cellular components, regulates seed dormancy | Involved in root growth inhibition and programmed cell death | Involved in leaf growth inhibition and programmed cell death | Involved in the regulation of flowering time |

b) ***Root Development:*** ROS signalling is involved in the formation and elongation of roots, which are critical for nutrient uptake and water absorption. ROS production is higher in the root tip, where cell division and differentiation occur. Studies have shown that ROS signalling is involved in regulating the balance between cell division and differentiation, which is necessary for proper root development. ROS also regulate the formation of root hairs, which increase the surface area of the root and enhance nutrient uptake (Schiefelbein, 2015).

c) ***Leaf Development:*** ROS play a role in leaf development by controlling cell division and differentiation. They also regulate the size and shape of leaves. Studies have shown that ROS signaling is involved in leaf vein patterning and stomatal development, which are critical for proper leaf function. ROS also regulate leaf senescence, which is the programmed death of leaves (Vainonen, 2015; Mhamdi, 2010).

d) ***Flowering:*** ROS signaling plays a critical role in the timing and coordination of flowering in plants. Studies have shown that ROS levels increase during the transition from vegetative growth to reproductive growth. ROS signaling is involved in regulating the expression of genes that control flowering, including the photoperiodic pathway, the autonomous pathway, and the vernalization pathway (Pucciariello, 2012).

e) ***Defense Against Pathogens and Pests:*** ROS production is a crucial component of plant defense against pathogens and pests. ROS can damage pathogen cell walls and activate defense genes. Studies have shown that ROS signaling is involved in the response to a wide range of pathogens, including bacteria, fungi, and viruses (Wang, 2013). ROS also play a role in the plant's response to herbivores, including insects and nematodes (Maffei, 2007).

f) ***Abiotic Stress Response:*** ROS signaling plays a vital role in the plant's response to abiotic stresses, such as drought, salinity, and high temperatures. ROS signaling helps activate stress-responsive genes and regulate stress-related physiological processes. Studies have shown that ROS signaling is involved in the response to a wide range of abiotic stresses, including drought, salinity, and high temperatures (Zhu, 2016; Chen, 2019).

g) ***Senescence and Programmed Cell Death:*** ROS play a role in senescence and programmed cell death by activating enzymes that degrade cellular components. Studies have shown that ROS signaling is involved in leaf senescence, which is the programmed death of leaves. ROS also play a role in the response to stress-induced programmed cell death, which occurs when plants are exposed to high levels of stress (Gechev, 2006).

**Table 3b.** ROS and its role in defense, abiotic stress, and senescence

| ROS Type | Role in Defense Against Pathogens and Pests | Role in Abiotic Stress Response | Role in Senescence and Programmed Cell Death |
|---|---|---|---|
| Superoxide radical | Microbicidal activity, signal transduction | Involved in signal transduction and defense response | Triggers senescence and cell death |
| Hydrogen peroxide | Antimicrobial activity, signal transduction | Signaling molecule, activates MAPK cascade, activates antioxidant enzymes, and stimulates stomatal closure | Activates senescence and cell death pathways, mediates the balance between cell survival and death |
| Hydroxyl radical | Microbicidal activity | Damages proteins, DNA, and membranes | Causes DNA damage and protein oxidation, triggers apoptosis |
| Singlet oxygen | Antimicrobial activity | Inhibits photosynthesis, activates stress response genes | Causes oxidative damage, promotes programmed cell death |
| Peroxynitrite | Microbicidal activity | Causes nitrosative stress, activates antioxidant enzymes | Causes DNA damage and protein oxidation, triggers apoptosis |

**Effect of ROS generation on cellular processes**

***a) ROS-mediated control of the cell cycle, cell division, cell expansion and cell death***

Although excessive ROS production has been linked to oxidative damage and cell death, recent research has demonstrated that ROS also play important roles in the regulation of cell cycle, cell division, cell expansion, and cell death. Although the mechanisms underlying this reaction are still largely unknown, stress in plants frequently results in reduced growth and cell cycle halt. It is understood that reductive and oxidative signals are necessary for transitions between the phases of the cell cycle and that redox cycles are conserved within the cell cycle (Menon and Goswami, 2007; Diaz-Vivancos *et al.,* 2015; de Simone *et al.,* 2017). Recent studies have clarified how ROS and changes in redox states can affect such phase-to-phase transitions and progressions, which are primarily controlled by a complex machinery of interacting cyclins (CYCs) and cyclin-dependent kinases (CDKs).

ROS have been implicated in the regulation of the cell cycle. During the G1 phase, low levels of ROS are produced, and these promote cell proliferation by activating several key signaling pathways, including the MAPK/ERK pathway and the PI3K/Akt pathway. As cells progress through the cell cycle, ROS levels increase and contribute to the regulation of the G2/M transition. ROS are known to activate the ATM/Chk2/p53 pathway, which is critical for the arrest of cells in the G2 phase and the prevention of DNA damage-induced cell death. Redox disturbances have an impact on both the activity and transcript levels of CYCs and CDKs (Reichheld *et al*., 1999; Foyer *et al*., 2018). For example, TEOSINTE BRANCHED1-CYCLOIDEA-PROLIFERATING CELL FACTOR1 (TCP) transcription factors directly influence cell cycle components as a result of redox processes (Kadota *et al.,* 2005). Moreover, CYCs levels were regulated by TCPs at transcription level, potentially through interactions with CYC promoters, and therefore, feature a conserved redox-sensitive cysteine residue that is necessary for DNA binding. This shows that the interaction between a TCP transcription factor and its promoter may be hindered under oxidising circumstances as a result of the creation of disulfide bonds (Viola *et al*., 2013, 2016).

ROS also play an important role in cell division. Studies have shown that ROS production is required for cytokinesis, the final stage of cell division. Specifically, ROS are thought to regulate the assembly and contraction of the contractile ring, which is required for the separation of daughter cells. ROS are also known to modulate the activity of microtubules, which are critical for the proper alignment and segregation of chromosomes during mitosis. Moreover, in wheat (Triticum sp.) and Arabidopsis root tip cells, pharmacological disruption of ROS homeostasis produces mostly aberrant tubulin polymer synthesis and disrupts effective cell plate assembly, ultimately leading to disturbed cytokinesis (Livanos *et al.,* 2012a, b). Similar to the genetic disruption of NADPH oxidases, which produce ROS, and mitogen-activated protein kinases, which are involved in ROS

signalling, tubulin becomes disorganised, which emphasises the need for a closely regulated ROS balance during cytokinesis (Takeda *et al*., 2008; Kosetsu *et al.,* 2010; Yao *et al.,* 2011).

ROS are also able to modulate cell expansion, via their effects on the cell wall. ROS are known to promote cell elongation and expansion by regulating cell wall remodeling and the activity of cell wall-loosening enzymes. Additionally, ROS have been shown to activate a number of signaling pathways, including the MAPK/ERK pathway, which is involved in the regulation of cell growth and differentiation. For instance, apoplastic $H_2O_2$, hydroxyl radicals, and superoxides alter the rigidity and relaxation of cell walls, which in turn affects the pace of cell expansion. Although several oxidant sources are acknowledged, little is known about how they are regulated. The peroxidative and hydroxylatic activities of apoplastic class III peroxidases have antagonistic effects on the stiffness of cell walls in addition to NADPH oxidases, amine, and oxalate oxidases (Passardi *et al*., 2004; Schmidt *et al.,* 2016). Peroxidases typically control $H_2O_2$ levels in a peroxidative mode by oxidising a variety of substrates. By doing this, they aid in the crosslinking of extensins and phenolics, which increases the stiffness and decreases the ability of cell walls to elongate. On the other hand, it has been shown that hydroxyl radical production can break pectins and xylogucans, which makes it easier to release cell walls (Fry, 1998; Passardi *et al.,* 2004). Genetic modifications of different class III peroxidases have shown that this property of peroxidases being connected with both cell elongation and growth-restricting processes is manifested in their divergent impacts on growth rates (Lu *et al*., 2014; Schmidt *et al.,* 2016).

Finally, ROS play a critical role in the regulation of cell death. Excessive ROS production can lead to oxidative damage and cell death via several mechanisms, including apoptosis, necrosis, and autophagy. However, ROS can also promote cell survival by activating several signaling pathways, including the PI3K/Akt pathway and the NF-kB pathway. In response to numerous stimuli, such as development and bacterial challenges, increased ROS production happens in either a temporary or permanent manner, also known as an oxidative burst, and can start cell death signalling (Van Breusegem and Dat, 2006). The tapetum, seed coat, endosperm, and lateral root cap are a few tissues and organs where development-associated programmed cell death (PCD) occurs (Daneva *et al.,* 2016). For instance, PCD occurs in tapetal cells, which is necessary for the production of microspores. Surprisingly, the rice (Oryza sativa) mutant defective in tapetum cell death 1 (dtc1) fails to accumulate ROS and demonstrates delayed tapetum PCD resulting in male sterile plants (Yi *et al.,* 2016).

Overall, the effects of ROS on basic cellular processes – the cell cycle, cell division, cell expansion and cell death – are thought to contribute, acting in concert via interactions between plant phytohormonal pathways, to the multiple functions of ROS during the plant life cycle.

***b) ROS in Cell Proliferation and Differentiation***

It has been clear in recent years that plants' reaction to biotic and abiotic environmental stimuli, as well as programmed cell death (PCD), are all regulated by ROS, which are crucial signalling molecules (Alvarez et al. 1998; Blokhina *et al.* 2003; Navrot *et al*. 2007). Throughout the process of respiration and photosynthesis, ROS are continuously created. In several processes related to plant growth and development, plant cells produce ROS, including superoxide and H2O2 (Schroeder *et al*. 2001b; Foyer &Noctor 2005). Moreover, the generation of bursts of superoxide at the plasma membrane is one of the primary ways that plants communicate information about changes in the environment (Doke *et al*. 1994). Yet, the prevalent opinion continues to consider them as an unavoidable burden balanced with the advantages of using oxygen as a respiratory electron acceptor.

Cell division and cellular differentiation are the primary processes that control growth and development in multicellular organisms. Early organogenesis termination results from disruption of the balance between these two stages, which may cause aberrant growth (Zhang *et al.,* 2008). ROS homeostasis controls the change from cellular proliferation to cell elongation during the early phases of differentiation (Tsukagoshi *et al*., 2010).

The example of such process involves that, at the beginning of each stage of cell differentiation in the fungus Neurosporacrassa, a hyperoxidant condition takes place that supports the development of conidia (Gessler *et al.,* 2007). The hyperoxidant state, according to Aguirre *et al*. (2005), develops when the amount of ROS produced surpasses the antioxidant capability of the cell. The fact that antioxidants impede developmental processes is well known as an outcome of this example, which raises the possibility that ROS are also necessary for similar processes in plants. On the other hand, it is expected that a lack of antioxidant enzymes will lead to increased ROS levels and enhanced cell differentiation. ROS are significant regulators of plant development because they play crucial functions in cell proliferation. The spatial control of ROS generation is a key factor influencing plant shape. NADPH oxidases (NOXs), which use NADPH as an electron donor to create the superoxide radical ($O_{2)}$, which has been proven to have a role in development, produce ROS (Gapper & Dolan 2006). The roots of plants homozygous for loss-of-function rhd2 mutations exhibit lower levels of ROS and are 20% shorter than the wild type, showing that cell growth is faulty in these plants

(Foreman *et al*. 2003). ROS are significant regulators of plant development because they play crucial functions in cell proliferation. The spatial control of ROS generation is a key factor influencing plant shape. NADPH oxidases (NOXs), which use NADPH as an electron donor to create the superoxide radical ($O_2^-$), which has been proven to have a role in development, produce ROS (Gapper & Dolan 2006). The roots of plants homozygous for loss-of-function rhd2 mutations exhibit lower levels of ROS and are 20% shorter than the wild type, showing that cell growth is faulty in these plants (Foreman *et al*. 2003; Renew *et al.* 2005). Inhibitors like diphenylene iodonium (DPI) were employed by Liszkay *et al.* (2004) to demonstrate how NOX-derived ROS regulate cell growth in maize (Zea mays) roots. ROS are crucial for both wall cross-linking, which prevents cell expansion during the stoppage of growth and cell differentiation, and cell-wall loosening in developing tissues (Potikha *et al.* 1999; Liszkay *et al.* 2004; Ros-Barcelo et al. 2002).The oxidative cross-linking of cell wall glycoproteins and polysaccharides by peroxidase, which reduces cell wall extensibility, is a critical mechanism by which H2O2 modulates extension development in plants (Schopfer 1996).On the other hand, the secretory pathway's H2O2 production may encourage the development of substantial hemicellulose coagula, which will have a wall-loosening impact (Fry *et al*. 2000). OH radicals, which are found in the cell walls of elongating organs in vivo (Liszkay *et al.* 2004; Renew et al. 2005), control growth by permitting walls to extend through the scission of xyloglucan polymers (Fry 1998). Membrane-bound NAD(P)H oxidases, apoplastic oxalate oxidases, peroxidases, and amine oxidases are the primary potential ROS-delivering processes in the cell wall. Amine oxidases are ubiquitous polycationic enzymes that catalyse the oxidative de-amination of polyamines, which are engaged in essential cell-life activities (Bagni and Tassoni 2001; Seiler 2004). The polyamine oxidases that contain flavin and the copper-containing amine oxidases (CuAO) are examples of amine oxidases (PAOPlant amine oxidases are more than just a way to control cellular polyamine levels; through their reaction byproducts, aminoaldehydes, 1,3-diaminopropane (DAP), and hydrogen peroxide, they contribute to crucial physiological activities (Bouchereau *et al.* 1999; Walters 2003). As amine oxidases are widely distributed in tissues that are undergoing lignification or significant wall-stiffening processes, it is possible that these enzymes may have an impact on plant growth and development by stiffening and hardening cell walls (Cona *et al.* 2005; Paschalidis&Roubelakis-Angelakis 2005).

***c) The role of ROS during germination***

Reactive oxygen species (ROS) have been found to play a crucial role in various aspects of plant growth and development, including seed germination and meristem development. Seed germination is a complex process that involves the activation of various biochemical pathways and physiological changes. ROS are known to play a crucial role in seed germination by regulating cell cycle progression, cell wall remodeling, and hormone signaling. In Arabidopsis thaliana, ROS production is known to be required for germination, as inhibition of ROS production leads to reduced germination rates (Oracz, 2009). ROS are thought to regulate germination by modulating the activity of enzymes involved in the breakdown of cell wall polysaccharides and by activating signaling pathways involved in hormone responses.

Plant embryos and the surrounding endosperm in dry, dormant seeds exhibit very limited metabolic activity, and ROS generation is therefore assumed to be very low (Bailly *et al.,* 2008). However, metabolism quickly resumes after seed imbibition and throughout germination (Rajjou *et al*., 2012), and this quick metabolic start appears to be associated with enhanced ROS generation via a number of pathways and at a number of subcellular locations. This entails mitochondrial respiration, lipid catabolism, lipid -oxidation in the glyoxysomes, and synthesis via NADPH oxidases (Rajjou *et al.,* 2012; Wojtyla *et al.,* 2016; Ishibashi *et al*., 2017). Experiments showing that exogenously applied oxidants, such as $H_2O_2$, and a pharmacologically or genetically influenced decrease in catalase or in other antioxidant activities, were shown to positively influence the release of dormancy and the beginning of germination, have been used to support the spatiotemporal correlation of increased ROS production and accumulation during the onset of germination (Leymarie *et al*., 2012; Basbouss-Serhal *et al.,* 2017). Moreover, it has been demonstrated that overexpressing CAT in barley (Hordeum vulgare) seeds inhibits early germination (Ishibashi *et al*., 2017). Increased ROS levels are therefore essential for successful germination and serve as promising signs for the breaking of dormancy (Bailly *et al.,* 2008). After seed imbibition, ROS levels rise and serve as a primary force for germination. Yet, over a specified limit, ROS are either too strong to negatively impact embryo viability and prohibit or delay germination, or too low to allow germination (Bailly et al., 2008). The requirement to strictly regulate ROS homeostasis during germination results in the creation of an "oxidative window" for germination, which limits effective seedling development within specific limits of elevated ROS levels. Moreover, the increase in ROS concentration was also observed during the processes such as the weakening of endosperm, the cell walls loosening, and the radicle lengthening, etc. (Barba-Espin *et al.,* 2010).

After germination, the apical meristem of the seedling is responsible for the continued growth and development of the plant. ROS are known to play an

important role in meristem development by regulating cell proliferation and differentiation. In particular, ROS have been shown to regulate the balance between stem cell maintenance and differentiation in the apical meristem (Tsukagoshi, 2019). ROS are thought to activate several signaling pathways, including the MAPK/ERK pathway and the WUSCHEL-RELATED HOMEOBOX (WOX) pathway, which are involved in the regulation of stem cell fate. Recent research has also shown that ROS can modulate the activity of transcription factors involved in the regulation of meristem development. For example, the transcription factor NAC1 is known to be involved in the regulation of meristem size and differentiation. ROS have been shown to regulate NAC1 activity by inducing its degradation via the 26S proteasome pathway. Additionally, ROS have been shown to regulate the activity of other transcription factors, including MYB30 and ARF6, which are involved in the regulation of meristem development (Xie, 2000).In conclusion, ROS play a crucial role in seed germination and meristem development by regulating cell cycle progression, cell wall remodeling, hormone signaling, and stem cell fate. The modulation of ROS levels and signaling pathways may represent a potential target for the improvement of seed germination rates and the regulation of meristem development.

***d) ROS homeostasis drives organ growth***

Reactive oxygen species (ROS) play a crucial role in organ growth and development by regulating various cellular processes. ROS homeostasis, which refers to the balance between ROS generation and scavenging, is essential for proper organ growth and development in plants. Studies have shown that ROS homeostasis is critical for root and shoot growth in plants. For example, in Arabidopsis thaliana, the transcription factor NAC016 has been shown to regulate ROS homeostasis and promote root growth by enhancing the expression of ROS scavenging genes (Li *et al.*, 2020). Similarly, the transcription factor MYB36 has been shown to control ROS homeostasis and promote shoot growth by regulating the expression of genes involved in ROS scavenging and cell wall biosynthesis.

The majority of plant roots exhibit indeterminate growth, which involves not only ongoing primary root cell division and expansion but also the growth of lateral roots (LRs) and root hairs. Studies have demonstrated that all of these processes are impacted by altered ROS homeostasis, which inhibits primary root growth, stimulates LR emergence, and increases root hair growth. (Foreman *et al*., 2003; Orman-Ligeza *et al.*, 2016). Tsukagoshi (2016) recently given an overview of ROS function in regulating root growth and development. He emphasises that interactions between ROS and auxin signalling, which are essential in determining root architecture (Du and Scheres, 2018), partially control root growth and development.For instance, in root hairs, at least two auxin-regulated transcriptional regulators—ROOT HAIR DEFECTIVE 6-LIKE 4 (RSL4) and MEDIATOR 25 (MED25)—promote root hair elongation through the auxin-controlled transcriptional regulation of NADPH oxidases and class III peroxidases (Foreman et al., 2003; Sundaravelpandian *et al.*, 2013; Mangano et al., 2017). Also, a proper balance between $H_2O_2$ and superoxide levels may serve as a signal to control the development of root hair cells, according to research on ROS levels (Sundaravelpandian *et al*., 2013). The misexpression of parts of the ROS processing system has been linked to a number of mutants that exhibit growth problems, including a non-exhaustive list of mutants with leaf growth defects. Moreover, studies have shown that ROS homeostasis also plays a role in plant response to environmental stimuli, such as light and temperature. For example, in Arabidopsis thaliana, the photoreceptor cryptochrome 1 regulates ROS homeostasis and promotes seedling growth under blue light (Wang *et al.*, 2016). Similarly, in rice plants, the transcription factor OsJAZ9 regulates ROS homeostasis and controls thermotolerance by modulating the expression of ROS scavenging genes (Hu *et al*., 2019).New information has been gathered from researching cat2 mutants in particular, which exhibit growth inhibition as a result of increased photorespiratory $H_2O_2$availability, which causes SA aggregation and photoperiod-dependent activation of a pathogenesis-related pathway (Queval *et al*., 2007; Mhamdi *et al*., 2010a). Furthermore, it has been demonstrated that certain ROS components serve specific roles in the transmission of $H_2O_2$ signals and in connecting $H_2O_2$ to phytohormone pathways, even though they are not necessary for the normal growth and placement of leaves (i.e. into a "rosette" formation) in Arabidopsis. (Tognetti *et al.*, 2010; Han *et al*., 2013a; Rahantaniaina *et al.*, 2017).

In addition to promoting organ growth, ROS homeostasis also regulates organ size and shape. For instance, in tomato plants, the transcription factor SlCDF1 regulates ROS homeostasis and controls leaf morphology by affecting cell proliferation and expansion (Xie *et al.*, 2018). Similarly, in Arabidopsis thaliana, the transcription factor TCP4 has been shown to regulate ROS homeostasis and control leaf shape by affecting cell proliferation and differentiation (Kieffer *et al.*, 2011). In addition to influencing cell proliferation throughout development, ROS may also play a role in regulating organ number and initiation, according to Sagi et al. (2004). ROS and glutathione are among the signals that aid in the development of the legume-rhizobia symbiosis (Shaw & Long 2003; Pauly *et al.* 2006). In a semiaquatic legume, ethylene and ROS serve as positive transducers downstream of the Nod factor response and are necessary for the genesis of root nodules. Moreover, many studies have linked antioxidants and ROS to nodule senescence (Becana

*et al*. 2000; Matamoros *et al.* 2003). Many plant hormone responses have been linked to the involvement of ROS as second messengers (Kwak *et al.* 2006). Overall, these studies suggest that ROS homeostasis plays a critical role in plant growth and development by regulating various cellular processes, including cell proliferation, expansion, and differentiation. Further research is needed to elucidate the molecular mechanisms underlying ROS homeostasis and its regulation of organ growth and development in plants.

***e) Redox signalling in flower development***

Reactive oxygen species (ROS) play a crucial role in the redox signaling pathway, which regulates various cellular processes including flower development. The redox signaling pathway involves the generation of ROS as a result of metabolic processes and environmental stresses, which are then rapidly detoxified by the antioxidant defense system to maintain ROS homeostasis. However, in certain cases, ROS can act as signaling molecules and trigger downstream signaling events by oxidizing and modifying proteins, lipids, and nucleic acids (Han, 2019). In flower development, ROS have been shown to regulate various processes such as cell proliferation, differentiation, and senescence. For example, ROS are involved in the regulation of floral organogenesis, which is the process by which floral organs such as petals and sepals are formed. ROS signaling also plays a role in regulating the timing of floral transition and in the development of floral organs (Mittler, 2017; Hu, 2017).

Recent studies have addressed the critical role that ROS play in the development of plant reproductive organs and tissues (Jiménez-Quesada *et al*., 2016; Schippers *et al*., 2016). The buildup of ROS at the tip of pollen tubes is required for their successful development towards the female gametophyte, according to pharmacological methods and ROS-staining tests (Potock *et al*., 2012). The activation of these NADPH oxidases by calcium and phosphorylation is required for appropriate growth, and genetic evidence for the involvement of two RBOH genes (RBOHH and RBOHJ) in pollen tube growth has been reported (Duan *et al.*, 2014; Lassig et al., 2014). Recent studies have identified several transcription factors and signaling pathways that are regulated by ROS during flower development. For instance, the transcription factor AGAMOUS-LIKE 15 (AGL15) is involved in the regulation of floral meristem identity and floral organogenesis, and its expression is modulated by ROS levels. Similarly, ROS have been shown to regulate the expression of several genes involved in flower development, including those encoding MADS-box transcription factors, which are critical regulators of flower development. Several studies have also shown that ROS are involved in regulating pollen development, fertilization, and seed formation in plants. For example, ROS are required for pollen tube growth and guidance towards the ovule during fertilization. In addition, ROS signalling has been shown to play a role in the regulation of seed dormancy and germination (Mhamdi, 2018).Overall, these studies demonstrate the important role of ROS in flower development through their involvement in redox signalling pathways.

## CONCLUSIONS

Reactive oxygen species (ROS) are generated in different organelles of plant cells, including chloroplasts, mitochondria, and peroxisomes, as by-products of various metabolic processes or under stress conditions. ROS play a dual role in plant development, acting as signalling molecules that regulate various cellular processes, such as growth, differentiation, and programmed cell death, and as oxidative stress factors that can damage cellular components and impair plant development. During germination, ROS are essential for the activation of various enzymes and signalling pathways that promote seed germination and seedling growth. However, excessive ROS accumulation can lead to oxidative damage and inhibit germination. In flower development, ROS play a crucial role in regulating the balance between cell proliferation and differentiation, as well as in the formation and differentiation of floral organs. ROS also participate in the signal transduction pathways that control the expression of genes involved in flower development.

In conclusion, the site of ROS generation in plants, and the amount of ROS produced, can significantly affect plant development and cellular processes, including cell proliferation and differentiation, seed germination, organ growth, and flower development, etc. Understanding the molecular mechanisms underlying ROS production and signalling in plants is essential for developing strategies to enhance plant growth and productivity under stress conditions.

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