Chapter 4
Reactive Oxygen Species Production and Scavenging During Seed Germination of Halophytes

Aysha Rasheed, Sarwat Ghulam Rasool, Bilquees Gul, M. Ajmal Khan, and Abdul Hameed

Contents

Abstract Reactive oxygen species (ROS) are excited or partially reduced forms of atmospheric oxygen, which are continuously produced during aerobic metabolism like many physiochemical processes operating throughout seeds' life. ROS were previously known merely as cytotoxic molecules, but now it has been established that when tightly regulated to low levels they perform numerous beneficial functions in plants including many critical roles in seed physiology. This ROS homeostasis is achieved owing to the presence of a well-coordinated antioxidant system, which is composed of many enzymatic and nonenzymatic components. ROS reportedly facilitate seed germination via cell wall loosening, endosperm weakening, signaling, and/or decreasing abscisic acid levels. Most of the existing knowledge about ROS homeostasis and functions is based on the seeds of crops and model plants. This information about the seeds of non-crops such as halophytes is limited to just a few studies. Furthermore, mechanisms underlying ROS functions such as downstream targets, cross talk with other molecules, and alternative routes are still obscure. The objective of this article is to present an overview about (i) general mechanisms of

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ROS homeostasis in plants, (ii) ROS homeostasis in dry seeds, (iii) ROS metabolism in germinating seeds under optimal conditions, and (iv) ROS flux in germinating seeds under stress conditions with special emphasis on halophytes.

Keywords Antioxidant defense system · Halophyte · Oxidative damage · Salinity · Seed germination · Reactive oxygen species

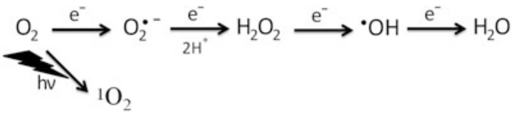
Abbreviations

$^{\bullet}OH$	Hydroxyl radical
ABA	Abscisic acid
AOI	Active oxygen intermediates
AOS	Active oxygen species
APX	Ascorbate peroxidase
AsA	Ascorbate
CAT	Catalase
DHAR	Dehydroascorbate reductase
GPOX	Guaiacol peroxidase
GPX	Glutathione peroxidase
GR	Glutathione reductase
GSH	Reduced glutathione
GSSG	Oxidized glutathione
GST	Glutathione S-transferases
H_2O_2	Hydrogen peroxide
MDAR	Monodehydroascorbate reductase
NaCl	Sodium chloride
NADPH	Nicotinamide adenine dinucleotide phosphate
$O_2^{\bullet -}$	Superoxide radical
O_2	Oxygen
$^1O_2$	Singlet oxygen
POD	Peroxidase
Prx	Thiol peroxidase type II peroxiredoxin
ROI	Reactive oxygen intermediates
ROS	Reactive oxygen species
SOD	Superoxide dismutase

4.1 Introduction

Reactive oxygen species (ROS) are excited or partially reduced forms of atmospheric oxygen, generated in all living cells by the transfer of one, two, or three electrons to oxygen to produce a superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide

Fig. 4.1 Formation of common ROS



(H_2O_2), or hydroxyl radical ($^\bullet$OH), respectively, or by the energetic excitation of oxygen to produce singlet oxygen ($^1O_2$) (Fig. 4.1). Different terminologies such as active oxygen species (AOS), reactive oxygen intermediates (ROI), active oxygen intermediates (AOI), and sometimes oxygen free radicals are also used for ROS (Gutteridge and Halliwell 2000; Apel and Hirt 2004; Ray et al. 2012; Suzuki et al. 2012; Diaz-Vivancos et al. 2013; Waszczak et al. 2018). ROS appeared on Earth about 2.5 billion years ago along with atmospheric oxygen and since then have played a key role in the evolution of both prokaryotic and eukaryotic organisms (Anbar et al. 2007; Ślesak et al. 2012).

Although conventionally reported as toxic chemical species, under optimal conditions ROS are generally formed in low quantities and serve as signaling molecules for many cell processes (Suzuki et al. 2012; Baxter et al. 2013; Mittler 2017; Turkan 2017). Being signaling molecules, ROS are quite versatile because of their reactivity, diverse production sites, and their potential permeability for biological membranes (Møller et al. 2007; Møller and Sweetlove 2010; Farmer and Mueller 2013). It has been well-established that ROS have large number of beneficial/regulatory roles in living organisms including plants, animals, and other eukaryotes (Halliwell 2006; del Río 2015; Choudhury et al. 2017; Mittler 2017; Turkan 2017). For instance in higher plants, ROS have a vital role in the regulation of different developmental processes, stress signaling, interactions with other organisms, systemic responses and programmed cell death, etc. (Gutteridge and Halliwell 2000; del Río 2015; Choudhury et al. 2017). ROS are produced as metabolic by-product primarily in chloroplasts, mitochondria, and peroxisomes but are also reported to be synthesized in many other cell compartments where there are proteins or any other molecule with a redox potential high enough to excite or donate an electron to atmospheric oxygen (Fig. 4.2; Apel and Hirt 2004; Farmer and Mueller 2013; Mittler 2017). Under optimal conditions, a synchronized action of different antioxidant enzymes and substances helps plant cells to maintain ROS homeostasis (Foyer and Noctor 2005, 2009; Gill and Tuteja 2010; Mittler 2017). However, under stress conditions, production of ROS overwhelms the capacity of cell's intrinsic antioxidant defense to detoxify them; as a result, oxidative damage to different cell components such as membrane lipids, proteins, and nucleic acids occurs (Jithesh et al. 2006; Ozgur et al. 2013; Shabala 2017). These deleterious effects of ROS are often termed as oxidative stress (Inzé and Van Montagu 1995; Mittler 2002; Shabala 2017). Currently, a large number of articles including many reviews exist on ROS homeostasis and redox metabolism in the vegetative tissues of the plants (Foyer and Noctor 2009; Gill and Tuteja 2010; Choudhury et al. 2017; Turkan 2017; Czarnocka and Karpiński 2018). However, there is generally a dearth of knowledge about production, scavenging, and roles of ROS in seeds, especially during their germination stage (Bykova et al.

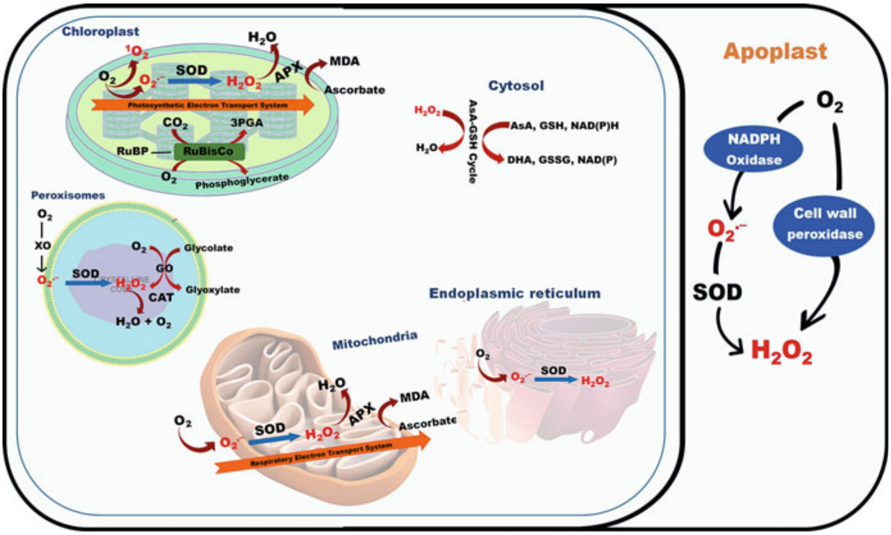


Fig. 4.2 General outline of ROS production and scavenging in plants. ROS are produced at several sites in the plant cells such as chloroplasts, mitochondria, peroxisomes, apoplast, endoplasmic reticulum, etc.

2015; Pehlivan 2017). This information is even scarcer for the seeds of halophytes (Kranner and Seal 2013), which are naturally salinity tolerant plants of saline habitats and hold immense potential to become non-conventional crops for arid saline lands in the future (Panta et al. 2014; Shabala 2017). The aim of this article is to present an overview of the findings on (i) general mechanisms of ROS homeostasis in plants, (ii) ROS production and scavenging in dry seeds, (iii) ROS metabolism in germinating seeds under optimal conditions, and (iv) ROS flux in germinating seeds under stress conditions.

4.2 ROS Production and Scavenging in Plants: General Outline

Plants metabolize atmospheric oxygen (O_2) in a number of processes including photosynthesis, photorespiration, and respiration; consequently, ROS are continuously produced as a by-product of aerobic metabolism (Foyer and Noctor 2005). During these aerobic processes, formation of ROS by activation of O_2 occurs by two mechanisms: (i) stepwise monovalent reduction of O_2 leads to the formation of $O_2^{\bullet-}$, H_2O_2, and $^{\bullet}OH$ and (ii) energy transfer to O_2 that leads to the formation of $^1O_2$. In green tissues of the plants, main sites for ROS production are the chloroplasts, which produce $O_2^{\bullet-}$, H_2O_2, and O_2^1 as a by-product of photosynthesis (Miller et al. 2010), whereas mitochondria produce $O_2^{\bullet-}$ and H_2O_2 as a by-product of respiration and peroxisomes generate H_2O_2 as a by-product of photorespiration (Miller et al. 2010). ROS are also produced due to the activation of the apoplast and plasma membrane-bound ROS-producing enzymes such as NADPH oxidases, various peroxidases, and superoxide dismutases (SODs) (Mittler 2002; Apel and Hirt 2004; Miller et al. 2010; Mittler et al. 2011; Czarnocka and Karpiński 2018). NAD(P)H-dependant electron transport involving Cty P450 in endoplasmic reticulum could be another source of $O_2^{\bullet-}$ production (Mittler 2002). Under stress conditions, accumulation of $O_2^{\bullet-}$ and H_2O_2 in the presence of heavy metals (e.g., Fe^{2+} and Cu^{+}, etc.) generates hydroxyl radical ($^{\bullet}OH$) via Haber-Weiss reactions, which is considered the highly toxic ROS and has been reported in many organelles such as chloroplasts and apoplasts (Koppenol 2001; Demidchik 2015).

Under optimal conditions, ROS content is tightly regulated to low levels via a well-coordinated antioxidant system, which is composed of many enzymatic and nonenzymatic antioxidants (Mittler 2002; Apel and Hirt 2004; Czarnocka and Karpiński 2018). Enzymatic components of antioxidant defense include superoxide dismutases (SODs), catalases (CATs), and enzymes of Foyer-Halliwell-Asada pathway, while key nonenzymatic components are ascorbate, glutathione, tocopherol, and phenolic compounds (Jithesh et al. 2006; Sharma et al. 2012). Many of these antioxidants such as SODs and CATs are believed to be originated as early as 4.1–3.6 billion years ago, even prior to the great oxidation event (Inupakutika et al. 2016), that made it possible for the organisms to deal with ROS which appeared on Earth about 2.5 billion years ago along with atmospheric oxygen (Anbar et al. 2007; Inupakutika et al. 2016).

Superoxide dismutases (SODs; EC 1.15.1.1) act as “the first line of defense against ROS” by converting $O_2^{\bullet-}$ into H_2O_2. Three major types of SODs, i.e., cytosolic Cu-Zn SOD, mitochondrial Mn-SOD, and chloroplastic Fe-SOD, have been reported from plants (Alscher et al. 2002). Often a positive relationship between SOD activity and salinity tolerance is reported in both glycophytes and halophytes (Jithesh et al. 2006; Prashanth et al. 2008; Ozgur et al. 2013; Bose et al. 2014). However, halophytes are known to possess comparatively higher levels of SOD activity/expression as compared to the glycophytes. For example, SOD activity invoked promptly and to a higher level in *Cakile maritima* (halophyte) as compared to *Arabidopsis thaliana* (glycophyte) upon salt exposure (Ellouzi et al. 2011). Similarly, SOD activities in mangrove *Rhizophora stylosa* were more than 40 times than those of peas (Cheeseman et al. 1997). Hence, a quick and stronger induction of SOD activity in halophyte might be a key player in stress signaling in halophytes.

Catalases (CATs; *EC* 1.11.1.6) are haem-containing tetrameric antioxidant enzymes involved in detoxification of H_2O_2 into water and oxygen (Willekens et al. 1997). CATs perform multifaceted roles in plants such as in photorespiration (Canvin 1990), scavenging of H_2O_2 during β-oxidation of fatty acids in germinating seeds (Willekens et al. 1995), and stress tolerance (Anjum et al. 2016). Often multiple isoforms of CATs are found in plants, which are mainly localized in peroxisomes in most plants (Jithesh et al. 2006; Su et al. 2014) and also in mitochondria of some plants (Scandalios 1990; Shugaev et al. 2011). The reaction catalyzed by CATs is very fast with reaction rate constant of $K \approx 10^7\ \mathrm{M}^{-1}\ \mathrm{s}^{-1}$which means each unit of CAT can detoxify millions of molecules of H_2O_2 per second (Deisseroth and Dounce 1970). Degradation constant of the CAT protein is 0.263 day^{-1} (Eising and Süselbeck 1991), while K_M value of CATs for H_2O_2 ranges between 40 and 600 mM (Del Río et al. 1977; Arabaci 2011). CATs, unlike other antioxidant enzymes, detoxify H_2O_2 in an energy-efficient manner, as they do not need reducing equivalent for activity, hence considered indispensable for ROS quenching under stress conditions (Anjum et al. 2016). Jithesh et al. (2006) reviewed that exposure to salinity may lead to all the possible (i.e., rise, decline, and unchanged) responses of CAT activity/expression in halophytes. However, halophytes generally tend to possess higher CAT activity/expression levels than the glycophytes (Bose et al. 2014). For instance, halophyte *Hordeum marinum* showed higher constitutive levels of CAT compared to *H. vulgare* (Seckin et al. 2010).

Enzymes of Foyer-Halliwell-Asada pathway (also known as ascorbate-glutathione cycle), namely, ascorbate peroxidase (APX; EC 1.11.1.11), monodehydroascorbate reductase (MDAR; EC 1.6.5.4), dehydroascorbate reductase (DHAR; EC 1.8.5.1), and glutathione reductase (GR; EC 1.8.1.7) with the help of some antioxidant metabolites (i.e., ascorbate, glutathione, and NADPH), also play an important role in detoxification of H_2O_2 (Fig. 4.3; Noctor and Foyer 1998; Jithesh et al. 2006). In plants, this antioxidant pathway reportedly operates in the cytosol, mitochondria, plastids, and peroxisomes (Jimenez et al. 1998; Noctor and Foyer 1998; Jithesh et al. 2006; Das and Roychoudhury 2014). This pathway is very efficient and helps in fine-scale homeostasis of H_2O_2, as APX (the first enzyme of the pathway) has a higher affinity for H_2O_2 (at μM level) than the CATs (at mM level) (Gill and Tuteja 2010). Hence, enzymes of Foyer-Halliwell-Asada pathway especially APXs are considered important component of plants' stress tolerance machinery (Mittler 2002; Jithesh et al. 2006; Bose et al. 2014). For instance, an

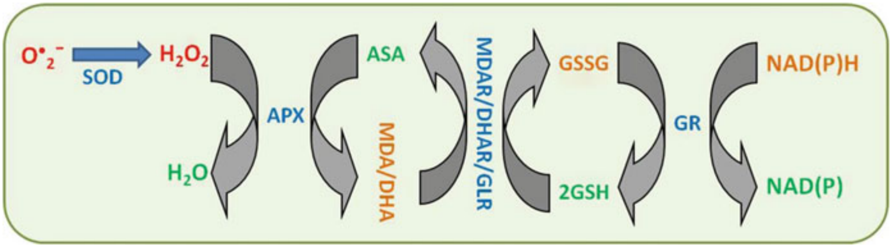


Fig. 4.3 An outline of Foyer-Halliwell-Asada pathway (also known as ascorbate-glutathione cycle) that quenches ROS (i.e., $O_2^{\bullet -}$ and H_2O_2) in the cytosol, chloroplast stroma, and mitochondria of plant cells. SODs convert $O_2^{\bullet -}$ into H_2O_2, which is detoxified into water by the action of APX that consumes ascobate (AsA). Oxidized forms of ascorbate [monodehydroascorbate (MDA) and dehydroascorbate (DHA)] are recycled back to AsA by MDAR (monodehydroascorbate reductase) and DHR (dehydroascorbate reductase) or GLR (glutaredoxin) at the expense of glutathione (GSH). Oxidized glutathione (GSSG) is reduced back to GSH by the action of glutathione reductase (GR) that consumes NAD(P)H as regeneration power

increase in APX and GR was found in response to salinity in halophytes *Bruguiera parviflora* (Parida et al. 2004) and *Salicornia brachiata* (Parida and Jha 2010). Many other antioxidant enzymes such as glutathione peroxidase (GPX; EC 1.11.1.9), glutathione *S*-transferases (GST; EC 2.5.1.18), thiol peroxidase type II peroxiredoxin (Prx; EC 1.11.1.15), and guaiacol peroxidase (GPOX; EC 1.11.1.7) have also been reported from plants and contribute toward ROS homeostasis (Jithesh et al. 2006; Ozgur et al. 2013; Bose et al. 2014).

To keep ROS levels within the tolerable range, plants also utilize low-molecular-weight nonenzymatic antioxidants such as ascorbate (AsA, a sugar derivative also known as vitamin C), glutathione (GSH; a thiol tripeptide γ-glutamyl-cysteinyl-glycine), and tocopherols (Foyer and Halliwell 1976; Jithesh et al. 2006; Ozgur et al. 2013). Often a positive relationship between plant salinity tolerance and levels of these antioxidants are reported. AsA and GSH are the most common nonenzymatic antioxidants of plants, which are found in all major compartments of the plant cells where they can scavenge ROS directly as well as with the help of Foyer-Halliwell-Asada pathway and many other antioxidant enzymes (Ozgur et al. 2013). Their role in salinity tolerance is well-established. For example, levels of AsA and GSH increased with increasing salinity in the halophytic species *Sphaerophysa kotschyana* (Yildiztugay et al. 2013) and *Limonium stocksii* (Hameed et al. 2015). Tocopherols (also known as vitamin E) are lipid-soluble molecules, which exist in four (i.e., α-, β-,γ-, and γ-) forms and are known as an active antioxidant defense for biological membranes (Falk and Munné-Bosch 2010; Ozgur et al. 2013). Among the four isoforms, α-tocopherol is the predominant form in plants, which is synthesized in plastids and plays an important role in quenching ROS especially $^1O_2$ (Bose et al. 2014; Ozgur et al. 2013). Its role in salinity tolerance of plants including halophytes is also frequently reported (Seal et al. 2010; Ellouzi et al. 2011; Ozgur et al. 2013). In addition, many other substances such as phenolic compounds, proline, glycine-betaine, polyamines, polyols, many sugars, and ferritin (iron-binding proteins) have also been reported as nonenzymatic antioxidants of plants (Jithesh et al. 2006; Ozgur et al. 2013; Bose et al. 2014).

A coordinated action of aforementioned enzymatic and nonenzymatic antioxidants keeps the levels of various ROS within low/tolerable range, which in fact is essential for the regulation/signaling of various plant processes (Fig. 4.4; Jithesh et al. 2006; Ozgur et al. 2013; Bose et al. 2014). For instance, ROS are involved in regulation of seed germination and dormancy (Schopfer et al. 2001; Oracz et al. 2007), growth and development (Gapper and Dolan 2006; Gechev et al. 2006), stress acclimation (Gechev et al. 2006), and programmed cell death (Jabs 1999; Dangl and Jones 2001; Van Breusegem and Dat 2006). However, these benefits are strictly dose-dependent (Fig. 4.4; Gechev et al. 2006; Quan et al. 2008). Under environmental stresses production of ROS exceeds the capacity of cells to detoxify them; as a result higher cellular levels of ROS cause oxidative damage to various cellular components like nucleic acids, membrane lipids, and proteins (Beckman and Ames 1998; Apel and Hirt 2004; Ozgur et al. 2013; Bose et al. 2014).

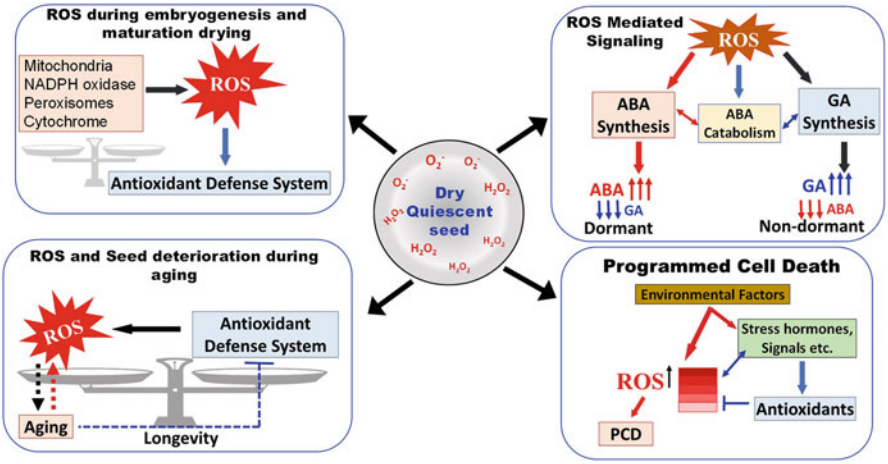


Fig. 4.4 Model indicting the dual roles of ROS in plants. Under optimal conditions, low levels of ROS perform various positive functions in plants, while under environmental stresses, their production overwhelms the capacity of cells to detoxify them; as a result their accumulation causes oxidative damages to lipids, proteins, and nucleic acids

4.3 ROS Production and Scavenging in Dry Seeds

Seeds are the perpetuation units of plants and composed of an embryo, food-laden tissues, and protective coverings (Bewley and Black 1994; Matilla et al. 2005; Khan and Gul 2006; Kranner et al. 2010a, b). Seeds by protecting the embryo and being able to travel long distances ensure the establishment of next generation, thereby the continuity of a plant species on the temporal and spatial scale (Hilhorst 1995; Koornneef et al. 2002; Gul et al. 2013). Seeds of many plant species are extremely tolerant to harsh environmental conditions such as high salinity and drought as long as they are in the dry quiescent state. Hence, seeds of most species can last in soil for a long period (weeks, months, or even years) in the dry state of metabolic quiescence while retaining their ability to germinate (Bewley and Black 1994; Rajjou and Debeaujon 2008; Gul et al. 2013). Seeds of most plants including those of halophytes are orthodox in nature with low ($\leq 5\%$) moisture content (Roberts 1973). Development of orthodox seeds includes the embryogenesis, accumulation of food reserve, and desiccation or maturation drying which results in a mature quiescent seed (Müntz 1982; Bewley and Black 1994). Production of ROS is obligatory at every step from seed development to seed germination and also during seedling establishment (Bailly 2004; Bailly et al. 2008; Pehlivan 2017). Hence, an efficient antioxidant system is essential for seed development, longevity, and germination (Bailly 2004; Kranner et al. 2010a, b; Hameed et al. 2014).

A growing body of literature indicates the presence of ROS in the "dry" orthodox seeds (Fig. 4.5; Bailly 2004; Bailly et al. 2008; Kranner et al. 2010a, b; Hameed et al. 2014; Pehlivan 2017). Although an ample number of articles exist now about ROS

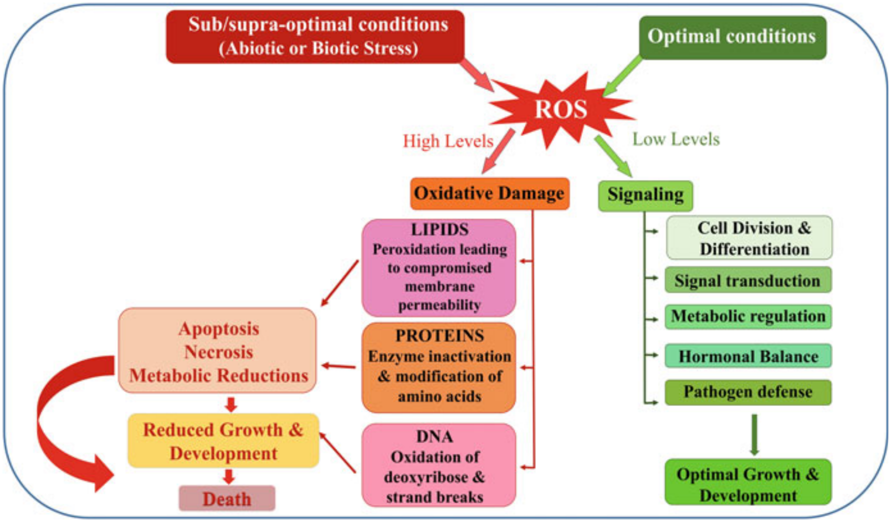


Fig. 4.5 Production and functions of ROS in dry quiescent seeds of orthodox nature

production in the seeds of crop plants (Bailly et al. 2008; Pehlivan 2017), this information about the seeds of halophytes is scant (Kranner et al. 2010a, b; Hameed et al. 2014). Hameed et al. (2014) reported that H_2O_2 and malondialdehyde (MDA, a common indicator of oxidative membrane damage) were present in freshly collected dry seeds of two halophytes *Suaeda fruticosa* and *Limonium stocksii*. Bailly et al. (2008) reviewed that the H_2O_2 content of the seeds first declines during maturation drying (i.e., seed development), remains constant afterward during quiescence or dormancy stage, and finally increases with after-ripening (i.e., dormancy breakage) and with aging (i.e., deterioration). Owing to low (5–15%) moisture content, enzymatic processes are not active in dry orthodox seeds. Hence, nonenzymatic processes such as Amadori and Maillard reactions and lipid autoxidation may be responsible for ROS production and MDA accumulation in a dry state (McDonald and Vanlerberghe 2004; Varghese and Naithani 2008; Bailly et al. 2008).

Dry seeds are generally devoid of AsA and APX owing to their depletion during maturation drying stage. However, there may be present an ASA-independent antioxidant system comprised of components like SOD, CAT, GSH, tocopherols, etc. (De Tullio and Arrigoni 2003; Bailly 2004; Chen and Arora 2011). However, such information about halophyte seeds is limited to just a few studies (Kranner et al. 2010a, b; Hameed et al. 2014). Hameed et al. (2014) reported that the dry seeds of *S. fruticosa* and *L. stocksii* were devoid of AsA but had GSH, SOD, CAT, GPX, and GR. Weitbrecht et al. (2011) indicated that owing to low moisture in dry seeds, antioxidant enzyme activities are limited/impossible in most parts of the seeds, and GSH plays key antioxidant function.

The ROS signaling pathways in quiescent seeds are not yet fully understood, and it is still fascinating how seeds sense ROS in the “dry” (i.e., maturation, seed bank/

storage) states (Fig. 4.5). Many recent studies have shown that ROS play crucial roles in releasing seed dormancy and the mechanism involved in this process might be the oxidation of certain proteins during after-ripening (Oracz et al. 2007; Kumar et al. 2015). Bahin et al. (2011) showed that the interaction of ROS and phytohormones alleviated the seed dormancy in *Hordeum vulgare* seeds. Similar cross talk of ROS with the phytohormones was reported for the seeds of *Bunium persicum* (Amooaghaie and Ahmadi 2017) and *Avena fatua* (Cembrowska-Lech et al. 2015). ROS also play a pivotal role in protection against pathogens, as their accumulation in infected cells acts as safeguard for the seeds either by affecting pathogens directly or indirectly by provoking the hypersensitive reaction leading to programmed cell death (Grant and Loake 2000). Besides the aforementioned positive impacts, ROS are also implicated in seed deterioration and result in the loss of viability during the aging (either natural or accelerated aging) (Bailly 2004; Bailly et al. 2008). Hence, seeds' intrinsic antioxidant constituents are of immense importance for the longevity of the seeds in soil seed bank and also for *ex situ* seed conservation banks (Bailly et al. 2008; Kranner et al. 2010a, b; Donà et al. 2013).

4.4 ROS Production and Scavenging in Germinating Seeds Under Optimal Conditions

Seed germination is a complex process of transformation of dry seeds from quiescent to metabolically active state that demands energy and hence is accompanied by rapid oxygen consumption for respiratory oxidative phosphorylation (Bewley and Black 1994). This reactivation of metabolism upon water uptake especially the oxidative phosphorylation and transition of damaged mitochondrial membranes from gel to liquid-crystalline state result in an oxidative burst by the production of ROS (Crowe and Crowe 1992; Tommasi et al. 2001; Nonogaki et al. 2010; Pergo and Ishii-Iwamoto 2011). Generally, about 2–3% of the oxygen used by the mitochondria can be transformed into superoxide and hydrogen peroxide (Oracz et al. 2007). Peroxisomes of germinating seeds also generate ROS, as fatty acid β-oxidation during conversion of stored lipids into sugars produces H_2O_2 and oxidation of xanthine into uric acid by xanthine oxidase produces superoxide in the peroxisomal matrix (Corpas et al. 2001; Bailly 2004). Plasma membrane-bound NADPH oxidases are another source of ROS in imbibed seeds, as they transfer electrons from cytoplasmic NADPH to oxygen that leads to the formation of superoxide radical and subsequently H_2O_2 (Colville and Kranner 2010).

To deal with continuously producing ROS during germination, nondormant imbibed seeds utilize a well-coordinated antioxidant defense system (Bailly 2004; Bailly et al. 2008; El-Maarouf-Bouteau and Bailly 2008; Miller et al. 2010; Hameed et al. 2014). However, generally little is known about antioxidant defense mechanism of halophyte seeds (Kranner and Seal 2013; Hameed et al. 2014; Rasheed et al. 2016). Activities of SOD, APX, and GR increased, while CAT and GPX activities decreased with time in water-imbibed seeds of two halophytes *S. fruticosa* and *L. stocksii* (Hameed et al. 2014). The dry seed of *Spinacia oleracea* maintained a SOD- and CAT-based antioxidant system which was replaced by APX-based system in osmoprimed germinating seeds (Chen and Arora 2011), while peroxidase (POD) activity was not detected during seed germination in *Chenopodium murale*, indicating the little role of peroxidases during seed germination (Bogdanović et al. 2008). In case of germinating sunflower seeds, CAT and GR activities increased before radicle protrusion (Bailly et al. 2000).

Ascorbate (AsA), although absent in dry orthodox seeds, seems to be synthesized during germination (De Gara et al. 1997; Bailly 2004; Bailly et al. 2008; Hameed et al. 2014). For example, AsA was detected in germinating seeds of halophytes *C. rubrum* (Dučić et al. 2003), *S. fruticosa*, and *L. stocksii* (Hameed et al. 2014) soon after attaining complete hydration. Rise in AsA content may be a result of its de novo synthesis (Tommasi et al. 2001) and/or recycling from the oxidized form (De Tullio and Arrigoni 2003). Besides antioxidant function, AsA is also a cofactor for enzymes involved in the synthesis of germination-regulating hormones like gibberellins and ethylene (De Tullio and Arrigoni 2003) and is also implicated in promoting cell division essential for seedling formation (Noctor and Foyer 1998; De Tullio et al. 1999; De Tullio and Arrigoni 2003). Reduced glutathione (GSH) content also increased in seeds of pine (Tommasi et al. 2001) and pea (Spragg et al. 1962) during the initial 24 h of germination. GSH content peaked at the time of radicle emergence in *Chenopodium rubrum* (Dučić et al. 2003). Similarly, GSH content also increased with time in germinating unstressed seeds of *S. fruticosa* and *L. stocksii* (Hameed et al. 2014). Tommasi et al. (2001) and Hameed et al. (2014) reported a decline in the content of the oxidized form of glutathione (GSSG) alongside increased GSH that indicates the prevalence of an efficient recycling machinery of GSH from GSSG.

ROS production during germination has conventionally been considered detrimental for seed germination; however, an increasing body of evidence suggests that they play important roles during germination (Fig. 4.6; Bailly et al. 2008; Soundararajan et al. 2016). ROS accumulation during early phase of germination creates an “oxidative window” (sensu Bailly et al. 2008) under optimal conditions that facilitates seed germination via cell wall loosening (Müller et al. 2009), signaling (El-Maarouf-Bouteau and Bailly 2008), and/or decreasing ABA levels (Fig. 4.6; Wang et al. 1995, 1998). According to Levine et al. (1994), H_2O_2 production in low quantity during seed germination protects emerging seedlings from pathogens.

4.5 ROS Production and Scavenging in Germinating Seeds Under Stress Conditions

All environmental stresses such as salinity, drought, heat, cold, heavy metals, high irradiance, and biotic stresses lead to excessive production of ROS, which cause oxidative damage to key cell components such as membrane lipids, proteins, and nucleic acids (Jithesh et al. 2006; Gill and Tuteja 2010; Kranner et al. 2010a, b;

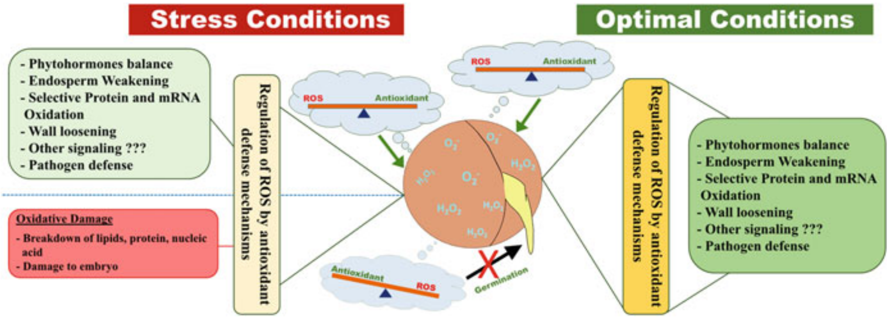


Fig. 4.6 Roles of ROS and antioxidants in germinating seeds under optimal and stress conditions. Change (i.e., dark vs light) in the intensity of colors (green, red, yellow) indicates the intensity of the phenomenon in different box

Choudhury et al. 2017). Generally, germination of the seeds is inhibited under stress or non-optimal conditions, and often this inhibition is linked to oxidative stress (Fig. 4.6; McDonald 1999; Tommasi et al. 2001; Lee et al. 2010; Xu et al. 2013). Thus the success of seed germination is dependent on the efficiency of an antioxidant defense system that operates during germination (De Gara et al. 1997; Bailly 2004). Most studies are related to ROS production in seeds of crops during storage under non-optimal conditions such as high temperature (Rajjou and Debeaujon 2008; Rajjou et al. 2012). Generally, little is known about stress-related ROS homeostasis in germinating seeds (Kranner et al. 2010a, b) especially of halophytes (Hameed et al. 2014; Rasheed et al. 2016).

Exposure to salinity caused an increase in endogenous H_2O_2 and malondialdehyde in two halophytes *S. fruticosa* and *L. stocksii* (Hameed et al. 2014) as well as in seedlings of *Sorghum bicolor* (Chai et al. 2010). Wang et al. (2009) showed that after 4 days of salinity treatment (300 mM NaCl), seeds of *Medicago sativa* and *Melilotus officinalis* had much higher malondialdehyde contents than in those of the control, whereas malondialdehyde content of germinating seeds of *Salsola drummondii* did not vary with increases in salinity, but sub-/supra-optimal temperature, and dark resulted in higher malondialdehyde as compared to optimal temperature and 12 h photoperiod, respectively (Rasheed et al. 2016). Hence, ROS production and oxidative damage responses of the halophyte seeds seem to vary with species and type of stresses; however, current knowledge is just confined to few studies and warrants the importance of more studies in this regard.

An increase in the activities of different antioxidant enzymes is often ascribed important for successful seed germination especially under stress conditions (Bailly 2004; Kranner and Seal 2013; Hameed et al. 2014; Panuccio et al. 2014; Rasheed et al. 2016). For instance, an increase in the activities of SOD and CAT after 48 h of exposure to NaCl was reported in germinating seeds of *Cucumis melo* (Pinheiro et al. 2016). SOD, CAT, and APX activities increased in germinating seeds of *Chenopodium quinoa* 3 days after sowing in various NaCl solutions (Panuccio et al. 2014). Similarly, an increase in CAT and GPX activities was reported in the germinating seeds of *Suaeda fruticosa* and *Limonium stocksii* under saline treatments (Hameed et al. 2014). Similarly, an increase in SOD, CAT, GPX, and APX activities was observed in the germinating seeds of *Salsola drummondii* under non-optimal temperatures and dark but not under saline conditions (Rasheed et al. 2016). Hence, an induction of antioxidant enzyme activities particularly of CAT appears key to successful seed germination under stress conditions.

Generally, little is known about the variations in the content of different nonenzymatic antioxidants of germinating seeds under stress conditions. This information about halophyte seeds is confined to just a few studies. Hameed et al. (2014) indicated that salinity inhibited seed germination of coastal halophytes *Suaeda fruticosa* and *Limonium stocksii* by decreasing ascorbate-dependent antioxidant system. Similarly, there was some decline in AsA content of germinating seeds of *Salsola drummondii* under high salinity and non-optimal temperatures (Rasheed et al. 2016). In the absence of AsA, GSH acts as the key antioxidant in orthodox seeds and thereby appears important for seed germination (Bailly 2004; Tommasi et al. 2001; Kranner and Seal 2013; Hameed et al. 2014). However, environmental stresses may cause a decline in its levels. For instance, GSH decreased with increasing salinity in germinating seeds of *L. stocksii*, *Suaeda fruticosa* (Hameed et al. 2014), and *Melilotus officinalis* (Wang et al. 2009). GSH content did not vary with variations in salinity, temperature, and light in *Salsola drummondii* (Rasheed et al. 2016). In contrary, total antioxidant capacity and total phenols increased in germinating seeds of *Chenopodium quinoa* 3 days after sowing in various NaCl solutions (Panuccio et al. 2014). Hence, it appears that responses of different nonenzymatic antioxidants of germinating seeds may vary with species and stresses, thus demanding more research for a better understanding.

4.6 Conclusions

Production of ROS is ubiquitous to aerobic metabolism and is therefore observed during every stage of a plant’s life cycle and throughout seeds’ life. ROS, although conventionally known for their cytotoxic effects, have emerged as key signaling molecules implicated in regulating a number of plant processes including seed germination/dormancy. It is believed that tightly regulated levels of ROS constitute an “oxidative window” (*sensu* Bailly et al. 2008) that facilitates the germination of most seeds. Seeds’ antioxidant defense system which is composed of both enzymatic and nonenzymatic antioxidants plays a pivotal role in the tight regulation of ROS levels. ROS reportedly facilitate seed germination through cell wall loosening, endosperm weakening, signaling, and/or decreasing abscisic acid levels. Therefore, it appears that ROS and antioxidants play a broader role in seed biology than often acknowledged. Despite an increasing amount of literature on ROS homeostasis during seed germination and dormancy loss, generally, there is a dearth of this knowledge about the seeds of non-crop plants such as halophytes. In addition, detailed mechanisms of ROS functions such as downstream targets, cross talk with other molecules and alternative routes, etc. also need to be clarified.

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