



# Reactive Oxygen Species; Oxidative Damage or Oxidative Signaling?

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## Abstract

Salt stress induces osmotic stress, ionic toxicity and most drastically causes oxidative damage. High salt stress levels cause oxidative damage, associated with the production of different reactive oxygen species (ROS). Conventionally ROS were considered as bad guys and plants exhibited high antioxidants activities, can tolerate oxidative stress. Nonetheless recent evidences showed that ROS also act as signaling molecules which plays very crucial role in plant stress adaptation. This has prompted to reconsider conventional role of ROS as oxidative species and to further examine role of ROS as oxidative signaling in breeding programs to enhance salt stress tolerance in plants. Moreover, along with considering diversity of antioxidants, ROS production and ROS scavenging both at inter and intra-cellular level should be considered.

**Keywords:** Antioxidant activity; Redox regulation; Oxidative signaling; H<sub>2</sub>O<sub>2</sub>

**Abbreviations:** ROS: Reactive Oxygen Species

## Perspective

Salt stress is amongst most drastic a biotic stresses that can significantly reduce crop yields [1,2]. Salt stress causes osmotic stress and specific ion toxicity however in recent years oxidative damage has been added to this list [3,4]. Under salt stress, reduction of O<sub>2</sub> occurred and converted into H<sub>2</sub>O, and reactive oxygen species (ROS) (such as superoxide radical (O<sub>2</sub><sup>-</sup>), hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), and hydroxyl radical (OH<sup>-</sup>) [5]. These ROS at first instance acts as signaling molecules and trigger plant defense mechanism in plants to cope with salt stress however due to inability of plants to maintain a balance between over production of ROS, these ROS cause

oxidative damage to plants and disrupt numerous plant processes [6]. ROS are highly toxic and due to their highly cytotoxic and reactive nature, their accumulation in plant tissues and intracellular compartments must be tightly controlled. In response to ROS, plants possess very effective ROS scavenging mechanism, termed as antioxidant defense system which scavenges ROS and protects plant cells from salt stress induced oxidation process [7]. From last two decades, articles focusing on conventional concept of antioxidant defense system, higher antioxidant activity better the plant to cope ROS have been increased exponentially. Increase in antioxidant activity with increase in salt concentration has been considered as salt stress tolerance mechanism in plants (especially in halophytes) [8,9], nonetheless, many other reports question the validity of this approach, reporting no or a negative correlation between activity of

antioxidant enzymes and plant salinity stress tolerance  
(Table 1).

Antioxidants response	Plant species	Antioxidant response	Reference
<b>SOD</b>	Rice	Increase	Lee et al. 2001 [10]
	Brassica napus	Increase	Ashraf and Ali 2008 [11]
	Wheat	Increase	Sairam et al. 2005 [12]
	Rice	Decrease	Khan and Panda 2008 [13]
	Maize	Decrease	De Azevedo Neto et al. 2006 [14]
	Foxtail millet	Decrease	Sreenivasulu et al. 2000 [15]
<b>CAT</b>	Chickpea	Increase	Eyidogan and Oz 2005; [16]
	Rice	Increase	Khan and Panda 2008 [13]
	Pea	Increase	Hernandez et al. 2000 [8]
	Rice	Decrease	Khan and Panda 2008 [13]
	Pea	Decrease	Noreen and Ashraf 2009 [17]
<b>APX</b>	Rice	Increase	Khan and Panda 2008 [13]
	Wheat	Increase	Mandhanian et al. 2006 [18]
	Alfalfa	Increase	Wang et al. 2009 [19]
	Maize	Decrease	de Azevedo Neto et al. 2006 [14]
	Foxtail millet	Decrease	Sreenivasulu et al. 2000 [15]
	Pea	No change	Hernandez et al. 2002 [8]
	Rice	No change	Demiral and Türkan 2005 [20]
<b>GPX</b>	Rice	Increase	Vaidyanathan et al. 2003 [21]
	Tobacco	Increase	Roxas et al. 2000 [22]
	Tomato	Increase	Wang et al. 2005 [19]
	Pea	No change	Hernández et al. 2002 [18]
<b>Proline</b>	Wheat	Increase	Sairam et al. 2002 [12]
	Sugar beet	Increase	Ghoulam et al. 2002 [23]
	Sesame	Increase	Koca et al. 2007 [24]
	Cassia angustifolia	Decrease	Agarwal and Pandey 2004 [25]
	Rice	Decrease	Lutts et al. 1996 [26]
<b>Tocopherol</b>	Cotton	Increase	Gossett et al. 1994 [27]
	Pea	Increase	Noreen and Ashraf 2009 [17]
	Pea	Decrease	Noreen and Ashraf 2009 [17]
	Rice	Decrease	Turan and Tripathy 2013 [28]

Table 1: Selected examples of different response of antioxidants activity in different plant species.

Nonetheless in recent years new concept of oxidative signaling rather than oxidative stress has been suggested (Foyer and Noctor 2005). Plants utilize ROS as effective and most likely first signaling molecules to trigger or control different physiological mechanisms (e.g.) stomatal density and size [29], cell division and expansion (Foreman et al. 2003), hormones production [30], floral development [31]. In many cases, production of ROS is genetically programmed, and superoxide and  $H_2O_2$  are used as second messengers (Foyer and Noctor 2005). Demidchik et al. [32] further supported these arguments by showing that free oxygen radical can regulate  $K^+$  and

$Ca^{2+}$  permeable channels in plant root cells, thus plays important signaling compounds under salt stress. This has provoked to reconsider conventional concept of oxidative damage and redox regulation and introduce new concept of oxidative signaling in breeding programs to enhance salt stress tolerance in plants. Evidences have been increased significantly showing differential response of antioxidant production under salt stress in various plant parts at various time points (Box 1). Therefore, along with considering diversity of antioxidants, ROS production and ROS scavenging both at inter and intra-cellular level should be considered.

## Box 1

**Antioxidant response at different time points of salt stress**

Antioxidant production and their ROS scavenging activity also displays a pronounced time dependency on salt stress duration and therefore might be different at different time points. In *Medicago truncatula* roots, activities of POD, SOD, and CAT were increased only upto 24 hours after salt stress imposition however these activities were lost after 48 hours of salt stress [33]. Similarly, Hernández et al. [8] showed that glutathione reductase activity was increased only after 24 of salt stress while SOD production was continuously increased up to 48 hours of salt stress. In tomato, ROS scavenging by SOD, CAT, MDHAR and APX was noticed up to 16 days after salt stress however GR activity was continuously decreased from the beginning of salt stress impositions [34]. All these studies showed differential response of antioxidant at different time points, suggested that variation might be due to plant species, experimental condition and data collection.

**Different antioxidant response in different plant tissue and organelles**

ROS scavenging by antioxidants are tissue specific, for instance in maize polyphenol contents and total antioxidant activity were enhanced with subsequent increase in salt stress levels in mature leaves and roots however no change was noticed in young leaves. Moreover proline contents were higher in young leaves only and no change was noticed in roots or older leaves (Hamada et al. 2016). Some other studies also reported tissue specific response of antioxidants in different plant species. In tomato leaves, ascorbic acid and tocopherol contents were increased with increase in salt stress level [35] however they declined in rice leaves under salt stress [28]. According to Bandoğlu et al. [36], higher activity of SOD, GR and APX was observed in roots while little activity was noted in shoot. Similarly in *Phaseolus vulgaris* higher activity of APX and SOD was observed in roots while no activity was noted in nodules under salt stress [37]. These contrasting findings could be owing to plant species or tissue specificity. Furthermore plant age related variation in antioxidants production and their responses could also explain the reason behind the inter-specific or intra-specific aspects of ROS production and antioxidant activity. Kraxchik and Bernstein [38] supported these arguments by showing that young leaves of maize are less sensitive to salt stress as compared with mature leaves. These studies indicated possible role of ROS in the systemic signaling from roots to leaves and activation of antioxidant for better protection against oxidative stress and/or salt stress. Along with tissue specific antioxidant response, organelles specific antioxidant activities have also been reported. For example Hernandez et al. [8] documented high activity of SOD activity in pea apoplast while higher activity of GR, MDHAR and DHAR in symplast. Similarly, Mittova et al. [39] reported that mitochondria and peroxisomes of the salt treated roots of wild tomato had increased levels of lipid peroxidation and  $H_2O_2$  coupled with decreased activities of SOD, POD, ASC and GSH, suggesting that improving endogenous production of antioxidant at mitochondria and/or peroxisome could improve salt stress tolerance. In another study, higher activity of SOD, APX and GR was noted in chloroplastic fraction as compared with mitochondrial fraction and cytosolic fraction [40].

Some other arguments also highlighted that salt stress tolerant plant do not allow ROS production in first instance and thus require no antioxidant activity [6]. Plants can use these ROS and do some other jobs such as amelioration of ion toxicity. This can be done by either excluding excessive sodium from cytosol into apoplast or vacuole [40,41]. Halophytes use such strategy to cope with high salt stress levels. Halophytes also exhibited higher antioxidant production and converts excessive free oxygen radical into  $H_2O_2$  at initial stages of salt stress and after that use  $H_2O_2$  as signaling molecule to trigger other physiological and genetic processes [42]. However it is still unknown, when halophytes decide that salt stress induced  $H_2O_2$  should be used as signaling compound in plant adaptive mechanism and redox regulation [43]. Moreover, owing to similar signaling signatures between  $H_2O_2$  and  $Ca^{2+}$ , the role of other enzymatic antioxidants may be attributed to the need to decrease the basal levels

of  $H_2O_2$ , once the signaling has been processed. In this context, role of CAT and APX in the shaping of  $H_2O_2$  signature may be similar to those that  $Ca^{2+}$  efflux systems [44].

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