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Polyamines as redox homeostasis regulators during salt stress in plants

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The balance between accumulation of stress-induced polyamines and reactive oxygen species (ROS) is arguably a critical factor in plant tolerance to salt stress. Polyamines are compounds, which accumulate in plants under salt stress and help maintain cellular ROS homeostasis. In this review we first outline the role of polyamines in mediating salt stress responses through their modulation of redox homeostasis. The two proposed roles of polyamines in regulating ROS—as antioxidative molecules and source of ROS synthesis—are discussed and exemplified with recent studies. Second, the proposed function of polyamines as modulators of ion transport is discussed in the context of plant salt stress. Finally, we highlight the apparent connection between polyamine accumulation and programmed cell death induction during stress. Thus, polyamines have a complex functional role in regulating cellular signaling and metabolism during stress. By focusing future efforts on how polyamine accumulation and turnover is regulated, research in this area may provide novel targets for developing stress tolerance.

Keywords: polyamine signaling, ROS, plant abiotic stress, salinity stress, redox homeostasis

Introduction

Global climate change and agronomic practices have contributed to increased soil salinity, which currently affects an estimated 45 million hectares of irrigated land (Rengasamy, 2010). Salt stress limits crop productivity and is imposed by an accumulation of cations (Na^+, K^+, Mg^{2+}, Ca^{2+}) and anions (Cl^-, SO_4^{2-}, HCO_3^-) originating from water-soluble salts such as Na_2SO_4, $NaHCO_3$, NaCl, and $MgCl_2$ as well as less water-soluble salts including $CaSO_4$, $MgSO_4$, and $CaCO_3$. These salts accumulate due to factors such as mineral erosion and crop irrigation with mineralized water or ocean water (Todorova et al., 2013).

High salt concentrations in soil cause both hyperionic and hyperosmotic stress in the intracellular environment. During the initial stages of salt stress, the high external solute concentration decreases the cellular water potential, which eventually imposes turgor loss and pleiotropic physiological responses including stomatal closure, growth inhibition, reduced pollen viability, inhibition of photosynthetic enzyme activity, sucrose accumulation, and inactivation of photosynthetic electron transport (Munns and Tester, 2008; Chaves et al., 2009; Biswal et al., 2011; Silva et al., 2011; Mittal et al., 2012; Shu et al., 2012; Jajoo, 2013). Long-term salt stress results in hyperaccumulation of Na^+ leading to suppression of enzymatic activity, increased H_2O_2 and lipid peroxidation that ultimately causes leaf senescence (Sairam et al., 2002; Chinnusamy and Zhu, 2003; Allu et al., 2014).

Under normal conditions, the cytosol contains 100–200 mM of K^+ and 1–10 mM of Na^+ (Taiz and Zeiger, 2002). Excess NaCl is the most common cause of salt stress in plants and induces overaccumulation of Na^+ and Cl^- and depletion of K^+ ions in the cell. This imbalance in the Na^+:K^+ ratio is a result of the competition between the ions for transport into the cell and is thought to produce detrimental effects due to changes in osmotic potential, nutrient limitation and ionic toxicity. Plants counteract these effects using multiple strategies including: (i) producing osmolytes like soluble sugars, organic acids, free amino acids, and accumulating potassium ions (Ahmad and Sharma, 2008; Ahmad et al., 2012), (ii) activating transporters that export sodium from the cell, (iii) limiting Na^+ uptake into roots and leaves, (iv) sequestering Na^+ ions into subcellular compartments, (v) altering photosynthetic rates, (vi) changing membrane structure, (vii) inducing antioxidative enzymes, and (viii) decreasing stomatal conductance (Jithesh et al., 2006; Ozgur et al., 2013). In addition, plant cells rapidly accumulate reactive oxygen species (ROS) in response to salt and other stresses, a response widely known as the "oxidative burst" (Mittler, 2002; Miller et al., 2008). The oxidative burst has an important role in inducing signaling events and is dependent on enzymes located in several subcellular compartments (Foyer and Noctor, 2005; Baxter et al., 2014). However, it is essential that ROS production be regulated, as excess ROS accumulation results in membrane lipid peroxidation, DNA damage, protein denaturation, carbohydrate oxidation, pigment breakdown, and ultimately leads to cell death (Scandalios, 1993; Noctor and Foyer, 1998). To counteract the potentially damaging effects of the oxidative burst, plants produce a diverse set of antioxidants whose regulation is not yet fully understood. While the interplay between ROS turnover and antioxidant accumulation during stress is quite complex, it is essential to understand how this system works for its potential in enhancing plant stress tolerance (Noctor and Foyer, 1998).

Mechanisms of ROS Production During Salt Stress

ROS are highly reactive forms of molecular oxygen and include the hydroxyl radical ($HO^{\cdot}$), superoxide ($O2^{\cdot -}$), hydrogen peroxide (H_2O_2), and singlet oxygen ($^1O_2$) (Dowling and Simmons, 2009; Shapiguzov et al., 2012). The reactivity and half-life of different ROS species are correlated to their mobility and diffusion distance in the cellular space. Among the ROS species present in plants, hydrogen peroxide is the most stable having a half-life of 1 ms, whereas singlet oxygen ($^1O_2$), superoxide ($O_2^{\cdot -}$) and hydroxyl radicals ($OH^{\bullet}$) are short-lived species with half-lives of 1–4 μs to 1 nanosecond (Gechev et al., 2006; Moller et al., 2007). Although numerous subcellular compartments contribute to ROS production, the major sites of ROS generation include the chloroplast, mitochondria, and peroxisome (**Figure 1**) (Foyer et al., 2003; Mittler et al., 2004; Asada, 2006; Rhoads et al., 2006).

The chloroplast produces the highest levels of ROS under both normal conditions and salt stress. ROS generation occurs within both Photosystem I (PSI) and Photosystem II (PSII) reaction centers in the thylakoid membrane. During salt stress, ROS production is enhanced due to changes in membrane fluidity and protein complex formation, blocking the electron transfer from water to PSII (Chaves et al., 2009; Biswal et al., 2011; Silva et al., 2011; Jajoo, 2013). Another important site for ROS production is the mitochondria. During salt stress, mitochondrial respiration is disrupted; over-reduction of the ubiquinone pool facilitate the leakage of electrons from complexes I and III of the mitochondrial electron transport chain to molecular oxygen, resulting in $O_2^{\cdot -}$ production (Noctor et al., 2007; Miller et al., 2010). Excess O_2in the cell also increases the photorespiration rate, which produces $O_2^{\cdot -}$ and $^1O_2$ as by products (Allakhverdiev et al., 2002; Foyer and Noctor, 2003). Peroxisomes, which cater as a site for numerous metabolic processes such as photorespiration, β-oxidation of fatty acid, flavin oxidase pathway, dismutation of superoxide radicals and polyamine catabolism, also contribute significantly to ROS accumulation in plants subjected to salinity stress (Moschou et al., 2008a,b; Mohapatra et al., 2009). The effects of salt stress on peroxisomes and chloroplasts are interconnected. Reduced water availability and stomatal closure during salt stress causes reduction in the CO_2 to O_2 ratio in mesophyll cells. This facilitates the affinity of Rubisco to O_2, thus increasing photorespiration and production of glycolate in chloroplasts. The end product of chloroplasts (glycolate) is oxidized by glycolate-oxidase in peroxisomes—a major pathway of H_2O_2 production (Noctor et al., 2002; Karpinski et al., 2003). In addition to organelles, enzymes localized in other cellular compartments, including the cytosolic polyamine oxidase (PAO) and diamine oxidase (DAO), plasma membrane NADPH oxidases, cell wall-associated peroxidases (POXs) and oxalate oxidases participate in ROS synthesis and may play a minor role in ROS production during salt stress (Kawano, 2003; Parida and Das, 2005; Ahmad and Sharma, 2008).

Enzymatic and Non-Enzymatic Regulation of ROS in Plants

High levels of ROS can damage the cell by inactivating enzymes, initiating lipid oxidation of membranes, and breaking DNA strands (Van Breusegem et al., 2001; Halliwell, 2006). Plants modulate ROS accumulation during salinity stress via enzymatic and non-enzymatic pathways. The cytosolic enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and enzymes that participate in the ascorbate-glutathione cycle (**Figure 2**). Non-enzymatic antioxidants include the lipid-soluble membrane-associated α-tocopherol, and β-carotene, which are products of lipid peroxidation. Polyamines belong to the category of water-soluble compounds with antioxidative properties alongside glutathione (GSH), ascorbate (ASC), polyphenols (flavonoids, tannins, and anthocyanins), proteinaceous thiols, proline, and glycine-betaine (Mittler, 2002; Ozgur et al., 2013; Todorova et al., 2013). Glycine-betaine is a key regulator in ROS homeostasis, which stabilizes PSII by preventing high salt (Na^+ and Cl^-)-induced dissociation of the regulatory extrinsic proteins (Papageorgiou and Murata, 1995). Some plants also use the alternative oxidase enzyme (AOX) to remove electrons from the ubiquinone pool and transfer them to oxygen to form water, thus preventing the over-reduction of ubiquinones and resulting in decrease of salt-induced ROS production in mitochondria (Smith et al., 2009; Miller et al., 2010). Unlike metazoans, plant cells do not have a mechanism to detoxify $OH^{\cdot}$ enzymatically and to regulate the accumulation of $OH^{\cdot}$, rely on non-enzymatic

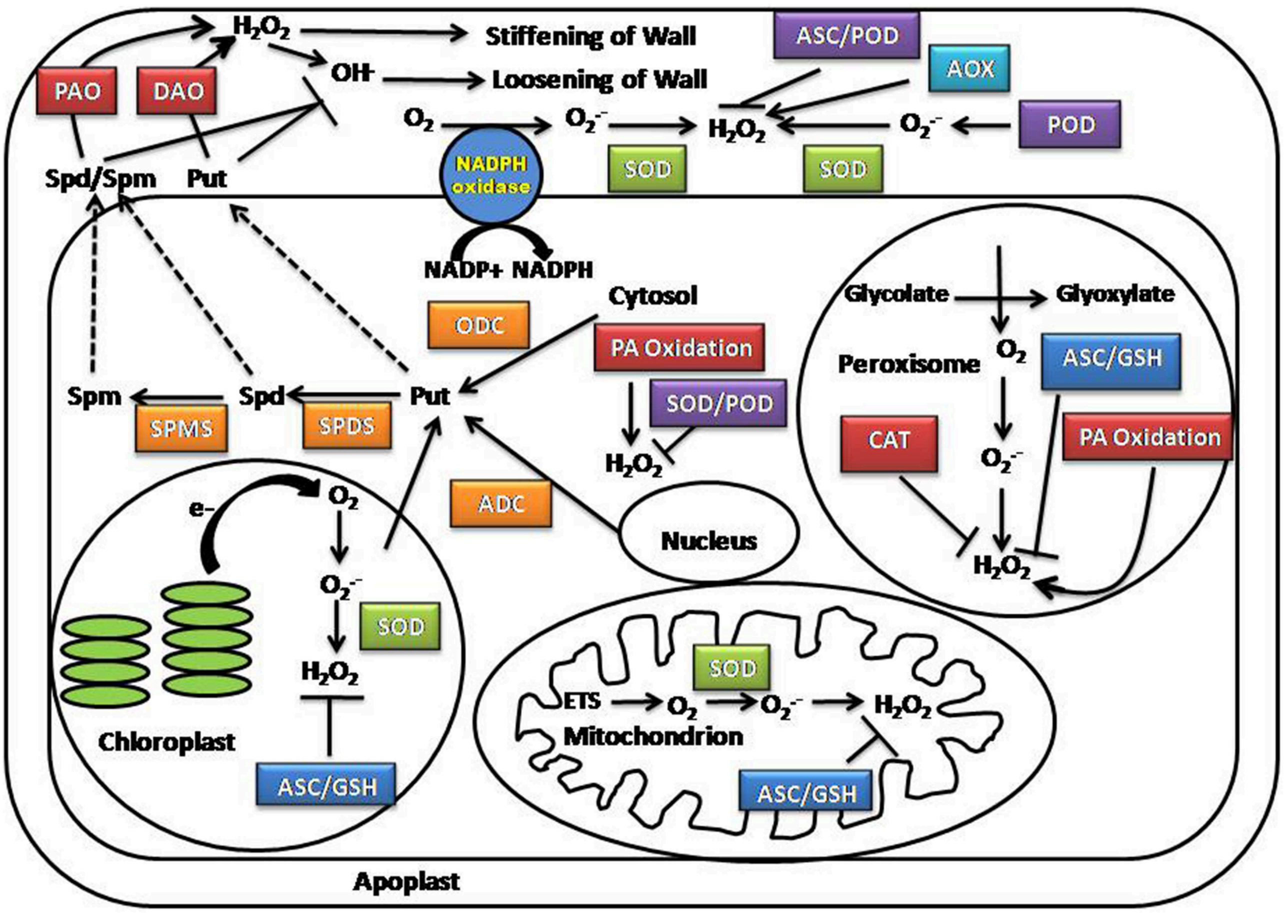

FIGURE 1 | Location of ROS and polyamine production in the cell. AOX, Alternative oxidase; ADC, Arginine decarboxylase; ASC, Ascorbate; APX, Ascorbate peroxidase; CAT, Catalase; DAO, Diamine oxidases; ETS, Electron transport chain; GSH, Glutathione; ODC, Ornithine decarboxylase; PA, Polyamine; PAO, Polyamine oxidases; SPDS, Spermidine synthase; SPMS, Spermine synthase; SOD, Superoxide dismutase.

antioxidants, and various mechanisms to prevent $OH^{\cdot}$ formation (Bose et al., 2014).

Numerous studies have shown a correlation between antioxidant accumulation and plant salt stress tolerance; however recent evidence hints that this relationship is more complex than previously thought. Several polyols accumulating during salt stress (sorbitol, mannitol, myo-inositol, pinitol, and others) may be involved in scavenging hydroxyl radicals (Williamson et al., 2002). In particular, the osmolyte proline seems to be associated with the activation of ROS-scavenging enzymes during salt stress (Saradhi and Mohanty, 1997; Szabados and Savouré, 2010; Gupta and Huang, 2014). For example, exogenous application of proline improves salt tolerance in melon, and was associated with increased chlorophyll content, photosynthetic rate, reduced $O_2^{\cdot -}$, and H_2O_2 accumulation, and increased levels of antioxidants (SOD, POD, CAT, APX, DHAR, and GR) (Yan et al., 2011). In addition, heightened levels of proline were observed in salt-tolerant transgenic rice overexpressing the DEAD-box helicase *PDH45* which correlated with increased activation of antioxidant enzymes including SOD, APX, GPX, and GR under salt stress (Gill et al., 2013). It has also been shown that exogenous application of compatible solutes like glycine betaine, proline, mannitol, trehalose or myo-inositol, considerably reduced $OH^{\cdot -}$ generated K^+ efflux during salt stress through an unknown mechanism (Cuin and Shabala, 2007).

Thus, ROS production and detoxification during salt stress appears to involve multiple cellular locations and molecular mechanisms. While polyamines are only one of several compounds with antioxidative properties that accumulate in stressed plants, they seem to play a significant role in regulating stress tolerance as outlined below.

Polyamines

Overview

Polyamines, small aliphatic amines with proposed antioxidant effect, are ubiquitous across all living organisms (Hussain et al., 2011; Gupta et al., 2013). Endogenous levels of polyamines increase during exposure to abiotic stresses such as drought, salinity, chilling, heat, hypoxia, ozone, UV, and heavy metal exposure and are ubiquitously produced in all cells and tissues

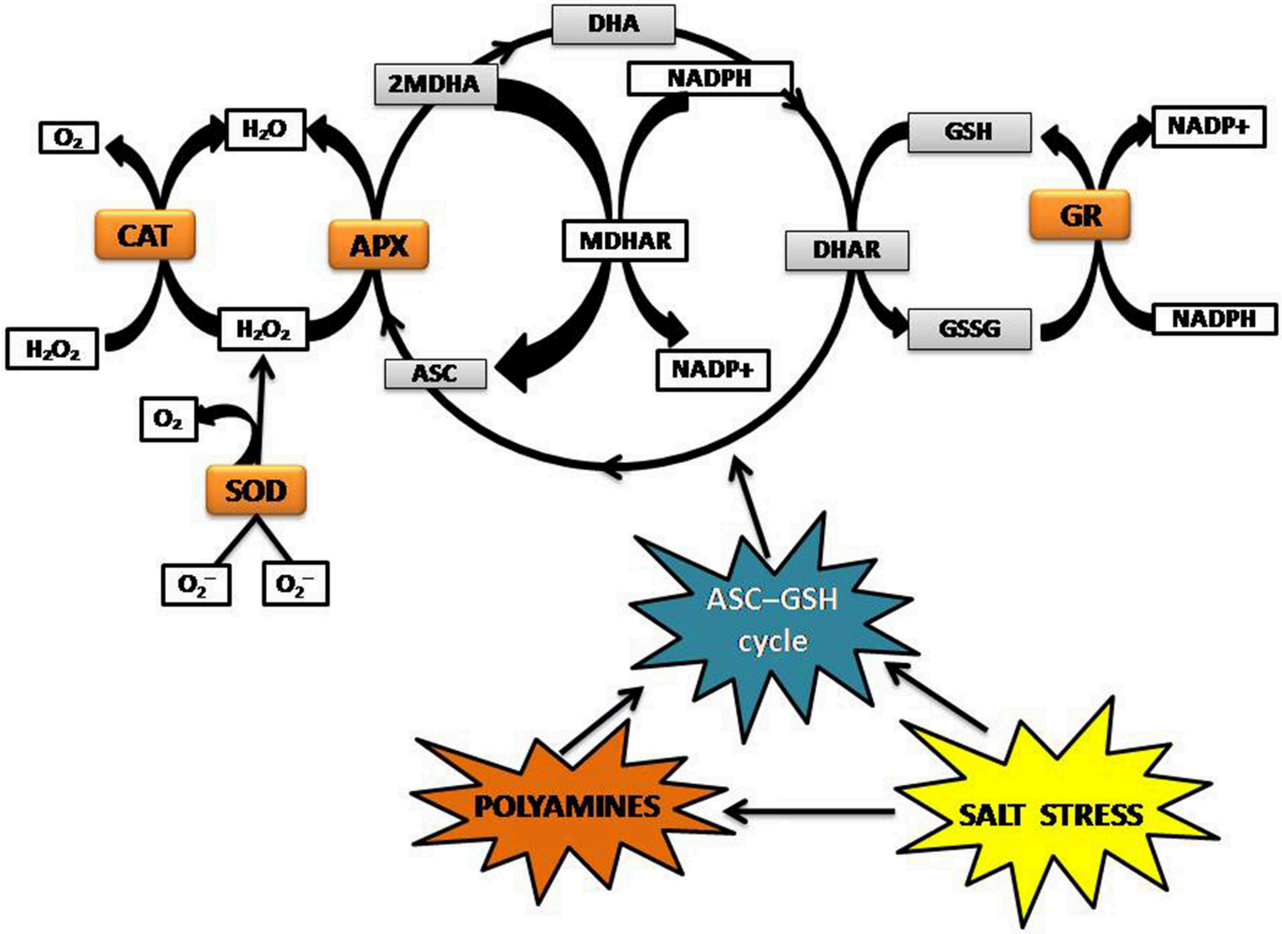

FIGURE 2 | ROS detoxification mediated by ASC-GSHcycle. ASC, Ascorbate; APX, Ascorbate peroxidase; CAT, Catalase; DHA, Dehydroascorbate; GSH, Glutathione; GR, Glutathione reductase; GSSG, glutathione disulphide; MDHA, Monodehydroascorbate; MDHAR, NAD(P)H-dependent oxido-reductase; SOD, Superoxide dismutase.

(Alcázar et al., 2010; Gill and Tuteja, 2010). The most abundant plant polyamines include putrescine (Put, 1, 4- diaminobutane), spermidine (Spd, N -3-aminopropyl-1, 4-diaminobutane) and spermine (Spm, bis (N -3-aminopropyl)-1,4-diaminobutane). Beside these, cadaverine (Cad, 1, 5-diaminopentane) has also been detected in several plant species, in particular in *Gramineae, Leguminoseae* and *Solanaceae* (Lutts et al., 2013). Another polyamine, thermospermine—a structural isomer of spermine—is synthesized by the action of thermospermine synthase (Takano et al., 2012). Putrescine (Put) is primarily synthesized by ornithine decarboxylase using ornithine as a substrate (**Figure 1**). Another alternative pathway for Put synthesis occurs through the action of arginine decarboxylase (ADC) followed by two successive steps catalyzed by agmatine iminohydrolase (AIH) and *N*-carbamoyl-Put amidohydrolase (CPA) (Fuell et al., 2010). Put can be used as a substrate to generate Spd by spermidine synthase (SPDS) and Spd can then converted to Spm by spermine synthase (SPMS). Other polyamine oxidation products include hydrogen peroxide and γ-aminobutyric acid, which are involved in plant development and stress responses (Tiburcio et al., 2014). The unique polycationic structure of polyamines suggest that they may be free radical scavengers, in line with some observations that their accumulation correlates with plant tolerance to biotic and abiotic stresses (Mehta et al., 2002; Walters, 2003; Groppa and Benavides, 2008; Gill and Tuteja, 2010; Gupta et al., 2013).

The interactions between polyamines, ROS and antioxidants are complex and induce diverse and apparently contradictory physiological effects during stress (Bhattacharjee, 2005; Gill and Tuteja, 2010; Pottosin et al., 2012, 2014; Velarde-Buendia et al., 2012). In particular, increased levels of cellular polyamines during abiotic stress (e.g., salinity) have shown dual effects. On one hand, exogenous polyamine application was correlated with higher plant tolerance to abiotic stress, partly due to the increased ability to inactivate oxidative radicals. On the other hand, polyamines were reported to decrease plant's capacity to withstand stress, possibly due to the increased levels of H_2O_2 resulted from polyamines' catabolism (Minocha et al., 2014). Indeed, both the anabolism and catabolism of the polyamine species were reported to increase during abiotic stress, with the net effect of raised cellular levels of ROS as well as antioxidant enzymes and metabolites (Pottosin et al., 2012, 2014; Minocha et al., 2014). In this review we have attempted to clarify the complex relationship between polyamines and ROS, focusing on the potential role of polyamine as a redox homeostasis manager during plant abiotic stress response.

Polyamines: One of the Prominent Regulators in ROS Homeostasis during Salt Stress

Plant polyamines are thought to contribute to cellular responses during salt stress through modulation of ROS homeostasis via two distinct mechanisms (Takahashi and Kakehi, 2010). First, polyamines promote ROS degradation by scavenging free radicals and activating antioxidant enzymes during stress conditions (Gupta et al., 2013). Free polyamines are responsible for the detoxification of superoxide anions and hydrogen peroxide, while the conjugated polyamines are involved in scavenging other ROS (Langebartels et al., 1991; Kubis, 2005). Kuznetsov and Shevyakova (2007) have reported that conjugated polyamines show more antioxidant ability than free polyamines. Second, polyamines promote ROS production through polyamine catabolism in the apoplast (Yoda et al., 2006; Marina et al., 2008; Mohapatra et al., 2009; Campestre et al., 2011). While it is difficult to determine which of these mechanisms is most important during salt stress, manipulation of the polyamine biosynthetic pathways is correlated to abiotic stress resistance in several studies. For example, impaired expression of *ADC1* or *ADC2* significantly decreased Put levels and increased susceptibility to salt stress (Urano et al., 2004). When mouse ornithine decarboxylase (ODC) was introduced in *Nicotiana tabacum,* free polyamine content increased by 2-4 fold and germination increased by 33–45% on high salt medium (Kumria and Rajam, 2002). Transgenic *Nicotiana tabacum* plants overexpressing a S-adenosylmethionine decarboxylase *(SAMDC)* gene also demonstrated enhanced of soluble polyamines as well as increased seed weight, photosynthetic rate and expression of antioxidant enzymes (APX, MnSOD, and glutathione S-transferase) relative to untransformed lines (Wi et al., 2006). Increased polyamine accumulation (4–7%) was also observed in tobacco plants expressing the S-adenosylmethionine synthetase (*SsSAMS2*) gene, which supported up to 20% higher photosynthetic rates and biomass accumulation compared to the control (Qi et al., 2010). Similarly, introduction of *SAMDC* cDNA from *Tritordeum* into *Oryza sativa* produced higher free polyamine content (Put, Spd, Spm), and a reduction in salt-induced shoot growth repression compared to non-transgenic rice plants (Roy and Wu, 2002). Ectopic expression of *SPDS* orthologs from different source plants also improved growth and survival of young plants in *Arabidopsis*, European pear (*Pyrus communis* L.) and tomato suggesting the importance of this enzyme to cope up with saline environmental condition across diverse plant species (Kasukabe et al., 2004; Wen et al., 2008; Neily et al., 2011). Exogenous application of polyamines has also been shown to have a significant effect on the plant, and has been suggested to be a potential strategy to increase plant survival during salt stress. For example, Spm application promoted osmotic and salt stress tolerance in *Arabidopsis* and rice, which was thought to be due to enhanced polyphenol accumulation, CAT, and SOD enzyme activities (Sreenivasulu et al., 2000; Cheruiyot et al., 2007; Roychoudhury et al., 2011; Zrig et al., 2011; Radhakrishnan and Lee, 2013). In cucumber, Spm treatment enhanced salt tolerance (growth, photosynthetic rates) in a salt-sensitive cultivar, which was correlated to higher antioxidative enzyme activity and proline accumulation (Duan et al., 2008). Put application also increased the activity of antioxidant enzymes and carotenoids in leaf tissues of salt stressed *Brassica juncea* seedlings and enhanced seedling growth relative to the untreated controls (Verma and Mishra, 2005). Together, these studies indicate that altering polyamine accumulation through manipulation of biosynthetic pathways or direct application could have an effect on physiological responses to salt stress. **Table 1** summarizes the effect of endogenously formed and exogenously applied polyamines in alleviating salt resistance via the modulation of cellular antioxidative components (enzymatic or non-enzymatic).

Engineering consistent polyamine accumulation may not be so simple however, as plants also exhibit increased polyamine degradation during salt stress and thus polyamine turnover appears to be highly regulated. During salt stress, intracellular polyamines are exported from the cytosol to the apoplast, against the electrochemical gradient, and oxidized by DAO and/or PAO to generate hydrogen peroxide that is further converted to $OH^{\cdot}$ via the Fenton reaction (Pottosin et al., 2014). For example, polyamine degradation occurs through oxidative deamination catalyzed by aminooxidases such as the copper-containing DAO and flavoprotein-containing PAO. DAO exhibits high affinity for diamines, while PAO oxidizes secondary amine groups from Spd and Spm (Alcazar et al., 2006). While dicotyledonous plants predominantly accumulate DAO, monocotyledonous plants usually accumulate more PAO than DAO (Šebela et al., 2001; Cona et al., 2006). The oxidative deamination of Put produces Δ 1-pyrroline, H_2O_2, and NH_3 by DAO whereas activity of PAO resulted in the formation of Δ1–pyrroline (from Spd oxidation) or 1-(3-aminopropyl)-pyrroline (from Spm oxidation), along with 1, 3-diaminopropane and H_2O_2 (Federico and Angelini, 1991). Both DAO and PAO are localized to the cytoplasm and cell wall and are involved in production of the hydrogen peroxide required for cell wall stiffening (Cona et al., 2003; Kuznetsov and Shevyakova, 2007) (**Figure 1**). These enzymes seem to contribute to changes in growth during salt stress since increased PAO accumulation in the expansion zone of maize leaves enhanced both ROS accumulation and elongation (Rodríguez et al., 2009; Shoresh et al., 2011). Moreover, high salt (400 mM NaCl) or ROS application induces DAO activity in the leaves and roots of the halophyte *Mesembryanthemum crystallinum* further implicating that these enzymes play a role in salt stress (Shevyakova et al., 2006).

Polyamines as Modulators of Ion Homeostasis

Polyamines are also hypothesized to promote salt stress tolerance through their direct or indirect effects on ion transport (**Figure 3**) (Demidchik and Maathuis, 2007; Pandolfi et al., 2010; Bose et al., 2011). For instance, polyamines including Spd, Spm, and Put affect ion transport indirectly by interacting with plasma membrane phospholipids and enhancing membrane stability. Polyamine-enhanced membrane stability has been shown

TABLE 1 | Effect of polyamines in the regulation of various enzymatic and non-enzymatic antioxidant components in salt stressed plants.

Polyamines	Transgenic gene name	Traits studied	References
Spd, Spm	–	GPX, CAT, APX	Roychoudhury et al., 2011
Put	–	GPX, CAT, GR	Ghosh et al., 2012
Put, Spd, Spm	Spermidine synthase	SOD, APX, MDHAR, GR	He et al., 2008
Put, Spd, Spm	S-adenosylmethionine decarboxylase	APX, MnSOD, GST	Wi et al., 2006
Spd	Spermidine synthase 1	APX	Neily et al., 2011
Cadaverine	–	Peroxidase	Kuznetsov et al., 2007
Put	–	SOD, CAT, POD, APX, GR	Verma and Mishra, 2005
Spd	–	SOD, POD, CAT	Duan et al., 2008
Put, Spd, Spm	–	APX, GR, SOD	Tang and Newton, 2005
Spm	–	APX, DHAR, MDAR, GR, POD, SOD	Shu et al., 2013
Put, Spd, Spm	–	SOD, POD, CAT, GR, MDHAR, DHAR, APX	Tanou et al., 2013
Spm	–	Proline, CAT, MDA, POX, GR	Chai et al., 2010
Put	–	CAT, POX, SOD, APX, GR, DHAR	Sheokand et al., 2008
Put	–	POD, CAT, Proline	Öztürk and Demir, 2003
Spd	–	CAT, POD, superoxide, reduced glutathione, total polyphenol content	Radhakrishnan and Lee, 2014
Put, Spd, Spm	–	Mn-SOD, CAT, APX	Sudhakar et al., 2015
Put	–	SOD, POX, CAT	Fariduddin et al., 2014
Put, Spd	–	SOD, POX, CAT	Ghahremani et al., 2014

to have a significant effect on both H^+/ATPase and Ca^{2+}/ATPase transporters during salinity stress (Roy et al., 2005; Pottosin and Shabala, 2014). Ca^{2+} channel regulation mediated by polyamines and H_2O_2 in response to salt stress leads to the rapid rise in the intracellular concentration of Ca^{2+} that, subsequently, enforces a positive feedback on the ROS production via the membrane-localized NADPH-oxidase (Takeda et al., 2008; Bose et al., 2014). Sudden exposure to salt stress is reflected in the alterations of turgor that is sensed by rapid increase in cellular cGMP, produced by the action of receptor kinase cyclase. This in turn activates the root-localized cyclic nucleotide-gated channels allowing the inward flow of Ca^{2+}, thus cGMP signal is converted to Ca^{2+} signal during salinity (Demidchik and Maathuis, 2007). On the other hand, a rise in cGMP can directly inactivate root voltage-independent non-selective cation channels (VI-NSCC) by reducing the influx of toxic Na^+ (Rubio et al., 2003). Salt-stress elicited Ca^{2+} signals activate signaling molecules including the *SOS3* calcium-binding protein and the serine/threonine protein kinase *SOS2* which in turn activate the membrane Na^+/H^+ antiporter SOS1 leading to Na^+ efflux (Zhu, 2003). If we consider the above mentioned reports, one can easily observe an indirect cumulative effect of polyamines and ROS in regulating the cellular Ca^{2+} that is important for salt response. In contrast, Spm may directly affect ion transport during salt stress by blocking inward-rectifying K^+ channels (KIRC) and non-selective cation channels (NSCCs), limiting Na^+ influx, and K^+ efflux (Liu et al., 2000; Shabala et al., 2007; Zhao et al., 2007; Zepeda-Jazo et al., 2008). Put and Spm have shown strong potential in reducing the hydroxyl radical-induced $K(^+)$ efflux and the respective non-selective current. This synergistic effect between ROS and polyamines was much more pronounced in a salt-sensitive barley variety than salt-tolerant one (Velarde-Buendia et al., 2012). Subsequently, an increased external $[Ca^{2+}]$ activated depolarization-activated NSCCs (DA-NSCCs), inhibited Na+ -induced K+ efflux, thus ameliorating Na^+ toxicity in plants (Shabala et al., 2006). During salinity, exogenous application of spermidine has been found to block VI-NSCC reducing the inward flow of Ca^{2+} and Na^+ and the outward flow of K^+ in barley seedlings (Zhao et al., 2007). It has been reported that polyamine accumulation under salt stress has a tendency to make the overall tonoplast cation conductance more K^+ selective, thus considered to lead to higher vacuolar Na^+ sequestration and an improved cytosolic K^+/Na^+ homeostasis (Zepeda-Jazo et al., 2008). Absence of Spm causes an imbalance in Ca^{2+} homeostasis in the *Arabidopsis* mutant plant and showed hypersensitivity to salinity, suggesting its involvement in modulating the activity of certain Ca^{2+}- permeable channels and changes in Ca^{2+} allocation compared to unstressed state, which may prevent Na^+ and K^+ entry into the cytosol, enhance Na^+ and K^+ influx into the vacuole, or suppress Na^+ and K^+ release from the vacuole (Yamaguchi et al., 2006). Moreover, vacuolar *Cation/H^+ Exchangers* (*CAX*) are found to be over-expressed and both FV and SV channels (FV, fact-activating vacuolar channel; SV, slow-activating vacuolar channel) suppressed during salinity, resulting into an overall increase in vacuolar Ca^{2+} (Cheng et al., 2004; Pottosin et al., 2004). Dobrovinskaya et al. (1999) reported that cellular polyamines strongly inhibited FV and SV channels whose reduced activity is essential for conferring salinity tolerance in the facultative halophyte *Chenopodium quinoa* (Bonales-Alatorre et al., 2013). However, more research is required to understand this interaction as well as the putative interactions between polyamines and vacuolar transport systems (Pottosin and Shabala, 2014).

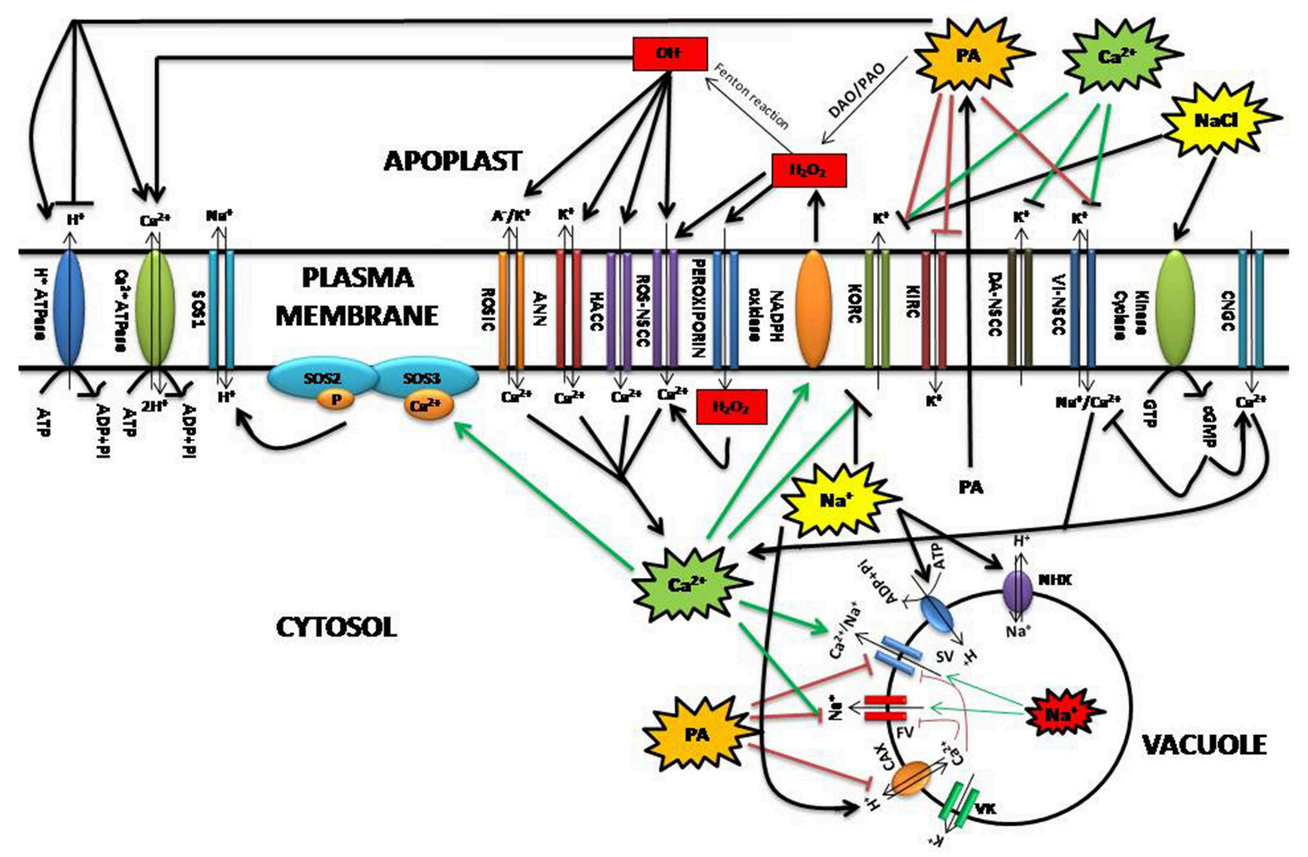

FIGURE 3 | Relationship between polyamines and ROS during salinity in the context of ion transport regulation at plasma membrane and vacuole. ANN, Annexin-formed channel; CAX, Cation/H+ exchangers; CNGCs, Cyclic nucleotide-gated channels; cGMP, cyclic guanyl cyclase; DA-NSCCs, Depolarization-activated NSCCs; DAO, Diamine oxidases; FV, Fast vacuolar channel; HACC, Hyperpolarization-activated Ca^{2+} influx channel; KIRC, K^+ inward-rectifying; KORC, K^+ outward rectifying; VK, K+-selective channels; ROSIC, Non-selective voltage-independent conductance; NHX, Na+/H+ antiporters; PA, Polyamine; PAO, Polyamine oxidases; ROS-NSCC, ROS activated Non-selective cation channel; SOS1, SOS2, SOS3, respectively, Salt overly sensitive 1,2,3; SV, Slow vacuolar channel; VI-NSCCs, Voltage-independent nonselective cation channels.

Cross Talk between Polyamines, ROS, NO, and ABA

Plants employ multi-level signal transduction to induce stress responses. The coordinated actions of hormones such as abscisic acid (ABA), ethylene, jasmonate, and auxin along with other signaling molecules like Ca^{2+}, cyclic nucleotides, ROS and reactive nitrogen species such as NO form a complex signaling network (Neill et al., 2003; Tuteja and Sopory, 2008). Interestingly, ABA was found to be involved in regulating both biosynthetic and catabolic pathways for polyamines in *Arabidopsis* (Urano et al., 2004; Hussain et al., 2011). For example, exogenous application of ABA has been found to modulate the transcription and biosynthesis of polyamine metabolic enzymes such as *ADC2, SPDS,* and *SPMS* during stress (Alcazar et al., 2006; Hussain et al., 2011). On the other hand Put has been found to serve as a modulator of indispensable ABA increase under cold stress thus representing and reciprocal relationship between Put and ABA biosynthesis during the period of stress in order to increase plant adaptive potential (Cuevas et al., 2008, 2009; Urano et al., 2009). The transgenic tobacco plants overexpressing the ABA-biosynthetic enzyme 9-cis-epoxycarotenoid dioxygenase is associated with the ABA-induced production of H_2O_2, NO, and the subsequent induction of antioxidant enzymes conferring salt tolerance (Zhang et al., 2009). Recently, it has been shown that polyamines can induce the production of NO that serves as a signal-inducing salt resistance by increasing the K^+ to Na^+ ratio by stimulating the expression of the plasma membrane H^+-ATPase and Na+/H+ antiport in the tonoplast (Zhao et al., 2004; Tun et al., 2006; Yamasaki and Cohen, 2006; Zhang et al., 2006). It was suggested that NO production induced by polyamines could be mediated either by H_2O_2, one reaction product of oxidation of polyamines by DAO and PAO, or by unknown mechanisms involving polyamines, DAO and PAO (Wimalasekera et al., 2011). Pre-treatment with H_2O_2 or sodium nitroprusside (NO donor) induced major antioxidant defense (SOD, catalase, APX, and GR), reduced protein carbonylation and accumulated leaf S-nitrosylated proteins, suggesting an overlap relation between NO and H_2O_2 signaling pathways in salinity acclimation (Tanou et al., 2009a,b).

In the light of these observations we have made an attempt to explore the interconnection(s) between polyamines, NO, ABA, and ROS as potential mediator(s) of stress responses. More research is needed to determine the exact nature of these intricate connections in the context of salt stress.

Polyamines and Programmed Cell Death

Plant cells employ dynamic activation of ROS production to regulate defense responses during stress. When ROS accumulation crosses a threshold value, cells enter into a genetically programmed necrotic process that leads to cellular suicide, which restricts the oxidative damage to a controlled number of cells and triggers pathways for nutrient recycling (de Pinto et al., 2006; Stowe and Camara, 2009). The key regulator of the switch between the cellular endurance and programmed cell death (PCD) under salt stress could be controlled by the interplay between polyamine and ROS homeostasis; specifically, the precise modulation of polyamine levels by the shift between polyamine anabolism and catabolism may result a lower polyamine concentration which, in turn may facilitate PCD (Moschou et al., 2008a; Toumi et al., 2010).

We have already discussed in our previous section that polyamines act as important regulators of ion homeostasis during salt stress. Modulation of the cellular K^+ and Ca^{2+} concentrations regulate stress-related PCD pathways in plants (Moschou and Roubelakis-Angelakis, 2014). Plant polyamines are found to affect intracellular dynamics of both ions, thus suggesting their direct involvement in PCD (Wu et al., 2010; Zepeda-Jazo et al., 2011). Low cellular concentrations of K^+ were shown to increase the activity of metacaspases and nucleases, thus promoting ROS- and salt-induced PCD (Demidchik et al., 2010). Salt stress led to high cytosolic [Ca^{2+}] which promoted the opening of mitochondrial permeability transition pore (MPTP) and PCD induction in tobacco protoplasts (Lin et al., 2005). Mitochondrial depolarization and cytochrome-c release is a hallmark event during the PCD (Logan, 2008; Andronis and Roubelakis-Angelakis, 2010). Takahashi's group showed that 0.5 mM Spm pretreatment of tobacco leaf discs induced expression of the *Salicylic acid (SA)-induced Protein Kinase*

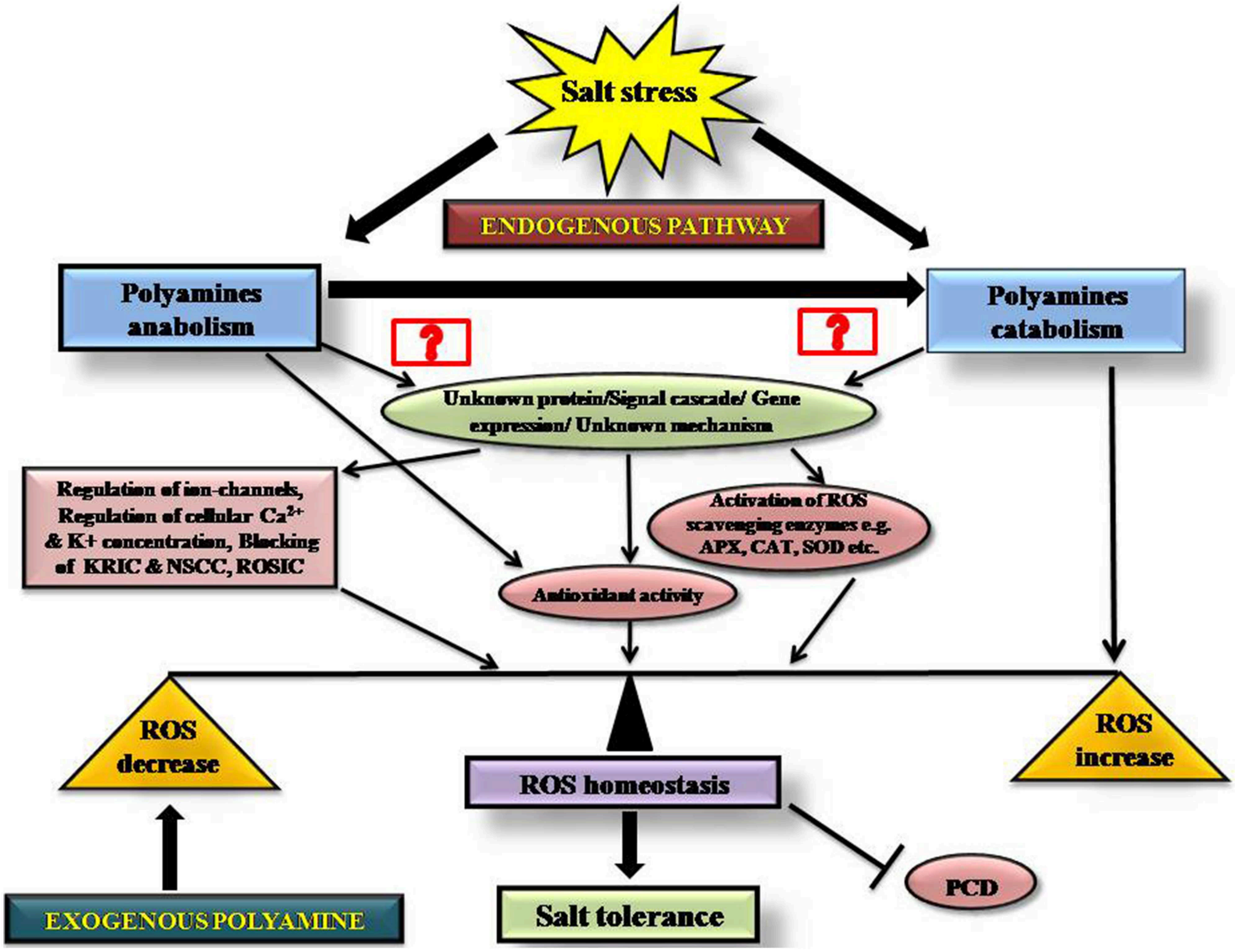

FIGURE 4 | Schematic diagram showing the role of endogenous and exogenous polyamines in maintaining redox homeostasis during salinity stress.

(*SIPK*) and *Wound-Induced Protein Kinase* (*WIPK*) and caused mitochondrial dysfunction similar to the one observed during PCD in tobacco leaves (Takahashi et al., 2003).

Accumulation of metabolic derivatives of polyamines may also indirectly control PCD pathways (Moschou and Roubelakis-Angelakis, 2014). For example, tobacco plants with reduced or increased *PAO* expression demonstrated increased salt tolerance or PCD depending on the availability of intracellular polyamines (Moschou et al., 2008c). Expression of the *Spm Oxidase* (*SMO*) can also be linked to hydrogen peroxide production and PCD, providing additional support to the above presented view of PAO-induced PCD (Moschou and Roubelakis-Angelakis, 2014). It has also been reported that overexpression of *PAO* activates mitogen-activated protein kinases (MAPK)-mediated pathways during biotic stress (Moschou et al., 2009).

In sum, a connection between polyamine metabolism and PCD can be inferred, but more work is needed to determine the molecular mechanisms underlying this relationship.

Conclusions and Future Prospects

This review outlines our current understanding of polyamines and their contributions to ROS homeostasis during salt stress, summarized in **Figure 4**. The figure depicts the possible cellular pathways by which polyamines modulate ROS homeostasis during salinity and the probable mode of action of endogenous and exogenous PAs into a single frame, so that one can easily view the current state of the field.

Our literature review suggests that the regulation of polyamine metabolism is a complex process where the exact roles of polyamines in regulating ROS, ion transport and PCD are still to be discovered. For the field to progress there is a need to address several important aspects: (i) The identity of the cellular components that mediate the link between ROS synthesis, ROS signaling and polyamines; (ii) The mechanisms that these mediator components employ; and (iii) The potential organ- or tissue-specific differences in the composition and regulation of polyamine-ROS networks.

To solve these questions one should focus on several relevant processes including polyamine biosynthesis, transport and catabolism in parallel with the tissue-, species-, and salt stress dependent expression of various ion channels and transporters. Additionally, one should consider the nature of various ROS and polyamine species that accumulate in plants under stress and the sites of their subcellular synthesis, alongside changes in the polyamine and ROS scavenging systems.

Salt stress constitutes a serious challenge to overcome in the quest of global increase in crop productivity. Understanding the underlying molecular mechanism of salt stress adaptation is the key to successful crop biotechnology.

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