Plant Abiotic Stress: Function of Nitric Oxide and Hydrogen Peroxide

Małgorzata Janicka, Małgorzata Reda, Natalia Napieraj, and Katarzyna Kabała

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Abstract The negative effect of various environmental stresses is partially due to the generation of reactive oxygen species (ROS). ROS were originally considered to be detrimental to cells. However, it is now recognized that hydrogen peroxide functions as a trigger for induction of many genes encoding enzymes involved in cellular protection under stress. In a number of abiotic responses, NO generation occurs in parallel with H_2O_2, and both molecules can act synergistically and/or independently. Studies have shown that NO and H_2O_2 function as stress signals in plants, mediating a range of resistance mechanisms. The main place of the signal perception of worsening environmental conditions is the plasma membrane. On the other hand, one of the major proteins of the plant cell membrane is the plasma membrane H^+-ATPase (PM H^+-ATPase), a key enzyme in adaptation of plants to abiotic stresses. In plants exposed to different abiotic stresses, e.g., salinity, heavy metals, and low or high temperature, an increase in permeability related to membrane damage is observed. Maintaining ionic balance and replenishing the loss of essential substances are important issues. Support of active transport of ions through the plasma membrane requires increased generation of an electrochemical proton gradient by PM H^+-ATPase, which results in a proton-motive force used by active transporters for assimilation of various nutrients, as well as for releasing toxic ions from cells. NO and H_2O_2 are important elements for understanding the mechanisms

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M. Janicka (✉) · M. Reda · N. Napieraj · K. Kabała
Department of Plant Molecular Physiology, Institute of Experimental Biology, University of Wrocław, Wrocław, Poland
e-mail: malgorzata.janicka@uwr.edu.pl

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of PM H^+-ATPase modification at both genetic and posttranslational level. Nowadays the role of NO and H_2O_2 as well as the signal cascades by which signaling molecules participate in plant responses to changing environmental conditions is under intensive study.

Keywords Abiotic stress · NO · H_2O_2 · Plasma membrane H^+-ATPase

1 Introduction

Plants are continuously subjected to numerous environmental stresses, such as heavy metals, salinity, drought, and low or high temperature. These adverse external factors limit plant growth and productivity. Understanding plant responses to abiotic stresses is essential for reasonable production of more resistant crop plants. The process by which plant cells sense the stress signals and transmit them to cellular machinery for activation of adaptive responses is referred as signal transduction. In plants, the signal transduction pathways are still elucidated. Despite many physiological and molecular studies, the knowledge of how plants sense and transduce extreme temperature, drought, salinity, or heavy metals needs to be explained. The negative effect of various environmental stresses is partially due to the generation of reactive oxygen species (ROS). Accumulation of ROS is a general feature of abiotic stresses and together with changes in cell antioxidant capacity can lead not only to oxidative damage but also to ROS signaling (Tanou et al. 2009; Foyer and Noctor 2009; Groβ et al. 2013; Arora et al. 2016). In a number of abiotic responses, H_2O_2 generation occurs in parallel with NO (nitric oxide), and these molecules can act both synergistically and independently (Clarke et al. 2000; Neill et al. 2002; Zhang et al. 2007; Qiao et al. 2014). NO is a key signaling molecule that mediates a variety of physiological functions and defense mechanisms against abiotic stresses in plants (Qiao and Faan 2008).

In general, extreme temperature mainly results in mechanical embarrassment, whereas heavy metals, salinity, and drought exert their scathing effects mainly by disrupting the ionic and osmotic equilibrium of the cell. In plants exposed to abiotic stresses, an increase in permeability related to membrane damage is observed (Guy 1990; Breckle and Kahle 1991; Devi and Prasad 1999). Moreover, under heavy metals or salt stress, accumulation of toxic ions in plant cells occurs. Ion homeostasis is the physiological fundament for living cells. Maintaining ionic balance and replenishing the loss of essential substances in repair processes are important issues under such conditions (Janicka-Russak 2011). Support of active transport of ions and organic compounds through the plasma membrane requires increased generation of a proton gradient by plasma membrane H^+-ATPase (Serrano 1989). The generation of an electrochemical proton gradient across the membrane results in a proton-motive force that is used by active transporters for uptake of various nutrients as well as for releasing toxic ions and substances from cells (Janicka-Russak 2011). It has been proven that the activity of the plasma membrane H^+-ATPase (PM H^+-ATPase) is a key index of plant adaptation to abiotic stresses (Kłobus and Janicka-Russak 2004; Janicka-Russak et al. 2008, 2012a, b, 2013; Sahu and Shaw 2009; Lopez-Pérez et al. 2009). Moreover, the reported studies show that signaling molecules are important elements for understanding the mechanisms of modification of the plasma membrane proton pump activity. Both NO and H_2O_2 play an essential role in regulation of PM H^+-ATPase activity under stress conditions (Zhang et al. 2007; Siddiqui et al. 2010; Janicka-Russak and Kabała 2012; Janicka-Russak et al. 2012a; Janicka et al. 2018). The pathways by which signaling molecules participate in plant responses to changes in environmental conditions are under intensive study. The purpose of this chapter is to explain the role of NO and H_2O_2 in plant adaptation to abiotic stresses.

2 Abiotic Stress in Plants

Stress is a physical definition. In biological terms, it is problematic to define stress. A physiological condition, stressful for one plant, may be optimal for another plant. The most applied definition of biological stress is an adverse force or a condition which limits the normal functioning of biological systems such as plants (Jones and Jones 1989). It is well known that NO and H_2O_2 play key functions in the regulation of plant tolerance to environmental stress factors such as drought, salinity, low or high temperature, heavy metals, and wounding (Neil et al. 2002, 2008; Vandenabeele et al. 2003; Shapiro 2005; Suzuki and Mittler 2006; Volkov et al. 2006; Qiao and Faan 2008; Janicka et al. 2018).

Exposure to high salinity can affect all the major plant processes, including protein synthesis, photosynthesis, and lipid metabolism (Parida and Das 2005). A high concentration of salt in the soil is one of the stressogenic stimuli. Excessive salinity imposes two stress factors on plants: an osmotic component that results from the reduced water availability caused by an increase in osmotic pressure in the soil and an ionic stress resulting from a solute imbalance, causing changes in the K^+/Na^+ ratio and increasing the concentration of Na^+ and Cl^- in the cytosol (Alvarez et al. 2003). Sodium toxicity results from the similarity of the Na^+ and K^+ ions that compete for plant transporters and binding sites in enzymes (Silva and Geros 2009). Osmolytes like proline, glycine-betaine, trehalose, mannitol, and sorbitol that are abundantly produced and accumulated in salt-treated plants represent an important component of salt stress responses. These compounds lower the osmotic potential of cells or protect various cellular structures and proteins against stress-induced damage (Sahi et al. 2006). It is well established that the efficient exclusion of Na^+ excess from cytoplasm is the most important step toward the maintenance of ion homeostasis inside the cell (Zhu 2003; Silva and Geros 2009). Majority of plants adapted to salinity maintain a relatively low concentration of Na^+ in the cytosol achieved through the active exclusion of sodium ions in the apoplast and vacuole. Removal of sodium ions out of the cell, catalyzed by the specific plasma membrane and tonoplast Na^+/H^+ antiporters, depends on the membrane electrochemical proton gradient (Chinnusamy et al. 2005; Silva and Geros 2009; Kabała and Janicka-Russak 2012). The only pump which generates proton gradient across the plasma membrane is H^+-ATPase. For this reason, it is believed that plant plasma membrane H^+-ATPase plays a major role in salt stress tolerance. The importance of the proton pump in plant adaptation to salinity was indicated by the observations carried out on salt-tolerant plants, showing increased activity of this enzyme in both normal and salt conditions (Vera-Estrella et al. 1994; Chen et al. 2007; Sahu and Shaw 2009). Moreover, the salinity induces the activities of the plasma membrane proton pumps both in halophytes and glycophytes (Kłobus and Janicka-Russak 2004; Sahu and Shaw 2009; Lopez-Pérez et al. 2009; Janicka-Russak et al. 2013). NaCl stress induces the expression of PM H^+-ATPase genes (Niu et al. 1993; Janicka-Russak and Kłobus 2007; Janicka-Russak et al. 2013). The positive correlation between accumulation of mRNAs of H^+-ATPase and salt tolerance is well documented (Niu et al. 1993; Perez-Prat et al. 1994; Janicka-Russak and Kłobus 2007; Sahu and Shaw 2009). It seems that both NO and H_2O_2 are generated under salt stress to activate resistance mechanisms in plants. These signal molecules maintain adequate K nutrition and a favorable K^+ to Na^+ ratio in cytosol (Zhu 2003). It was shown that NO produced under salt stress can serve as a second messenger to induce H_2O_2 generation mediated by the induction of plasma membrane NADPH oxidase expression (Zhang et al. 2007). Subsequently, the H_2O_2 contributes to induce the expression of PM H^+-ATPase that creates an electrochemical proton gradient for the establishment of ionic homeostasis to confer salt resistance (Zhang et al. 2007; Janicka et al. 2018).

Unpredictable falls in temperature are a common phenomenon in a temperate climate. Membranes are most susceptible to damage resulting from low temperature. An increase in membrane permeability and a change in its viscosity and fluidity result in a decrease of cell turgor due to low temperature (Guy 1990). It is well known that lipids containing saturated fatty acids solidify at temperatures higher than those containing unsaturated fatty acids. Therefore, the relative proportion of unsaturated fatty acids in the membrane strongly influences its fluidity (Mahajan and Tuteja 2005). Membrane changes at cold concern positional redistribution of saturated and unsaturated fatty acids. Membrane reconstruction has been observed in response of plants to low temperature. Chilling-sensitive plants usually have a higher proportion of saturated fatty acids. On the other hand, chilling-resistant species are marked by higher proportion of unsaturated fatty acids (Mahajan and Tuteja 2005). Probably, the change in membrane fluidity in sensitive species initiates a signal chain reaction that leads to acclimation to cold stress. Furthermore, the increase in H_2O_2 accumulation at low temperatures occurs (Kocsy et al. 2001). Glutathione is an important component of the ascorbate-glutathione cycle, which is indirectly involved in the regulation of H_2O_2 concentration in plants (Foyer et al. 1997). At low temperature, high GSH content and NADPH-dependent glutathione reductase (GR) activity were detected in plants indicating their possible contribution to chilling tolerance and cold acclimation. Changes in H_2O_2 concentration and GSH/GSSG ratio alter the redox state of the cells and activate specific defense mechanisms through a redox signaling chain (Kocsy et al. 2001). ROS produced in response to low temperature contributes to membrane damage. The integrity of intracellular organelles is also disrupted, leading to a loss of compartmentalization and impairing of photosynthesis, protein synthesis, and general metabolic processes. Low temperatures induce alteration in cellular components, including unsaturated fatty acids, glycerolipids, proteins, and carbohydrate composition as well as the activation of ion channels (Knight et al. 1996). Cold acclimation results in protection and stabilization of the integrity of cellular membranes, enhancement of the antioxidative mechanisms, increased intracellular sugar level, as well as accumulation of cryoprotectants like polyamines (Krishna et al. 1995; Polisensky and Braam 1996; Xiong and Zhu 2001; Mahajan and Tuteja 2005; Chinnusamy et al. 2006). Cold acclimation involves precise signaling and regulation of the transcriptome. Cold-induced ROS (such as H_2O_2) may activate a mitogen-activated protein kinase cascade that regulates tolerance to freezing (Chinnusamy et al. 2006). Altered transcript levels of PM H^+-ATPase genes were also observed (Ahn et al. 1999; Janicka-Russak et al. 2012a) due to exposure of plants to low temperature. Published data also indicate that activity of PM H^+-ATPase is modulated under low temperature by changes in plasma membrane lipids (Martz et al. 2006). The activity of plasma membrane H^+-ATPase may increase more than twofold following cold acclimation (Martz et al. 2006). Moreover, fatty acid-regulated PM proton pump activity is involved in the cellular response underlying cold acclimation and de-acclimation (Martz et al. 2006).

Temperature is a major factor in determining the natural distribution of plants. High temperatures can damage several plant metabolic and physiological processes (Larkindale and Huang 2004; Johnston et al. 2007). Plants are able to sense, respond to, and acclimate to mild high temperatures. This property allows them to survive extreme temperature shocks. High temperature causes protein dysfunction. Maintaining proteins in their functional conformations and preventing their aggregation are important for cell survival under high temperature stress (Wang et al. 2004; Timperio et al. 2008). The treatment of plants with temperatures near the upper limit for survival induces a specific set of proteins, the heat shock proteins (HSPs). This response is common to all living organisms. Königshofer et al. (2008) observed that as the final indicator of the heat signaling cascade, the synthesis of HSPs occurs. Their results indicated that elevated production of hydrogen peroxide, in the early stages of the heat signaling pathways, which responds rapidly to changes in membrane fluidity, is required for the activation of HSP synthesis. Similar observations were made by Miller and Mittler (2006) and Volkov et al. (2006). It was demonstrated that increased H_2O_2 production in apoplast under abiotic stresses occurs as a result of elevated levels of ABA (Hu et al. 2005, 2006). There is some evidence that ABA may be involved in heat stress responses in plants (Robertson et al. 1994; Gong et al. 2002). It was shown that ABA added to plants protected them from heat-induced oxidative damage (Larkindale and Knight 2002; Larkindale and Huang 2004).

Bioaccumulation of heavy metals in the environment has become a problem for all living organisms including plants. Heavy metals have the competence to interact with several cellular biomolecules such as proteins and DNA. Elevated levels of heavy metals lead to the increased generation of reactive oxygen species and induction of oxidative stress (Howlett and Avery 1997; Pál et al. 2005; Hossain et al. 2012). In response to heavy metals, plants are equipped with a range of mechanisms to counteract their toxicity. These mechanisms include chelation of metals by forming complexes with phytochelatins or metallothioneins, which is followed by the removal of heavy metals ions from cytoplasm. The plant plasma membrane may be regarded as the first structure that is a target for heavy metal toxicity. An increase in permeability related to membrane damage is observed in plants that have been subjected to heavy metal stress (Demidchik et al. 1997; Murphy and Taiz 1997; Murphy et al. 1999). It is well known that metal ions are easily bound to both the sulfhydryl groups of proteins and hydroxyl part of phospholipids (Devi and Prasad 1999). They can also replace the calcium ions at essential sites of cell membranes (Breckle and Kahle 1991). All these events result in disruption of membrane integrity and ionic homeostasis of cells. A factor that may be important in the maintenance of plasma membrane integrity in the presence of heavy metals could be enhanced membrane repair after damage (Salt et al. 1998). This could involve heat shock proteins. Moreover maintaining ionic balance and replenishing the loss of essential substances are important under heavy metal stress. A few observations have indicated that H^+-ATPase activity was changed under heavy metal stresses (Demidchik et al. 1997; Astolfi et al. 2003, 2005; Janicka-Russak et al. 2008, 2012b; Kabała et al. 2008). Moreover, the relative expression of PM-H^+-ATPase genes in cucumber roots was affected due to Cd treatment (Janicka-Russak et al. 2012b).

Many studies indicate that NO and H_2O_2 could be a common and mutual elements of different signaling pathways activated by plants in response to adverse environmental factors. Hydrogen peroxide and nitric oxide are involved in both salt and heat stress tolerance. Pretreatment of seedlings with H_2O_2 or SNP (NO donor) before salt or heat treatment caused decreases in deleterious effects of stress in plants (Uchida et al. 2002). Cross-resistance factors are able to reduce the effects of other stresses. For instance drought-hardened maize plants become more chilling-tolerant as well (Pérez de Juan et al. 1997). These phenomena are common in wide range of stresses (Uchida et al. 2002). This suggests that environmental factors activate similar signal transduction pathways. Stress conditions often lead to similar disturbances in plants, including dehydration and membrane damage. Control of ion movement across plasma membrane is an essential element of cellular adaptation to abiotic stresses. Because active transport of ions across the plasma membrane requires increased generation of a proton gradient by PM H^+-ATPase, it is suspected that this enzyme could play a key role in abiotic stress tolerance.

3 Plasma Membrane H^+-ATPase

The main place of the signal perception of worsening environmental conditions is the outer cell membrane, i.e., the plasma membrane. One of the most important proteins of the plant cell membrane is PM H^+-ATPase. This protein belongs to a large superfamily of pumps termed P-type ATPases. Plasma membrane H^+-ATPase is a tightly bound and integral transmembrane protein. The enzyme is a single polypeptide of ~100 kDa. By the use of the chemical energy of ATP hydrolysis, PM ATPases extrude protons from cells to apoplast to generate an electrochemical proton gradient (Serrano 1989). PM H^+-ATPase as a proton pump plays a central role in many physiological functions such as nutrient uptake, intracellular pH regulation, stomatal opening, and cell growth. Besides regulation of physiological processes, this proton pump also participates in the adaptation of plants to changing environmental conditions, especially stress conditions (Janicka-Russak 2011). Generation of an electrochemical proton gradient across the membrane is necessary for active transporters involved in accumulation of nutrients as well as removal of ions and other toxic substances from cells. Thus, the plasma membrane H^+-ATPase can be a key element for resistance mechanisms activated under various stress conditions. Therefore, the regulation of enzyme activity may represent an important cellular mechanism for abiotic stress resistance. Modification of the plasma membrane H^+-ATPase activity could take place at the genetic and posttranslational level.

The molecular study of plant H^+-ATPase has shown that this enzyme is encoded by a multigene family. In addition to tissue-specific expression, the plasma membrane H^+-ATPase genes are differentially expressed by environmental factors. Several studies have indicated that the H^+-ATPase genes might be activated by various abiotic stresses. With such a phenomenon, the amount of H^+-ATPase might be increased under conditions requiring greater transport activity. The external signals resulting in changes in plant plasma membrane H^+-ATPase gene expression include salinity (Niu et al. 1993; Janicka-Russak and Kłobus 2007), low temperature (Ahn et al. 1999; Janicka-Russak et al. 2012a), heavy metals (Janicka-Russak et al. 2008, 2012b), and mechanical stress (Oufattole et al. 2000). It was shown that signaling molecules NO and H_2O_2 contribute to increased activity of PM H^+-ATPase by stimulation of expression of gene encoding this enzyme (Zhang et al. 2007; Janicka et al. 2018).

As to posttranslational regulation, the best known mechanism described to date involves the auto inhibitory action of the C-terminal domain (approximately 100 amino acids) of the enzyme protein. The activity of the enzyme is well known to be regulated by 14-3-3 proteins, the association of which requires phosphorylation of the penultimate H^+-ATPase residues of Thr 947 (Svennelid et al. 1999; Fuglsang et al. 2006). The binding of 14-3-3 regulatory protein displaces the inhibitory domain, activating the enzyme. One 14-3-3 protein dimer binds two C-terminal polypeptides simultaneously, so a high activity state of H^+-ATPase could involve formation of dimers or multimeric complexes (Kanczewska et al. 2005). Recent studies have shown that NO participates in posttranslational modifications of plasma membrane proton pump because it leads to an increased level of enzyme phosphorylation and to an increased H^+/ATP coupling ratio (Janicka et al. 2018).

It is well known that the plant plasma membrane H^+-ATPase requires lipids for activity. This lipid dependency suggests a possible mode of regulation via modification of lipid environment (Kasamo 2003). Abiotic stresses lead to changes in the plasma membrane lipid composition altering the fluidity of the membrane. The modulation of the phospholipid environment of the plasma membrane regulates the activity of H^+-ATPase (Kasamo 2003). The activation of H^+-ATPase is dependent on the degree of saturation or unsaturation of the fatty acyl chain and its length. The activity decreased with an increase in the length of the chain and in the degree of unsaturation (Kasamo 2003; Martz et al. 2006).

4 Function of H_2O_2 in Abiotic Stress in Plants

It is known that the negative effect of the various environmental stresses, e.g., salinity, heavy metals, and extreme temperature, is partially due to the generation of reactive oxygen species and the inhibition of the systems which defend against them (Alscher et al. 1997; Quan et al. 2008). The reactive oxygen species H_2O_2 is a harmful cellular metabolite. To some extent, excess H_2O_2 accumulation can lead to oxidative stress in plants, which then triggers cell death (Quan et al. 2008). Although ROS were originally considered to be detrimental to cells, they are now widely recognized as key factors modulating cellular activities (Suzuki and Mittler 2006; Quan et al. 2008). There are several possible sources of H_2O_2 in plants which can be activated during abiotic stress, e.g., electron transport chains in chloroplast and mitochondria, photorespiration in peroxisomes, or enzymatic sources including plasma membrane NADPH oxidase and cell wall-bound peroxidases/amine oxidase. However, under stress conditions, much attention is focused on plasma membrane and apoplast compartments, in which increases in H_2O_2 could be associated with the activities of NADPH oxidases and peroxidases (Bolwell et al. 2002). Plants tolerate much higher concentration of endogenous H_2O_2 than other organisms (Queval et al. 2008). This increased tolerance could be attributed to the fact that accumulation preferentially occurs in the apoplast and that intracellular concentrations are much lower. ROS originating from the plasma membrane NADPH oxidase have been focus in ROS signaling (Jiang and Zhang 2002). It has been shown that NADPH oxidase is involved in plant growth and development and in plant responses to pathogens, elicitors, and wounding (Sagi and Fluhr 2006), chilling (Piotrovskii et al. 2011), drought (Jiang and Zhang 2002), and salt stress (Yang et al. 2007). This enzyme oxidizes cytoplasmic NADPH and transfers an electron to molecular O_2 to form O_2^-; the latter is then converted to H_2O_2 by superoxide dismutase (SOD) (van Gestelen et al. 1997). NADPH is mainly generated by the pentose phosphate pathway (Yu et al. 2014). Glucose-6-phosphate dehydrogenase (G6PDH) is the rate-limiting enzyme of this pathway. Recent studies demonstrated that G6PDH plays important role under salt stress and heavy metals (Wang et al. 2008; Jakubowska et al. 2015). However, studies that have been carried to elucidate the physiological role of this protein in plant tolerance to abiotic stresses are still limited.

In addition, apoplastic ROS generation can be mediated by two amine oxidases, the diamine oxidase (DAO) and polyamine oxidase (PAO). DAO and PAO are localized in peroxisomes and the apoplast (Moschou et al. 2008). DAO oxidizes putrescine, whereas PAO oxidizes spermidine and spermine and yields Δ^1-pyrroline and 1,5-diazbicyclononane, respectively, along with 1,3-diaminopropane and H_2O_2. Increased DAO activity resulted in increased tolerance to salinity (Waie and Rajam 2003). It was also shown that upon salt stress spermidine is secreted into apoplast and catabolized by PAO to produce H_2O_2 (Moschou et al. 2008). Polyamines (PAs) are low molecular weight polycationic compounds present ubiquitously in all living cells. Data suggest that PAs are able to affect the activity of H_2O_2-scavening enzymes, moderating this signal at molecular level (Kubiś 2003). Some evidence has shown that PA oxidation is directly involved in plant adaptation to abiotic stresses (Moschou et al. 2008). H_2O_2 derived from PA catabolism could also exert signaling effects. Toumi et al. (2010) have shown that the intrinsic ABA signal upregulates PA metabolism, which in turn increases endogenous H_2O_2 load through the apoplastic PAs exodus/catabolism pathway. Also Paschalidis et al. (2010) have indicated that ABA is partly responsible for the induction of the polyamine exodus pathway in plants. They demonstrated that ABA is an upstream signal for the induction of the polyamine catabolic pathway.

Increasing evidence indicates that hydrogen peroxide functions as a signaling molecule responsible for induction of many genes encoding enzymes involved in cellular protection under stress conditions (Vandenabeele et al. 2003; Volkov et al. 2006; Quan et al. 2008). It was observed that treatment of plants with H_2O_2 contributes to increased expression of PM H^+-ATPase genes in cucumber roots (Janicka-Russak et al. 2012a, 2018). Furthermore, it was shown that abscisic acid causes enhanced generation of ROS (Pei et al. 2000; Laloi et al. 2004). ABA is known as a stress hormone, which mediates responses to a variety of stress factors. Some studies demonstrated that increased H_2O_2 production in apoplast under abiotic stresses occurs as a result of elevated levels of ABA (Hu et al. 2005, 2006). Furthermore, ABA stimulates H_2O_2 production by NADPH oxidases (Hu et al. 2005). So, it seems that under abiotic stress, the elevated level of H_2O_2 could partly result from increased amounts of ABA.

5 Function of NO in Abiotic Stress in Plants

Nitric oxide is a small, highly diffusible, gaseous molecule with ubiquitous bioactivity. It is synthesized in plant cells either during physiological or stress conditions. Endogenously generated NO and NO-derived compounds referred as reactive nitrogen species (RNS) are involved in many primary physiological processes including seed germination, root growth and development, control of stomatal movements, flowering, regulation of pollen tube growth, ripening of fruits, and senescence (Domingos et al. 2015; Sami et al. 2018). NO and RNS play also an extensive role in triggering the plant defense mechanisms in plant response to abiotic stresses such as salinity, drought, high and low temperature, and heavy metals (Corpas et al. 2011; Sahay and Gupta 2017; Sami et al. 2018).

Biosynthesis of NO occurs in certain cellular compartment including cytoplasm, chloroplasts, mitochondria, peroxisomes, and apoplast space (Tischner et al. 2004; Jasid et al. 2006; del Río et al. 2003; Stöhr and Stremlau 2006). Several oxidative and reductive and enzymatic and nonenzymatic pathways for NO biosynthesis have been discovered in plants. Reductive route of NO production involves reduction of nitrite ions and is dominantly associated with catalytic activity of cytoplasmic nitrate reductase (cNR). To date, the numerous studies confirmed the role of cNR in NO production in plants during physiological processes and under abiotic stresses (Kolbert et al. 2010; Hancock 2012; Sun et al. 2014). Further, during anoxia, mitochondrial inner membrane can also participate in reductive pathways of NO biosynthesis (Tischner et al. 2004; Gupta and Igamberdiev 2011). Xanthine oxidoreductase (XOR), a molybdenum-containing enzyme is responsible for NO production occurring in peroxisomes (Weidert et al. 2014). In root apoplast space, NO_2^- conversion to NO is performed by plasma membrane-associated nitrite-nitric oxide reductase (Ni-NOR), which is closely related to plasma membrane nitrate reductase (PM-NR) (Stöhr and Ullrich 2002; Eick and Stöhr 2012). The oxidative pathways include the enzymatic production of NO from L-arginine. In animals, nitric oxide synthases (NOS) oxidizing L-arginine to NO via L-citrulline are well recognized. Despite many years' explorations, there is no direct molecular evidence for existence of homologous NOS in higher plants, although NO production sensitive to mammalian NOS inhibitors has been detected (Corpas et al. 2009; Santolini et al. 2017).

The action mechanism of nitric oxide in plant response to abiotic stresses can be manifested through affecting the function and activity of numerous proteins due to their gene expression and/or protein posttranslational modifications (PTM). S-nitrosylation of cysteine residue, nitration of tyrosine, and metal nitrosylation are the main ones (Astier and Lindermayr 2012). *S*-nitrosylation consists a reversible covalent binding of NO moiety to the thiol group of cysteine (Cys) residue of target proteins. This reaction is resulting in the formation of *S*-nitrosothiol (Astier et al. 2011). *S*-nitrosylation can alter proteins activity, stability, conformation, subcellular localization, and protein-protein interactions (Farnese et al. 2016). The evidences indicate that this PTM is a crucial component of primary metabolism and photosynthesis and contributes to plant signaling and responses to abiotic stresses (Yu et al. 2014; Sami et al. 2018). To date, several proteins, such as H^+-ATPase, NADPH oxidase, ascorbate peroxidase glutathione reductase, or nitrosoglutathione reductase, concerned with stress reaction or ROS production and/or detoxification undergo modifications through *S*-nitrosylation (Tanou et al. 2009; Yun et al. 2011; Romero-Puertas et al. 2013).

Tyrosine (Tyr) nitration is another NO-mediated protein modification which involves addition of nitro group ($-NO_2$) transferring from peroxynitrite ($ONOO^-$) to the aromatic ring of Tyr residue (Corpas et al. 2009). Tyr nitration leads to structural and functional changes in target proteins and leads to altered cell and tissue homeostasis. Several stress-related proteins, such as some antioxidant enzymes, were identified to undergo Tyr nitration (Mata-Pérez et al. 2016). Metal nitrosylation consists of reversible NO binding to transitions metal, e.g., iron, zinc, and copper, in metalloproteins to form metal-nitrosyl complexes (Astier and Lindermayr 2012; Farnese et al. 2016). This PTM induces changes of protein conformation that affects the activity or reactivity of target proteins (Astier and Lindermayr 2012). Besides posttranslational proteins modifications, NO can affect gene expression of several protein related to and involved in plant response to abiotic stresses. Other studies showed that exogenous NO induces the expression of plasma membrane H^+-ATPase in plants under salt stress (Siddiqui et al. 2010).

Many studies have documented the essential role of NO for the plant's tolerance to elevated salt concentrations. Generally, it was shown that during salt treatment, NO improved biomass of shoots and roots (Egbichi et al. 2014), enhanced relative water content and chlorophyll level, decrease leakage of electrolyte, and protect from and reduces membrane injury and lipid peroxidation (Liu et al. 2016). Plant's exposure to raised NaCl concentration leads to accumulation of NO in cucumber tissues (Janicka et al. 2018). Salt-induced NO synthesis is associated with NR-dependent and/or NOS-like-dependent NO biosynthesis pathway (Zhao et al. 2007; Reda et al. 2018). Moreover, NO enhances K^+/Na^+ ratio by increasing activity of plasma membrane and tonoplast proton pumps and Na^+/H^+ antiport (Zhang et al. 2006; Kabała and Janicka-Russak 2012). In plants, both extremely high and low temperatures lead to accumulation of *S*-nitrosothiols and rise of protein nitration (Corpas et al. 2011; Farnese et al. 2016; Sami et al. 2018). To date, extreme temperatures usually promote a rapid increase in the endogenous NO and other RNS levels (Corpas et al. 2011; Li et al. 2013; Yu et al. 2014; Janicka et al. 2018). Moreover, exogenous application of NO to plants subjected to high temperature stress enhances the activity of several antioxidant enzymes (Sami et al. 2018). It was shown that activation of plasma membrane H^+-ATPase occurring during low temperature acclimation is NO mediated (Janicka et al. 2018). Additionally, action of NO on plasma membrane proton pump was tightly associated with H_2O_2 (Janicka et al. 2018). A growing body of evidence shows changes in NO generation in various plants subjected to heavy metals. However, intensity of NO production seems to be strictly dependent on form and concentration of metal used (Chmielowska-Bąk et al. 2014). Exogenously applied NO alleviates Cd toxicity by increasing pectin and cellulose content in cell walls leading to increasing Cd deposition in root cell walls (Xiong et al. 2009). NO can also promote incorporation of metals into vacuole by increasing phytochelatin synthesis (Arasimowicz-Jelonek et al. 2011) or metal removal from the cell by enhancing the activity of plasma membrane proton pump (Janicka-Russak et al. 2012a, b).

6 Conclusion

Recent studies show that NO and H_2O_2 interact to alleviate the negative influence of abiotic stress on plant growth, metabolism, and development. Both NO and H_2O_2 are generated in plant cells to activate different resistance mechanisms. As the plasma membrane is the main place of the signal perception related to unfavorable conditions, the PM-bound H^+-ATPase, responsible for proton gradient generation, seems to be a key enzyme involved in plant adaptation to changing environment. The activity, phosphorylation status, and gene expression of plasma membrane proton pump are modulated under abiotic stress conditions. It was demonstrated that enhanced PM H^+-ATPase functioning is one of the main adaptive mechanisms enabling plant survival under salinity, heavy metals, and low and high temperatures. Recently, NO and H_2O_2 were recognized as signaling molecules, which can affect PM proton pump action. Therefore, it is postulated that both NO and H_2O_2 signaling pathways are involved in the regulation of this enzyme and improvement of stress-induced cell disorders (Fig. 1).

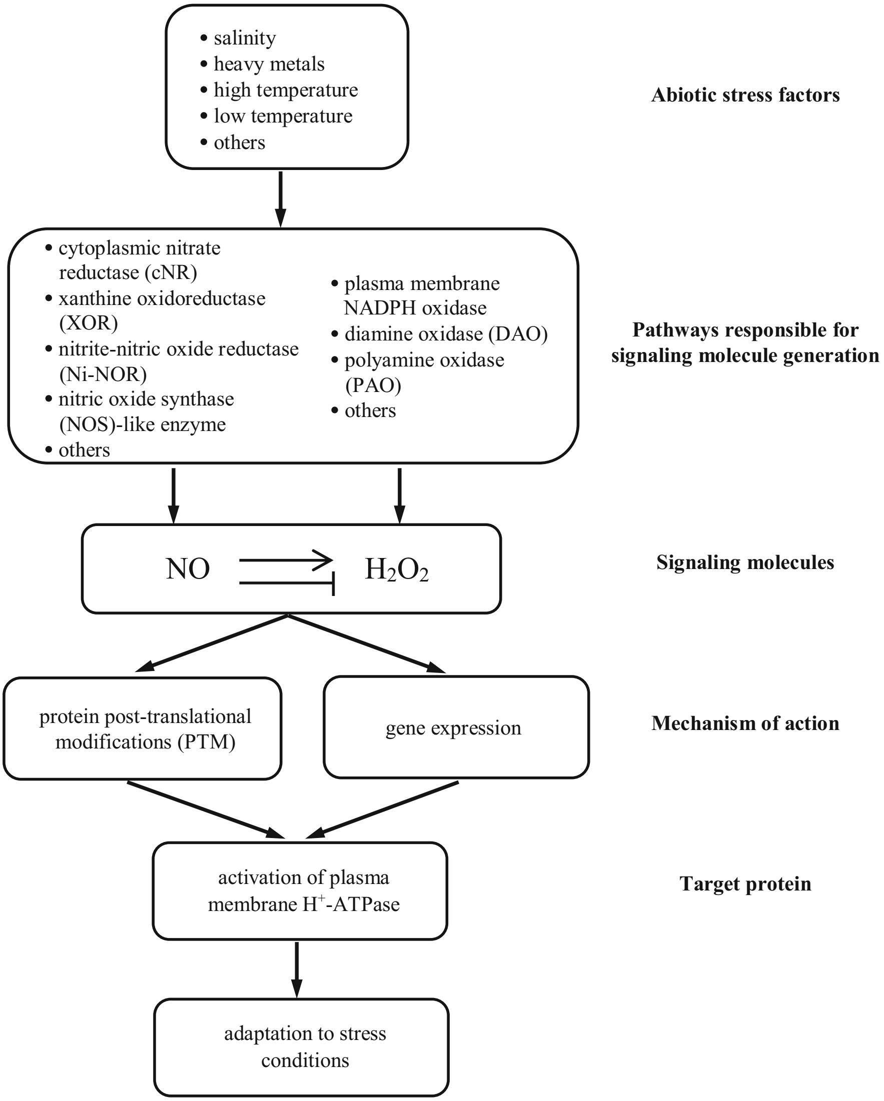

Fig. 1 Model of NO and H_2O_2 signaling pathways, induced under abiotic stress conditions, responsible for activation of plasma membrane H^+-ATPase involved in plant stress tolerance. Abiotic stresses, including salinity, heavy metals, and low as well as high temperatures, are known to induce NO and H_2O_2 generation. Increase in NO and H_2O_2 levels occurs as a result of enhanced activity of different enzymatic systems existing in plant cells. Additionally, NO can affect H_2O_2 accumulation, elevating or inhibiting it. Both NO and H_2O_2 act as signaling molecules which modulate the function and activity of numerous proteins due to their gene expression and/or posttranslational modifications (PTM), such as reversible phosphorylation, *S*-nitrosylation, or Tyr-nitration. The PM-bound H^+-ATPase, responsible for proton gradient generation, is a key enzyme involved in plant adaptation to environmental stresses. NO as well H_2O_2 can activate PM proton pump at both genetic and protein levels and in this way participate in plant tolerance

References

Ahn SJ, Yang IJ, Chung GC, Cho BH (1999) Inducible expression of plasma membrane H^+-ATPase in the roots of figleaf gourd plants under chilling root temperature. Physiol Plant 106:35–40

Alvarez I, Tomaro LM, Bernavides PM (2003) Changes in polyamines, proline and ethylene in sunflower calluses treated with NaCl. Plant Cell Tissue Organ Cult 74:51–59

Alscher RG, Donahue JL, Cramer CL (1997) Reactive oxygen species and antioxidants: relationship in green cells. Physiol Plant 100:224–233

Arasimowicz-Jelonek M, Floryszak-Wieczorek J, Gwóźdź EA (2011) The message of nitric oxide in cadmium challenged plants. Plant Sci 181:612–620

Arora D, Jain P, Singh N, Kaur H, Bhatla SC (2016) Mechanisms of nitric oxide crosstalk with reactive oxygen species scavenging enzymes during abiotic stress tolerance in plants. Free Radic Res 50:291–303

Astier J, Lindermayr C (2012) Nitric oxide-dependent posttranslational modification in plants: an update. Int J Mol Sci 13:15193–15208

Astier J, Rasul S, Koen E, Manzoor H, Besson-Bard A, Lamotte O, Jeandroz S, Durner J, Lindermayr C, Wendehenne D (2011) *S*-nitrosylation: an emerging post-translational protein modification in plants. Plant Sci 181:527–533

Astolfi S, Zuchi S, Chiani A, Passera C (2003) In vivo and in vitro effects of cadmium on H^+-ATPase activity of plasma membrane vesicles from oat (*Avena sativa* L.) roots. J Plant Physiol 160:387–393

Astolfi S, Zuchi S, Passera C (2005) Effect of cadmium on H^+-ATPase activity of plasma memebrane vesicles isolated from roots of different S-supplied maize (*Zea mays* L.) plants. Plant Sci 169:361–368

Bolwell GP, Bindschedler LV, Blee KA, Butt VS, Davies DR, Gardner SL, Gerrish C, Minibayeva F (2002) The apoplastic oxidative burst in response to biotic stress in plants: a tree component system. J Exp Bot 53:1367–1137

Breckle SW, Kahle H (1991) Effects of toxic heavy metals (Cd, Pb) on growth and mineral nutrition on beech (*Fagus sylvatica* L). Plant Ecol 101:43–53

Chen Z, Pottosin II, Cuin TA, Fuglsang AT, Tester M, Jha D, Zepeda-Jazo I, Zhou M, Palmgren MG, Newman IA, Shabala S (2007) Root plasma membrane transporters controlling K^+/Na^+ homeostasis in salt-stressed barley. Plant Physiol 145:1714–1725

Chinnusamy V, Jagendorf A, Zhu J (2005) Understanding and improving salt tolerance in plants. Crop Sci 45:437–448

Chinnusamy V, Zhu J, Zhu J (2006) Gene regulation during cold acclimation in plants. Physiol Plant 126:52–56

Chmielowska-Bąk J, Gzyl J, Rucińska-Sobkowiak R, Arasimowicz-Jelonek M, Deckert J (2014) The new insight into cadmium sensing. Front Plant Sci 5:245

Clarke D, Durner J, Navarre DA, Klessig DF (2000) Nitric oxide inhibition of tobacco catalase and ascorbate peroxidase. Mol Plant-Microbe Interact 13:1380–1384

Corpas FJ, Leterrier M, Valderrema R, Airaki M, Chaki M, Palma JM, Barroso JB (2011) Nitric oxide imbalance provokes a nitrosative response in plants under abiotic stress. Plant Sci 181:604–611

Corpas FJ, Palma JM, del Rio LA, Barroso JB (2009) Evidence supporting the existence of L-arginine-dependent nitric oxide synthase activity in plants. New Phytol 184:9–14

del Rio LA, Corpas FJ, Sandalio LM (2003) Plant peroxisomes, reactive oxygen metabolism and nitric oxide. IUBMB Life 55:71–81

Demidchik V, Sokolik A, Yurin V (1997) The effect of Cu^{2+} ion transport systems of the plant cell plasmalemma. Plant Physiol 114:1313–1325

Devi S, Prasad M (1999) Membrane lipid alterations in heavy metal exposed plants. In: Prasad MNV, Hagemeyer J (eds) Heavy metal stress in plants. From molecules to ecosystems. Springer, Berlin, pp 99–116

Domingos P, Pardo AM, Wong A, Gehring C, Feijo JA (2015) Nitric oxide: a multitasked signaling gas in plants. Mol Plant 8:506–520

Egbichi I, Keyster M, Ludidi N (2014) Effect of exogenous application of nitric oxide on salt stress responses of soybean. South Afr J Bot 90:131–136

Eick M, Stöhr C (2012) Denitrification by plant roots? New aspects of plant plasma membrane-bound nitrate reductase. Protoplasma 249:909–918

Farnese FS, Menezes-Silva PE, Gusman GS, Oliveira JA (2016) When bad guys become good ones: the key role of reactive oxygen species and nitric oxide in the plant responses to abiotic stress. Front Plant Sci 7:471

Foyer CH, Lopez-Delgado H, Dat JF, Scott IM (1997) Hydrogen peroxide- and glutathione-associated mechanisms of acclimatory stress tolerance and signalling. Physiol Plant 100:241–254

Foyer CH, Noctor G (2009) Redox regulation in photosynthetic organisms: signaling, acclimation, and practical implications. Antioxid Redox Signal 11:861–890

Fuglsang A, Tulinius G, Ciu N, Palmgren M (2006) Protein phosphatases 2A scaffolding subunit A interacts with plasma membrane H^+-ATPase C-terminus in the same region as 14-3-3 protein. Physiol Plant 128:334–340

Gill SS, Hasanuzzaman M, Nahar K, Macovei A, Tuteja N (2013) Importance of nitric oxide in cadmium stress tolerance in crop plants. Plant Physiol Biochem 63:254–261

Gong M, Li YJ, Chen SZ (2002) Abscisic acid-induced thermotolerance in maize seedlings is mediated by calcium and associated with antioxidant systems. J Plant Physiol 153:488–496

Groβ F, Durner J, Gaupels F (2013) Nitric oxide, antioxidants and prooxidants in plant defence responses. Front Plant Sci 4:419

Gupta KJ, Igamberdiev AU (2011) The anoxic plant mitochondrion as a nitrite: NO reductase. Mitochondrion 11:537–543

Guy C (1990) Cold acclimation and freezing stress tolerance: role of protein metabolism. Annu Rev Plant Physiol Plant Mol Biol 41:187–223

Hancock JT (2012) NO synthase? Generation of nitric oxide in plants. Period Biol 114:19–24

Hossain MA, Piyatida P, da Silva JAT, Fujita M (2012) Molecular mechanism of heavy metal toxicity and tolerance in plants: central role of glutathione in detoxification of reactive oxygen species and methylglyoxal and in heavy metal chelation. J Bot 2012:37

Howlett NG, Avery SV (1997) Relationship between cadmium sensitivity and degree of plasma membrane fatty acid unsaturation in *Saccharomyces cerevisiae*. Appl Microbiol Biotechnol 48:539–545

Hu X, Jiang M, Zhang A, Lu J (2005) Abscisic acid induced apoplastic H_2O_2 accumulation up-regulates the activities of chloroplastic and cytosolic antioxidant enzymes in maize leaves. Planta 223:57–68

Hu X, Zhang A, Zhang J, Jiang M (2006) Abscisic acid is a key inducer of hydrogen peroxide production in leaves of maize plants exposed to water stress. Plant Cell Physiol 47:1484–1495

Jakubowska D, Janicka-Russak M, Kabała K, Migocka M, Reda M (2015) Modification of plasma membrane NADPH oxidase activity in cucumber seedling roots in response to cadmium stress. Plant Sci 234:50–59

Janicka M, Reda M, Czyżewska K, Kabała K (2018) Involvement of signalling molecules NO, H_2O_2 and H_2S in modification of plasma membrane proton pump in cucumber roots subjected to salt or low temperature stress. Funct Plant Biol 45:428–439

Janicka-Russak M (2011) Plant plasma membrane H+-ATPase in adaptation of plants to abiotic stresses. In: Shanker A, Venkateswarlu B (eds) Abiotic stress response in plants- physiological, biochemical and genetic perspectives. InTech, Rijeka, pp 197–218

Janicka-Russak M, Kabała K, Burzyński M, Kłobus G (2008) Response of plasma membrane H^+-ATPase to heavy metal stress in *Cucumis sativus* roots. J Exp Bot 59:3721–3728

Janicka-Russak M, Kabała K (2012) Abscisic acid and hydrogen peroxide induce modification of plasma membrane H^+-ATPase from *Cucumis sativus* L. roots under heat shock. J Plant Physiol 1969:1607–1614

Janicka-Russak M, Kabała K, Wdowikowska A, Kłobus G (2012a) Response of plasma membrane H^+-ATPase to low temperature in cucumber roots. J Plant Res 125:291–300

Janicka-Russak M, Kabała K, Burzyński M (2012b) Different effect of cadmium and copper on H^+-ATPase activity in plasma membrane vesicles from *Cucumis sativus* roots. J Exp Bot 63:4133–4142

Janicka-Russak M, Kabała K, Wdowikowska A, Kłobus G (2013) Modification of plasma membrane proton pumps in cucumber roots as an adaptation mechanism to salt stress. J Plant Physiol 170:915–922

Janicka-Russak M, Kłobus G (2007) Modification of plasma membrane and vacuolar H+-ATPase in response to NaCl and ABA. J Plant Physiol 164:295–302

Jasid S, Simontacchi M, Bartoli CG, Puntarulo S (2006) Chloroplasts as a nitric oxide cellular source. Effect of reactive nitrogen species on chloroplastic lipids and proteins. Plant Physiol 142:1246–1255

Jiang M, Zhang J (2002) Involvement of plasma membrane NADPH oxidase in abscisic acid-and water stress-induced antioxidant defense in leaves of maize seedlings. Planta 215:1022–1030

Johnston MK, Jacob NP, Brodl MR (2007) Heat shock-induced changes in lipid and protein metabolism in the endoplasmic reticulum of barley aleurone layers. Plant Cell Physiol 48:31–41

Jones HG, Jones MB (1989) Introduction: some terminology and common mechanisms. In: Jones HG, Flowers TJ, Jones MB (eds) Plants under stress. Cambridge University Press, Cambridge, pp 1–10

Kabała K, Janicka-Russak M (2012) Na^+/H^+ antiport activity in plasma membrane and tonoplast vesicles isolated from NaCl treated cucumber roots. Biol Plant 56:377–382

Kabała K, Janicka-Russak M, Burzyński M, Kłobus G (2008) Comparison of heavy metal effect on the proton pumps of plasma membrane and tonoplast in cucumber root cells. J Plant Physiol 165:278–288

Kanczewska J, Marco S, Vandermeeren C, Maudoux O, Rigaud J, Boutry M (2005) Activation of the plant plasma membrane H^+-ATPase by phosphorylation and binding of 14-3-3 proteins convert a dimer into a hexamer. Proc Natl Acad Sci U S A 102:11675–11680

Kasamo K (2003) Regulation of plasma membrane H^+-ATPase activity by the membrane environment. J Plant Res 116:517–523

Kłobus G, Janicka-Russak M (2004) Modulation by cytosolic components of proton pump activities in plasma membrane and tonoplast from *Cucumis sativus* roots during salt stress. Physiol Plant 121:84–92

Knight H, Trewavas AJ, Knight MR (1996) Cold calcium signaling in *Arabidopsis* involves two cellular pools and a change in calcium signature after acclimation. Plant Cell 8:489–503

Kolbert Z, Ortega L, Erdei L (2010) Involvement of nitrate reductase (NR) in osmotic stress-induced NO generation of *Arabidopsis thaliana* L. roots. J Plant Physiol 167:77–80

Kocsy G, Galiba G, Brunold C (2001) Role of glutathione in adaptation and signaling during chilling and cold acclimation in plants. Physiol Plant 113:158–164

Königshofer H, Tromballa HW, Löppert HG (2008) Early events in signaling high temperature stress in tobacco BY2 cells involve alterations in membrane fluidity and enhanced hydrogen peroxide production. Plant Cell Environ 31:1771–1780

Krishna P, Sacco M, Cherutti JF, Hill S (1995) Cold-induced accumulation of hsp-90 transcripts in *Brassica napus*. Plant Physiol 107:915–923

Kubiś J (2003) Polyamines and “scavenging system”: influence of exogenous spermidine on catalase and guaiacol peroxidase activities, and free polyamines level in barley leaves under water deficit. Acta Physiol Plant 25:337–343

Laloi C, Apel K, Danon A (2004) Reactive oxygen signalling: the latest news. Curr Opin Plant Biol 7:323–328

Larkindale J, Huang B (2004) Changes of lipid composition and saturation level in leaves and roots for heat-stress and heat-acclimated creeping bentgrass (*Agrostis stolonifera*). Environ Exp Bot 51:57–67

Larkindale J, Knight MR (2002) Protection against heat stress-induced oxidative damage in *Arabidopsis* involves calcium, abscisic acid, ethylene and salicylic acid. Plant Physiol 128:682–695

Li W, Wei Z, Qiao Z, Wu Z, Cheng L, Wang Y (2013) Proteomics analysis of alfalfa response to heat stress. PLoS One 8:82725

Liu A, Fan J, Gitau MM, Chen L, Fu J (2016) Nitric oxide involvement in Bermuda grass response to salt stress. J Amer Soc Hort Sci 141:425–443

Lopez-Pérez L, Martínez Ballesta M, Maurel C, Carvajal M (2009) Changes in plasma membrane lipids, aquaporins and proton pump of broccoli roots, as an adaptation mechanism to salinity. Phytochemistry 70:492–500

Mahajan S, Tuteja N (2005) Cold, salinity and drought stress: an overview. Arch Biochem Biophys 444:139–158

Martz F, Sutinen M, Kiviniemi S, Palta J (2006) Changes in freezing tolerance, plasma membrane H^+-ATPase activity and fatty acid composition in *Pinus resinosa* needles during cold acclimation and de-acclimation. Tree Physiol 26:783–790

Mata-Pérez C, Begara-Morales JC, Chaki M, Sánchez-Calvo B, Valderrama R, Padilla MN, Corpas FJ, Barroso JB (2016) Protein tyrosine nitration during development and abiotic stress response in plants. Front Plant Sci 7:1699

Miller G, Mittler R (2006) Could heat shock transcription factors function as hydrogen peroxide sensors in plants. Ann Bot 98:279–288

Moschou PN, Paschalidis AK, Delis ID, Andriopoulou AH, Lagiotis GD, Yakoumakis DI, Roubelakis-Angelakis KA (2008) Spermidine exodus and oxidation in the apoplast induced by abiotic stress is responsible for H_2O_2 signatures that direct tolerance responses in tobacco. Plant Cell 20:1708–1724

Murphy A, Taiz L (1997) Correlation between potassium efflux and copper sensitivity in 10 *Arabidopsis* ecotypes. New Phytol 136:211–222

Murphy A, Eisinger WR, Shaff JE, Kochian LV, Taiz L (1999) Early copper-induced leakage of K^+ from *Arabidopsis* seedlings is mediated by ion channels and coupled to citrate efflux. Plant Physiol 121:1375–1382

Neil S, Barros R, Bright J, Desikan R, Hancock J, Harrison J et al (2008) Nitroc oxide, stomatal closure, and abiotic stress. J Exp Bot 59:165–176

Neill SJ, Desikan D, Clarke A, Hurst RD, Hancock JT (2002) Hydrogen peroxide and nitric oxide as signaling molecules in plants. J Exp Bot 53:1237–1242

Niu X, Narasimhan M, Salzman R (1993) NaCl regulation of plasma membrane H^+-ATPase gene expression in *Glycophyte* and *Halophyte*. Plant Physiol 103:712–718

Oufattole M, Arango M, Boutry M (2000) Identification and expression of three new *Nicotiana plumbaginifolia* genes which encode isoforms of a plasma membrane H^+-ATPase, and one which is induced by mechanical stress. Planta 210:715–722

Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: a review. Ecotoxicol Environ Saf 60:324–349

Pál M, Horwáth E, Janda T, Páldi E, Szalai G (2005) Cadmium stimulates the accumulation of salicylic acid and its putative precursors in maize (*Zea mays*) plants. Physiol Plant 125:356–364

Paschalidis AK, Toumi I, Moschou NP, Kalliopi A, Roubelakis-Angelakis A (2010) ABA-dependent amine oxidases-derived H_2O_2 affects stomata conductance. Plant Signal Behav 5:1153–1156

Pei ZM, Murata Y, Benning G, Thomine S, Klüsener B, Allen GJ, Grill E, Schroeder JI (2000) Calcium channels activated by hydrogen peroxide mediate abscisic acid signalling in guard cells. Nature 17:731–734

Pérez de Juan J, Irigoyen J, Sánchez-Díaz M (1997) Chilling of drought-hardened and non-hardened plants of different chilling-sensitive maize lines changes in water relations and ABA contents. Plant Sci 122:71–79

Perez-Prat E, Narasimhan M, Niu X, Botella M, Bressan R, Valupesta V, Hasegawa PM, Binzel ML (1994) Growth cycle stage dependent NaCl induction of plasma membrane H^+-ATPase mRNA accumulation in de-adapted tobacco cells. Plant Cell Environ 17:327–333

Piotrovskii MS, Shevyreva TA, Zhestkova IM, Trofimova MS (2011) Activation of plasmalemmal NADPH oxidase in etiolated maize seedlings exposed to chilling temperatures. Russ J Plant Physiol 58:234–242

Polisensky DH, Braam J (1996) Cold shock regulation of the *Arabidopsis* TCH genes and the effects of modulating intracellular calcium levels. Plant Physiol 111:1271–1279

Qiao W, Faan LM (2008) Nitric oxide signaling in plant responses to abiotic stresses. J Integr Plant Biol 50:1238–1246

Qiao W, Li C, Fan LM (2014) Cross-talk between nitric oxide and hydrogen peroxide in plant responses to abiotic stresses. Environ Exp Bot 100:84–93

Quan LJ, Zhang B, Shi WW, Li HY (2008) Hydrogen peroxide in plants: a versatile molecule of the reactive oxygen species network. J Integr Plant Biol 50:2–18

Queval G, Hager J, Gakière B, Noctor G (2008) Why are literature data for H_2O_2 contents so variable? A discussion of potential difficulties in quantitative assays of leaf extracts. J Exp Bot 59:135–146

Reda M, Golicka A, Kabała K, Janicka M (2018) Involvement of NR and PM-NR in NO biosynthesis in cucumber plants subjected to salt stress. Plant Sci 267:55–64

Robertson AJ, Ishikawa M, Gusta LV, MacKenzie SL (1994) Abscisic acid induced heat tolerance in *Bromus inermis* lees cell suspension cultures. Plant Physiol 105:181–190

Romero-Puertas MC, Rodríguez-Serrano M, Sandalio ML (2013) Protein S-nitrosylation in plants under abiotic stress: an overview. Front Plant Sci 4:373

Sagi M, Fluhr R (2006) Production of reactive oxygen species by plant NADPH oxidases. Plant Physiol 141:336–340

Sahay S, Gupta M (2017) An update on nitric oxide and its benign role in plant responses under metal stress. Nitric Oxide 67:39–52

Sahi C, Singh A, Blumwald E, Grover A (2006) Beyond osmolytes and transporters novel plant salt-stress tolerance-related genes from transcriptional profiling data. Physiol Plant 127:1–9

Sahu BB, Shaw BP (2009) Salt-inducible isoform of plasma membrane H^+-ATPase gene in rice remains constitutively expressed in natural halophyte, *Suaeda maritima*. J Plant Physiol 166:1077–1089

Salt DE, Smith RD, Raskin I (1998) Phytoremediation. Annu Rev Plant Physiol Plant Mol Biol 49:643–668

Sami F, Faizan M, Faraz A, Siddiqui F, Yusuf M, Hayat S (2018) Nitric oxide-mediated integrative alterations in plant metabolism to confer abiotic stress tolerance, NO crosstalk with phytohormones and NO-mediated post translational modifications in modulating diverse plant stress. Nitric Oxide 73:22–38

Santolini J, André F, Jeandroz S, Wendehenne D (2017) Nitric oxide synthase in plants: where do we stand? Nitric Oxide 63:30–38

Serrano R (1989) Structure and function of plasma membrane ATPase. Annu Rev Plant Physiol Plant Mol Biol 40:61–94

Shapiro AD (2005) Nitric oxide signaling in plants. Vitam Horm 72:339–398

Siddiqui MH, Al-Whaibi MH, Basalah MO (2010) Role of nitric oxide in tolerance of plants to abiotic stress. Protoplasma 248:447–455

Silva P, Geros H (2009) Regulation by salt of vacuolar H^+-ATPase and H^+-pyrophosphatase activities and Na^+/H^+ exchange. Plant Signal Behav 4:718–726

Stöhr C, Stremlau S (2006) Formation and possible roles of nitric oxide in plant roots. J Exp Bot 57:463–470

Stöhr C, Ullrich WR (2002) Generation and possible roles of NO in plant roots and their apoplastic space. J Exp Bot 53:2293–2303

Sun C, Lu L, Liu L, Liu W, Yu Y, Liu X, Hu Y, Jin C, Lin X (2014) Nitrate reductase-mediated early nitric oxide burst alleviates oxidative damage induced by aluminum through enhancement of antioxidant defenses in roots of wheat (*Triticum aestivum*). New Phytol 201:1240–1250

Suzuki N, Mittler R (2006) Reactive oxygen species and temperature stresses: a delicate balance between signaling and destruction. Physiol Plant 26:45–51

Svennelid F, Olsson A, Piotrowski M, Rosenquist M, Ottman C, Larsson C, Oecking C, Sommarin M (1999) Phosphorylation of Thr-948 at the C-terminus of the plasma membrane H^+-ATPase creates a binding site for regulatory 14-3-3 protein. Plant Cell 11:2379–2391

Tanou G, Job C, Rajjou L, Arc E, Belghazi M, Diamantidis G, Molassiotis A, Job D (2009) Proteomics reveals the overlapping roles of hydrogen peroxide and nitric oxide in the acclimation of citrus plants to salinity. Plant J 60:795–805

Timperio AM, Egidi MG, Zolla L (2008) Proteomics applied on plant abiotic stresses: role of heat shock proteins (HSP). J Proteom 71:391–411

Tischner R, Planchet E, Kaiser WM (2004) Mitochondrial electron transport as a source for nitric oxide in the unicellular green alga *Chlorella sorokiniana*. FEBS Lett 576:151–155

Toumi I, Moschou PN, Paschalidis KA, Bouamama B, Ben Salem-Fnayou A, Ghorbel AW, Mliki A, Roubelakis-Angelakis KA (2010) Abscisic acid signals reorientation of polyamine metabolism to orchestrate stress responses via the polyamine exodus pathway in grapevine. J Plant Physiol 167:519–525

Uchida A, Jagendorf AT, Hibino T, Takabe T, Takabe T (2002) Effects of hydrogen peroxide and nitric oxide on both salt and heat stress tolerance in rice. Plant Sci 163:515–523

Van Gestelen P, Asard H, Caubergs RJ (1997) Solubilization and separation of a plant plasma membrane NADPH-superoxide ($O^{\cdot}_2{}^{-}$)-synthase from other NAD(P)H-oxidoreductases. Plant Physiol 115:543–550

Vandenabeele S, Van Der Kelen K, Dat J, Gadjev I, Boonefaes T, Morsa S, Rottiers P, Slooten L, van Montagu M, Zabeau M, Inze D, van Breusegem F (2003) A comprehensive analysis of hydrogen peroxide-induced gene expression in tobacco. Proc Natl Acad Sci U S A 100:16113–16118

Vera-Estrella R, Barkla B, Higgins V, Blumwald E (1994) Plant defense response to fungal pathogens (activation of host-plasma membrane H^+-ATPase by elicitor-induced enzyme dephosphorylation). Plant Physiol 104:209–215

Volkov RA, Panchuk II, Mullineaux PM, Schoffl F (2006) Heat stress-induced H_2O_2 is required for effective expression of heat shock genes in *Arabidopsis*. Plant Mol Biol 61:733–746

Waie B, Rajam M (2003) Effect of increased polyamine biosynthesis on stress responses in transgenic tobacco by introduction of human S-adenosylmethionine gene. Plant Sci 164:727–734

Wang W, Vinocur B, Shoseyov O, Altman A (2004) Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. Trend Plant Sci 9:244–253

Wang X, Ma Y, Huang C, Li J, Wan Q, Bi Y (2008) Involvement of glucose-6-phosphate dehydrogenase in reduced glutathione maintenance and hydrogen peroxide signal under salt stress. Plant Signal Behav 3:394–395

Weidert ER, Schoenborn SO, Cantu-Medellin N, Choughule KV, Jones JP, Kelly EE (2014) Inhibition of xanthine oxidase by the aldehyde oxidase inhibitor raloxifene; implications for identifying molybdenum nitrite reductases. Nitric Oxide 37:41–45

Xiong J, An L, Lu H, Zhu C (2009) Exogenous nitric oxide enhances cadmium tolerance of rice by increasing pectin and hemicellulose contents in root cell wall. Planta 230:755–765

Xiong L, Zhu J (2001) Abiotic stress signal transduction in plants: molecular and genetic perspectives. Physiol Plant 112:152–166

Yang Y, Xu S, An L, Chen N (2007) NADPH oxidase-dependent hydrogen peroxide production, induced by salinity stress, may be involved in the regulation of total calcium in roots of wheat. J Plant Physiol 164:1429–1435

Yu M, Lamattina L, Spoel SH, Loake GJ (2014) Nitric oxide function in plant biology: a redox cue in deconvolution. New Phytol 202:1142–1156

Yun BW, Feechan A, Yin M, Saidi NB, le Bihan T, Yu M, Moore JW, Kang JG, Kwon E, Spoel SH, Pallas JA, Loake GJ (2011) S-nitrosylation of NADPH oxidase regulates cell death in plant immunity. Nature 478:264–268

Zhang JZ, Wang L, Liu Y, Zhang Q, Wei Q, Zhang W (2006) Nitric oxide enhances salt tolerance in maize seedlings through increasing activities of proton pump and Na^+/H^+ antiport in tonoplast. Planta 224:545–555

Zhang F, Wang Y, Yang Y, Wu H, Wang D, Liu J (2007) Involvement of hydrogen peroxide and nitric oxide in salt resistance in the calluses from *Populus euphratica*. Plant Cell Environ 30:775–785

Zhao MG, Tian QY, Zhang WH (2007) Nitric oxide synthase-dependent nitric oxide production is associated with salt tolerance in *Arabidopsis*. Plant Physiol 144:206–217

Zhu JK (2003) Regulation of ion homeostasis under salt stress. Curr Opin Plant Biol 6:1–5