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REVIEW PAPER

Nitric oxide in plants: an ancient molecule with new tasks

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Abstract

Multitasking capability of nitric oxide (NO) makes it a highly investigating signaling molecule in plant biology. In plants including inflection of hormonal levels, fruit ripening, wound suppression and defensive responses, and regulation of programmed cell death, much progress in NO signaling cascades has been achieved. Additionally, growing evidences suggest the interactive behavior of NO with auxin, salicylic acid, abscisic acid, jasmonic acid and thus regulates their signaling pathways. Parallel to this, reactive oxygen species (ROS) along with NO are supposed to accomplish various developmental and stress responses. Under biotic stress, signaling initiated by NO was found to be mediated by two specific protein i.e. pathogenesis-related 1 (PR-1) and phenylalanine ammonia lyase. The above mentioned genes were also promoted by second messengers like cyclic GMP (cGMP) and cyclic ADP-ribose (cADPR), which further initiate and regulate NO signaling. In plants, important mechanism is programmed cell death regulating various growth and developmental aspects by acting as a damage control. Under stress condition the infected cells are removed by involving signaling agents i.e. NO and ROS which is a matter of crosstalk in recent years. Keeping above facts into consideration, present work mainly deals with NO signaling under adverse conditions as well as its interaction with different phytohormones and ROS.

Keywords Abiotic stress tolerance · Phytohormones · Programmed cell death · Reactive oxygen species · Second messengers

Introduction

Nitric oxide (NO), an effective biological factor involved in signaling cascade and a gaseous reactive nitrogen species (RNS), is mostly known for its multitasking role in plants (Domingos et al. 2015). A number of reports have recognized the NO generation endogenously in both higher plants as well as in algae, lichens and also in some non-flowering plants including ferns and gymnosperms (Domingos et al. 2015; Chakraborty and Acharya 2017; Tiwari et al. 2019). Among many vital components, NO is considered as a lipophilic, ubiquitous biologically active signaling molecule which is now recognized as a possible intercessor for regulating responses of plants against stress (Asgher et al. 2017; Begara-Morales et al. 2018). NO is an elementary molecule which governs signaling and controls metabolic processes of plants and makes them able to combat with stressful situations (Arasimowicz et al. 2009; Baudouin 2011; Asgher et al. 2017; Singh et al. 2017; Begara-Morales et al. 2018; Corpas and Palma 2018). Previously, NO was considered as a significant messenger involved in signaling process during pathogens attack (Huang et al. 2004). However in the recent years, NO has attracted more attention due to its omnipresence and the diversity of physiological functions. Figure 1 depicts the role of NO in plant development, gene expression, defense responses (expression of antioxidant enzymes) and stomatal movement under stress condition. Figure 2 illustrates the crosstalk of NO with other signaling molecules and involvement of NO in plant protein modifications through nitration and *S*-nitrosylation process. Under abiotic stress, NO reacts with superoxide radical ($O_2^{\cdot-}$) and gets converted into peroxinitrite ($ONOO^-$) which is a powerful oxidant RNS molecule which further involved in nitration

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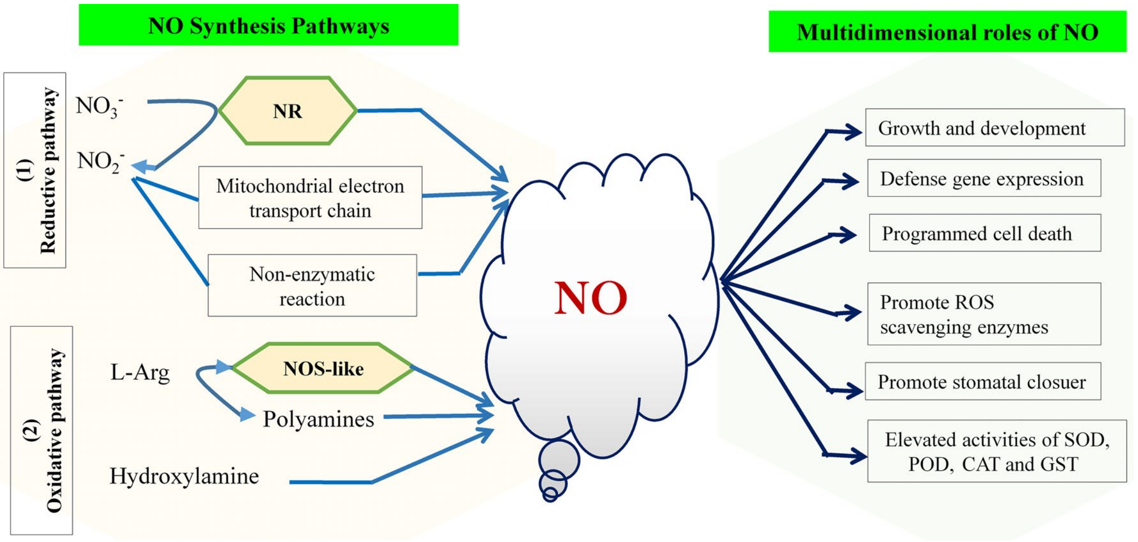


Fig. 1 A systematic representation of synthesis of NO and its multidimensional roles under stress

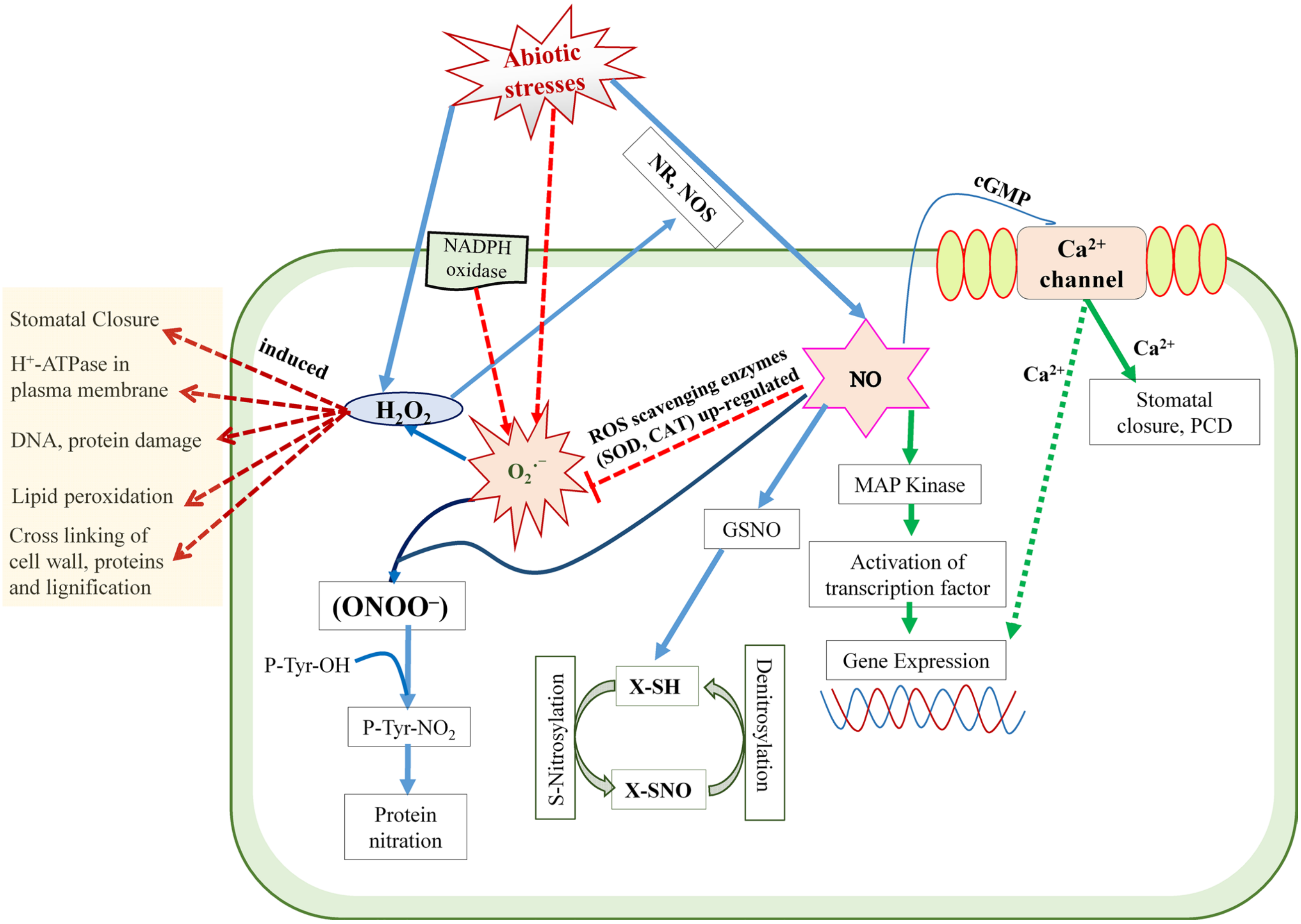


Fig. 2 NO signaling and its interaction with other signaling molecules

process for post translational modifications. In nitration reaction addition of nitro group (–NO_2) to the proteins, fatty acids or nucleic acids takes place. Nitro-tyrosine is a most studied modification found in case of protein modification (Corpas et al. 2009; Kolbert et al. 2017). Peroxinitrite is toxic to animals but in plant cells its toxic effect may depend on its concentration. Several researchers have reported its role in defense, apoptosis and gene expression in plants (Groß et al. 2013; Qiao et al. 2014). On the other hand, the covalent attachment of NO with thiol (-SH) group in the side chain of cysteine (Cys) is depicted as *S*-nitrosylation process (Fig. 2) (Fares et al. 2011; Broniowska and Hogg 2012). Fröhlich and Durner (2011) demonstrated that $_{\text{L}}$-arginine is as a foremost source of endogenous NO production in animals. But in case of higher plants, more investigations are required to know the occurrence of such enzymes similar to mammalian nitric oxide synthase (NOS). There are several studies are available to detect the precise characteristic feature of a gene like mammalian NOS. For instance, nitric oxide associated-1 gene (*s*) was activated by Ca^{2+} in plants (Galatro and Puntarulo 2014). On the other hand, Chakraborty and Acharya (2017) reported two ways for NO production (i.e. reductive and oxidative) in plants (Fig. 1) and also revealed the signaling role of NO in plants. The multitasking role of NO has been proven during few decades because of its multidimensional role along with interactive behavior with biomolecules and phytohormones (Domingos et al. 2015). Under drought conditions, higher plants are required to check the water loss. In this unfavorable condition, guard cells are known to balance the opening and closing of stomata to equilibrate the gaseous interchange for active photosynthesis. Nitric oxide governs stomatal movement induced by abscisic acid (ABA), a water-stress hormone (Freschi 2013). Thus, another important role of NO is to make plants more capable against drought condition (García-Mata and Lamattina 2007; Shabbir et al. 2016). According to Wendehenne et al. (2004), programmed cell death (PCD) has been observed under synchronised increase of NO and H_2O_2 in tobacco cells; however in soybean cells, PCD does not successfully occur in lack of reactive oxygen species (ROS). This indicates that only increased level of NO is not much enough to drive end of cell life. In recent years, several reports showed that NO and its related RNS have the capacity to govern every single step of plant developmental process (Table 1) by balancing antioxidants and ROS under stress conditions as described in Fig. 4 (Begara-Morales et al. 2018). Though there are many studies carried out to understand the nature and signaling of NO that triggers the gene expression to modulate plant metabolic processes, but the facts are still remained unclear. In spite of many evidences which show the behavior and role of NO as a plant growth regulator under stress, the current information regarding NO synthesis and signaling pathways in plants is still limited. In this review, we have tried to appraise the plant signaling governed by NO and its cross talks with ROS and different phytohormones, and other second messengers under stress conditions.

Synthesis of NO in plants

Production of NO is not only limited via enzymatic action but can also be formed as a by-product of various processes like respiration, nitrogen fixation and denitrification (Domingos et al. 2015). Chakraborty and Acharya (2017) demonstrated two pathways of NO synthesis i.e. oxidative and reductive. The former one is arginine or hydroxylamine-dependent pathway and latter one is nitrate dependent pathway (Fig. 1). Previous studies show that NO primarily produced through the family of NOS enzymes in mammalian cells. Each NOS enzyme catalyzes the production of NO from $_{\text{L}}$-arginine i.e. NADPH-dependent simultaneously producing $_{\text{L}}$-citrulline (Li and Poulos 2005; Domingos et al. 2015). There are fewer evidences for NOS existence or similar enzymes in plant system but Guo et al. (2003) described some possibility and identification of *AtNOS1* gene in *Arabidopsis thaliana*. Further, *AtNOS1* has been renamed to *AtNOA1* as nitric oxide associated- 1 gene (Crawford et al. 2006). Zemojtel et al. (2006) have reported the involvement of GTPase implied *AtNOA1*-gene in NO formation from $_{\text{L}}$-arginine in mitochondrial biogenesis. However, according to the latest available literature, there is a possible existence of *AtNOA1* that encrypts cGTPase which is localized in the chloroplast, possibly engaged in process of mRNA translation resulting in protein formation (Flores-Pérez et al. 2008; Moreau et al. 2008). The more recent evidences regarding the presence of NOS like gene sequence in land plants as well as in algal system have been shown by Jeandroz et al. (2016). On the basis of comparative gene sequencing of mammalian NOS with algal and plant NOS they found more compatibility with algal system. Overall findings still not clearly prove the presence of NOS enzyme in higher plants and there are much contradictions about its major role in synthesis of NO. Several reports have noticed that nitrite found as a foremost substrate for sequential process of NO synthesis in higher plants (Santolini et al. 2017). There are two ways of NO productions through nitrite involving enzymatic along with non-enzymatic pathways (Fig. 1). Nitrate reductase (NR) is mainly known to reduce nitrate and converts it into nitrite by utilizing NADPH as a reducing agent, but it also produces NO from nitrite by both in vitro as well as in vivo processes (Yamasaki and Sakihama 2000; Rockel et al. 2002; Santolini et al. 2017). Mohn et al. (2019) observed two isoforms (NIA1 and NIA2) of NR in *A. thaliana*. They also found that NIA1 mainly involved in NO production whereas nitrate reduction is the main function

Table 1 Nitric oxide and its implication in plant developmental processes

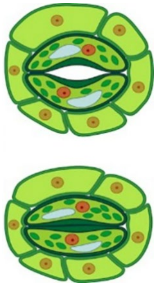
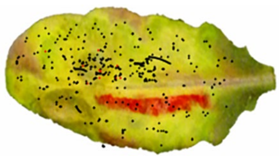
Developmental map	Process	NO-mediated effect(s)	Hormone involved	References
	Seed germination	Promotes germination	Up-regulation of gibberellins Down regulation of ABA	Arc et al. (2013)
		Down regulates ABA catabolism in *Arabidopsis* mutants *cyp707a1* and *cyp707a3*	Down regulation of ABA	Liu et al. (2009)
	Etiolation	Promotes De-etiolation	Up-regulation of gibberellins and cytokinins	Beligni and Lamattina (2000)
	Hypocotyl	Reduces hypocotyl elongation	Inhibition of gibberellins	Beligni and Lamattina (2000)
	Stomatal movement	NO induces stomatal closure and participates in ABA and UV signalling	ABA guided NO production to close stomata	García-Mata and Lamattina (2001, 2002, 2007), Garcia-Mata et al. (2003) and Desikan et al. (2004)
		NO regulates stomatal movement in *uvr8-1* mutant	—	Tossi et al. 2014
	Root organogenesis	Inhibits root elongation, Induces lateral root growth and root hair formation, Promotes adventitious roots	Induction of auxins and cytokinins	Correa-Aragunde et al. (2004), Pagnussat et al. (2004), and Lombardo et al. (2006)
		nia1, *nia2*, *Atnoa1* mutant plants showed reduced lateral root formation, in *Arabidopsis* but NO donor induced formation of lateral root.	—	Méndez-Bravo et al. (2010)
	Senescence	NO delays leaf senescence	Stimulation of ethylene	Leshem and Pinchasov (2000), Mishina et al. (2007), and Liu and Guo (2013)

Table 1 (continued)

Developmental map	Process	NO-mediated effect(s)	Hormone involved	References
	During pathogen attack	Stimulation of endogenous NO by MAPK cascade leads to Ca^+ mediated response Down-regulates Hb1-coding gene *GLB1* in wild type *Arabidopsis* plants	Salicylic acid mediated signaling Accumulation of salicylic acid, jasmonic acid, and ethylene	Domingos et al. (2015) and Yun et al. (2016) Groß et al. (2013)

of NIA2. Some biochemical and genetic-based approaches show that during ABA signaling and hypoxia, NR is the enzyme which chiefly acts as a mediator for NO synthesis (Desikan et al. 2002; Dordas et al. 2004; Bright et al. 2006). Another aspect of non-enzymatic conversion of nitrite to NO in the apoplast has been found at low pH having reductant ascorbic acid (Bethke et al. 2004). Still controversy exists regarding the co-involvement of $_L$-arginine and NR dependent pathways in NO production in plants (Rasul et al. 2012).

Some recent studies describe that polyamines also participate in synthesis of NO in some cases (Fig. 1). In *Arabidopsis* seedlings, Tun et al. (2006) described spermidine and spermine, two polyamines which are known to induce quick generation of NO in root tip (in elongation zone) and also in primary leaves (in the trichomes and veins).

Cross talk of NO with other second messengers (Ca^{2+}, cGMP and cADPR)

In animals, it has been reported that guanylate cyclase (sGC) in soluble state is involved in NO signaling. Mechanism includes the binding of NO with sGC heme triggering the enzymatic action and thereby, increase in the level of ubiquitous cGMP as a second messenger was noticed which is for a short time activates various respective goals (Besson-Barda et al. 2008). Further, it has also been reported that similar mechanism runs in Tobacco (Durner et al. 1998) and cucumber (Pagnussat et al. 2003) hence, attests the fact that cGMP amount increased after the exogenous application of NO. Besides this, Wendehenne et al. (2004) demonstrated in tobacco plant that sGC inhibitors chunk the behavioral role of gene phenylalanine ammonia lyase (PAL) and its enzymatic action, as well as root development in cucumber which is dependent on NO and auxin interactions (Pagnussat et al. 2003). However, several major constituents of the NO/cGMP pathway and its role are still to be identified.

Additionally, cGMP by inducing cyclic ADP-ribose (cADPR) and Ca^{2+} mobilization, NO may pose its functions in both plants and animals. Another second messenger i.e. cADPR, stimulates the release of Ca^{2+} through intracellular channel permeable to Ca^{2+} i.e. RYR (ryanodine receptor channels) (Wendehenne et al. 2001). In animals, cGMP dependent pathway mediates cADPR synthesis which directly activates NO (Fig. 3) by acting as downstream messenger for NO and also by up-regulating *PAL* and *PR-1* genes and ultimately Ca^{2+} mobilization is enhanced which directly governs the response against signaling (Wendehenne et al. 2001). NO is known to regulate signaling cascade i.e. cADPR-dependent action governed by *PAL* and *PR-1* genes is simultaneously sensitive to RYR inhibitors (Wendehenne et al. 2004). Whereas 8- Br-cADPR plays opponent role against cADPR and

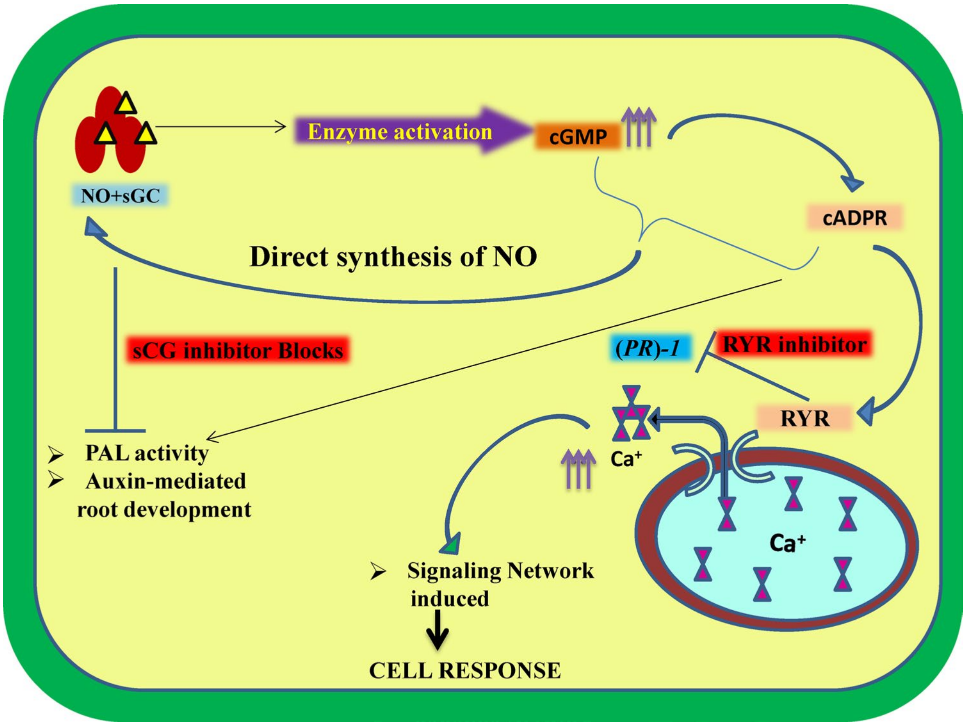


Fig. 3 NO combines with sCG and activates the enzymatic activity resulting in production of secondary messenger i.e. cGMP which further induces cADPR activity and is also directly involved in the process of NO synthesis. Simultaneously, sCG inhibitor deactivates PAL activity as well as auxin mediated root development by inhibiting the role of NO. cGMP with cADPR increases the Ca^+ release intracellularly and further signaling cascade regulates the cell response. Mobilization of Ca^+ through RYR channel is sensitive to its inhibitor which also blocks the *PR-1* gene mediated PAL activity directed by cGMP and cADPR messengers induced by NO

suppresses the induction caused by *PR-1* and NO (Klessig et al. 2000). In guard cells of *Vicia faba*, it has been described that NO promots the levels of cytosolic Ca^{2+} (Garcia-Mata et al. 2003). As in above mentioned evidences, NO regulates its function through cGMP (Beligni and Lamattina 2001) and cADPR through activated intracellular Ca^{2+}-permeable channels and liberating free cytosolic Ca^{2+} as reported earlier in cells of tobacco that are reacting against cryptogein (Lamotte et al. 2004). Hossain et al. (2014) showed positive interaction of cADPR with NO and ROS in methyl jasmonate mediated guard cells movement. In addition, NO shows its importance against fight with drought condition by mediating ABA mediated opening and closing of stomatal guard cells along with cGMP and cADPR (Garcia-Mata and Lamattina, 2001). With regards to the role of NO in stomatal closure in *Vicia faba*, c-PTIO affect the Ca^{2+}-dependent ABA induced processes i.e. c-PTIO inactivates the inward-movement mediated by K^+ channel while activates the outward-movement mediated by Cl^- channel (Garcia-Mata et al. 2003). Hence, it is cleared that NO involved in the regulatory process of plants but their regulatory pathway(s) have yet not been demarcated. The study concludes that NO regulates the genes that are involved in maintaining the level of intrinsic Ca^{2+} through its channels and also via the modulators of cGMP and cADPR which are NO/redox-sensitive processes (Fig. 3).

Crosstalk of NO and phytohormones

Nitric oxide, being a signaling bioactive molecule, shows its interaction with phytohormones and with its related reactive nitrogen species (RNS: $ONOO^-$, N_2O_3, NO_2) regulates metabolic processes against pathogenic attack and environmental stresses in plants. Its mechanism of targeting in overall metabolic process in order to counter stress responses is still not properly known. Over the last few decades some findings have enlighten the rapid induction and potential role of NO in plant growth regulation as described in Table 1. The intrinsic level of NO increased during stress condition and simultaneously involved in plant growth and developmental processes (Delledonne 2005). Hao and Zhang (2010) suggested a governing factor "ABA–H_2O_2–NO–MAPK-antioxidant existence sequence" that indicates the ABA performed ameliorative functions during water stress. Nitric oxide has been shown to act as a dynamic signaling intermediate resulting in vital phenomena i.e. closure of stomata to moderate the dehydration along with triggering the antioxidant defense system to respond to damage caused by oxidative species (Shabbir et al. 2016). In another study the interactive role of NO has been implicated in regulating metabolism in CAM plants by up-regulating the cytosolic Ca^{2+} (Freschi et al. 2010; Mioto and Mercier 2013). Seed dormancy during germination is mainly decided by the stability between ABA and gibberellins (Table 1), hence acts as signals triggered by environmental factors to further proceed the physiological and metabolic functions (Arc et al. 2013). The studies demonstrated that exogenous NO application is also capable of breaking the seed dormancy in *Arabidopsis* and barley, and its role was further confirmed by the use of NO scavenger (c-PTIO) (Bethke et al. 2004, 2006a, b; Libourel et al. 2006). Evidences showed that exogenous ABA application promotes NO production endogenously in tobacco and *Arabidopsis* (Guo et al. 2003; Bright et al. 2006; Liu et al. 2009), and similar phenomena was also noticed in the aleurone layer specifically in apoplast cell throughout the process of germination in barley (Bethke et al. 2004). Likewise, various responses mediated by auxin, for instance- development of root (Pagnussat et al. 2003; Correa-Aragunde et al. 2004), root movement towards gravity (Hu et al. 2005), process of root re-differentiation (Correa-Aragunde et al. 2004; Pagnussat et al. 2004; Lanteri et al. 2006), formation of nodules in root (Pii et al. 2007) are also modulated by ABA and NO (Table 1). Several other responses such as development of root under deficiency of iron (Chen et al. 2010), cell division, embryonic development (Ötvös et al. 2005) and induction of NR activity (Du et al. 2008) are also synergistically regulated by auxin and NO. In *Arabidopsis,* exogenously applied NO reduced the PIN1-dependent acropetal auxin transport in root apical meristem thereby inhibits the polar transport of auxin indicating NO acts downstream regulator of auxin (Fernández et al. 2011; Fernández-Marcos et al. 2012).

Previous reports underlined that NO inhibits the hypocotyl elongation (Table 1) in *Arabidopsis* and lettuce grown in the absence of light (Beligni and Lamattina 2000). Furthermore, Tonón et al. (2010) have noticed that in etiolated *A. thaliana* seedlings, NO together with superoxide and ATP regulates hypocotyl elongation. Gibberellic acid (GA) has been shown to regulate NO mediated signaling pathway by a possible mechanism in which PIF and DELLA proteins are also actively involved. Hence, it was concluded that increase in DELLA proteins and growth-promoting PIF gene products are also coordinated by NO (Lozano-Juste and León 2011). In recent past, accumulating evidences suggest a complex interaction between NO and CKs. For example zeatin (a kind of CK) has been shown to induce NO production in *Arabidopsis* seedlings (Tun et al. 2008). However, other evidences point out either unchanged response or quite low level of NO production after CK treatment/in mutant or transgenic plants with increased level of CK (Xiao-Ping and Xi-Gui 2006; Romanov et al. 2008; Liu et al. 2013). The synergistic role of CKs with NO has been clearly demonstrated in the plants treated with NO scavengers/NOS inhibitors or in mutant plants deprived of NO production demolish the expression of CKs induced gene *CYCD3;1* (transcriptional gene for cell cycle activation). Furthermore, Freschi (2013) has also pointed out the antagonistic effect of CKs with NO in epidermal strips of *Vicia faba* where SNP as a donor of NO reduced the generation of NO inside the guard cell.

In the last decade, several observations focused on a probable role of NO and it is considered as a crucial game changer against hypersensitivity like wounding/cutting or other power-driven stresses (Pedroso et al. 2000; Garcês et al. 2001). Work of Liu et al. (2016) on tomato reflected the role of NO as wound healer. Nitric oxide acts as a downstream mediator of jasmonic acid (JA) synthesis, by hindering the H_2O_2 production and inhibiting proteinase gene expression. Now, it is clear that during pathogenesis, the role of those genes which express themselves when wound occurs was down-regulated by NO. The inhibition of this defense gene was not dependent on salicylic acid (SA), which is an antagonistic phenomenon against JA synthesis and/or its activity (Alavi et al. 2014). Though, systemic acquired resistance (SAR) induced by SA has been weaken by the application of inhibitors of NOS enzyme and scavengers of NO and thereby, these results revealed that both SA and NO are dependent on each other. In this phenomenon nitric oxide required for the action and biosynthesis of SA and NO requires SA for its functions (Ji et al. 2016). After detailed observations based on these studies it can be pretended that NO is a key component to regulate phytohormones homeostasis. Moreover, some researchers have considered that NO itself as an “artificial plant hormone” for its extraordinary performance (Qian et al. 2009).

NO regulates gene expression to maintain hormonal balance in plants

Neill et al. (2002) have reported interactive relation between ROS and NO and came to a conclusion that NO has the capability of modifying the way of working of many genes in plant cells. Like in soybean and tobacco plants, NO triggers the expression of several proteins such as PR-1 which is related to pathogenesis while PAL and GST show a vibrant role in defensive routes inside the cell (Delledonne et al. 1998; Durner et al. 1998). del Rio et al. (2003) described that expression of genes related to diverse form of peroxidases, ferritin, and biosynthesis of crucial enzymes of jasmonic acid are induced by NO. In *Arabidopsis*, it has been reported that NO induces expression of genes encoding several enzymes like GST, CHS (chalcone synthase), GPX (glutathione peroxidase), and AOX1a (alternative oxidase) which detoxify stress biomarkers and also down regulate ascorbate peroxidase (tAPX), present in thylakoid region (Huang et al. 2002). The SnRK2 kinase regulated by abscisic acid (ABA) and SRK2C/SnRK2.8 in *Arabidopsis* notified as a drought resistant factor in plants by up-regulating

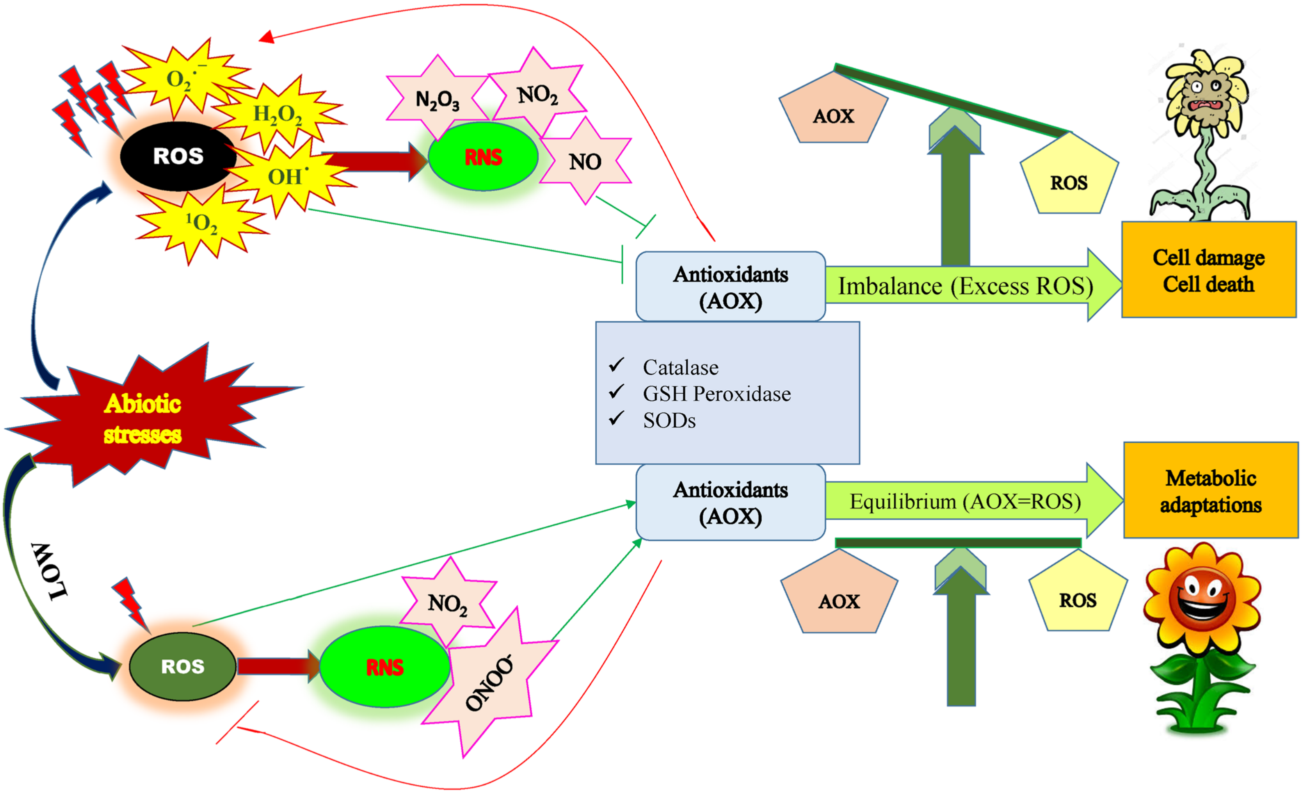


Fig. 4 An active interaction between NO and ROS affects antioxidant defense system under abiotic stress. Under low stress condition, moderately produced ROS act as signals for NO synthesis that enhances antioxidant defense system to provide protection to stressed plants. Whereas under heavy stress situation, excessively produced ROS promotes production of RNS that tends to create imbalance in AOX and ROS. This imbalance causes cell damage or cell death

DREB1A/CBF3 which encodes transcription factor regulating those genes which are responsive under stress condition (Umezawa et al. 2004). In addition, to activate AREB1 and TRAB1 they are activated by phosphorylation of SnRK2 kinases in both *Arabidopsis* as well as rice plant, respectively (Kobayashi et al. 2005; Furihata et al. 2008) and regulate ABA-responsive genes. Beside this, osmotic stress facing cells might use NO as an initial signaling factor to promote the defensive pathway guided by *SnRK2* (Courtois et al. 2008). Guo et al. (2003) have also observed that stomatal opening guided by lower light and resistivity towards drought in *Arabidopsis* was due to mutant nitrate transporter *Chl1* gene. Similarly, Meyer et al. (2005) revealed the role of *AtNOS1* which is dually involved in NO production and in ABA responsive closure of stomata in *Arabidopsis*. Groß et al. (2013) have also noticed that in wild type *Arabidopsis* plant, higher accumulation of SA, JA and ethylene occurred during pathogen attack. As a result of this, the endogenous accumulation of NO inside the cell ultimately suppresses the Hb1-coding gene *GLB1* in order to resist plants against pathogen attack (Table 1).

NO and ROS crosstalk: nitric oxide-induced programmed cell death (PCD)

Reactive oxygen species (ROS) are mainly consequential result of a sequential processes involved in cellular metabolism (Halliwell and Gutteridge 2007). Sharma et al. (2012) considered their excessive accumulation as necessary evil and in excess caused deleterious effect on plants and animals. As Fig. 4 shows that plants possess an effective endogenous defensive mechanism including a wide network of antioxidant machinery which defends them from harm caused by ROS, and hence harmonizing their internal ratio (Wrzaczek et al. 2013). Figure 4 depicts a group of oxidative molecules/ions: (1) superoxide anion, (2) hydroxyl free radical, (3) hydrogen peroxide and (4) oxygen species having single electron are considered as ubiquitous ROS in cell (Gechev et al. 2006; Sharma et al. 2012; Singh et al. 2016). In plant cells, the major sites of oxidative biomarkers production are chloroplasts, mitochondria, and peroxisomes (Sharma et al. 2012; Kong et al. 2013; Sandalio et al. 2013; Singh et al. 2016). Previous studies have considered ROS as signaling molecules in many cellular processes (Mittler et al. 2011; Wrzaczek et al. 2013). Equilibrium of ROS is a crucial phenomenon i.e. production of ROS and their scavenging decide their fate as damaging or signaling molecules (Fig. 4). ROS level in cell triggers different signaling networks which depend on multiple aspects such as: (1) chemical individuality of ROS, (2) concentration of ROS, (3) signal intensity, (4) site of ROS production, (5) plant developing stage, and (6) crosstalk among ROS, hormones, and NO (Chaudhuri et al. 2013; Mor et al. 2014; Singh et al. 2016). Klepper (1979) had first time reported generation of NO within cell. Thereafter, Delledonne et al. (1998) reported NO as a key factor in *Arabidopsis* and tobacco which is involved in defense response. Although, NO may pause destructing effect of ROS depending on its rate and site of production (Beligni and Lamattina 1999). Crosstalk among NO and ROS decides the fate of cells under stress conditions and also determined the physiological phenomena inside the cell (Rodríguez-Serrano et al. 2009). In fact, targets of *S*-nitrosylation process i.e. attachment of NO to cysteine thiol within a protein to form an *S*-nitrosothiol (SNO) (Fig. 2) which operates the signaling for the action of antioxidant enzymes against ROS suggesting a perfect balance between NO and ROS (de Pinto et al. 2013; Romero-Puertas et al. 2013). NO has a short life time and considered as a free radical which limits its effect on surrounding environment. Apart from NO, S-nitrosylated glutathione (GSNO) is relatively a stable reservoir and transportable form of NO (Kovacs et al. 2016). GSNO level inside cell is either guided by its production or by enzymatic action catalyzed by GSNO reductase (GSNOR). Mutation in *GSNOR* gene caused deteriorated plant growth (Lee et al. 2008; Xu et al. 2013). The *gsnor-ko* plants contain increased level of S-nitrothiols (SNO) and nitroso species reflecting the controlled activity of GSNOR for both GSNO and protein-SNOs (Lee et al. 2008).

Programmed cell death (PCD) is an active plus genetically controlled phenomenon promoting the cell death in plants which includes cellular metabolic processes that occurs throughout plant life and considered as an essential process for normal development against biotic and abiotic stresses (van Doorn 2005; Gechev et al. 2006; Bozhkov and Lam 2011; Singh et al. 2016). Every cell completes its life cycle by a sequential event PCD which includes several peculiar proceedings: (1) transformed morphology of nucleus, (2) inflammation of vacuoles along with mitochondria, plus ER, (3) protoplast contraction, and (4) cytoskeleton reformation (Serrano et al. 2015). Additional demarcations are fragmentation of DNA, caspase mediated activity, and an increase of ROS and RNS (Xu and Huang 2017). According to de Pinto et al. (2012), ROS and NO are considered as the important component for PCD in plants. Plant develops a multifaceted response i.e. innate and immune which is collectively called as hypersensitivity (HR). This is mainly evolved to defend themselves against insects and microbial pathogen which can uniquely end in systemic acquired resistance (SAR) (Domingos et al. 2015). This was mainly regulated by increase in the Ca^{2+} level inside the cell through CNGC (cyclic nucleotide-gated ion channels) (Ali et al. 2007). CNGC is cGMP-mediated channel which is mainly regulated by peptide signaling molecule, AtPeps, and their receptor, AtPepR1 (Qi et al. 2010). Further, the increase in endogenous Ca^{2+} triggers salicylic acid (SA) (Yun et al. 2016), NO and ROS generation leads to PCD in the area of infection, in that way limits the pathogen growth (Domingos et al. 2015). Nitric oxide and H_2O_2 play crucial role in governing hypersensitivity (Grant and Loake 2000; Kovacs et al. 2016) (Table 1). Delledonne et al. (2001) mentioned in their work that cell death phenomena are determined by the ratio of NO to H_2O_2. Interestingly, tropospheric ozone (O_3) induces ROS production and enhances the HR programme in the apoplast and thereby, considered as an ideal for regulation of end of life of cell by the initiating and proliferating the death signals (Overmyer et al. 2003). In animal cell, infection (also considered as HR) results in PCD phenomena and similar to the plants, NO and H_2O_2 are considered as responsible molecules for the same (Wang et al. 2013). Either of them could be responsible for functioning of cytochrome *c* and also for the regulation of signaling cascade guided by caspase leading to the hypersensitivity as coated by Mur et al. (2006) and Tan et al. (2013). Besides these, certain other significant machineries are also involved in defense signaling pathway i.e. activation of protein kinases (MAPKs) and phosphatases which are also influenced by ROS and NO and therefore, cumulative role of NO and H_2O_2 enhanced by the stimulation of central MAPK cascade against pathogen infection (Domingos et al. 2015). In plants, leaf senescence is also a consequence of PCD, which is considered as the ultimate leaf developmental phase which is controlled by age of organ and environmental conditions as conveyed by Jing et al. (2005). The work of Cui et al. (2013) verified that at senescence stage, the amount of H_2O_2 increases leading to cell death in *Arabidopsis*. Along with oxidizing properties, H_2O_2 also transduces the signals and regulates the gene expression involved in the senescence process. With this context, several senescence-associated genes (SAG) are characterized from *Arabidopsis* which is ROS-induced expressions of these genes as reported by Navabpour et al. (2003) clarifying the role of ROS in senescence. Apart from ROS, NO can provoke as well as hinder senescence process which dependents upon its amount and place of act (Wang et al. 2013). It may increase the ROS toxicity resulting in leaf senescence (Niu and Guo 2012). Kong et al. (2013) observed that H_2O_2 was implicated in NO-mediated PCD in maize.

Conclusions and future perspectives

To maintain all the primary and basic functions of the cell, NO manages an internal environment that pretends to change gene expression patterns and thus modulates chemical homeostasis of the cell. By this way, NO successfully makes a cell capable of alleviating impact of different stress. Nitric oxide suppresses Hb1 coded *GLB1* genes during hypoxia and pathogen attack in *Arabidopsis* that clear its role in defense gene regulation and protein modifications which provide a base for further study in this area. Involvement of NO signaling in several post translational modifications also provide a significance to its crucial role in defense machinery. Further in defense mechanism, the NPR1/TGA interaction is critical for regulating responses by salicylic acid action (Astier and Lindermayr 2012). Few reports proposed the efficient role of NO in defense signaling, over the modulation of PCD mediated by ROS and some new assessments regarding organic and bio molecular information intended for this crucial functional intermediary component are also explained in Fig. 4. Some recent discoveries described plant NOSs that have little sequential similarities to their mammalian counterparts. Intrinsic NO production by pathways involved in different biosynthesis processes in varied cellular sections including different organelles, involving physiological, biochemical and molecular events in response to specific ecological stimulus is still having an area of curiosity. Although NO, is known for its extraordinary faith for all around growth and developmental processes, however, it is not only limited to plants but also applied for animals as well as various organisms like algae, bacteria, lichen, fungi etc. Therefore, multidimensional studies will be helpful for further researches regarding role of NO in plant biology. Future research involving investigation on intricate NO signaling network in plants will certainly witness exciting outcomes.

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