Chapter 6

Cross Talk between Nitric Oxide and Phytohormones Regulate Plant Development during Abiotic Stresses

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Abstract

Plants, being sessile, are concurrently exposed to various biotic and abiotic stresses. The perception of stress signals in plants involves a wide spectrum of signal transduction pathways that interact to induce tolerance against adverse environmental conditions. This functional overlapping among various stress signaling cascades also leads to the expression of genes that regulate biosynthesis or action of other hormones. Phytohormonal signals, activated by both developmental and environmental responses, play a crucial role to develop stress tolerance in plants. Nitric oxide (NO) is one of the major players in plant signaling networks. Emerging evidence supports that NO interplays with signaling pathways of auxins, gibberellins, abscisic acid, ethylene, jasmonic acid, brassinosteroids, and other plant hormones to control metabolism, growth, and development in plants. This chapter focuses on the current state of knowledge of cross talk between signaling pathways of NO and phytohormones in plants exposed to various abiotic stresses.

Keywords: nitric oxide, phytohormones, abiotic stresses, signaling cascades, plant growth

1. Introduction

Exposure to a wide array of environmental stresses is one of the most crucial factors that negatively influence plant growth and productivity worldwide. Plants respond to such adverse conditions through perception of endogenous and exogenous stress factors via hormone signaling networks along with the coordination of several downstream signal transduction mechanisms involving cyclic nucleotides, calcium ions, and reactive oxygen (such as hydrogen peroxide) or nitrogen (e.g., nitric oxide) species. Acclimation to abiotic stresses is achieved through turgor maintenance [1], accumulation of osmolytes [2], regulation of photosynthetic and transpiration rate, and activation of antioxidant machinery [3]. Moreover, stress-induced alterations in gene expression and metabolism stimulate several anti-stress compounds, which help to modify physiology, phenology, growth, and reproduction of plants exposed to adverse environmental conditions [4].

Nitric oxide (NO) is an important metabolite and stress signaling molecule that influences multitude of physiological and developmental functions in plants. It serves as a key component of the signaling cascades involved in plant growth, metabolism, and adaptive responses to various biotic and abiotic stresses. It is well established that NO regulates a plethora of physiological processes ranging from seed germination to plant senescence. Emerging evidence suggests this potential plant growth regulator interplays with various phytohormones (PHs) to control metabolism, growth, and development in plants.

During the last few years, extensive research has been carried out to explore the multiple and diversified mechanisms underlying PHs interactions with NO. There is virtually no doubt that NO acts either upstream or downstream of PHs [5, 6]. It seems that NO modulates the biosynthesis, distribution, degradation, and conjugation of elements involved in PHs transport and signaling [7–11]. However, further studies are required to explain how NO concomitantly interacts with hormone-related proteins at post-transcriptional or even translational level. Similarly, the understanding of mechanisms underlying intersection of NO signaling with signaling cascades of auxins (AUXs), gibberellins (GBs), cytokinins (CKs), ethylene (ETs), absicic acid (ABA), salicylic acid (SA), jasmonic acid (JA), polyamines (PAs), brassinosteroids (BRs), and strigolactones (SLs) under abiotic stress conditions remains elusive. Considering the common function played by these plant growth regulations in enhancing plant tolerance to biotic and abiotic stresses, it can be speculated that PHs-mediated stress responses are linked with NO synthesis. Therefore, this chapter would focus on the current state of knowledge of cross talk between signaling pathways of NO and PHs in plants exposed to various abiotic stresses (**Table 1**).

Type of stress	Phytohormone	Plant species	Response	Relation with NO	References
Drought stress	ABA	*Zea mays*	Increased expression of ABA biosynthetic gene *vp14*	+	Zhang et al. [26]
	AUX	*Tagetes erecta*	Development of adventitious roots	+	Liao et al. [33]
	SA	*Triticum aestivum*	Increased tolerance against osmotic stress	+	Alavi et al. [41]
	CK	*Zea mays*	Regulation of photosynthetic machinery	+	Shao et al. [42]

Type of stress	Phytohormone	Plant species	Response	Relation with NO	References
Cd toxicity	ET	*Pisum sativum*	Promoted the Cd-induced senescence processes	–	Rodríguez-serrano et al. [64]
	PAs	*Triticum aestivum*	Inhibition of root growth	+	Groppa et al. [66]
	AUX	*Arabidopsis thaliana*	Stabilization of AUX repressor protein IAA17 through suppression of AUX carriers PIN1/3/7	–	Yuan and Huang [67]
		Medicago truncatula	Improved antioxidative capacity and reduced degradation of AUX in roots	+	Xu et al. [68]
	SA	*Lolium perenne*	Increased activities of antioxidative enzymes	+	Wang et al. [72]
		Arachis hypogaea	Restricted Cd distribution to organelles	+	Xu et al. [78]
Ni toxicity	SA	*Brassica napus*	Enhanced chlorophyll contents and reduced lipid peroxidation and proline accumulation	+	Kazemi et al. [77]
Cu toxicity	BR	*Raphanus sativus*	Increased ABA synthesis resulted in improved tolerance	+	Choudhary et al. [80]
Al toxicity	GA	*Triticum aestivum*	Promoted apical root growth	+	He et al. [50]
Salinity stress	ABA	*Gossypium hirsutum*	Decreased salt-induced leaf senescence by regulating the expression of ABA biosynthesis genes (*NCED2 and NCED9*)	–	Kong et al. [88]
	ET	*Lycopersicon esculentum*	Reduced ROS levels and blocked ET synthesis resulting in lower dead cell ratio in cell suspension cultures	–	Poór and Tari [85]
	AUX	*Arabidopsis thaliana*	Repressed AUX signaling through stabilization of AUXIN RESISTANT3 (AXR3)/INDOLE-3-ACETIC ACID17 (IAA17)	–	Liu et al. [94]
	SA	*Fagus sylvatica*	Reduced H_2O_2 accumulation, limited Na^{2+} uptake and increased influx of H^+-ATPase to plasma membrane	+	Dong et al.[97]
	PAs	*Cucumis sativus*	Reduced free putrescine, spermidine and polyamine oxidase (PAO) activity	–	Fan et al. [103]

Type of stress	Phytohormone	Plant species	Response	Relation with NO	References
Temperature stress	ABA	*Phragmites australis*	Improved the thermotolerance of plant calluses	+	Song et al. [109]
		Medicago sativa	Enhanced *MfSAMS1* expression to increase acclimation against cold stress	+	Guo et al. [123]
	PAs	*Lycopersicon esculentum*	Increased putrescine and spermidine levels and stimulated the expression of genes encoding Spd synthase (*LeSPDS*), arginine decarboxylase (*LeADC. LeADC1*) and ornithine decarboxylase (*LeODC*) to improve chilling stress tolerance	+	Diao et al. [121]
		Zingiber officinale	Conversion of putrescine into spermidine or spermine conferred cold tolerance	+	Li et al. [124]
	SA	*Spinacia oleracea*	Increased NR activity reduced chilling injury	+	Aydin and Nalbantoğlu [128]
	JA	*Cucumis sativus*	Increased CAT activity to scavenge H_2O_2, leading to reduced chilling injury	+	Liu et al. [129]

Table 1. Summary of representative reports on the interaction of nitric oxide with phytohormones during various abiotic stresses.

2. NO-phytohormone cross talk under drought stress

Drought stress is one of the major limiting factors affecting multiple aspects of plant growth and productivity [2]. The typical mechanism of plants response to water stress, frequently caused by drought, is closure of stomata to conserve water. NO and ABA are the two most important stress-related molecules that intensively cross talk during environmental challenges like drought to induce plant adaptive responses such as stomatal closure and activation of antioxidant machinery [5, 11]. Evidence suggests that NO acts downstream of ABA as decreased NO synthesis reduces ABA-induced responses in plant tissues exposed to stress conditions [12, 13]. However, NO is also reported to counteract ABA during events not linked to stress adaptation such as breaking of seed dormancy [14, 15]. It indicates a certain level of specificity in NO-ABA cross talk mechanisms, which seems to depend on the type of plant cell, tissue or organ studied, or nature of physiological event under analysis.

Generation of ROS (H_2O_2) under adverse environmental conditions triggers NO-mediated ABA responses such induction of stomatal closure [16], activation of antioxidant enzymes [17], and up-regulation of transcription factors [18]. In addition, cGMP and type 2C protein phosphatases (PP2Cs) have also been identified to participate in downstream of NO-mediated ABA signal transduction and upstream of cytosolic Ca^{2+} during the regulation of stomatal apparatus [19–21]. Moreover, the calcium/calmodulin system and mitogen-activated protein kinases (MAPKs) have also been demonstrated as key downstream elements involved in ABA or H_2O_2-induced NO signaling during plant antioxidant defense mechanisms [22, 23]. Cross talk between NO and ABA in the ABA-dependant signaling network up-regulated the cytosolic Ca^{2+} to regulate Crassulacean acid metabolism (CAM) expression in bromeliads that significantly improved plant tolerance in a water-limited environment [21, 24]. It seems that ABA-induced NO production is associated with increased nitrate reductase (NR) activity that controls stomatal movements in *Arabidopsis* [19] and CAM expression in bromeliads [24]. The expression of CYP707A2 gene, induced by NO biosynthesis, during seed germination initiated ABA catabolism and increased ABA levels to enhance plant resistance against drought stress [11, 25]. BR treatment of water-stressed *Zea mays* leaves induced NO generation in mesophyll cells and up-regulated the expression of ABA biosynthetic gene *vp14* to enhance water stress tolerance in *Zea mays* [26].

Interestingly, NO serves as a second messenger in the signaling cascades of various plant hormones such as GA, JA, ET, CK, and AUX involved in the regulation of stomata under environmental stress conditions [27, 28]. Interactions between NO and AUX signaling pathways are complex and need to be explored in plants exposed to water-limited environment. It is well established that both NO and AUX interplay during growth and development of plant roots [29, 30]. Association of AUX with ET to regulate root morphology and development is considered a key aspect of drought tolerance in plants [31]. Development of adventitious roots in cucumber hypocotyl cuttings involves the cross talk between AUX and NO signaling networks activated by Ca^{2+} dependent protein kinase activity [32]. Since NO is intensively involved in lateral root formation during drought stress [33], it may be speculated that AUX and NO signaling cascades interact and influence the architecture and development of root hair and root meristem size [34, 35] for the extraction of more water under drought stress conditions.

Drought stress influences the signaling of various JA-associated genes [36]. JA stimulates CDPK production by increasing Ca^{2+} influx and the resultant signal cascade results in ABA-regulated stomatal closure. A rapid loss in turgor and subsequent reduction in stomatal aperture were noted in excised *Arabidopsis* leaves treated with either ABA or methyl JA (MeJA) [37]. Suppression of MeJA-induced Ca^{2+} oscillations in guard cells of ABA-deficient mutants [38] implies that MeJA cross talk with ABA involves Ca^{2+} signal transduction pathways. Moreover, treatment with ABA or MeJA induces the formation of NO and ROS in guard cells [37]. Studies involving *Arabidopsis* revealed that ABA mediated Ca^{2+} influx into cytoplasm involves CPK6, which acts downstream of NO and ROS signaling and therefore may be a target of NO-stimulated Ca^{2+} influx into the cytoplasm [39]. In 2008, Palmieri et al. demonstrated that NO treatment up-regulated several genes involved in the JA biosynthetic pathway, indicating a potential regulation of JA signaling through the ROS/NO pathway [40]. NO also acts downstream of SA signaling to scavenge ROS in water-stressed plants. Coordinated action of NO and SA was found to alleviate the damaging effects of polyethylene (PEG)-induced osmotic stress in *Triticum aestivum* seedlings [41].

A positive interaction between NO and CK under water-limited environment was reported by Shao et al. [42]. Treatment of plants with CK plus NO scavenger (Hemoglobin) revealed that CK promoted NO signaling, probably mainly through a NR source in plants exposed to water stress conditions. CK interaction with NO signaling cascades regulated photosynthetic machinery and increased the adaptability to drought stress in *Zea mays* [42]. Contrasting reports indicate antagonistic interaction between NO and CK, for example, CK-induced reduction in NO levels promoted stomatal opening in dark grown *Vicia fabia* seedlings [43]. Presumably, CKs activate plasma membrane H1-ATPase through decreasing NO levels in guard cells, and then stimulate stomatal opening in darkness. Wilhelmova et al. [44] reported similar results in transgenic tobacco plants. Negative interaction between NO and CKs was evident during leaf development as increased NO production reduced CKs level in aging leaves. Evidence suggests that reaction of zeatin with peroxynitrite, a NO derivative, reduces its availability in plants [45].

3. NO-phytohormone cross talk under heavy metals stress

Heavy metals (HMs) are phytotoxic elements that can damage plant growth and metabolism at very low concentrations [46]. The involvement of plant hormones such as IAA, CK, and ET to alleviate HMs-induced toxicity is well reported [47–49]. Some recent studies suggest that NO acts in concert with signaling pathways of phytohormones to induce tolerance against excess elements [50, 51]. However, the exact nature of NO-hormone interactions still needs to be explored and is largely dependent on the species, the plant organ as well as concentration of metal and duration of stress [52].

Cadmium is one of the most widely distributed HM in agricultural soils [53]. Cd-induced increase in endogenous levels of NO is associated with its role as a bioactive molecule to quench ROS [54]. Alterations in hormonal homeostasis are potential signals that directly affect plant responses to Cd stress, including interplay between hormones and the whole plant signaling network, such as the ROS [55], MAPK [56], and NO signaling pathways [57]. Exposure to short-term Cd stress revealed an interrelation of ET with NO generation, polyamine metabolism, and MAPK cascades in young *Glycine max* seedlings [58]. It is well documented that exposure to HMs enhances the production of ET [59] due to increased 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (ACS) activity in metal stressed plants [60]. Cross talk between ET and stress signaling molecules like NO is important to understand the mechanisms of plant adaptation to HM-induced oxidative stress [61–63]. More recently, Thao et al. [51] suggested a possible link between NO and ET through MAPKs in plants exposed to HM stress. Accumulation of ET reduced NO levels and promoted the Cd-induced senescence processes in *Pisum sativum* [64]. Similarly, integration of ET, NO, PA, and MAPKs pathways improved tolerance in young *Glycine max* seedlings against short-term Cd stress [52]. The potential involvement of ETHYLENE INSENSITIVE2 (EIN2) in improving resistance against lead (Pb) stress has also been demonstrated in *Arabidopsis* [65]. Treatment of *Triticum aestivum* seedlings with Cd and PAs (spermine and putrescine) was found to induce NO generation in roots leading to root growth inhibition [66].

Experiments with *Arabidopsis* showed that Cd toxicity triggers NO accumulation, which in turn promotes the stabilization of AUX repressor protein IAA17 through suppression of AUX carriers PIN1/3/7 [67]. Xu et al. [68] found that exogenous NO supply improved the antioxidative capacity and reduced the degradation of AUX in roots of *Medicago truncatula* seedlings exposed to Cd stress. In another study, it was noted that NO acts downstream of AUX on modulating root architecture in *Arabidopsis seedlings* exposed to Cd stress [69]. Rodríguez-Serrano et al. [70] demonstrated that Cd toxicity strongly depressed the activity of NO-synthase dependent NO production in *Pisum sativum* seedlings; however, exogenous Ca supply ameliorated this effect due to enhanced JA and ET production. Interplay among NO, H_2O_2, and SA has also been reported in lupine seedlings [71] and ryegrass plants [72] under Cd stress. Application of putrescine (Put) and NO in combination was reported to alleviate Cd toxicity in *Vigna radiate* by triggering the activity of both enzymatic and nonenzymatic antioxidant machinery and a parallel increase in phytochelatin synthesis [73].

Interplay between NO and GA has been reported to influence a wide spectrum of physiological processes, including seed germination, primary root growth, and inhibition of hypocotyl elongation [8, 29]. Interaction of NO with GA was observed to promote apical root growth in *Triticum aestivum* roots exposed to aluminum (Al) toxicity [50]. Contrary reports of Zhu et al. [74] showed that GA mediated alleviation of Cd toxicity in *Arabidopsis* was linked to reduction of Cd-induced NO accumulation and suppression of up-regulation of *IRT1*. Antagonistic relationship between NO and GA was also reported by Wu et al. [75] who noticed that NO accumulation inhibited the stimulatory effect of GA on primary root growth under low phosphorous (P) conditions. They suggested that GA interacts with NO and P pathways on DELLA-SLY module. Studies have shown the positive interaction between NO and CK, for example, Shen et al. [76] found that NO deficiency inhibited the activation CK-induced gene CYCLIN-D3;1 (CYCD3;1), which in turn promoted callus initiation from somatic plant tissues. Recent reports of Liu et al. [45] revealed that CK directly interact with NO to reduce endogenous NO levels in *Arabidopsis* implying the protective role of CK against nitrosative stress; however, no study has yet provided definitive evidence for NO and CK interaction under metal stress.

Combined NO and SA application was observed to counteract the toxic effects of Ni in *Brassica napus* through enhanced chlorophyll contents and reduced lipid peroxidation and proline accumulation [77]. Similarly, NO and SA increased Cd contents in cell walls of Cd-stressed *Arachis hypogaea* that reduced the distribution of Cd to organelles [78]. In recent years, accumulating evidence indicates the involvement of BRs induced NO production in root architecture and development [79]. Choudhary et al. [80] found that BR induced increased NO production promoted ABA synthesis that alleviated the toxic effects of Cu in *Raphanus sativus* seedlings.

Cross talk between plant hormones and NO is also considered critical for Fe-deficiency signaling [81]. Evidence obtained in *Arabidopsis* suggests interplay between ET and NO for up-regulation of genes (A*tFIT*, *AtbHLH39*, *AtFRO2*, *AtNAS1*, *AtNAS2*, *AtFRD3*, *AtMYB72*) related to Fe-deficiency [82]. Although, it is well reported that enhanced NO generation helps to maintain root growth under Cd stress [83]; however, the exact role of NO under excess Fe conditions is rudimentary and demands further investigation.

4. NO-phytohormone cross talk under salinity stress

Salinity stress is considered one of the most harmful stresses due to its high magnitude and worldwide distribution [84]. Phytohormones play a key role in enhancing the tolerance and adaptability of plants against salinity stress. Some recent studies suggest that NO acts in concert with signaling pathways of phytohormones to induce tolerance against salt stress [85, 86]. Presumably, plant hormones such as ABA, ET, and AUX are transported from salt-treated roots to leaves to trigger NO synthesis or transport throughout the plant [87]. NO-induced alleviation of oxidative damage in salt-stressed plants is associated with increased antioxidant activities and decreased thiobarbituric acid reactive substances content [69]. ABA stimulates H_2O_2 accumulation that results in increased NO generation, leading to the activation of MAPK and up-regulation of genes associated with antioxidant enzymes [17, 18] in plants exposed to abiotic stresses like salinity. However, NO does not always positively interplay with ABA. In cotton, exogenous NO supply (using SNP as NO donor) reduced salt-induced leaf senescence by decreasing ABA content and down regulating the expression of ABA biosynthesis genes (*NCED2* and *NCED9*) [88].

In general, it is believed that ET biosynthesis corresponds to increased damage in plants. However, recent studies indicate ET as a stress-signaling hormone that interacts with signaling cascades of other phytohormones to enhance tolerance against various biotic/abiotic stresses [70, 86]. Studies involving tobacco seedlings showed that transcriptional activation of ethylene response factor (ERF) in ethylene-signaling process improved salt stress tolerance by decreasing ROS accumulation [89]. Treatment of *Arabidopsis* callus with 100 mM NaCl triggered the accumulation of NO that promoted ET emission, resulting in increased expression of the plasma membrane H^+-ATPase genes [90]. Hence, both NO and ET participate in up-regulation of plasma membrane H^+-ATPase that modulates ion homeostasis for improved salt tolerance. NO and ET also cooperate to stimulate the alternative respiratory pathway under salt stress conditions [91, 92]. Contrary reports of Poór and Tari [85] showed antagonistic relationship between NO and ET in tomato cell suspension cultures treated with NaCl (100 and 250 mM). Increased ET synthesis promoted ROS generation leading to high dead cell ratio in salt-stressed cell culture. However, NO generation decreased ROS levels and blocked ET synthesis resulting in lower dead cell ratio. In another study, absence of ET and NO in apical root segments and cell suspension culture, respectively, caused ionic imbalance (Na^+/K^+) that resulted in increased susceptibility to salinity stress [93]. AUX and NO involvement in inhibition of root meristem growth in salt-stressed *Arabidopsis* was revealed by Liu et al. [94]. They reported that salinity stress repressed root meristem growth by inhibiting the expression of *PINFORMED* (*PIN*) genes, thereby reducing AUX levels. Moreover, stabilization of AUXIN RESISTANT3 (AXR3)/INDOLE-3-ACETIC ACID17 (IAA17) repressed AUX signaling via NO accumulation.

Participation of both NO and ROS in SA-induced stomatal closure is also reported in literature [95]. Activation of a peroxidase (sensitive to the inhibitor salicylhydroxamic acid) by SA promotes ROS accumulation and NO generation in guard cells, leading to stomatal closure. Experiment with soybean seedlings showed that combined application of SNP (as NO donor) and SA alleviated the toxicity of NaCl-induced salt stress by increased proline accumulation and activation of CAT, APX, and GPX. Similar results were reported by Liu et al. [96] and Dong et al. [97] in *Gossypium hirsutum* and *Fagus sylvatica*, respectively. SA interaction with signaling cascades of NO modulated photosynthetic machinery and reduced H_2O_2 accumulation that promoted the influx of H^+-ATPase to plasma membrane. Moreover, synergistic effect of SA and NO improved Ca^{2+}/Mg^{2+} absorption and reduced Na^{2+} uptake under salt stress conditions [97].

Sulfur (S) is a major component of metabolites such as reduced glutathione (GSH), coenzyme A, methionine, cysteine (Cys), sulfo-lipids, iron-sulfur (Fe-S) clusters, and thioredoxin system involved in regulation of physiological processes under salt stress conditions [98]. Evidence suggests that NO promotes S-assimilation, which is linked to ET production through Cys synthesis [86]. Hence, it may be speculated that NO and S interact to modulate ABA and ET levels in guard cells that may influence the stomatal and photosynthetic response under salt stress conditions. NO combines with GSH to generate S-nitrosoglutathione (GSNO), leading to enhanced S requirement of plants for improved tolerance under environmental stress conditions [99, 100]. Coordinated effect of NO and S regulated the utilization of S and GSH resulting in improved growth and photosynthetic activity in salt-stressed mustard plants [86]. NO is a key regulatory signal that activates several biochemical processes and interacts with sulfhydryl groups and nitro groups in the process of nitration to enhance tolerance against salt stress [101]. NO also cooperates with other signaling molecules such as H_2S to enhance tolerance against salinity stress in plants. NO and H_2S cross talk helped to maintain low Na^+ levels with up-regulation of *HvHA1* and *HvSOS1* and increased plasma membrane H^+-ATPase levels in cytoplast of salt stressed barley seedlings [102]. Moreover, transcriptional activation of vacuolar Na^+/H^+ antiporter (*HvVNHX2*) and H^+-ATPase subunit β (*HvVHA-β*) up-regulated the expression of vacuolar Na^+/H^+ antiporter (NHE1) that helped to modulate Na^+ compartmentation into the vacuoles.

Recently, it has been proposed that NO negatively regulates CK signaling by limiting phosphorelay activity via S-nitrosylation [103]. Contrasting reports of Kong et al. [88] showed that foliar applied SNP (as NO donor) delayed salt-induced leaf senescence in cotton seedlings by up-regulating the expression of CK biosynthesis gene, isopentenyl transferase (*IPT*). NO induced reduction in total free PAs, free Put, spermidine (Spd), and polyamine oxidase (PAO) activity that was reported by Fan et al. [103] in cucumber seedlings exposed to NaCl stress. These reports provide a strong evidence for NO cross talk with plant hormones to induce salt stress tolerance in plants; however, further in depth studies to understand interplay among these plant growth regulators in terms of transcriptional regulation, signal transduction, and ion detoxification are needed.

5. NO-phytohormone cross talk under temperature stress

Temperature stress negatively influences the vegetative and reproductive growth phases of plants. Coordinated action between NO and plant hormones (ABA, JA, GA, CK) induce thermotolerance in plants by activating the antioxidant machinery and up-regulating the expression of genes encoding heat shock proteins [104–106]. Studies involving *Arabidopsis* mutants impaired in ABA biosynthesis (*aba1-1*) and signaling (*abi 1-1*) showed that drought and heat stress induced stomatal closure involved JA and H_2O_2 signaling that triggered NO levels [106] and Ca^{2+} and SLAC1 function [107, 108]. However, SA antagonized JA function to induce stomatal opening in *abi1-1* [106]. In *Phragmites communis*, ABA treatment triggered NOS activity and increased NO levels that improved the thermotolerance of plant calluses [109]. Treatment of *Stylosanthes guianensis* seedlings with ABA stimulated the activities of CAT, SOD, and APX suggesting that ABA-induced NO generation leads to the production of antioxidant enzymes [110]. Evidence supports the antagonist relationship between SA and ET in improving heat tolerance in plants by increasing proline contents and enhancing photosynthetic-NUE [111]. SA cross talk with AUX, ET, JA, and BR has been demonstrated in specific bioassays [112]. SA triggered increase in GST activity was noted to induce heat stress tolerance in *Zea mays* [113]. Presumably, SA reduced H_2O_2 accumulation through NO generation; however, direct evidences of NO interaction with plant hormones (SA, GA, AUX, BR, and JA) in improving plant heat stress tolerance are lacking. BRs are also thought to interact with ABA, SA, and ET to induce heat stress signaling through complex networks [114, 115]. BR treatment of *Brassica napus* seedlings subjected to short-term heat shocks was noted to enhance endogenous ABA concentration [116]. BR induced increase in ABA level has also been reported in cellular culture of *Chlorella vulgaris* [117].

Low temperature severely restricts plant growth and causes both structural and metabolic damages in plants [118]. Exposure to low temperature induces oxidative and nitrosative stress thereby promoting NO synthesis [119], which serves as a potential link between PA and ABA to induce stress responses in plants [120]. Literature indicated extensive cross talk among NO, ABA, PAs, and H_2O_2 to modulate various physiological and stress responses under low temperature conditions [110, 121]. Interplay among NO, SA, and ABA was noted to enhance the antioxidative activities (CAT, SOD, POX) that contributed to improved chilling injury in *Zea mays* seedlings [122]. Guo et al. [123] found that coordinated action between NO and ABA up-regulated cold-induced *MfSAMS1* expression, resulting in enhanced acclimation against cold stress in *Medicago sativa* subsp. *falcata*. Moreover, expression of *MfSAMS1* altered the levels of Spm, Put, and Spd and activities of PAO and copper-containing amine oxidase, which regulate anti-oxidant machinery during cold acclimation. Exogenous NO supply increased Put and Spd levels and stimulated the expression of genes encoding Spd synthase (*LeSPDS*), arginine decarboxylase (*LeADC. LeADC1*), and ornithine decarboxylase (*LeODC*) to improve chilling stress tolerance in *Lycopersicon esculentum* leaves. However, the expression of genes encoding Spm synthase (*LeSPMS*) and *S*-adenosylmethionine decarboxylase (*LeSAMDC*) was not influenced by NO treatment [121]. Reports of Li et al. [124] showed that NO treatment converts Put into Spd or Spm to confer cold tolerance in *Zingiber officinale* seedlings. Pretreatment of *Orzya sativa* seedlings with various ammonium concentrations decreased the effects of cold stress by increasing Put and Spd contents [125], suggesting the possible involvement of NO in stress tolerance. In a recent article, Wang et al. [126] reported the coordinated action of NO and PAs to induce chilling tolerance in cold-stored banana. NO treatment increased the activities of PAO, diamine oxidase (DAO) and glutamate decarboxylase (GAD), leading to γ-aminobutyric acid (GABA) accumulation to prevent chilling injury in fruits.

NR and NOS pathway are the most widely known NO sources in plants [19, 127]. Evidence obtained by Aydin and Nalbantoğlu [128] showed that SA pretreatment of *Spinacia oleracea* leaves influenced NR activity to induce chilling stress tolerance. A recent study indicated the involvement of JA in NO synthesis that increased CAT activity to scavenge H_2O_2, leading to reduced chilling injury in *Cucumis sativus* [129]. Therefore, it is concluded that NO cross talk with other hormones safeguards the quality of stored fruits and vegetables. Another study on NO revealed that it increases the expression of *MaCAT, MaPOD, MaSOD,* and *MaAPX* genes to alleviate damages caused by low temperature in banana (Wu et al. [75]). In *Elymus nutans*, interaction between NO and 5-aminolevulinic acid (ALA) stimulated antioxidant defense to reduce chilling injury [130]. Further investigations involving influence of NO on BR, CK, JA, and ET pathways are suggested which would provide important information about signaling cascades of these regulatory substances in cold stressed plants.

6. NO-phytohormone cross talk under other abiotic stresses

Ever increasing human population and industrial productivity has resulted in alarming rise in air pollutants, causing extensive damages to natural habitats of plant [131]. Ozone is characterized as one of the most phytotoxic air pollutants severely restricting plant growth and development [132]. Plants use many transportable chemical signals such as NO to turn the sensing of ozone from guard cells to adjacent epidermal and mesophyll cells [133]. Presumably, NO generation in relation to ozone stress induces ET and ABA synthesis and interferes with stomatal ABA response, potentially by inhibiting K^+ efflux at the guard cells [134]. The involvement of alternative oxidase (*AOX*) in the inhibition of ozone-induced toxicity has also been demonstrated to require both NO- and ET-dependent pathways [135]. Interestingly, Rao and Davies [136] observed that NO treatment caused leaf injury due to increased levels of ozone-induced ET production. Both SNP and ozone treatment up-regulated the expression of the ET biosynthesis related genes (*ACS6* and *ACC oxidase*), which correlates with ET formation [137]. In *Arabidopsis*, exogenous NO supply in combination with ozone stress was noted to attenuate the induction of SA biosynthesis and other defense-related genes [132].

Destruction of ozone layer in upper atmosphere, as a result of increased concentrations of air pollutants, has exposed living organisms to UV-radiation particularly UV-B that induces oxidative stress in plants [138, 139]. Although it is well known that NO interacts with ABA, ET, MeJA to control guard cell signaling in response to various environmental stresses [140, 141], only few reports are available with regard to NO, ET, and ABA cross talk in stomatal regulation under UV-B stress [142]. Studies involving *Lactuca sativa* seedlings showed that exogenous NO supply (using SNP as a NO donor) prevented UV-B induced inhibition of GA and IAA synthesis [143]. NO stimulated decrease in SA and ABA levels was found to be associated with reduced H_2O_2 and malondialdehyde contents. In contrast, coordinated action of NO and SA was observed to reduce UV-B stress in *Triticum aestivum* seedlings [144].

A transient NO burst is among the earliest responses to wounding [145]. NO production in wounded parts involves several pathways including cross talk with signaling cascades of hormones and endogenous signals [146, 147]. It was shown that NO and AUX actively take part in wound-healing response in plants [145, 148]. Imanishi et al. [149] presented evidence for the involvement MeJA and mechanical wounding in expression of the *Ipomoelin* gene (*IPO*) in sweet potato. Later, Jih et al. [150] demonstrated that SNP-derived NO delayed wounding-induced *IPO* expression, providing evidence for antagonistic association between NO and JA. In *Arabidopsis*, NO treatments led to elevated expression of key enzymes of the octadecanoid pathway, like *LOX2, AOS, or OPR3,* in wounded leaf epidermis [151]. However, this induction did not influence JA responsible genes, like PDF*1.2*, hence supporting the earlier evidences about NO and JA association. NO-induced wound-responses could act as a modulator of cell death initiation together with H_2O_2 accumulation, and delay of IPO-expression [152]. Contrasting reports in *Lycopersicon esculentum* demonstrated neither wound-induced NO burst, nor NO-induced elevation of endogenous SA levels [153]. Moreover, SNP-derived NO inhibited the expression of the proteinase inhibitors *Inh1, Inh2*, cathepsin D inhibitor (*CDI*), and metallocarboxypeptidase inhibitor (*CPI*) and increased *AOS* or *LOX* activity. Nevertheless, these studies demonstrate clearly that induction of a wound-response in plants involve cross talk among various stress signaling molecules.

Initiation of senescence in plants is controlled by various factors such as nutrient supply, light conditions, leaf age, and environmental stress [154]. Plant hormones such as ET and CK influence senescence by either promoting or delaying the process, respectively [155, 156]. Evidence supports the interaction of NO with other plant hormones to floral senescence and fruit maturation [157]. Recently, Ji et al. [158] demonstrated that SA treatment at low concentrations induced NOA1-dependent NO signaling and activated antioxidant defense to counteract MeJA-induced leaf senescence. NO plays a conceivable role to counteract the ABA- and jasmonate-induced senescence in rice by inhibiting H_2O_2 accumulation and lipid peroxidation [159]. Mishina et al. [160] found that delayed leaf senescence in *Arabidopsis* involves NO-induced reduction in SA levels. During fruit ripening, NO cross talk with SA and ET involves the regulation of levels of secondary metabolites such as anthocyanins [161]. NO-induced suppression of cell wall softening related enzymes such as polygalacturonase (PG), pectin methylesterase (PME), and pectate lyase (PL) was found to delay softening and ripening of stored *Carica papaya* by reducing ABA, IAA and zeatin ribose (ZR) levels [123].

7. Conclusion and future perspectives

Although our understanding of NO interactions with plant hormones has increased dramatically in past few years, many pieces of the puzzle are still missing. It is well established that NO coordinates with plant hormones to regulate gene expression and activities of anti-oxidative enzymes under adverse environmental conditions. However, our current knowledge about NO-phytohormone interactions is derived chiefly from NO-induced posttranslational modifications of transcription factors and biosynthetic enzymes. Future work is needed to explore the interplay among NO, plant hormones, ROS, protein kinases, and cytoskeletal proteins in order to understand the complicated network of NO signaling under abiotic stress conditions. Interestingly, most of the studies related to NO-phytohormonal interactions involve experiments in controlled laboratory environments, very little is known about the

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cross talk between these signaling molecules during flower initiation or grain development. Moreover, plants growing under natural conditions face multiple stresses; hence, future studies will need to address how NO interacts with the signaling cascades of phytohormones in plants exposed to two or more abiotic stresses.

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