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), abscisic 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]      |
|                | SA           | *Medicago truncatula* | Improved antioxidative capacity and reduced degradation of AUX in roots   |                  | Xu et al. [68]           |
| 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$_2$O$_2$ accumulation, limited Na$^+$ 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]         |
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 ($\text{H}_{2}\text{O}_{2}$) 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

| 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 Nalbantoglu [128] |
| | JA | *Cucumis sativus* | Increased CAT activity to scavenge $\text{H}_{2}\text{O}_{2}$, 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
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_{2}O_{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$_2$O$_2$, 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 (*AtFIT*, *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$_2$O$_2$ 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 PIFORMED (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$_2$O$_2$ 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$_2$S to enhance tolerance against salinity stress in plants. NO and H$_2$S 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 $\beta$ (*HvVHA-$\beta$) 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$_2$O$_2$ 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$_2$O$_2$ 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$_2$O$_2$ 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$_2$O$_2$, 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$_2$O$_2$ 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 of 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 PDF1.2, 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$_2$O$_2$ 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$_2$O$_2$ 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...
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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**References**

[1] Waraich EA, Ahmad R, Ashraf MY. Role of mineral nutrition in alleviation of drought stress in plants. Australian Journal of Crop Science. 2011;5:764-777

[2] Shabbir RN, Waraich EA, Ali H, Nawaz F, Ashraf MY, Ahmad R, Awan MI, Ahmad S, Irfan M, Hussain S, Ahmad Z. Supplemental exogenous NPK application alters biochemical processes to improve yield and drought tolerance in wheat (Triticum aestivum L.). Environmental Science and Pollution Research. 2016;23:2651-2662

[3] Nawaz F, Ashraf MY, Ahmad R, Waraich EA, Shabbir RN, Bukhari MA. Supplemental selenium improves wheat grain yield and quality through alterations in biochemical processes under normal and water deficit conditions. Food Chemistry. 2015;175:350-357

[4] Penuelas J, Sardans J, Estiarte M, Ogaya R, Carnicer J, Coll M, Barbeta A, Rivas-Ubach A, Llusia J, Garbulsky M, Filella I. Evidence of current impact of climate change on life: A walk from genes to the biosphere. Global Change Biology. 2013;19:2303-2338

[5] Hancock JT, Neill SJ, Wilson ID. Nitric oxide and ABA in the control of plant function. Plant Science 2011;181:555-559
Simontacchi M, García-Mata C, Bartoli CG, Santa-María GE, Lamattina L. Nitric oxide as a key component in hormone-regulated processes. Plant Cell Reports. 2013;32:853-866

Manjunatha G, Lokesh V, Neelwarne B. Nitric oxide in fruit ripening: Trends and opportunities. Biotechnology Advances. 2010;28:489-499

Lozano-Juste J, León J. Nitric oxide regulates DELLA content and PIF expression to promote photomorphogenesis in Arabidopsis. Plant Physiology 2011;156:1410-1423

Terrile MC, Paris R, Calderón-Villalobos LI, Iglesias MJ, Lamattina L, Estelle M, Casalangué CA. Nitric oxide influences auxin signaling through S-nitrosylation of the Arabidopsis TRANSPORT INHIBITOR RESPONSE 1 auxin receptor. The Plant Journal. 2012;70:492-500

Feng J, Wang C, Chen Q, Chen H, Ren B, Li X, Zuo J. S-nitrosylation of phosphotransfer proteins represses cytokinin signaling. Nature Communications. 2013;4:1529

Freschi L. Nitric oxide and phytohormone interactions: Current status and perspectives. Frontiers in Plant Science. 2013;4:1-22

Tossi V, Cassia R, Bruzzzone S, Zocchi E, Lamattina L. ABA says NO to UV-B: A universal response?. Trends in Plant Science. 2012;17:510-517

Zhang M, Yuan B, Leng P. The role of ABA in triggering ethylene biosynthesis and ripening of tomato fruit. Journal of Experimental Botany. 2009;60:1579-1588

Lozano-Juste J, Leon J. Enhanced abscisic acid-mediated responses in nia1nia2noa1-2 triple mutant impaired in NIA/NR- and AtNOA1-dependent nitric oxide biosynthesis in Arabidopsis. Plant Physiology. 2010;152:891-903

Lozano-Juste J, León J. Nitric oxide modulates sensitivity to ABA. Plant Signaling & Behavior. 2010;5:314-316.

Bright J, Desikan R, Hancock JT, Weir IS, Neill SJ. ABA-induced NO generation and stomatal closure in Arabidopsis are dependent on H$_2$O$_2$ synthesis. The Plant Journal. 2006;45:113-122

Lu G, Gao C, Zheng X, Han B. Identification of OsbZIP72 as a positive regulator of ABA response and drought tolerance in rice. Planta. 2009;229:605-615

Zhang A, Jiang M, Zhang J, Ding H, Xu S, Hu X, Tan M. Nitric oxide induced by hydrogen peroxide mediates abscisic acid-induced activation of the mitogen-activated protein kinase cascade involved in antioxidant defense in maize leaves. The New Phytologist. 2007;175:36-50

Desikan R, Griffiths R, Hancock J, Neill S. A new role for an old enzyme: Nitrate reductase-mediated nitric oxide generation is required for abscisic acid-induced stomatal closure in Arabidopsis thaliana. Proceedings of National Academy of Sciences. 2002;99:16314-16318
[20] Dubovskaya LV, Bakakina YS, Kolesneva EV, Sodel DL, McAinsh MR, Hetherington AM, Volotovski ID. cGMP-dependent ABA-induced stomatal closure in the ABA-insensitive Arabidopsis mutant abi1-1. The New Phytologist. 2011;191:57-69

[21] Mioto PT, Mercier H. Abscisic acid and nitric oxide signaling in two different portions of detached leaves of Guzmania monostachia with CAM up-regulated by drought. Journal of Plant Physiology. 2013;170:996-1002

[22] Neill S, Barros R, Bright J, Desikan R, Hancock J, Harrison J, Morris P, Ribeiro D, Wilson I. Nitric oxide, stomatal closure, and abiotic stress. Journal of Experimental Botany. 2008;59:165-176

[23] Sang J, Jiang M, Lin F, Xu S, Zhang A, Tan M. Nitric oxide reduces hydrogen peroxide accumulation involved in water stress-induced subcellular Anti-oxidant defense in maize plants. Journal of Integrative Plant Biology. 2008;50:231-243

[24] Freschi L, Rodrigues MA, Domingues DS, Purgatto E, Van Sluys MA, Magalhaes JR, Kaiser WM, Mercier H. Nitric oxide mediates the hormonal control of Crassulacean acid metabolism expression in young pineapple plants. Plant Physiology. 2010;152:1971-1985

[25] León J, Castillo MC, Coego A, Lozano-Juste J, Mir R. Diverse functional interactions between nitric oxide and abscisic acid in plant development and responses to stress. Journal of Experimental Botany. 2014;65:907-921

[26] Zhang A, Zhang J, Zhang J, Ye N, Zhang H, Tan M, Jiang M. Nitric oxide mediates brassinosteroid-induced ABA biosynthesis involved in oxidative stress tolerance in maize leaves. Plant and Cell Physiology. 2011;52:181-192

[27] Saito N, Yoshimasa N, Mori IC, Murata Y. Nitric oxide functions in both methyl jasmonate signaling and abscisic acid signaling in Arabidopsis guard cells. Plant Signaling & Behavior. 2009;4:119-120

[28] Liu Y, Ye N, Liu R, Chen M, Zhang J. H$_2$O$_2$ mediates the regulation of ABA catabolism and GA biosynthesis in Arabidopsis seed dormancy and germination. Journal of Experimental Botany. 2010;61:2979-2990

[29] Sanz L, Albertos P, Mateos I, Sánchez-Vicente I, Lechón T, Fernández-Marcos M, Lorenzo O. Nitric oxide (NO) and phytohormones crosstalk during early plant development. Journal of Experimental Botany. 2015;66:2857-2868

[30] Sugawara S, Mashiguchi K, Tanaka K, Hishiyama S, Sakai T, Hanada K, Kinoshita-Tsujimura K, Yu H, Dai X, Takebayashi Y, Takeda-Kamiya N. Distinct characteristics of indole-3-acetic acid and phenylacetic acid, two common auxins in plants. Plant and Cell Physiology. 2015;56:1641-1654

[31] Kohli A, Sreenivasulu N, Lakshmanan P, Kumar PP. The phytohormone crosstalk paradigm takes center stage in understanding how plants respond to abiotic stresses. Plant Cell Reports. 2013;32:945-957
[32] Pagnussat GC, Simontacchi M, Puntarulo S, Lamattina L. Nitric oxide is required for root organogenesis. Plant Physiology. 2002;129:954-956

[33] Liao WB, Huang GB, Yu JH, Zhang ML. Nitric oxide and hydrogen peroxide alleviate drought stress in marigold explants and promote its adventitious root development. Plant Physiology and Biochemistry. 2012;58:6-15

[34] Hunt PW, Klok EJ, Trevaskis B, Watts RA, Ellis MH, Peacock WJ, Dennis ES. Increased level of hemoglobin 1 enhances survival of hypoxic stress and promotes early growth in Arabidopsis thaliana. Proceeding of the National Academy of Sciences. 2002;99:17197-17202

[35] Chen J, Zhang HQ, Hu LB, Shi ZQ. Microcystin-LR-induced phytotoxicity in rice crown root is associated with the cross-talk between auxin and nitric oxide. Chemosphere. 2013;93:283-293

[36] Huang D, Wu W, Abrams SR, Cutler AJ. The relationship of drought-related gene expression in Arabidopsis thaliana to hormonal and environmental factors. Journal of Experimental Botany. 2008;59:2991-3007

[37] Munemasa S, Oda K, Watanabe-Sugimoto M, Nakamura Y, Shimoishi Y, Murata Y. The coronatine-insensitive 1 mutation reveals the hormonal signaling interaction between abscisic acid and methyl jasmonate in Arabidopsis guard cells. Specific impairment of ion channel activation and second messenger production. Plant Physiology. 2007;143:1398-1407

[38] Hossain KK, Nakamura T, Yamasaki H. Effect of nitric oxide on leaf non-photochemical quenching of fluorescence under heat-stress conditions. Russian Journal of Plant Physiology. 2011;58:629-633

[39] Munemasa S, Hossain MA, Nakamura Y, Mori IC, Murata Y. The Arabidopsis calcium-dependent protein kinase, CPK6, functions as a positive regulator of methyl jasmonate signaling in guard cells. Plant Physiology. 2011;155:553-561

[40] Palmieri MC, Sell S, Huang X, Scherf M, Werner T, Durner J, Lindermayr C. Nitric oxide-responsive genes and promoters in Arabidopsis thaliana: A bioinformatics approach. Journal of Experimental Botany. 2008;59:177-186

[41] Alavi SM, Arvin MJ, Manoochehri Kalantari K. Salicylic acid and nitric oxide alleviate osmotic stress in wheat (Triticum aestivum L.) seedlings. Journal of Plant Interactions. 2014;9:683-688

[42] Shao R, Wang K, Shangguan Z. Cytokinin-induced photosynthetic adaptability of Zea mays L. to drought stress associated with nitric oxide signal: Probed by ESR spectroscopy and fast OJIP fluorescence rise. Journal of Plant Physiology. 2010;167:472-479

[43] Xiao-Ping S, Xi-Gui S. Cytokinin and auxin-induced stomatal opening is related to the change of nitric oxide levels in guard cells in broad bean. Physiology Planta. 2006;128:569-579
[44] Wilhelmova N, Fuksova H, Srbova M, Mikova D, Mýtinová Z, Prochazkova D, Vytášek R, Wilhelm J. The effect of plant cytokinin hormones on the production of ethylene, nitric oxide, and protein nitrotyrosine in ageing tobacco leaves. Biofactors. 2006;27:203-211

[45] Liu WZ, Kong DD, Gu XX, Gao HB, Wang JZ, Xia M, Gao Q, Tian LL, Xu ZH, Bao F, Hu Y. Cytokinins can act as suppressors of nitric oxide in Arabidopsis. Proceedings of the National Academy of Sciences. 2013;110:1548-1553

[46] Rascio N, Navari-Izzo F. Heavy metal hyperaccumulating plants: How and why do they do it? And what makes them so interesting?. Plant Science. 2011;180:169-181

[47] Potters G, Pasternak TP, Guisez Y, Palme KJ, Jansen MA. Stress-induced morphogenic responses: Growing out of trouble?. Trends in Plant Science. 2007;12:98-105

[48] Piotrowska-Niczyporuk A, Bajguz A, Zambrzycka E, Godlewska-Żykiewicz B. Phytohormones as regulators of heavy metal biosorption and toxicity in green alga Chlorella vulgaris (Chlorophyceae). Plant Physiology and Biochemistry. 2012;52:52-65

[49] Lin YC, Chang-Chien GP, Chiang PC, Chen WH, Lin YC. Multivariate analysis of heavy metal contaminations in seawater and sediments from a heavily industrialized harbor in Southern Taiwan. Marine Pollution Bulletin. 2013;76:266-275

[50] He HY, He LF, Gu MH, Li XF. Nitric oxide improves aluminum tolerance by regulating hormonal equilibrium in the root apices of rye and wheat. Plant Science. 2012;183:123-130

[51] Thao NP, Khan MI, Thu NB, Hoang XL, Asgher M, Khan NA, Tran LS. Role of ethylene and its cross talk with other signaling molecules in plant responses to heavy metal stress. Plant Physiology. 2015;169:73-84

[52] Chmielowska-Bąk J, Gzyl J, Rucińska-Sobkowiak R, Arasimowicz-Jelonek M, Deckert J. The new insights into cadmium sensing. Frontiers in Plant Science. 2014;5:245

[53] Arasimowicz-Jelonek M, Floryszak-Wiezorek J, Gwóźdź EA. The message of nitric oxide in cadmium challenged plants. Plant Science. 2011;181:612-620

[54] Singh HP, Batish DR, Kaur G, Arora K, Kohli RK. Nitric oxide (as sodium nitroprusside) supplementation ameliorates Cd toxicity in hydroponically grown wheat roots. Environmental and Experimental Botany. 2008;63:158-167

[55] Yu Y, Li ZH, Xing DA. Nitric oxide promotes MPK6-mediated caspase-3-like activation in cadmium-induced Arabidopsis thaliana programmed cell death. Plant, Cell & Environment. 2013;36:1-5

[56] Zhao FY, Hu F, Zhang SY, Wang K, Zhang CR, Liu T. MAPKs regulate root growth by influencing auxin signaling and cell cycle-related gene expression in cadmium-stressed rice. Environmental Science and Pollution Research. 2013;20:5449-5460

[57] Wang Y, Loake GJ, Chu C. Cross-talk of nitric oxide and reactive oxygen species in plant programmed cell death. Frontiers in Plant Science. 2013;4:314
[58] Chmielowska-Bąk J, Lefèvre I, Lutts S, Deckert J. Short term signaling responses in roots of young soybean seedlings exposed to cadmium stress. Journal of Plant Physiology. 2013;170:1585-1594

[59] Maksymiec W. Signaling responses in plants to heavy metal stress. Acta Physiologiae Plantarum. 2007;29:177-187

[60] Khan MI, Nazir F, Asgher M, Per TS, Khan NA. Selenium and sulfur influence ethylene formation and alleviate cadmium-induced oxidative stress by improving proline and glutathione production in wheat. Journal of Plant Physiology. 2015;173:9-18

[61] Thapa G, Sadhukhan A, Panda SK, Sahoo L. Molecular mechanistic model of plant heavy metal tolerance. Biometals. 2012;25:489-505

[62] Montero-Palmero MB, Martín-Barranco A, Escobar C, Hernández LE. Early transcriptional responses to mercury: A role for ethylene in mercury-induced stress. The New Phytologist. 2014;201:116-130

[63] Montero-Palmero MB, Ortega-Villasante C, Escobar C, Hernández LE. Are plant endogenous factors like ethylene modulators of the early oxidative stress induced by mercury?. Frontiers in Environmental Science 2014;2:34

[64] Rodríguez-serrano MA, Romero-puertas MC, Zabalza AN, Corps FJ, Gómez M, Del Rio LA, Sandalio LM. Cadmium effect on oxidative metabolism of pea (Pisum sativum L.) roots. Imaging of reactive oxygen species and nitric oxide accumulation in vivo. Plant, Cell & Environment. 2006;29:1532-1544

[65] Cao S, Chen Z, Liu G, Jiang L, Yuan H, Ren G, Bian X, Jian H, Ma X. The Arabidopsis Ethylene-Insensitive 2 gene is required for lead resistance. Plant Physiology and Biochemistry. 2009;47:308-312

[66] Groppa MD, Rosales EP, Iannone MF, Benavides MP. Nitric oxide, polyamines and Cd-induced phytotoxicity in wheat roots. Phytochem. 2008;69:2609-2615

[67] Yuan HM, Huang X. Inhibition of root meristem growth by cadmium involves nitric oxide-mediated repression of auxin accumulation and signalling in Arabidopsis. Plant, Cell & Environment. 2016;39:120-135

[68] Xu J, Wang W, Yin H, Liu X, Sun H, Mi Q. Exogenous nitric oxide improves antioxidative capacity and reduces auxin degradation in roots of Medicago truncatula seedlings under cadmium stress. Plant and Soil 2010;326:321. DOI: 10.1007/s11104-009-0011-4

[69] Xu J, Wang W, Sun J, Zhang Y, Ge Q, Du L, Yin H, Liu X. Involvement of auxin and nitric oxide in plant Cd-stress responses. Plant and Soil. 2011;346:107

[70] Rodríguez-Serrano M, Romero-Puertas MC, Pazmino DM, Testillano PS, Risueño MC, Luis A, Sandalio LM. Cellular response of pea plants to cadmium toxicity: Cross talk between reactive oxygen species, nitric oxide, and calcium. Plant Physiology. 2009;150:229-243
[71] Arasimowicz-Jelonek M, Floryszak-Wieczorek J, Deckert J, Rucińska-Sobkowiak R, Gzyl J, Pawlak-Sprada S, Abramowski D, Jelonek T, Gwóźdź EA. Nitric oxide implication in cadmium-induced programmed cell death in roots and signaling response of yellow lupine plants. Plant Physiology and Biochemistry. 2012;58:124-134

[72] Wang Q, Liang X, Dong Y, Xu L, Zhang X, Hou J, Fan Z. Effects of exogenous nitric oxide on cadmium toxicity, element contents and antioxidative system in perennial ryegrass. Plant Growth Regulation. 2013;69:11-20

[73] Nahar K, Hasanuzzaman M, Alam MM, Rahman A, Suzuki T, Fujita M. Polyamine and nitric oxide crosstalk: Antagonistic effects on cadmium toxicity in mung bean plants through upregulating the metal detoxification, antioxidant defense and methylglyoxal detoxification systems. Ecotoxicology and Environmental Safety. 2016;126:245-255

[74] Zhu XF, Jiang T, Wang ZW, Lei GJ, Shi YZ, Li GX, Zheng SJ. Gibberellic acid alleviates cadmium toxicity by reducing nitric oxide accumulation and expression of IRT1 in Arabidopsis thaliana. Journal of Hazardous Materials. 2012;239:302-307

[75] Wu AP, Gong L, Chen X, Wang JX. Interactions between nitric oxide, gibberellic acid, and phosphorus regulate primary root growth in Arabidopsis. Biologia Planta. 2014;58:335-340

[76] Shen Q, Wang YT, Tian H, Guo FQ. Nitric oxide mediates cytokinin functions in cell proliferation and meristem maintenance in Arabidopsis. Molecular Plant. 2013;6:1214-1225

[77] Kazemi N, Khavari-Nejad RA, Fahimi H, Saadatmand S, Nejad-Sattari T. Effects of exogenous salicylic acid and nitric oxide on lipid peroxidation and antioxidant enzyme activities in leaves of Brassica napus L. under nickel stress. Scientia Horticulture. 2010;126:402-407

[78] Xu LL, Fan ZY, Dong YJ, Kong J, Bai XY. Effects of exogenous salicylic acid and nitric oxide on physiological characteristics of two peanut cultivars under cadmium stress. Biologia Planta. 2015;59:171-182

[79] Tossi V, Lamattina L, Cassia R. Pharmacological and genetical evidence supporting nitric oxide requirement for 2, 4-epibrassinolide regulation of root architecture in Arabidopsis thaliana. Plant Signaling & Behavior. 2013;8:e24712

[80] Choudhary SP, Kanwar M, Bhardwaj R, Yu JQ, Tran LS. Chromium stress mitigation by polyamine-brassinosteroid application involves phytohormonal and physiological strategies in Raphanus sativus L. PLoS One. 2012;7:e33210

[81] Brumbarova T, Bauer P, Ivanov R. Molecular mechanisms governing Arabidopsis iron uptake. Trends in Plant Science. 2015;20:124-133

[82] García MJ, Lucena C, Romera FJ, Alcántara E, Pérez-Vicente R. Ethylene and nitric oxide involvement in the up-regulation of key genes related to iron acquisition and homeostasis in Arabidopsis. Journal of Experimental Botany. 2010;61:3885-3899
[83] Alemayehu A, Zelinová V, Bočová B, Huttová J, Mistrík I, Tamás L. Enhanced nitric oxide generation in root transition zone during the early stage of cadmium stress is required for maintaining root growth in barley. Plant and Soil. 2015;390:213-222

[84] Hussain RA, Ahmad R, Nawaz F, Ashraf MY, Waraich EA. Foliar NK application mitigates drought effects in sunflower (Helianthus annuus L.). Acta Physiologica Plantarum. 2016;38:1-4

[85] Poór P, Tari I. Ethylene-regulated reactive oxygen species and nitric oxide under salt stress in tomato cell suspension culture. Acta Biologica Szegediensis. 2011;55:143-146

[86] Fatma M, Masood A, Per TS, Khan NA. Nitric oxide alleviates salt stress inhibited photosynthetic performance by interacting with sulfur assimilation in mustard. Frontiers in Plant Science. 2016;7

[87] Molassiotis A, Tanou G, Diamantidis G. NO says more than ‘YES’ to salt tolerance: salt priming and systemic nitric oxide signaling in plants. Plant Signaling & Behavior. 2010;5:209-212

[88] Kong X, Wang T, Li W, Tang W, Zhang D, Dong H. Exogenous nitric oxide delays salt-induced leaf senescence in cotton (Gossypium hirsutum L.). Acta Physiologica Plantarum. 2016;38:1-9

[89] Wu L, Zhang Z, Zhang H, Wang XC, Huang R. Transcriptional modulation of ethylene response factor protein JERF3 in the oxidative stress response enhances tolerance of tobacco seedlings to salt, drought, and freezing. Plant Physiology. 2008;148:1953-1963

[90] Wang H, Liang X, Wan Q, Wang X, Bi Y. Ethylene and nitric oxide are involved in maintaining ion homeostasis in Arabidopsis callus under salt stress. Planta. 2009;230:293-307

[91] Wang P, Du Y, Li Y, Ren D, Song CP. Hydrogen peroxide–mediated activation of MAP kinase 6 modulates nitric oxide biosynthesis and signal transduction in Arabidopsis. The Plant Cell. 2010;22:2981-2998

[92] Wang CL, Wu J, Xu GH, Gao YB, Chen G, Wu JY, Wu HQ, Zhang SL. S-RNase disrupts tip-localized reactive oxygen species and induces nuclear DNA degradation in incompatible pollen tubes of Pyrus pyrifolia. Journal of Cell Science. 2010;123:4301-4309

[93] Poór P, Gémes K, Horváth F, Szepesi A, Simon ML, Tari I. Salicylic acid treatment via the rooting medium interferes with stomatal response, CO2 fixation rate and carbohydrate metabolism in tomato, and decreases harmful effects of subsequent salt stress. Plant Biology. 2011;13:105-114

[94] Liu W, Li RJ, Han TT, Cai W, Fu ZW, Lu YT. Salt stress reduces root meristem size by nitric oxide-mediated modulation of auxin accumulation and signaling in Arabidopsis. Plant Physiology. 2015;168:343-356

[95] Khokon MD, Okuma EI, Hossain MA, Munemasa S, Uraji M, Nakamura Y, Mori IC, Murata Y. Involvement of extracellular oxidative burst in salicylic acid-induced stomatal closure in Arabidopsis. Plant, Cell & Environment. 2011;34:434-443
[96] Liu N, Tu L, Tang W, Gao W, Lindsey K, Zhang X. Small RNA and degradome profiling reveals a role for miRNAs and their targets in the developing fibers of *Gossypium barbadense*. The Plant Journal. 2014;80:331-344

[97] Dong F, Simon J, Rienks M, Lindermayr C, Rennenberg H. Effects of rhizospheric nitric oxide (NO) on N uptake in *Fagus sylvatica* seedlings depend on soil CO₂ concentration, soil N availability and N source. Tree Physiology. 2015;35:910-920

[98] Khan A, Ahmad I, Shah A, Ahmad F, Ghani A, Nawaz M, Shaheen F, Fatima HU, Pervaiz F, Javed S, Hayat F. Amelioration of salinity stress in wheat (*Triticum aestivum* L) by foliar application of phosphorus. Fyton. 2013;82:281-287

[99] Barroso JB, Corpas FJ, Carreras A, Rodríguez-Serrano M, Esteban FJ, Fernández-Ocaña A, Chaki M, Romero-Puertas MC, Valderrama R, Sandalio LM, del Río L.A. Localization of S-nitrosoglutathione and expression of S-nitrosoglutathione reductase in pea plants under cadmium stress. Journal of Experimental Botany. 2006;57:1785-1793

[100] Wang D, Liu Y, Tan X, Liu H, Zeng G, Hu X, Jian H, Gu Y. Effect of exogenous nitric oxide on antioxidative system and S-nitrosylation in leaves of *Boehmeria nivea* (L.) Gaud under cadmium stress. Environmental Science and Pollution Research. 2015;22:3489-3497

[101] Leterrier M, Chaki M, Airaki M, Valderrama R, Palma JM, Barroso JB, Corpas FJ. Function of S-nitrosoglutathione reductase (GSNOR) in plant development and under biotic/abiotic stress. Plant Signaling & Behavior. 2011;6:789-793

[102] Chen YS, Lo SF, Sun PK, Lu CA, Ho TH, Yu SM. A late embryogenesis abundant protein HVA1 regulated by an inducible promoter enhances root growth and abiotic stress tolerance in rice without yield penalty. Plant Biotechnology Journal. 2015;13:105-116

[103] Fan HF, Du CX, Guo SR. Nitric oxide enhances salt tolerance in cucumber seedlings by regulating free polyamine content. Environmental and Experimental Botany. 2013;86:52-59

[104] Uchida A, Jagendorf AT, Hibino T, Takabe T, Takabe T. Effects of hydrogen peroxide and nitric oxide on both salt and heat stress tolerance in rice. Plant Science. 2002;163:515-523

[105] Song L, Ding W, Zhao M, Sun B, Zhang L. Nitric oxide protects against oxidative stress under heat stress in the calluses from two ecotypes of reed. Plant Science. 2006;171:449-458

[106] Zandalinas SI, Balfagón D, Arbona V, Gómez-Cadenas A, Inupakutika MA, Mittler R. ABA is required for the accumulation of APX1 and MBF1c during a combination of water deficit and heat stress. Journal of Experimental Botany. 2016;67:5381-5390

[107] Daszkowska-Golec A, Szarejko I. Open or close the gate–stomata action under the control of phytohormones in drought stress conditions. Frontiers in Plant Science. 2013;4:138

[108] Murata Y, Mori IC, Munemasa S. Diverse stomatal signaling and the signal integration mechanism. Annual Review of Plant Biology. 2015;66:369-392
[109] Song L, Ding W, Shen J, Zhang Z, Bi Y, Zhang L. Nitric oxide mediates abscisic acid induced thermotolerance in the calluses from two ecotypes of reed under heat stress. Plant Science. 2008;175:826-832

[110] Zhou B, Guo Z, Xing J, Huang B. Nitric oxide is involved in abscisic acid-induced antioxidant activities in Stylosanthes guianensis. Journal of Experimental Botany. 2005;56:3223-3228

[111] Khan AL, Waqas M, Hamayun M, Al-Harrasi A, Al-Rawahi A, Lee JI. Co-synergism of endophyte Penicillium resedanum LK6 with salicylic acid helped Capsicum annuum in biomass recovery and osmotic stress mitigation. BMC Microbiology. 2013;13:51

[112] Clouse SD, Sasse JM. Brassinosteroids: Essential regulators of plant growth and development. Annual Review of Plant Biology. 1998;49:427-451

[113] Cetinkya H, Dinler BS, Tasci E. Investigation of comparative regulation on antioxidant enzyme system under copper treatment and drought stress in maize. Notulae Botanicae Horti Agrobotanici Cluj-Napoca. 2014;42:363

[114] Larkindale J, Huang B. Thermotolerance and antioxidant systems in Agrostis stolonifera: Involvement of salicylic acid, abscisic acid, calcium, hydrogen peroxide, and ethylene. Journal of Plant Physiology. 2004;161:405-413

[115] Larkindale J, Hall JD, Knight MR, Vierling E. Heat stress phenotypes of Arabidopsis mutants implicate multiple signaling pathways in the acquisition of thermotolerance. Plant Physiology. 2005;138:882-897

[116] Kurepin LV, Qaderi MM, Back TG, Reid DM, Pharis RP. A rapid effect of applied brassinolide on abscisic acid concentrations in Brassica napus leaf tissue subjected to short-term heat stress. Plant Growth Regulation. 2008;55:165-167

[117] Bajguz A. Brassinosteroid enhanced the level of abscisic acid in Chlorella vulgaris subjected to short-term heat stress. Journal of Plant Physiology. 2009;166:882-886

[118] Atıcı Ö, Nalbantoğlu B. Antifreeze proteins in higher plants. Phytochem. 2003;64:1187-1196

[119] Corpas FJ, Leterrier M, Valderrama R, Airaki M, Chaki M, Palma JM, Barroso JB. Nitric oxide imbalance provokes a nitrosative response in plants under abiotic stress. Plant Science. 2011;181:604-611

[120] Wimalasekera R, Villar C, Begum T, Scherer GF. COPPER AMINE OXIDASE1 (CuAO1) of Arabidopsis thaliana contributes to abscisic acid-and polyamine-induced nitric oxide biosynthesis and abscisic acid signal transduction. Molecular Plant. 2011;4:663-678

[121] Diao Q, Song Y, Shi D, Qi H. Interaction of polyamines, abscisic acid, nitric oxide, and hydrogen peroxide under chilling stress in tomato (Lycopersicon esculentum Mill.) seedlings. Frontiers Plant Science. 2017;8
[122] Esim N, Atici O. Nitric oxide improves chilling tolerance of maize by affecting apoplastic antioxidative enzymes in leaves. Plant Growth Regulation. 2014; 72:29-38

[123] Guo Q, Wu B, Chen W, Zhang Y, Wang J, Li X. Effects of nitric oxide treatment on the cell wall softening related enzymes and several hormones of papaya fruit during storage. Revista de Agroquimica y Tecnologia de Alimentos. 2014; 20:309-317

[124] Li Y, Van den Ende W, Rolland F. Sucrose induction of anthocyanin biosynthesis is mediated by DELLA. Molecular Plant. 2014; 7:570-572. DOI: 10.1093/mp/stt161

[125] Yamamoto E, Yonemaru JI, Yamamoto T, Yano M. OGRO: The overview of functionally characterized genes in rice online database. Rice. 2012; 5:26

[126] Wang Y, Luo Z, Mao L, Ying T. Contribution of polyamines metabolism and GABA shunt to chilling tolerance induced by nitric oxide in cold-stored banana fruit. Food Chemistry. 2016; 197:333-339

[127] Guo FQ, Okamoto M, Crawford NM. Identification of a plant nitric oxide synthase gene involved in hormonal signaling. Science. 2003; 302:100-103

[128] Aydin B, Nalbantoğlu B. Effects of cold and salicylic acid treatments on nitrate reductase activity in spinach leaves. Turkish Journal of Biology. 2011; 35:443-448

[129] Liu Y, Yang X, Zhu S, Wang Y. Postharvest application of MeJA and NO reduced chilling injury in cucumber (Cucumis sativus) through inhibition of H2O2 accumulation. Postharvest Biology and Technology. 2016; 119:77-83

[130] Fu J, Chu X, Sun Y, Miao Y, Xu Y, Hu T. Nitric oxide mediates 5-aminolevulinic acid-induced antioxidant defense in leaves of Elymus nutans griseb. Exposed to chilling stress. PLoS One. 2015;10:e0130367

[131] Tamaoki M. The role of phytohormone signaling in ozone-induced cell death in plants. Plant Signaling and Behavior. 2008;3:166-174

[132] Ahlfors R, Brosché M, Kollist H, Kangasjärvi J. Nitric oxide modulates ozone-induced cell death, hormone biosynthesis and gene expression in Arabidopsis thaliana. The Plant Journal. 2009; 58:1-2

[133] Wilkinson S, Davies WJ. Drought, ozone, ABA and ethylene: New insights from cell to plant to community. Plant, Cell & Environment. 2010; 33:510-525

[134] Kwak JM, Nguyen V, Schroeder JI. The role of reactive oxygen species in hormonal responses. Plant Physiology. 2006; 141:323-329

[135] Ederli L, Morettini R, Borgogni A, Wasternack C, Miersch O, Reale L, Ferranti F, Tosti N, Pasqualini S. Interaction between nitric oxide and ethylene in the induction of alternative oxidase in ozone-treated tobacco plants. Plant Physiology. 2006; 142:595-608
[136] Rao MV, Davis KR. The physiology of ozone induced cell death. Planta. 2001;213:682-690

[137] Overmyer K, Tuominen H, Kettunen R, Betz C, Langebartels C, Sandermann H, Kangasjärvi J. Ozone-sensitive Arabidopsis rcd1 mutant reveals opposite roles for ethylene and jasmonate signaling pathways in regulating superoxide-dependent cell death. The Plant Cell. 2000;12:1849-1862

[138] Zlatev ZS, Lidon FJ, Kaimakanova M. Plant physiological responses to UV-B radiation. Emirates Journal of Food and Agriculture. 2012;24:481

[139] Hideg É, Jansen MA, Strid Å. UV-B exposure, ROS, and stress: Inseparable companions or loosely linked associates?. Trends in Plant Science. 2013;18:107-115

[140] Wilson ID, Neill SJ, Hancock JT. Nitric oxide synthesis and signalling in plants. Plant, Cell & Environment. 2008;31:622-631

[141] Gonugunta VK, Srivastava N, Raghavendra AS. Cytosolic alkalinization is a common and early messenger preceding the production of ROS and NO during stomatal closure by variable signals, including abscisic acid, methyl jasmonate and chitosan. Plant Signaling & Behavior. 2009;4:561-564

[142] He J, Yue X, Wang R, Zhang Y. Ethylene mediates UV-B-induced stomatal closure via peroxidase-dependent hydrogen peroxide synthesis in Vicia faba L. Journal of Experimental Botany. 2011;62:2657-2666

[143] Esringu A, Aksakal O, Tabay D, Kara AA. Effects of sodium nitroprusside (SNP) pretreatment on UV-B stress tolerance in lettuce (Lactuca sativa L.) seedlings. Environmental Science and Pollution Research. 2016;23:589-597

[144] Yan F, Liu Y, Sheng H, Wang Y, Kang H, Zeng J. Salicylic acid and nitric oxide increase photosynthesis and antioxidant defense in wheat under UV-B stress. Biologia Planta. 2016;60:686-694

[145] Arasimowicz M, Floryszak-Wieczorek J, Milczarek G, Jelonek T. Nitric oxide, induced by wounding, mediates redox regulation in pelargonium leaves. Plant Biology. 2009;11:650-663

[146] Lamattina L, García-Mata C, Graziano M, Pagnussat G. Nitric oxide: The versatility of an extensive signal molecule. Annual Review of Plant Biology. 2003;54:109-136

[147] Wendehenne D, Durner J, Klessig DF. Nitric oxide: A new player in plant signalling and defence responses. Current Opinion in Plant Biology. 2004;7:449-455

[148] París R, Lamattina L, Casalongué CA. Nitric oxide promotes the wound-healing response of potato leaflets. Plant Physiology and Biochemistry. 2007;45:80-86

[149] Imanishi S, Kito-Nakamura K, Matsuoka K, Morikami A, Nakamura K. A major jasmonate-inducible protein of sweet potato, ipomoelin, is an ABA-independent wound-inducible protein. Plant & Cell Physiology. 1997;38:643-652
[150] Jih PJ, Chen YC, Jeng ST. Involvement of hydrogen peroxide and nitric oxide in expression of the ipomoelin gene from sweet potato. Plant Physiology. 2003;132:381-389

[151] Huang X, Stettmaier K, Michel C, Hutzler P, Mueller MJ, Durner J. Nitric oxide is induced by wounding and influences jasmonic acid signaling in Arabidopsis thaliana. Planta. 2004;218:938-946

[152] Grün S, Lindermayr C, Sell S, Durner J. Nitric oxide and gene regulation in plants. Journal of Experimental Botany. 2006;57:507-516

[153] Orozco-Cárdenas ML, Ryan CA. Nitric oxide negatively modulates wound signaling in tomato plants. Plant Physiology. 2002;130:487-493

[154] Smart CM. Gene expression during leaf senescence. The New Phytologist. 1994;126:419-448

[155] Gan S, Amasino RM. Inhibition of leaf senescence by autoregulated production of cytokinin. Science. 1995;270:1986

[156] Grbić V, Bleecker AB. Ethylene regulates the timing of leaf senescence in Arabidopsis. The Plant Journal. 1995;8:595-602

[157] Hung KT, Kao CH. Hydrogen peroxide is necessary for abscisic acid-induced senescence of rice leaves. Journal of Plant Physiology. 2004;161:1347-1357

[158] Ji Y, Liu J, Xing D. Low concentrations of salicylic acid delay methyl jasmonate-induced leaf senescence by up-regulating nitric oxide synthase activity. Journal of Experimental Botony. 2016;67:erw280

[159] Hung KT, Kao CH. Nitric oxide counteracts the senescence of rice leaves induced by abscisic acid. Journal of Plant Physiology. 2003;160:871-879

[160] Mishina TE, Lamb C, Zeier J. Expression of a nitric oxide degrading enzyme induces a senescence programme in Arabidopsis. Plant, Cell & Environment. 2007;30:39-52

[161] Manjunatha G, Gupta KJ, Lokesh V, Mur LA, Neelwarne B. Nitric oxide counters ethylene effects on ripening fruits. Plant Signaling & Behavior. 2012;7:476-483
