CHAPTER

# 25

# Insights Into the Nitric Oxide Mediated Stress Tolerance in Plants

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OUTLINE

## 25.1 INTRODUCTION

Nitric oxide (NO) was first discovered by Joseph Priestley in 1772 as a colorless and odorless gas named “nitrous air”; just a couple of years later came his discovery of oxygen ($O_2$). NO was considered as a toxic gas for next two centuries, until it was shown to emit by air purging of herbicide-treated *Glycine max* leaves (Klepper, 1979). Thenceforward, NO has long been of major interest in both plant and animal research (Santisree et al., 2015), and in 1992, *Science* magazine crowned NO as “Molecule of the Year”. A joint

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discovery that NO is produced by the mammalian species as a signaling molecule by Robert F. Furchgott, Louis J. Ignarro, and Ferid Murad secured the Nobel Prize in Physiology or Medicine for 1998. During the last two decades, several other discoveries have revealed the biological significance of NO in both animals and plants. Despite rapid research in animals, NO research in plants has been gradual with increasing excitement.

### 25.1.1 Nitric Oxide Function in Plants

Although initial discoveries in plants recognized NO as an atmospheric toxic pollutant for plant foliage, it was eventually considered as a modulator of plant defense during pathogen attacks. The increasing number of reports demonstrated the role of NO in a plethora of plant development processes including seed germination (Arc et al., 2013), root formation, different stages of the seed development, gravitropism, stomatal movements, photosynthesis, mitochondrial functionality, senescence, plant maturation (Sun et al., 2017; Patel et al., 2017; Hasanuzzaman et al., 2018; Locato et al., 2016; Mostofa et al., 2015; Asgher et al., 2017), multiple abiotic (Fancy et al., 2017; Santisree et al., 2015; Parankusam et al., 2017; Adimulam et al., 2017; Tossi et al., 2012; Sehrawat et al., 2013; Ziogas et al., 2013) and biotic stress responses in plants (Vaishnav et al., 2018). In addition, a number of studies focused on describing the crucial role of NO in moderating various plant hormone-mediated development and stress responses (Asgher et al., 2017). Further, accumulation of NO has been shown to induce gene expression of defense proteins during stress conditions and recovery (Romero-Puertas et al., 2013; Fancy et al., 2017). Mounting evidence suggests the role of NO in maintaining cellular homeostasis by acting as an antioxidant and negating the intensity of oxidative damage caused by various stress treatments (Hasanuzzaman et al., 2012; Groß et al., 2013). Despite the emergent knowledge about NO-mediated plant stress responses such as decreasing reactive oxygen species (ROS) levels, protecting membranes from damage, osmolyte accumulation, and regulation of various hormone-mediated signaling events, its functional status has been far from clear. However, the short life and complex chemistry of this diffusible free radical makes NO research in living systems extremely challenging.

### 25.1.2 NO Synthesis in Plants

#### *25.1.2.1 Nitric Oxide Synthase (NOS)*

In animal tissues, NO generation occurs through at least three different nitric oxide synthase (NOS) genes namely neuronal NOS (nNOS), an endothelial enzyme (eNOS), and an inducible enzyme (iNOS). Though NO is known to exist functionally in plants, the origin and signaling of NO is inconclusive to date. The isolation of NOS enzymes in animals is really rapid compared with the decades of research in plants. It is speculated that NO is derived from four major sources in plants: NO synthase pathway, which is similar to that of animals (Negi et al., 2010), nitrate reductase (NR) pathway, and other enzymatic and nonenzymatic pathways (Sahay and Gupta, 2017). The generation of NO has also been suggested through reductive pathways including the mitochondrial electron transport system and from xanthine dehydrogenase/oxidase (Sahay and Gupta, 2017). Despite several possible NO generating pathways proposed in plants (Sahay and Gupta, 2017), identification of a definitive enzymatic pathway generating NO in plants is still awaiting. The first molecular evidence for gene encoding NOS like activity potentially involved in NO synthesis in plants came from *Arabidopsis thaliana* T-DNA insertion mutant (*atnos1*) based on the homology to a snail protein (Guo et al., 2014). However, later studies failed to detect any NOS activity in purified recombinant *AtNOS1* protein or in similar recombinant proteins encoded by orthologous genes from *Zea mays* and *Oryza sativa*. Moreover, this mutant also failed to induce NO synthesis in guard cells in response to abscisic acid (ABA) and other stimuli. These studies concluded AtNOS1 as a regulator of NO levels rather than the molecule of synthesis. Eventually it was renamed as *Arabidopsis thaliana nitric oxide associated* (*atnos1*) mutant (Parankusam et al., 2017). Even though a few other recent pharmacological studies in various plant species also suggested the existence of NOS-like enzyme in plants, the attempts of purifying the gene or protein are still underway (Negi et al., 2010; Fröhlich and Durner, 2011). Nonetheless, two genes with NOS like activity and approximately 40% homology to animal *NOS* genes have been reported in green algae *Ostreococcus tauri* and *Ostreococcus lucimarinus* (Foresi et al., 2015). Though we now have the first *NOS* genes identified in a green alga, identification of *NO synthase* gene in higher plants is still awaited. The divergence of this gene to a new nonanimal homologous during the course of evolution might have posed a challenge to isolate *NO synthase* genes from higher plants.

#### *25.1.2.2 Nitrate Reductase (NR)*

Apart from NOS, the other well-known NO-generating enzyme in plants is nitrate reductase (NR). It converts nitrite to NO in a NAD(P)H dependent manner. In *Arabidopsis*, NR is encoded by two genes, *NIA1* and *NIA2*. The double mutant of *NIA* genes accumulate much less NO in guard cells in response to ABA. Eventually the NO generation by NR has been confirmed in many other species, like *Helianthus annus*, *Spinacea oleracea*, *Zea mays*, *Cucumis sativus*, *Chlamydomonas reinhardtii*, *Triticum aestivum*, *Malaxis monophyllos*, and *Aloe vera* (Sakihama et al., 2002, Xu and Zhao, 2003). Additionally, NO can be generated nonenzymatically under low pH by the interaction of two nitrous acid ($HNO_2$) molecules derived from protonated nitrite, by reduction of $NO_2$ to NO by carotenoids under light or by oxidation of hydroxylamine, salicylhydroxamate in plant cell cultures, and also during electron transport processes in mitochondria and chloroplasts (Jasid et al., 2006). NO besides being endogenous in origin is also taken up by plants from the external environment. Endogenous NO is synthesized in parallel to ROS accumulation in various organelles like mitochondria, chloroplast, peroxisomes, and apoplast. Recently Gibbs et al. (2014) identified a unifying mechanism for NO sensing in plants based on targeted proteolysis of plant-specific group VII ERF transcription factors. They proposed N-end rule pathway proteolysis as an essential NO sensing mechanism throughout the plant life cycle. Though the research on NO is gaining popularity in recent years, the following controversial questions about NO are around the corner: (1) the major source of NO generation and biosynthesis mechanism, (2) the sensing mechanism of NO by different plant tissues, and (3) the degradation mechanism.

### 25.1.3 NO Signaling in Plants

As the sources of NO generation have begun to establish, the mechanisms of NO signaling are also increasingly being resolved in parallel. Being lipophilic and highly diffusible in nature, NO is involved in several signaling processes in plants (Baudouin, 2011). Invariably, it has been shown that NO modifies the activity of enzymes and some key signaling components, possibly through posttranslational protein modifications (PTMs). The major PTMs that are integral to NO signaling include protein *S*-nitrosylation and tyrosine nitration (Fancy et al., 2017). A number of S-nitrosylated proteins were identified in *Arabidopsis thaliana*, *Brassica juncea*, *Citrus aurantium*, and *Zea mays* after stress treatment (Mengel et al., 2013; Fan et al., 2014; Fancy et al., 2017). NO-mediated PTMs including nitrosylation, nitration, and carbonylation have been shown to influence ascorbate peroxidase activity under drought (Santisree et al., 2015). NO mediated S-nitrosylation prevented the inactivation of the antioxidant enzymes in *Antiaris toxicaria* thereby providing a way to mitigate the $H_2O_2$ concentration in plant cells and increasing desiccation tolerance of seeds (Fan et al., 2014; Santisree et al., 2015). Many target signaling components such as redox-associated proteins, the $K^+$ channel at the guard cell plasma membrane, AtRhobD, salicylic acid-binding protein 3, NPR1, TGA1, and auxin signaling TIR1 (Romero-Puertas et al., 2013; Lindermayr et al., 2010; Terrile et al., 2012) are known to be engaged in NO-mediated PTMs. Additionally, NO acts as a signaling molecule at the transcription level by enhancing the expression of stress related kinases and by its interaction with other signaling molecules and phytohormones (Lozano-Juste and León, 2011). NO stimulates myosin activated protein kinase (MAPK), which in turn causes the activation of stress related genes (Li and Xue, 2010). Another well-established method by which NO exerts its effect is by influencing the redox status of the cell. Modulation of guanylate cyclase represents an NO-specific mechanism of signaling and there are many reports showing that cyclic guanosine monophosphate (cGMP) is a facet of NO effects in plants (Mulaudzi et al., 2011). Recently, a novel guanylate cyclase that generates cGMP and binds NO has been described in *Arabidopsis thaliana* (Mulaudzi et al., 2011). Certain other molecules like $Ca^{2+}$ and cyclic ADP-ribose (cADPR) are found to be involved in the downstream signaling of NO in plant stress responses (Mioto and Mercier, 2013). Moreover, the emerging high throughput omics platforms have been very useful in identifying various candidate genes associated with NO and NO-mediated PTMs (nitrosylation, nitration, and carbonylation) influencing plant stress conditions (Astier and Lindermayr, 2012; Shi et al., 2013; Begara-Morales et al., 2014). It is now imperative to integrate all these molecules and events into our existing knowledge of NO networks.

### 25.1.4 Modulation of Endogenous Nitric Oxide Levels in Plants

Given that NO is an important signal in plant stress responses, there is increasing interest in understanding the impact of altered NO levels in plants. Notwithstanding, the in vivo level of NO appears to be regulated by mutations in diverse genes. Previous studies have reported few mutants of *Arabidopsis thaliana* including *nia1nia2*, *noa1*, and *nox1*, which failed to exhibit certain developmental and stress responses due to defective NO accumulation, while *noe1* mutation in *Oryza sativa* resulted in higher NO accumulation (Desikan et al., 2002). The mutation in *CUE1* gene encoding a chloroplast phosphoenolpyruvate/phosphate translocator led to an increase in NO content and delayed flowering in the mutant (He et al., 2004). Meanwhile, the null alleles of *Arabidopsis thaliana* *HOT5* locus encoding S-nitrosoglutathione reductase (GSNOR), showed decreased tolerance to temperature stress due to an increase in levels of nitrate, NO, and nitroso species (Santisree et al., 2017). Similarly, enhanced lateral root formation in arginase-negative mutant is associated with an increased NO levels (Santisree et al., 2015). Similarly mutation in *Arabidopsis* prohibitin (*PHB3*) gene leads to reduction in absicic acid (ABA)−mediated NO accumulation and auxin-induced lateral root formation (Wang et al., 2010a,b).

Although there is no NOS sequence identified in higher plants, few transgenic efforts have constitutively expressed rat and mammalian neural nitric oxide synthase (nNOS) genes in plants (Shi et al., 2014; Santisree et al., 2015). *35S::nNOS* transgenic lines of *Arabidopsis thaliana* displayed improved abiotic and biotic tolerance (Shi et al., 2011). Similarly, overexpression of rat *nNOS* increased NOS activity and endogenous NO level in transgenic *Oryza sativa* lines, that led to higher tolerance under both drought and salt stresses (Cai et al., 2015). Further, transgenic plants expressing *OtNOS* also displayed increased stomatal development and enhanced abiotic stress tolerance due to higher accumulation of NO (Santisree et al., 2015). The fragmentary molecular identities related to NO synthesis and signaling in plants makes the transgenic and genetic studies challenging.

Due to the inadequate molecular information, most of the current NO research in plants bank on exogenous application of NO-donors and inhibitors/scavengers (Table 25.1). So far this pharmacological approach has been used either to mimic an endogenous NO-related response or as a substitute for an endogenous NO deficiency. Exogenous NO donors or inhibitors have been combined with high throughput technologies to study the ability of NO in modulating plant stress responses at the genomic, proteomic, and postproteomic levels. A pioneering proteomic study in *Gossypium hirsutum* leaves treated with sodium nitroprusside (SNP) identified 166 differentially expressed proteins belonging to diverse pathways, followed by the identification of 167 phosphoproteins to be differentially phosphorylated in response to SNP (Meng et al., 2011). Similarly, proteome profiling revealed 172 downregulated and 76 upregulated proteins in *Cicer aritinum* leaves (Santisree et al., 2017). Few other studies attempted to understand the proteomic basis of NO mediated stress tolerance (Bai et al., 2011; Sehrawat et al., 2013; Yang et al., 2013; Fan et al., 2014). Nevertheless, high-throughput genomic and proteomic signatures of NO still need to be unfolded to further explore the complexity involved in its signaling under plant stress.

## 25.2 NO IN PLANT STRESS RESPONSES

High temperature and drought are perhaps the two major environmental factors limiting crop growth and yield worldwide (Prasad et al., 2011; Vile et al., 2012). Plants respond at the molecular, cellular, and physiological level by perception and transmission of stress signals followed by a series of responses (Fancy et al., 2017). Longer and severe stress episodes result in production of redox active molecules including reactive oxygen and reactive nitrogen species (RNS), respectively (Astier et al., 2016), which leads to abnormalities at the cellular level due to oxidation of proteins, lipids, and nucleic acids (Hayat et al., 2012). On the other hand, it was demonstrated that abiotic stress often induced NO generation that led to the activation of cellular processes for protection against oxidative stress. NO protects the plants from oxidative damage by enhancing the $H_2O_2$-scavenging enzymes activities thereby maintaining cellular redox homeostasis (Shi et al., 2014; Zheng et al., 2009). Moreover, exogenous NO donors have often been deployed successfully as priming agents to ward off abiotic stress induced losses in plants (Uchida et al., 2002; Hasanuzzaman et al., 2012; Santisree et al., 2015; Savvides et al., 2016). Although accumulation of NO during various stress conditions appears to be a general response in diverse plant species and tissues, its specificity has been established by using various inhibitors/scavengers such as 2-(4-Carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (c-PTIO) or L-$N^G$-Nitroarginine methyl ester; N(G)-Nitro-L-arginine methyl ester (L-NAME), which reversed these NO-mediated effects in many such studies (Santisree et al., 2015). NO plays a critical role in mitigating oxidative stress caused by unfavorable climate (Siddiqui et al., 2017; Table 25.2). Most of the studies reinforce the role of NO in detoxifying ROS either directly interacting with $O^{-2}$ or indirectly by enhancing function of the antioxidant system (Tewari et al., 2008). Interaction of NO with $O^{-2}$ forms peroxynitrite, which serves as a nitrating agent in regulating protein activity under stress conditions (Baudouin, 2011). Further, NO upregulated the activity and transcription of ascorbate peroxidase (APX) and glutathione reductase (GR), the two key enzymes in the ascorbic acid−glutathione (AsA-GSH) cycle in *Nicotiana tabacum* and *Cucumis sativus* leaves (Cui et al., 2011) and conferred resistance to abiotic stress. NO also rapidly reacts with oxygen species, hemes, thiols, and proteins to produce biochemical signals that directly and indirectly regulate enzymatic activity. However, the information available is sometimes contradictory, depending on the plant species, severity, and duration of the stress treatments (Begara-Morales et al., 2014). Despite an increasing number of reports on the role of NO as an endogenous signaling molecule in plants, there is still a large knowledge gap about underlying molecular mechanisms of its action that can sense and transduce NO signals.

**TABLE 25.1** Various Forms of Nitric Oxide Modulators Used in Plants to Demonstrate the Role of NO Under Plant Abiotic Stress

| | **Plant species** | **Stress imposed** | **References** |
|---|---|---|---|
| **NO donors** | *Medicago sativa;* | High temperature stress | Yu et al. (2014) |
| Sodium nitroprusside (SNP) | *Triticum aestivum; Zea mays; Vicia faba; Salpichora organifolia; Tagetes erecta; Lycopersicon esculentum* | Drought stress | Tian and Lei (2007); Hao et al. (2008); Gracia-Mata and Lamattina (2001); Gupta et al. (2013) |
| | *Triticum aestivum* | Chilling stress | Esim et al. (2014) |
| | *Chrysanthemum morifolium; zea mays; Phaseolus vulgaris; phragmitis communis; Oryza sativa; Phaseolus radiates; Phragmitis communis; Gingiber officinale; Festuca anundinacea; Solanum lycopersicon* | High temperature stress | Yang et al. (2011a,b); Li et al. (2013b); Song et al. (2008); Li et al. (2013); Chen et al. (2013); Siddiqui et al. (2017) |
| | *Citrus grandis; Hibiscus moscheutos; Artemisia annua; Lolium perene; Triticum aestivum; Vigna unguiculata* | Al[a] stress | Yang et al. (2016); Aftab et al. (2012); Bai et al. (2011); Sun et al. (2014); Sadeghipour (2016) |
| | *Brassica junica; Arachis hypogeae; Trifolium repens; Typha angustifolia* | Cd[a] stress | Dong et al. (2014); Zhao et al. (2016) |
| | *Triticum aestivum; Pistia stratiotes* | As[a] stress | Hasanuzzaman et al. (2013) |
| | *Phaseolus vulgaris; Helianthus annuus; Zea mays; Glycene max* | UV-B stress | Shi et al. (2005); Tossi et al. (2012) |
| S-nitroso-N_acetyl-D-penicillamine (SNAP) | *Cicer aritinum* | Salinity stress | Ahmad et al. (2016) |
| Diethylamine NONOate sodium | *Glycene max* | Salinity stress | Egbichi et al. (2014) |
| | *Medicago sativa* | | |
| **Inhibitors** | *Salpichora organifolia; Tradescantia* sp; *Medicago sativa;* | Drought stress | Garcia-Mata and Lamattina (2001); Tian and Lei (2007); Hao et al. (2008) |
| Carboxy-2-phenyl-4,4,5,5, -tetramethylimidazoline-1-oxyl 3-oxide (cPTIO) | *Lactuca sativa; Zea mays* | High temperature stress | Deng and Song (2012); Li et al. (2013b) |
| | *Nicotiana tabacam; Arabidopsis thaliana; Betula pendula* | Ozone stress | Ederli et al. (2008); Ahlfors et al. (2009a) |
| **Mutants** | *Atnoa1, nia1nia2, gsnor1-3, respiratory burst oxidase homolog* mutants of *Arabidopsis thaliana* | Drought stress | Lozano-Juste and León (2011); She et al. (2004) |
| | *nia1nia2* mutants of *Arabidopsis thaliana* | Chilling stress | Zhao et al. (2009); Liu et al. (2016) |
| | *atgsnor1-3/hot5-2* mutants of *Arabidopsis thaliana* | Heat stress | Santisree et al. (2017) |
| | Homozygous mutants deficient of *atips1* of *Arabidopsis thaliana* | UV-B stress | Lytvyn et al. (2016) |
| **Transgenics** | *Arabidopsis thaliana* and *Oryza sativa* transgenic plants overexpressing *oxide synthase* gene (*nNOS*), *OtNOS* transgenic lines; *35S::nNOS* transgenic lines of *Arabidopsis thaliana* | Drought stress<br>Salt stress | Cai et al. (2015); Shi et al. (2014) |
| | *Arabidopsis thalianat*GLB3 | Heat stress | Hossain et al. (2011) |
| | H7 plants overexpressing *Arabidopsis* hemoglobin 1 (*AHb1*), transgenic cucumber plants overexpressing *CsNOA1* | Chilling stress | Zhao et al. (2009); Cantrel et al. (2011); Bai et al. (2011); Xu et al. (2012a,b); Liu et al. (2016) |

[a] *Al, aluminum; Cd, cadmium; As, arsenic.*

### 25.2.1 NO in Drought Stress Tolerance

Prevailing water deficit conditions limit crop yields worldwide (Simontacchi et al., 2015). NO, which is known to involve in various physiological processes of the plants, also plays a vital role in mitigating drought stress conditions in plants (Santisree et al., 2015). Many studies have reported an increased production of NO in drought-stressed plants depending on the duration and severity of the given drought stress (Santisree et al., 2015). Roots of *Cucumis sativus* when subjected to a mild water deficit for less than 10 h had slightly enhanced NO synthesis, while it increased to a greater extent with prolonged drought imposition for 17 h (Arasimowicz-Jelonek et al., 2011). Moreover, accumulation of NO as a result of application of exogenous donors in many reported studies also correlated well with the amelioration of drought stress, while the use of NO scavengers/inhibitors reversed this effect (Arasimowicz-Jelonek et al., 2011; Planchet et al., 2014).

The increase in NO production under drought stress has been correlated significantly to the decrease in stomatal conductance in *Vitis vinifera* (Patakas et al., 2010). Given the ability of NO to induce dark-induced stomatal closure in *Vicia faba* epidermal strips (She et al., 2004), a good number of studies confirmed the generation of NO in guard cells in response to drought and ABA by using a NO-sensitive fluorescent dye 4,5-Diaminofluorescein diacetate (DAF-2DA) (Planchet et al., 2014; Zimmer-Prados et al., 2014). Exogenous NO induces ABA synthesis by upregulating the expression of a key genes including *9-cis-epoxycarotenoid dioxygenase* and also negatively regulates the ABA sensitivity thereby enhancing plant tolerance to drought stress (Santisree et al., 2015). While, ABA failed to induce stomatal closure in *Atnoa1*and *nia1nia2* mutants of *Arabidopsis thaliana* having reduced endogenous NO levels, NO-deficient triple mutant *nia1nia2noa1-2* plants were hypersensitive to dehydration and ABA treatment in stomatal closure providing genetic evidence for the involvement of NO in ABA-mediated stomatal closure (Planchet et al., 2014; Lozano-Juste and León, 2011). Furthermore, the overaccumulation of NO in guard cells of *Arabidopsis thaliana* GSNO reductase mutant (*gsnor1-3*) has led to the defective ABA-induced stomatal closure due to the constitutive S-nitrosylation of open stomata 1 (OST1) reinforcing NO as a key intermediate in ABA-induced stomatal closure (Adimulam et al., 2017). Moreover, reduced NO accumulation and stomatal closure were observed in *respiratory burst oxidase homolog* mutant of *Arabidopsis thaliana* having a mutation in nicotinamide adenine dinucleotide phosphate (NADPH) oxidase suggesting a link between $H_2O_2$ and NO accumulation (She et al., 2004). Broadly, NO enhances antioxidant enzyme activity and induce stomatal closure through ambiguous signaling pathways that require MAPKs, cGMP, and $Ca^{2+}$. In addition to MAPK, NO also activates other protein kinases such as osmotic stress-activated kinase, NtOSAK in *Nicociana tabacum* (Baudouin and Hancock, 2014). NO alters protein phosphorylation through the regulation of these kinases and also alters calcium flux to regain normal NO responses to occur in the guard cells under drought. NO increases the cGMP level, which acts as the secondary messenger in promoting the expression of stress related genes and secondary metabolites during water deficit conditions (Santisree et al., 2015).

It was reported that exogenous NO decreased drought-induced reduction in photochemical quenching in *Tagetes erecta* (Liao et al., 2012), while enhancing $CO_2$ assimilation and photosynthetic rate in *Rumex* leaves under osmotic stress (Li et al., 2013). In *Lycopersicon esculentum*, SNP treatment promoted the activity of *carbonic anhydrase* that catalyzes the interconversion of $CO_2$ and $HCO_3$, and thus indirectly maintain constant supply of $CO_2$ to *ribulose-1,5-bisphosphate carboxylase/oxygenase* (RuBisCo) in a concentration dependent manner. Additionally, NO ameliorates the stress effects on chloroplasts and combats drought-induced leaf senescence by antagonizing the effects of ethylene (Manjunatha et al., 2012). NO application has been shown to negate the drought-induced decrease in transcription of *psbA* gene encoding for D1 protein of PSII complex, thus protecting PSII functionality during grain filling (Wang et al., 2011; Procházková et al., 2013). Similarly, photochemical efficiency of photosystem II (PSII) increased by exogenous NO treatment in drought stressed *Populus przewalskii*, but decreased under prolonged drought stress conditions (Simontacchi et al., 2013). Conversely, thylakoids isolated from NO-treated *Spinacia oleracea* exhibited less photosynthetic activity indicating that NO can bind reversibly to PSII and inhibit electron transport (Misra et al., 2014).

Exogenous NO treatment under drought stress often results in reduced $H_2O_2$ content and lipid peroxidation in plants while high NO causes nitrosative stress (Farooq et al., 2009; Liao et al., 2012; Li et al., 2013). For instance, SNP treatment maintained higher relative water content and reduced ion leakage during drought stress in two turf grass species (Hatamzadeh et al., 2015). Similarly, NO-treated plants maintained high levels of antioxidant enzyme activities and less lipid peroxidation under drought stress in *Dendrobium huoshanense* and *Oryza sativa* (Farooq et al., 2009; Fan et al., 2014). Despite reducing the level of oxidative stress, NO also help in maintaining high concentrations of osmotically active solutes and amino acids. NO promoted drought-induced free proline accumulation in many plants (Farooq et al., 2009; Wang et al., 2011). NO also mediates the accumulation of glycine betaine by stimulating the activity of *betaine aldehyde dehydrogenase* in the leaves of drought stressed *Zea Mays* (Hao et al., 2008). Conversely, neither depleting endogenous NO by its scavenger nor inducing by NO donor had significant effect on the accumulation of proline in *Medicago* seedlings. Meanwhile, drought stress decreased the DNA methylation levels in *Dendrobium huoshanense*, while NO increased the methylated sites clearly suggesting the ability of NO to alter gene expression under drought (Fan et al., 2014). Transgenic plants overexpressing the rat *neural nitric oxide synthase* gene (*nNOS*) in *Arabidopsis thaliana* and *Oryza sativa* exhibit enhanced drought tolerance than their untransformed controls (Cai et al., 2015; Shi et al., 2014). Moreover, *OtNOS* transgenic lines also exhibited better stomatal development compared with control plants. Although our knowledge on the role of NO in drought stress is still emerging, we find enormous potential of NO in mitigating drought induced adversaries in plants.

## 25.2.2 NO in Plant Salt Stress Tolerance

Soil salinity is one of the major abiotic stress factors for crop production impacting more than 45 million hectares of cultivated land (Slinger and Tenison, 2009; Fatma et al., 2016). With continuous increase in the demand for food, farmlands are being artificially irrigated in greater amounts, leading to increased salt accumulation in the soil. Excess accumulation of NaCl in soil limits the plant water and mineral uptake (Khan et al., 2012). In addition, the excess salt intake into the cytosol leads to osmotic imbalance and imposes toxic effects on cell membranes (Abeer et al., 2014). Higher salt concentrations cause oxidative stress due to excess production of ROS and thus hinder several metabolic processes (Fatma et al., 2016; Naser Alavi et al., 2014). In the past decade, function of NO in salt stress tolerance has gained a lot of attention among plant researchers (Yang et al., 2011a,b; Mostofa et al., 2015). It was reported that endogenous NO generation has increased in *Nicotiana tabacum* plants in response to salinity stress. External application of NO donor, *S*-nitroso-*N*-acetylpenicillamine (SNAP), to salinized plants enhanced the growth parameters, leaf relative water content, photosynthetic pigment production, levels of osmolytes, as well as the antioxidant enzyme activities and gene expression in *Cicer aritinum* (Ahmad et al., 2016). Moreover, exogenous NO enhanced salt tolerance by mitigating the oxidative damage, stimulating proton-pump and $Na^+/H^+$ antiport activity in the tonoplast thus promoting $K^+/Na^+$ ratio (Santisree et al., 2015). NO influences salinity tolerance by regulating plasma membrane $H^+$-ATPase and $Na^+/K^+$ ratio thereby generating a $H^+$ gradient that offers the force for $Na^+/H^+$ exchange (Zhang et al., 2006). For instance, NO has been implicated in enhancing $K^+$, $Ca^{2+}$, and $Mg^{2+}$ content in salt-treated *Gossypium hirsutum* plants (Dong et al., 2014). Moreover, NO reacts with lipid radicals thus preventing salt stress induced lipid oxidation and decreasing membrane permeability (Kopyra, 2004; Fatma and Khan, 2014; Xu et al., 2010b). NO enhances the antioxidant defense systems in plants subjected to salinity by inducing the expression of redox-related genes (Zheng et al., 2009). The application of Diethylenetriamine-NONOate (DETA/NO) ameliorated long term salinity effects in *Glycene max* via the induction of antioxidant enzymes (Egbichi et al., 2014). Studies have provided evidence that NO mediated detoxification is partly by its ability to regulate ascorbate–glutathione cycle through S-nitrosylation (Camejo et al., 2013; Ziogas et al., 2013). It is evident from the studies that salt stress induces an increase in total S-nitrosylation especially S-nitrosylation of the glycine dehydrogenase P subunit, F1 ATPase β subunit, and isocitrate dehydrogenase (ICDH) implying the role of NO-mediated posttranslational modifications in controlling respiratory/photorespiratory pathways (Fares et al., 2011; Camejo et al., 2013; Abat and Deswal, 2009; Begara-Morales et al., 2015). Conversely, salt stress induced $O_2$ might also reduce the S-nitrosylation level by interacting with S-nitrosoglutathione (GSNO/RSNO) (Fancy et al., 2017). However, the enhanced antioxidant enzyme activity due to foliar spray of NO in various crop plants has also resulted in increased plant growth under salt stress (Wu et al., 2011; Fatma and Khan, 2014). Similarly, exogenous application of NO was also proved beneficial in enhancing plant dry weight, shoot, and root length of salt-stressed wheat plants (Kausar and Shahbaz, 2013). Not only that, NO participates in enhancement of photosynthesis by inducing the photosynthetic pigments, adenosine triphosphate (ATP) synthesis, and two respiratory electron transport pathways in mitochondria under salt stress (Ruan et al., 2002). This was further ascertained by an improved photosynthesis by quenching excess energy and increasing in quantum yield of PSII by using exogenous NO in *Solanum melongena* seedlings (Wu et al., 2013). The exogenous application of NO has been reported to control the activity of phosphoenolpyruvate carboxylase kinase in *Sorghum bicolor* under salt stress (Monreal et al., 2013). NO application enhanced the photosynthetic potential of *Brassica juncea* under salt stress (Fatma and Khan, 2014). The sustained photosynthesis after application of NO under salt stress in *Lycopersicon esculentum* has been attributed to improved gas exchange parameters and chlorophyll fluorescence (Wu et al., 2011). A recent study in

**TABLE 25.2** Various Studies Describing the Involvement of Nitric Oxide (NO) in Plant Abiotic Stress Tolerance

| Stress imposed | Plant species | Response | References |
|---|---|---|---|
| Salinity stress | *Brassica nigra; Brassica juncea; Arabidopsis thaliana; Triticum aestivum; Lycopersicon esculentum; Sorghum bicoclor; Hordium vulgare; Cicer aritinum; Glycene max; Zea mays; Linum ustiatissimum; morua alba; Gossypium hirsutum* | Lipid peroxidation,<br>ROS[a] scavenging<br>Activation of antioxidant enzymes<br>Altered gene transcription,<br>enhanced photosynthesis | Khan et al. (2012); Fatma et al. (2016); Fatma and Khan (2014); Monreal et al. (2013); Ahmad et al. (2016); Egbichi et al. (2014); Dong et al. (2014) |
| Drought stress | *Triticum aestivum; Zea mays; Hordeum vulgare; Oryza sativa; Vicia faba; Cucumis sativus; Salpicora organifolia; Tagetes erecta; Malus hupensis; Spinacea oleracia; Populus przewalskii; Lycopersecon esculentum* | Stomatal closure, enhanced antioxidant defense, increased adventitious root length, reduced lipid peroxidation, mediating ABA[a] signaling | Santisree et al. (2015); Garcıa-Mata and Lamattina (2002); Tian and Lei (2007); Hao et al. (2008); Cheong et al. (2002); Simontacchi et al. (2013); Gupta et al. (2013) |
| Chilling stress | *Helianthus annus; Capsicum annum; Arabidopsis thaliana; Chirospora bugeana; Baccaurea ramiflora; Brassica juncea; Camallia sinensis; Lycopersicon esculentum; Triticum aestivum* | Synthesis of osmolytes, reprogramming of lipid signaling, negatively regulates sphingolipid phosphorylation, increases spermidine and spermine levels, increases antioxidant enzyme activity | Cantrel et al. (2011); Ashraf and Foolad (2007); Zhao et al. (2009); Chaki et al. (2011); Airaki et al. (2012); Zhao et al. (2009); Liu et al. (2016); Zhao et al. (2009); Bai et al. (2011); Xu et al. (2012a,b); Abat and Deswal (2009); Wang et al. (2012); Diao et al. (2016); Esim et al. (2014); Baudouin and Jeandroz (2015) |
| High temperature stress | *Medicago sativa; Pisum sativum; Chrysanthemeum morifolium; Nicotiana gluca; Helianthus annus; Triticum aestivum; zea mays; Phaseolus vulgaris; phragmitis communis; Oryza sativa; Phaseolus radiates; Gingiber officinale; Festuca anundinacea; Solanum lycopersicon; Cicer aritinum* | ROS scavenging enzymes, alleviated the expression of HSPs,[a]<br>NO acts as signal molecule for the stress response, protects the plant from heat stress induced oxidative stress, plays an important role in $H_2O_2$[a] metabolism | Yu et al. (2014); Chaki et al. (2011); Hasanuzzaman et al. (2012); Li et al. (2013a); Song et al. (2008); Li et al. (2013); Chen et al. (2013); Siddiqui et al. (2017); Ziogas et al. (2013) |
| Heavy metal stress | *Oryza sativa*; *Arabidopsis thaliana; Nicotiana tabacum; Solanum lycopersicon; Panax ginseng; Brassica junica; Pisum sativum; Triticum aestivum; Citrus grandis; Hibiscus moscheutos; Artemisia annua; Phaseolus vulgaris; Secale cereal; Lolium perene; Vigna unguiculata; Antiaris toxicaria; Glycene max; Lupinus luteus; Arachis hypogeae; Pistia stratiotes* | NO helps challenge heavy metal stress by chelating the heavy metal at the root zone and preventing their accumulation in plant, regulating gene transcription level of APX,[a] GR,[a] and DHA,[a] increases the plasma membrane transport activity, and GSNOR[a] activity | Wang et al. (2011); Tewari et al. (2008); Mostofa et al. (2015); Xu et al. (2010a,b); Sun et al. (2014); He et al. (2012a,b); Aftab et al. (2012); Wang et al. (2010a,b); Bai et al. (2011, 2015); Sadeghipour (2016); Yang et al. (2016); Xiong et al. (2009); Arasimowicz-Jeloneck et al. (2012); Dong et al. (2014); Hasanuzzaman et al. (2013) |
| Ozone stress | *Arabidopsis thaliana; Nicotiana tabacam; Ginkgo biloba* | Exogenous application or endogenous synthesis of NO reduces the damaging effects of ozone by activating active oxygen scavenging enzymes | Ahlfors et al. (2009); Ederli et al. (2008); Xua et al. (2012) |
| UV-B | *Zea mays; Betula pendula; Pisum sativum; Solanum tuberosum; Helianthus annuus; Glycene max* | NO functions as a secondary messenger under UV-B stress, reduces UV induced photomorphogenic responses | Zhang et al. (2011); Tossi et al. (2012) |
| Wounding stress | *Arabidopsis thaliana; Pisum sativum; Nicotiana tabacum; Helianthus annus; Vicia faba; Triticum aestivum* | $Ca^{2+}$ influx and ROS[a] production in NO[a] dependent pathway, acts as downstream signal molecule in wounding signal transduction | Huang et al. (2004); Chaki et al. (2011); Si et al. (2017) |
| Flooding stress | *Arabidopsis thaliana; Hordeum vulgare; Brassica japonicum* | Induces ethylene biosynthesis, maintains ATP[a] levels to prevent cell death | Wang et al. (2000) |

[a] *ABA, abscisic acid; APX, ascorbate peroxidase; ATP, adenosine triphosphate; DHAR, dehydroascorbate reductase; GR, glutathione reductase; GSNOR, S-Nitrasoglutathione reductase;* $H_2O_2$*, hydrogen peroxide; HSPs, heat shock proteins; NO, nitric oxide; ROS, reactive oxygen species.*

mustard has suggested that NO improves photosynthetic performance under salt stress more effectively by enhancing sulfur assimilation (Fatma et al., 2016). Besides, exogenous NO induced the accumulation of protecting molecules including proline, GB, total soluble proteins and total soluble sugars in *Cicer arietinum*, *Linum ustiatissimum*, and *Morua alba*, thus confirming its role in mitigating the adverse effects of salinity stress (Khan et al., 2012).

### 25.2.3 NO and Chilling Stress Tolerance in Plants

Exposure of plants to chilling stress severely limits the crop yields due to its deleterious effects including poor seed germination, stunted growth, delayed flowering, and altered gene expression (Minami et al., 2005). Previous studies have documented that an increase in NO synthesis was associated with cold acclimation in a number of plant species including *Arabidopsis thaliana*, *Helianthus annus*, and *Capsicum annum* (Singh et al., 2009; Zhao et al., 2009; Chaki et al., 2011; Airaki et al., 2012). Although, the temperature range for NO generation has not been clearly defined, its formation has been observed at 8ºC in pea leaves, at 4ºC in *Arabidopsis thaliana*, and at 0ºC in *Chorispora bugeana* (Zhao et al., 2009; Liu et al., 2011; Cantrel et al., 2011). Moreover, both NO-sensitive fluorescent probe and chemiluminescence confirmed the accumulation of NO after 1−4 h of chilling treatment in *Arabidopsis thaliana* (Cantrel et al., 2011). This chilling induced NO production was impaired in the *nia1nia2* nitrate reductase mutant and H7 plants overexpressing *Arabidopsis* hemoglobin 1 (*AHb1*) further supporting its role in chilling tolerance. While NR has been implicated in NO synthesis in *Arabidopsis thaliana*, loquat fruit, and *Baccaurea ramiflora* embryos under chilling stress (Zhao et al., 2009; Cantrel et al., 2011; Bai et al., 2011; Xu et al., 2012a,b), NO synthase inhibitors blocked NO accumulation in *Chorispora bungeana* suggesting the involvement of both NR and NOS like enzymes for NO synthesis during chilling stress (Baudouin and Jeandroz, 2015). Eventually, a number of other studies also confirmed the role of NO in alleviating cold injury (Zhao et al., 2009; Liu et al., 2011; Yang et al., 2011a,b; Tan et al., 2013; Diao et al., 2016). Recently, transgenic cucumber plants overexpressing *CsNOA1* constitutively had greater accumulation of soluble sugars, starch, and a lower chilling damage index, while suppression of *CsNOA1* expression resulted in opposite effects. Furthermore, ectopic expression of cucumber *CsNOA1* in the *A. thaliana noa1* mutant enhanced chilling tolerance and rescued the mutant phenotype due to an increase in endogenous NO levels (Liu et al., 2016). Consistent with this, exogenous NO donor has been shown to induce cold acclimation through the synthesis of osmolytes such as glycine betaine and proline (Ashraf and Foolad, 2007; Zhao et al., 2009; Wang et al., 2012) and reprogramming of lipid signaling and composition. Moreover, NO negated the chilling induced transient synthesis of phytosphingosine phosphate and ceramide phosphate in *Arabidopsis thaliana* (Cantrel et al., 2011; Lynch and Steponkus, 1987; Kawaguchi et al., 2000). Not only that, SNP treatment alleviated chilling injury in *Cynodon dactylon* by decreasing malondialdehyde (MDA) content and electrolyte leakage due to the stimulation of superoxide dismutase (SOD) and peroxidase (POD) activities (Fan et al., 2015). Similarly, application of exogenous SNP to cold stressed *Triticum aestivum* seedlings increased the tolerance by enhancing the synthesis of antioxidant enzymes (Esim et al., 2014).

It was documented that cold stress resulted in highest S-nitrosothiol formation followed by drought, high temperature, and salinity in *Brassica juncia*. Besides, 20 proteins predominantly associated with plant defense, photosynthesis, glycolysis, and signaling were found to be potentially S-nitrosylated after cold stress treatment in *Brassica juncea* (Abat and Deswal, 2009; Zhao et al., 2009). Importantly, Rubisco carboxylase is one among those enzymes shown to be inactivated by cold stress induced S-nitrosylation (Abat and Deswal, 2009). Collectively, the emerging picture suggests that NO regulates cold stress signaling by cell wall remodeling and promoting ROS detoxification in plants.

### 25.2.4 NO and High Temperature Stress Tolerance in Plants

Heat stress is defined as temperature above the optimal temperature that causes an irreversible damage to the growth and metabolism of plants (Johkan et al., 2011; Yamori et al., 2014; Awasthi et al., 2016; Santisree et al., 2017). Heat stress promoted NOS and GSNOR activities thereby increasing the accumulation of NO and S-nitrosothiols in plants suggesting a role for NO in heat stress mitigation (Yu et al., 2014). While exogenous application of NO donors has been able to reduce heat-induced cellular damage, depleting endogenous NO levels by cPTIO reversed these effects, establishing the functional specificity of NO in plant heat stress amelioration (Hasanuzzaman et al., 2013). The importance of NO homeostasis in heat stress tolerance has been highlighted by a null mutation in *atgsnor1-3/hot5-2* locus or RNAi line of *Arabidopsis thaliana*, where overaccumulation of NO correlated with high heat sensitivity (Parankusam et al., 2017). Further, NO scavenger could able to rescue heat sensitivity of these mutant lines of *Arabidopsis thaliana* (Parankusam et al., 2017).

Another major challenge under heat stress is the maintenance of membrane integrity. Exogenous application of SNP reduced electrolyte leakage and MDA content that substantially enhanced the survival percentage of *Zea mays* seedlings (Li et al., 2013b). In another study, SNP treatment recovered RWC, chlorophyll content, electrolyte leakage in heat stressed *Gingiber officinale* leaves (Li et al., 2013a). Heat stress reduced chlorophyll (chl) biosynthesis and caused great damage to photosynthetic apparatus followed by reduced yield (Parankusam et al., 2017). NO has been shown to negate this heat induced chlorophyll loss and also maintain the activity of photosystem II thereby sustaining photosynthesis in plants (Pospíšil, 2016). For example, pretreatment of SNP resulted in enhanced photosynthetic electron transport in heat stressed *Festuca arundinacea* (Chen et al., 2013). Similarly, SNP application reduced the rate of nonphotochemical quenching in heat shocked *Triticum aestivum* leaf discs and diverted more energy to PSII (Hossain et al., 2011). However, excess NO has been shown to inhibit electron transport by reversibly binding to thylakoid membrane complexes of *Pisum sativum* (Ziogas et al., 2013). Furthermore, heat-induced structural and functional changes in the thylakoid membrane often result in ROS formation (Pospíšil, 2016). Several studies evident the ability of NO in maintaining the cellular redox homeostasis by neutralizing harmful ROS produced by heat stress (Ziogas et al., 2013). Pretreatment with SNP enhanced ascorbate and glutathione contents and activities of antioxidant enzymes including monodehydroascorbate reductase, dehydroascorbate reductase, and glyoxalase I and II in heat stressed *Triticum aestivum* seedlings (Hasanuzzaman et al., 2012). Additionally, foliar application of SNP enhanced carotenoid levels thereby protecting against photooxidative damage caused by heat stress in *Chrysanthemum morifolium* (Yang et al., 2011a,b). However, prolonged heat stress was found to induce nitrosative stress in *Pisum sativum* due to increased S-nitrosylation (SNO) content (Parankusam et al., 2017). SNP pretreatment also helped in osmotic adjustment under heat stress by upregulating the *P5CS* gene in *Oryza sativa* seedlings and reducing putricine (PUT)/polyamine (PAs) ratio in *Gingiber officinale* (Uchida et al., 2002). It was shown that nearly 13 tyrosine-nitrated proteins including enzymes like ferredoxin−NADP oxidoreductase and carbonic anhydrase got induced by heat stress in *Chrysanthemum morifolium* seedlings (Chaki et al., 2011). However, detailed global molecular profiling by omics approaches are needed to increase our knowledge on the effect of NO and NO-mediated PTMs at subcellular level to mitigate nitrosative stress impacts induced by high heat.

## 25.2.5 NO and Heavy Metal Stress Tolerance in Plants

Heavy metals are a group of metals and metalloids that can alter the normal metabolic processes and become toxic to the growth of the plant beyond permissible concentrations (Sahay and Gupta, 2017; Oz et al., 2015). Copper (Cu), cadmium (Cd), aluminum (Al), and arsenic (Ar) are the most commonly reported heavy metals toxic to plants (Sahay and Gupta, 2017). They accumulate in the soil due to the application of fertilizers, mining, agricultural wastes, application of sewage sludge, and industrial activities. Once they enter into the plant cells through plasma membrane transporters, they affect the plants by direct interaction with DNA, proteins, and binding to atoms such as oxygen, sulfur, etc. (Choudhury et al., 2013; Chmielowska-Bąk et al., 2014). NO mitigate heavy metal stresses in plants mainly by two strategies. One, NO helps plants to challenge metal stress conditions by upregulation of antioxidant enzyme activity or by upregulation of defensive gene expression (Ortega-Galisteo et al., 2012). Two, NO regulates cellular free metal concentration either by excluding the heavy metal entry into the root or by preventing their cellular accumulation to a toxic level (Oz et al., 2015). However, the results are sometimes contradictory, where on one hand several reports evidence the protective role of NO in alleviating heavy metal stress adversaries, but on the other hand, NO together with heavy metals has been shown to contribute to the toxicity and growth inhibition of plants (Wang et al., 2014; Yun et al., 2016). Hence, more detailed studies will facilitate understanding of the exact roles of NO in regulating cellular responses to heavy metals (Xiong et al., 2010).

Studies suggested an increased NO production in the Cu-treated plants mainly in the root tissues (Tewari et al., 2008). Moreover, application of SNP effectively reduced Cu-induced toxicity and $NH_4^+$ accumulation in the leaves of *Oryza sativa* as well as in the adventitious roots of *Panax ginseng* (Tewari et al., 2008). Experiments showed the ability of NO in alleviating the growth inhibition induced by $CuCl_2$ due to the induction of $H^+$-ATPase activity in plasma membrane and also by enhancing the antioxidant system through regulating GSH/GSSG ratio (Yu et al., 2014; Wang et al., 2015; Xu et al., 2010a,b). In addition to regulation of antioxidant defense, NO is also shown to increase the RuBisCo activity and mineral uptake in Cu-stressed *Nicotiana tabacum* and *Loleumk perenne* respectively (Pető et al., 2011; Khairy et al., 2016).

Al affects crop growth and yield in acidic soils mainly by inhibiting uptake of minerals and nutrients. Exogenous application of SNP alleviated the effects of Al on root elongation in *Hibiscus moscheutos* (He et al., 2012a,b). Moreover, SNP treatment promoted Al immobilization in roots by improving the root secretion of malate and citrate there by preventing Al accumulation inside the cells in *Artemisia annua* (He et al., 2012a,b; Aftab et al., 2012). Not only that, NO also enhances Al tolerance by regulating hormonal equilibrium in root apices of *Secale cereale* and *Triticum aestivum* (Sun et al., 2014). Besides, SNP treatment improved photosynthetic efficiency, gene transcription, and activity of major antioxidant enzymes of Al-stressed plants (Aftab et al., 2012; Sun et al., 2014; Bai et al., 2011; Sadeghipour, 2016). While increase in endogenous NO level has been observed by Cd-stress in soybean cell suspension cultures (Kopyra, 2004) and in roots of *Lupinus luteus* seedlings (Arasimowicz-Jelonek et al., 2011), a severe decline in the NOS-dependent NO production was observed under Cd stress in *Pisum sativum* leaves (Rodríguez-Serrano et al., 2009). Studies indicate that NO protects chlorophyll against cadmium stress in *Helianthus annuus* (Laspina et al., 2005; Groppa et al., 2008) and Cu stress in *Lolium perenne* (Dong et al., 2014). In another study, NO-induced Cd tolerance in *Oryza sativa* has been attributed to the ability of NO to restrict Cd entry by increasing pectin and hemicellulose content in the cell wall of roots, promoting phosphotic acid accumulation and phospholipase D activity in the plasma membrane (Xiong et al., 2009; Jhanji et al., 2012; Yang et al., 2016). Moreover, SNP treatment significantly decreased the level of ROS and lipid peroxidation due to the increased activities of antioxidant enzymes in Cd exposed *Lolium perenne* seedlings (Arasimowicz-Jelonek et al., 2011; Bai et al., 2011). Interestingly, SNP decreased the translocation of Cd metal in roots and stems of *Arachis hypogeae* followed by an increase in photosynthetic activity (Dong et al., 2014). Similarly, SNP treatment increased antioxidant enzyme activities in As stressed *Triticum aestivum* (Hasanuzzaman et al., 2013). Exogenous application of SNP also decreased As accumulation, which resulted in improved seed germination in mung bean (Ismail, 2012; Leterrier et al., 2012).

Zinc (Zn) is another essential micronutrient that becomes toxic to plants at higher concentration (Sahay and Gupta, 2017). Roots of *Triticum aestivum* display enhanced NOS activity followed by NO generation when exposed to Zn (Duan et al., 2007). Besides, exogenous NO also impacts Zn translocation from root to shoot, increase ascorbate content in *Triticum aestivum* plants (Buet et al., 2014). Meanwhile, NO treated *Triticum aestivum* plants show a decrease in $H_2O_2$ and nonprotein thiol content under Fe deficient conditions (Buet et al., 2014). Reports suggest that NO increased uptake of Fe and magnesium that subsequently resulted in improved chlorophyll synthesis, photosynthesis, and transpiration (Kong et al., 2016). Similarly, Nickel (Ni) induced oxidative stress was alleviated by exogenous application of NO in *Brassica junica*, *Solanum lycopersicum*, and *Triticum aestivum* (Mihailovic and Drazic, 2011; Kazemi, 2012; Wang et al., 2010a,b). Another study points to the reduced manganese (Mn) toxicity due to NO donor treatment in excised rice leaves (Srivastava and Dubey, 2012). Collectively, the available data on the involvement of NO in metal stress suggests that NO alleviates heavy metal toxicity by attenuating oxidative stress and enhancing the activity of antioxidant enzymes.

### 25.2.6 NO in Ozone Stress Tolerance

Ozone ($O_3$) is an oxidant gaseous molecule present in the stratosphere region protecting Earth from harmful UV-B radiation. The rising surface $O_3$ levels due to urbanization and the industrial revolution has become a serious concern for both for human health and vegetation (Monks et al., 2015). Increased accumulation of NO was observed in *Nicotiana tabacam* and *Arabidopsis thaliana* upon ozone exposure, which disappeared following the addition of 100 $\mu$M cPTIO (Ederli et al., 2008; Ahlfors et al., 2009; Xua et al., 2012). Moreover, *Atnoa1/rif1* mutant with decreased NO accumulation was found to be $O_3$ sensitive. Conversely, the $O_3$-sensitive *rcd1* mutant was found to be an NO overproducer suggesting the significance of NO generation during $O_3$ stress response. NO is required to modify hormone biosynthesis and signaling, and associated gene expression in plants during $O_3$ exposure (Ahlfors et al., 2009). Although both NO and ethylene dependent pathways are required for the $O_3$-induced upregulation of alternative oxidase *AOX1a*, only NO is indispensable for the activation of *AOX1a* gene expression. Activating alternative oxidase pathway is essential to reducing the formation of reactive oxygen species and thus allowing increased carbon flux through the tricarboxylic acid cycle to provide carbon skeletons for other cellular processes under limited ADP supply (Ederli et al., 2008). Interestingly, acute ozone fumigation of poplar has changed the total nitrite and nitrosothiol contents of leaves and altered the homeostasis of 32 S-nitrosylated proteins (Vanzo et al., 2014). Together, a total of 172 proteins have been shown to be S-nitrosylated in poplar callus and leaf due to ozone fumigation. Besides, ozone fumigation enhanced the activity of phenylalanine ammonia-lyase (PAL) by denitrosylation in poplar (Vanzo et al., 2014).

### 25.2.7 NO in UV-B Tolerance of Plants

In recent years the depleting ozone layer is allowing more UV-B radiation (280–320 nm) to reach Earth's surface. Exposure to high doses of UV-B radiation leads to numerous harmful consequences in plant cells including dimers formation in DNA, genomic instability, overproduction of ROS, lipid peroxidation, followed by damage to the photosynthetic apparatus and membranes, and ultimately to PCD (Lytvyn et al., 2016; Krasylenko et al., 2013). Plants initiate various defense reactions including the activation of ROS scavenging systems, synthesis of UV-absorbing phenolic compounds, activation of DNA repair mechanisms, and upregulation of UV-B sensitive oxidative defense genes (Hideg et al., 2013). Studies indicate that upregulation of chalcone synthase gene responsible for flavonoid production by UV-B requires NO in *Arabidopsis thaliana* (Mackerness et al., 2001), while NO scavengers counteract this upregulation further asserting NO's role in flavonoid accumulation. A recent study suggests that treatment of *Arabidopsis thaliana* with SNP donor recovered the plant from UV-B inhibited root growth and altered morphology as well as had damaging effects on microtubular organization (Krasylenko et al., 2013). Similarly, a role of NO in UV-B induced stem elongation has been suggested for *Pisum sativum*. Although NOS-like source for NO generation during UV-B stress has been suggested in *Ginkgo biloba* (Tossi et al., 2012), the mammalian NOS inhibitors had no effect on UV-B-induced NO generation (Zhang et al., 2011). Conversely, a direct correlation between NR activity, NO emission, and nitrite ($NO_2^-$) has been shown to be essential for flavonoid accumulation under UV-B radiation, while cPTIO abolished this response in *Betula pendula* (Zhang et al., 2011).

Homozygous mutants of *Arabidopsis thaliana* deficient for inositol-3-phosphate synthase 1 (*atips1*), a key enzyme for biosynthesis of *myo*-inositol and its derivatives, displayed greater tissue-specific resistance to the action of UV-B. Moreover, pretreatment with low doses of SNP before UV-B exposure resulted in a tissue-specific protective effect in wild type, which was further enhanced in *atips1* (Lytvyn et al., 2016). Exogenous NO partially alleviated the UV-B effect by a decrease in chlorophyll content and oxidative damage to the thylakoid membrane in bean seedlings. In addition, the enhanced NO levels also help in maintaining cellular redox homeostasis under UV-B stress by activating antioxidants and secondary metabolite production. Consistent with this, SNP pretreatment prevented the oxidative stress progression in UV-B exposed *Phaseolus vulgaris* seedlings by decreasing $H_2O_2$ content, increasing the thiol group content and upregulation of active oxygen scavenging genes. Moreover, NO scavenger or inhibitor or cGMP inhibitor partially prevented the negative impact of UV-B on pollen germination and pollen tube growth suggesting the operation of cGMP mediated NO pathway during UV-B responses of *Paulownia tomentosa*. However, cataloguing of NO responsive genes, proteins, and other signaling partners under UV-B stress would decipher NO-dependent mechanisms of UV-B stress tolerance in plants.

### 25.2.8 NO in Wounding Stress Tolerance

Wounding stress in plants represents a range of mechanical injuries caused by both biotic (herbivory and infect feeding) and abiotic stresses (raining, wind, touching, hailing, etc.) (Gilroy et al., 2016). In cultivated crops, wounding may also occur during manual manipulation such as harvesting, handling, and storage. In *Pisum sativum* leaves, NO accumulated 4 h after wounding followed by an increase in the content of SNOs due to the induction of NOS and GSNOR activities (Gilroy et al., 2016). Interestingly, wounding triggered accumulation of GSNO and some other SNOs due to the downregulation of GSNOR activity, but without affecting the NO content in *Helianthus annus* hypocotyls (Chaki et al., 2011). The NO released under wounding in turn acts as a signal to cause a transient increase in the cytoplasmic $Ca^{2+}$ concentration at the site of injury in *Vicia faba* and *Nicotiana tabacum* cell suspensions (Gilroy et al., 2016). More recently, extracellular ATP leaking from the injured cells was also suggested to act as a signal to carry stress response to surrounding healthy cells in plants as well as in animals (Casalongué et al., 2015). Intriguingly, extracellular ATP induced activation of $Ca^{2+}$ influx, ROS production, and altered gene expression was also mediated through NO-dependent pathway (Chivasa et al., 2005; Song et al., 2008). Another study revealed that systemic accumulation of $H_2O_2$ and NO at local wound site enhanced cross tolerance to freezing in untreated systemic leaves in *Triticum aestivum* (Si et al., 2017). The mechanical stress induced NO burst has also been implicated in DNA fragmentation in *Arabidopsis thaliana* (Garcês et al., 2001). Although these results strongly support the critical role played by NO in wounding stress in plants, additional work is required to understand the detailed mechanism of its signaling in plants.

### 25.2.9 NO in Flooding Stress Tolerance

Flooding is a major limiting factor for crops growing on as much as 12% of the world's soils that suffer excess water (Bailey-Serres et al., 2012). In general, plants respond to flooding by forming root aerenchyma, initiating a hyponastic response and by initiating a quiescence phase to conserve bioenergy. The decline in mitochondrial respiration under hypoxia leads to an increase in NADH and a drop in ATP levels. Flooding causes anaerobic conditions leading to intracellular $NO_2$ accumulation as an alternative source of $NAD^+$ to maintain a high glycolytic rate, which is often converted to NO by cytosolic NR in *Hordeum vulgare* roots (Dongen and Licausi, 2015). Besides NR, hypoxic stress-induced hemoglobin (Hb) also regulates NO levels in *Zea mays* cell cultures and *Medicago sativa* root cultures (Igamberdiev et al., 2005). The regulation of NO levels was also shown to be critical by maintaining high nitrate ($NO^{3-}$) concentrations and stress-induced Hb in *Arabidopsis thaliana* (Wang et al., 2000). Both increased Hb gene expression and activation of NR enzyme induce the generation of NO in order to maintain ATP levels and to prevent cell death under flooding (Igamberdiev et al., 2005). Detoxification of NO and nitrite produced due to denitrification in soybean nodules after flooding requires a functional plant oxygen carrier leghemoglobin (Sánchez et al., 2010). Hence, the reduction of nitrate by *Brassica japonicum* bacteroids leads to legheamoglobin-NO production within *Glycene max* nodules in response to hypoxia (Meakin et al., 2007). Moreover, flooding caused a decrease in *nifH* expression and nitrogenase activity in wild-type soybean nodules (Sánchez et al., 2010). Nevertheless, uncertainties not only on the source of NO, but also the complete NO-mediated mechanism under flooding, need to be thoroughly addressed.

## 25.3 NO AND PHYTOHORMONES CROSSTALK IN ABIOTIC STRESS TOLERANCE

Owing to its rich chemistry, NO involves interactions with a number of signaling molecules and phytohormones during abiotic stress responses in plants (Sami et al., 2017). A series of experimental reports established that NO modulates the biosynthesis, distribution, and degradation of phytohormones. The past decade has witnessed the interaction of NO with almost all the plant hormones mostly as a second messenger in the signaling cascades of various plant developmental and stress responses. For example, NO has been intensively involved with hormones such as GA, JA, ET, CK, and AUX during the regulation of stomata under environmental stress conditions (Sami et al., 2017; Nawaz et al., 2017). A majority of the research publications highlighted the interaction between ABA and NO under drought stress. Interestingly, both synergistic and antagonistic crosstalks have been described between NO and ABA depending on the physiological response and tissue during stress (Santisree et al., 2015). For example, NO is involved in the ABA induced stomatal closure by selectively activating intracellular $Ca^{2+}$ channels through a cGMP/cADPR-dependent signaling pathway in *Vicia faba* guard cells (Mioto and Mercier, 2013). ABA induced NOS activity and NO levels have been shown to improve the thermotolerance of *Phragmites communis* calluses (Song et al., 2008). Guo et al. (2014) found that coordinated action between NO and ABA upregulated cold-induced MfSAMS1 expression, resulting in enhanced acclimation against cold stress. Similarly, the study using vp14 maize mutant defective in ABA synthesis suggests that the requirement of ABA accumulation after UV-B perception is critical to trigger the elevation of cytosolic $Ca^{2+}$ concentration resulting in enhanced NOS-mediated NO production (Tossi et al., 2012). NO and Aux display an extensive signaling crosstalk during the development and remodeling of root architecture for the extraction of more water under drought stress Simontacchi et al., 2013. Additionally, several developmental studies indicate the involvement of NO in auxin mediated lateral and adventitious roots formation (Simontacchi et al., 2013). In agreement with this, interplay of NO-AUX was also evident by significant reduction in root meristem size in salt treated *Arabidopsis thaliana.* Interestingly, supplementation of NO reduces AUX degradation by downregulating IAA oxidase activity in *Medicago truncatula* under Cd stress as well as under Al toxicity in *Triticum aestivum* and *Secale cereale* (Xu et al., 2010a,b; He et al., 2012a,b). In another study, Cd induced NO accumulation promoted the stabilization of AUX repressor protein IAA17 in *Arabidopsis* through suppression of AUX carriers PIN1/3/7 (Kovacs and Lindermayr, 2013). Further, a positive correlation between AUX and NO has been suggested in enhancing ferric-chelate reductase activity in a Fe-deficient *Arabidopsis thaliana* plants (Chen et al., 2010). Similar to auxin, a positive interaction between NO and CK under drought was reported, wherein the treatment with CK regulated photosynthetic machinery by promoting NO signaling in *Zea mays* (Shao et al., 2010). Conversely, CK reduced NO levels to trigger stomatal opening in dark grown *Vicia faba* seedlings (Santisree et al., 2015). Foliar application of SNP delayed salt-induced leaf senescence by upregulating the expression of isopentenyl transferase (*IPT*) in *Gossypium hirsutum* seedlings (Kong et al., 2016). However, more studies are required to provide strong evidence for NO and CK interaction under abiotic stress. Previous studies have reported the participation of NO in SA-induced stomatal closure in *Arabidopsis thaliana* (Sun et al., 2010). A coordinated action of NO and SA was found to mitigate the damaging effects of osmotic stress in *Triticum aestivum* seedlings (Naser alavi et al., 2014). In another study, combined application of NO and SA improved Ca2+/Mg2+ absorption, increased proline accumulation while mitigating the salt stress adversaries in *Glycene max* seedlings. Similarly, combination of NO and SA has been shown to alleviate the toxic effects of Ni in *Brassica napus* and Cd in *Arachis hypogaea* (Kazemi et al., 2010; Xu et al., 2015).

The critical balance between NO and ethylene seems to be essential to prevent cold-induced injury during postharvest fruit ripening and seed conservation (Bai et al., 2011; Xu et al., 2012a,b). Akin to SA, ET induced by Cd stress reduced NO levels in *Pisum sativum* and *Glycine max* seedlings. Besides, both NO and ET are required to upregulate the plasma membrane $H^+$ -ATPase and alternative respiratory pathway to modulate ion homeostasis for improved salt tolerance (Wang et al., 2010a,b). A few studies indicate that NO treatment induces production of ethylene to regulate a few $O_3$ induced genes (Ahlfors et al., 2009). Additionally, NO plays a key role in programmed cell death (PCD) and the hyponastic responses by inducing ethylene biosynthesis during flooding stress (Pasqualini et al., 2012). It is well known from the literature that coordinated action between NO and plant hormones including ABA, JA, GA, and CK induce thermotolerance by activating the antioxidant machinery and upregulating the heat shock protein expression in plants (Zandalinas et al., 2016). Further, pretreatment of *Zea mays* seedlings with $H_2O_2$ rapidly induced endogenous $H_2O_2$, NO, and $H_2S$ accumulation under heat stress, which was reversed by $H_2O_2$ scavenger dimethylthiourea and NO scavenger cPTIO, indicating that $H_2O_2$ induced heat stress tolerance was involved in the crosstalk between downstream components NO and $H_2S$ (Li et al., 2013b). An interlink between NO and GA has also observed in promoting apical root growth in Al-stressed *Triticum aestivum* roots (He et al., 2012a,b). Additionally, NO induced reduction in total free polyamines, free put, spermidine (Spd), and polyamine oxidase activity was reported in salt stressed cucumber seedlings (Fan et al., 2013). Despite this evidence, the complete understanding of mechanisms underlying the intersection of NO signaling with other signaling molecules requires further study to explain how NO concomitantly interacts with hormone-related proteins at the posttranscriptional or translational level.

## 25.4 CONCLUDING REMARKS AND FUTURE PERSPECTIVES

As climate change continues, our appreciation of how plants respond to stress is becoming increasingly significant. Accumulating evidence demonstrated a reversible accumulation of NO under a range of abiotic stresses (Fig. 25.1). Several studies indicate that the NO accumulation potentially enhances plant survival under stress conditions mostly by increasing cellular antioxidant defense. However, the functionality of NO accumulation depends on its concentration, location, duration, plant growth, and developmental stage and many internal and external factors. Although NO is recognized as a multitasking molecule with innumerable functions in plant stress responses, many questions remain unanswered. Most importantly, how does the stress-specific NO accumulation translate into a biological function that helps in stress amelioration? Another pertinent question is how the small NO molecule can influence modification of a massive number of molecules that enhance plants tolerance to stress. Since the sensitivity to stress varies from species to species, the stress ameliorating effects of NO in the given species under given stress may not be extrapolated to other species with different sensitivity. In some of the experiments, in vitro stress treatments used may not be comparable with the natural stress conditions that occur at

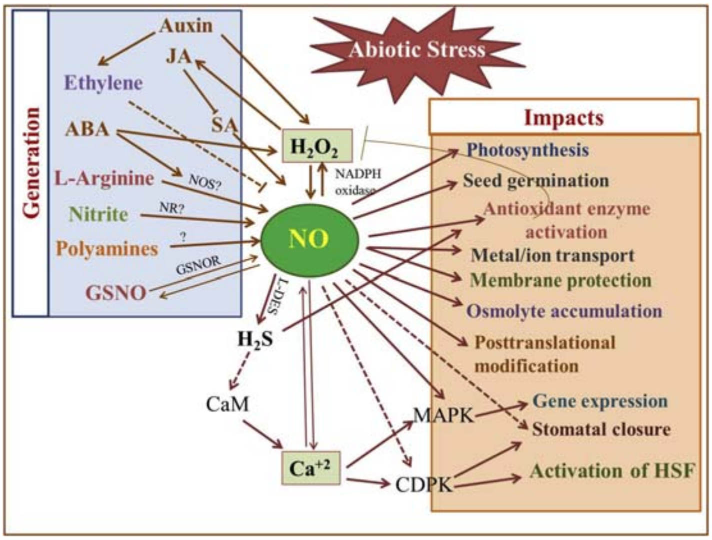

**FIGURE 25.1** Schematic illustration for synthesis and functional roles of nitric oxide (NO) in plant responses to abiotic stress.Abiotic stress factors in plants led to the generation of reactive oxygen species (ROS) and nitric oxide (NO), which can effect gene expression. NO participates actively in signal transduction by altering the expression of a number of genes, such as protein kinases and transcription factors (TFs), triggering various physiobiochemical responses, including changes in general metabolism and ion/metabolite transport, stress responses, as well as protein degradation. NO either stimulates (normal end arrow) or inhibits (blunt end arrow) plant processes in coordination with various other signaling molecules under abiotic stress. The dotted line denotes the pathways not studied clearly. The double-sided arrow indicates the mutual regulation of molecules. *ABA*, abscisic acid; *JA*, jasmonic acid; *MAPK*, mitogen activated protein kinase; *NOS*, nitric oxide synthase; *NR*, nitrite reductase; *ROS*, reactive oxygen species; *SA*, salicylic acid; *TF*, transcription factor.

the field level. Therefore, how the NO signaling pathways function in an open environment can only be addressed by field level studies. Further, detailed studies that are more directly linked to yield, such as the role of NO in increasing protection to photosynthesis and osmolyte accumulation under stress, will add more value to the established antioxidant role of NO.

Despite growing knowledge about NO-mediated plant functions, detailed information on its origin and signaling under individual stress conditions has so far been elusive. Hence, the genetic screens used to explore the consequences of NO deficiency may not be conclusive unless multiple NO generating sources are disabled simultaneously. Clearly, blocking the NO generating sources without complete elucidation of the responsible molecular identities presents a big challenge for genetic and transgenic researchers. Although the use of exogenous donors/inhibitors offers an alternative until the molecular identities of NO generation in plants are better deciphered, it is critical to consider the stress treatment and the tissue type used to critically analyze the results to avoid ambiguous conclusions. Moreover, the method of NO application needs to be validated considering the cost, impact, and ease of use under large scale applications. In this context, encapsulation of NO donors in nanomaterials looks promising and has several advantages such as improved efficiency and controlled release over direct exogenous applications (Savvides et al., 2016).

Although there is sufficient evidence on the potential involvement of NO in various hormone-mediated plant growth processes, the crosstalk studies remain fragmental under individual stress conditions. Moreover, the high throughput -omics analysis of NO-mediated stress responses remain largely untapped, but more research in this direction will facilitate research aimed at the identification of NO targets in stress conditions. Together, exploration of NO metabolism and its interacting partners in plants and their physiological relevance under stress will be helpful to enrich our knowledge on NO functions.

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