Reactive Nitrogen Species (RNS) in Plants Under Physiological and Adverse Environmental Conditions: Current View

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Contents

Abstract Nitric oxide (˙NO) and derived molecules, referred to as reactive nitrogen species (RNS), have become a new area of plant research. These molecules are involved in almost all physiological plant processes, ranging from seed germination, development, senescence, stomatal movement, fruit ripening, and reproduction to mechanisms of response to adverse environmental conditions possibly associated with nitro-oxidative stress. ˙NO can perform a dual function depending on its rate of production; at low concentrations, it acts as a signal molecule and, at high concentrations, like a stress molecule. Although in some cases the simultaneous high ˙NO production with other reactive oxygen species (ROS) can be useful to the cells as mechanism of defense, for example, against pathogens. All these processes are usually mediated by the chemical interactions of ˙NO whose functions

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are affected by other molecules. It is worth pointing out that the post-translational modifications of target proteins caused by nitration and *S*-nitrosylation have been best described in plants. However, $^{\cdot}NO$ can also regulate gene expression through direct interaction with DNA or through interaction with transcription factors. This review provides a comprehensive overview of the role played by RNS in the physiology of plants and their involvement in the mechanism of response to a diverse range of adverse environmental conditions.

1 Introduction

Endogenously generated nitric oxide ($^{\cdot}NO$) is currently one of the most studied bioactive gas molecules in plant cells. This is due to its involvement in a wide spectrum of plant physiological processes including seed germination, primary and lateral root growth, flowering, pollen tube growth regulation, stomatal movement, fruit ripening, and senescence; nevertheless, new functions of $^{\cdot}NO$ are gradually being added to the list. This key signaling molecule in different intracellular processes also participates in the mechanism of response to biotic and abiotic stresses (Neill et al. 2003; Lamotte et al. 2005; Besson-Bard et al. 2008; Corpas et al. 2011; Domingos et al. 2015; Corpas and Barroso 2015a). However, nitric oxide's versatility depends on its chemical properties, enabling it to interact with many molecules that affect its biochemical interactions and consequently its functions in plant cells (Pfeiffer et al. 1999).

2 Nitric Oxide and Reactive Nitrogen Species

The gasotransmitter nitric oxide, also referred to as nitrogen monoxide, is a free radical whose π orbital contains an unpaired electron represented by a dot on the N atom ($^{\cdot}NO$); however, for simplification purposes, this dot is omitted in many publications. Nitric oxide has a family of NO-derived molecules generally referred to as reactive nitrogen species (RNS). Table 1 shows the most representative RNS including radical and non-radical molecules. Thus, $^{\cdot}NO$ can react with many inorganic and organic molecules such as peptides, proteins, lipids, and nucleotides; this reactivity explains its numerous biochemical interactions. Figure 1 shows a simple model of $^{\cdot}NO$ metabolism in plant cells. $^{\cdot}NO$ in both its gas phase and aqueous solution form can react with O_2 to form dinitrogen trioxide (N_2O_3) and nitrogen dioxide ($^{\cdot}NO_2$). In aqueous solution, N_2O_3 and $^{\cdot}NO_2$ produce stoichiometric amounts of nitrite (NO_2^-) and nitrate (NO_3^-). Nitrogen dioxide is 1.5 times more soluble in a lipid membrane than in water (Signorelli et al. 2011). $^{\cdot}NO$ is also

Table 1 Main reactive nitrogen species (RNS) including inorganic and organic molecules

Non-radicals	Radicals
Inorganic molecules	
Nitroxyl anion (NO^-)	Nitric oxide ($^{\cdot}NO$)
Nitrosonium cation (NO^+)	Nitrogen dioxide ($^{\cdot}NO_2$)
Nitrous acid (HNO_2)	
Dinitrogen trioxide (N_2O_3)	
Dinitrogen tetroxide (N_2O_4)	
Peroxynitrite ($ONOO^-$)	
Peroxynitrous acid (ONOOH)	
Organic molecules	
Nitrotyrosine (Tyr-NO_2)	Lipid peroxyl radicals ($LOO^{\cdot}$)
Nitrosoglutathione (GSNO)	
Nitrosothiols (SNOs)	
Nitro-γ-tocopherol	
Nitro-fatty acids (FA-NO_2)	

able to react with the superoxide radical ($O_2^{\cdot -}$) to yield peroxynitrite ($ONOO^-$), with the rate constant (~ 10^{10} M^{-1} s^{-1}) for this reaction being considerably very high (Estévez and Jordán 2002), virtually ensuring that $ONOO^-$ will be formed in any plant cell or tissue where both radicals are present simultaneously. This chemical reaction is very fast given a rate constant of 2×10^9 M^{-1} s^{-1} for $O_2^{\cdot -}$ dismutation by the CuZn superoxide dismutase (SOD) enzyme (Gray and Carmichael 1992). The production site of $ONOO^-$ must therefore be associated with the sources of $O_2^{\cdot -}$ and $^{\cdot}NO$ including the main plant cell organelles, such as chloroplasts, mitochondria, and peroxisomes (Blokhina and Fagerstedt 2010; Corpas and Barroso 2014). Peroxynitrite, a powerful oxidant, plays a highly important role as it can mediate nitration processes and cause cellular injury (Szabó et al. 2007; Corpas et al. 2009a; Arasimowicz-Jelonek and Floryszak-Wieczorek 2011; Calcerrada et al. 2011; Berton et al. 2012; Szuba et al. 2015).

Nevertheless, one of the most controversial issues with respect to higher plants is the way in which $^{\cdot}NO$ is endogenously generated in the cell. At least two main enzymatic pathways for generating endogenous $^{\cdot}NO$, using the amino acid L-arginine and/or the nitrite-dependent pathway as well as non-enzymatic $^{\cdot}NO$ generation, have been described (Wojtaszek 2000). The involvement of at least one of these pathways in a specific process is supported by experimental data although it is important to note that, depending on the plant species, developmental stage, and/or environment conditions involved, the participation of both pathways cannot be ruled out. In the case of L-arginine-dependent nitric oxide synthase (NOS) activity, there is a strong biochemical evidence of the presence of this activity in plants, which requires the presence of all the co-factors of animal NOS using NADPH as an electron donor (see Corpas et al. 2009b); new data also confirm the existence of an NOS-like protein in the green alga *Ostreococcus tauri* (Foresi et al. 2010). Additionally, L-arginine is a precursor of the biosynthesis of polyamines which,

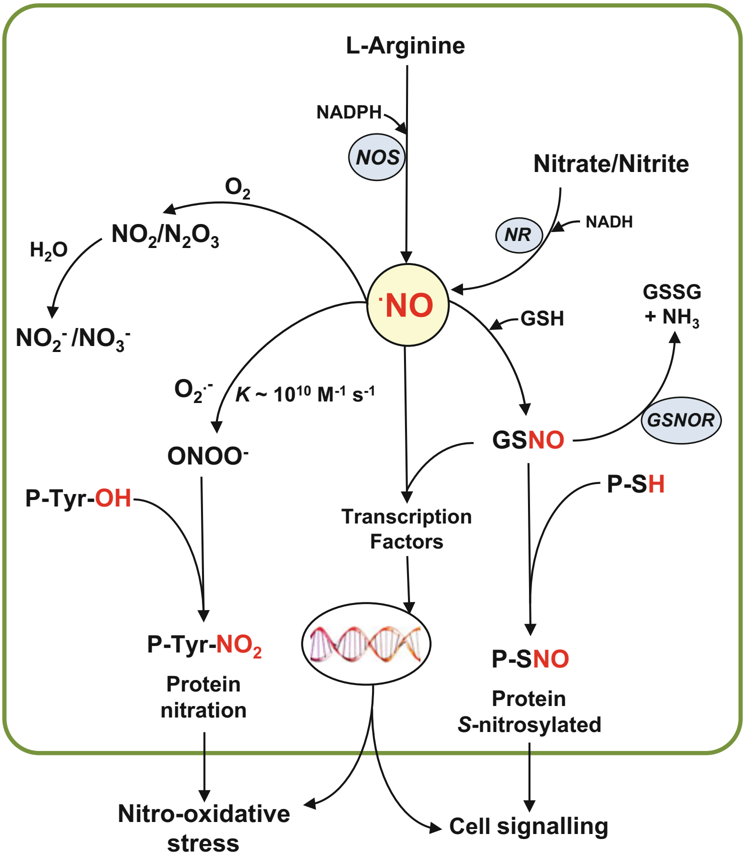

Fig. 1 Graphic model of nitric oxide (NO) metabolism in plant cells. L-Arginine-dependent nitric oxide synthase (NOS) and nitrate reductase (NR) generate NO which can react with reduced glutathione (GSH) in the presence of O_2 to form *S*-nitrosoglutathione (GSNO) through a process of *S*-nitrosylation. This metabolite can be converted by the enzyme GSNO reductase (GSNOR) into oxidized glutathione (GSSG) and NH_3. GSNO and other *S*-nitrosothiols can interact with specific sulfhydryl (-SH) groups to produce *S*-nitrosylated proteins in a process called *S*-transnitrosation which can mediate signaling processes. Nitric oxide in the presence of oxygen is converted into dinitrogen trioxide (N_2O_3) and nitrogen dioxide (NO_2) which, in aqueous solutions, are transformed into nitrite and nitrate. Nitric oxide can also react very rapidly ($K\sim 10^{10}\ M^{-1}\ s^{-1}$) with superoxide radicals (O_2^{-}) to generate peroxynitrite ($ONOO^{-}$), a powerful oxidant molecule that can mediate the tyrosine nitration of proteins. Nitric oxide and related molecules could be part of cell signaling or nitro-oxidative stress processes

according to some experimental data, could be involved in ·NO biosynthesis (Tun et al. 2006; Wimalasekera et al. 2011a, b). The production of ·NO by the nitrite-dependent pathway depends on nitrate reductase (NR) activity which uses NADH as an electron donor instead of NADPH. This classic enzyme is involved in the nitrogen metabolism and has been widely accepted as an ·NO source candidate (Yamasaki et al. 1999; Rockel et al. 2002; Lozano-Juste and Leon 2010).

As mentioned previously, $^{\cdot}$NO directly or indirectly performs its biological actions through different RNS by interacting with many other molecules. In the case of proteins, the most studied post-translational modifications (PTMs) in plant cells are nitration and *S*-nitrosylation (Fig. 1). On the other hand, regulation of gene expression by $^{\cdot}$NO has also been reported to produce specific transcriptional responses (Begara-Morales et al. 2014a), indicating that $^{\cdot}$NO is perceived differentially. This could occur through the impact of $^{\cdot}$NO on transcription factors or through direct interaction with the DNA (Serpa et al. 2007; Tavares et al. 2014).

3 Post-translational Modifications Mediated by RNS

3.1 Nitration

Nitration is a chemical reaction that enables a nitro group (-NO_2) to be added to molecules including proteins, lipids, and nucleotide acids (Rubbo and Radi 2008). In proteins, some amino acids, such as tyrosine (Tyr), cysteine (Cys), methionine (Met), and tryptophan (Trp), are preferentially nitrated. However, in plants, most studies focus on tyrosine nitration (Tyr-NO_2), which involves adding a nitro group to one of the two equivalent ortho-carbons of the aromatic ring of tyrosine residues. This transforms Tyr into a negatively charged hydrophilic Tyr-NO_2 moiety and causes a marked shift in the hydroxyl group's local p*K*a from 10.1 in tyrosine to 7.5 in nitrotyrosine. This process depends on different intrinsic and extrinsic features such as protein structure, nitration mechanism, and the environmental compartments where the targeted protein is located (Corpas et al. 2013). These covalent changes may result in several potential effects such as protein function loss, gain, or no functional change, with loss of function being the most common. It is important to remember that there is a physiological nitration in plant cells; however, under internal or external adverse conditions, an increase in protein nitration or free nitrotyrosine could be regarded as a reliable marker of nitrosative stress (Corpas et al. 2007; Berton et al. 2012). Many new potential target proteins, which undergo this PTM in plant cells under physiological or stress conditions, have been identified (Corpas et al. 2015). However, this process is closely associated with the ROS metabolism and consequently with oxidative stress, therefore it should be called nitro-oxidative stress (Corpas and Barroso 2013). A good example of this connection is the way in which important antioxidant enzymes, such as catalase (Clark et al. 2000; Chaki et al. 2015a), ascorbate peroxidase (Begara-Morales et al. 2014b), monodehydroascorbate reductase (Begara-Morales et al. 2015), and SOD (Holzmeister et al. 2015), are negatively regulated by nitration (see Table 2).

A new promising area of plant research is the identification and characterization of nitro-fatty acids (Sánchez-Calvo et al. 2013). These molecules together with their signaling component have been under intense study in animal cells; they can

Table 2 Examples of identified plant enzymes involved in ROS metabolism which are post-translationally affected by either nitration and/or *S*-nitrosylation and their effects

Enzymes involved in ROS metabolism	Plant species	*S*-Nitrosylation	Nitration	Reference
Catalase	*Nicotiana tabacum, Capsicum annuum*	Inhibition	Inhibition	Clark et al. (2000), Ortega-Galisteo et al. (2012) and Chaki et al. (2015a)
Superoxide dismutase isozymes (MnSOD1, CuZn SOD3, FeSOD3)	*Arabidopsis thaliana*	No effect	Inhibition	Holzmeister et al. (2015)
Peroxiredoxin II E and F	*Arabidopsis thaliana, Pisum sativum*	Inhibition	NT	Romero-Puertas et al. (2007) and Camejo et al. (2015)
Enzymes of ascorbate–glutathione cycle				
Cytosolic ascorbate peroxidase (APX)	*Pisum sativum*	Increased activity	Decreased activity	Clark et al. (2000), Fares et al. (2014), Begara-Morales et al. (2014b), and Yang et al. (2015)
Dehydroascorbate reductase (DHAR)	*Arabidopsis thaliana, Solanum tuberosum*	NT	NT	Fares et al. (2014) and Kato et al. (2013)
Monodehydroascorbate reductase (MDAR)	*Pisum sativum*	Inhibition	Inhibition	Begara-Morales et al. (2015)
Glutathione reductase	*Pisum sativum*	No effect	No effect	Begara-Morales et al. (2015)
Superoxide-generating system				
NADPH oxidase also called respiratory burst oxidase homologue (RBOH)	*Arabidopsis thaliana*	Inhibition	NT	Yun et al. (2011)

NT not tested

trigger signaling cascades via covalent and reversible PTMs of susceptible nucleophilic amino acids in target proteins which have important physiological functions such as an anti-inflammatory mechanism (Trostchansky et al. 2013). However, there are very few experimental data on this area of research in plants (Fazzari et al. 2014).

3.2 S-*Nitrosylation*

S-Nitrosylation, more appropriately called *S*-nitrosation, consists of the covalent attachment of an $^{\cdot}$NO group to the thiol (-SH) side chain of cysteine (Cys) present in peptides or proteins in order to produce a family of NO-derived molecules called *S*-nitrosothiols (SNOs). This covalent modification is highly labile under physiological conditions as their stability depends on the presence of trace metal ions (such as copper and iron) or reducing agents (such as thiols and ascorbate) which enhance their degradation (Askew et al. 1995; Vanin et al. 1997), thus making it difficult to study SNOs in cells. Furthermore, this process, which is selective and reversible, can alter protein conformation and/or protein properties. Different biochemical approaches such as biotin switch assays, resin-assisted capture (SNO-RAC), fluorescence switch, or protein microarray-based analysis (Jaffrey 2005; Han et al. 2008; Foster et al. 2009; Wang and Xian 2011; Fares et al. 2014) combined with mass spectrometry techniques have facilitated the study of SNO modulation and identification of a significant number of potential protein targets in different plant species under physiological and stress conditions (Lindermayr et al. 2005; Vanzo et al. 2014; Chaki et al. 2015b).

4 Nitric Oxide in Plant Development

Plant development involves many phases including seed germination, plant growth and differentiation of cells, tissues, and organs, flower formation, fruit ripening, and senescence. In all these processes, the direct involvement of $^{\cdot}$NO or indirectly through its interaction with different phytohormones (auxins, ethylene, and abscisic acids) and molecules such as ROS (superoxide radical, H_2O_2) has been described to some degree (Zhao 2007; Freschi 2013; Airaki et al. 2015; Corpas and Barroso 2015b; Sanz et al. 2015).

Many metabolic pathways are involved in seed germination and seedling establishment which begin with water imbibition, a catabolic and anabolic process using lipid mobilization to support the development of the new seedling during the transition from dark to light conditions until the seedling can initiate photosynthesis. $^{\cdot}$NO acts as a stimulator of germination and photo-morphogenesis (Beligni and Lamattina 2000; Kopyra and Gwózdz 2003; Simontacchi et al. 2004; Gniazdowska et al. 2010). Moreover, an increasing amount of data shows that $^{\cdot}$NO interacts with other molecules including calcium, H_2O_2, auxin, and gibberellins in the regulation of primary and lateral root growth, which eventually determines root architecture (Pagnussat et al. 2002; Correa-Aragunde et al. 2004; Guo et al. 2008; Fernández-Marcos et al. 2011; Duan et al. 2014; Sanz et al. 2015). During seedling development in different plant species such as pea, Arabidopsis, and pepper, cellular analyses employing specific NO-sensitive fluorophores and confocal laser scanning microscopy (CLSM) reveal that the steady-state levels of $^{\cdot}$NO content change depending on cell type in the main organs including roots, stems, and leaves (Corpas et al. 2006, 2009a; Airaki et al. 2015). Furthermore, in some cases, a temporal correlation between organ development and $^{\cdot}$NO production from L-arginine-dependent NOS activity has been described (Corpas et al. 2004, 2006). In addition, in the presence of other NO-derived molecules such as *S*-nitrosoglutathione and peroxynitrite, protein nitration has also been reported to be modulated during organ development (Airaki et al. 2015; Begara-Morales et al. 2013), indicating that these organs have a highly active ·NO metabolism.

The enzyme nitrosoglutathione reductase (GSNOR) is a conserved protein in prokaryotes and eukaryotes which catalyzes the NADH-dependent reduction of GSNO to GSSG and NH_3 regulating the level of GSNO and consequently cellular SNO homeostasis (Sakamoto et al. 2002; Leterrier et al. 2011). This activity is necessary for normal development under optimal growth conditions (Lee et al. 2008; Kubienová et al. 2013; Xu et al. 2013). Analysis of GSNOR in *Arabidopsis thaliana* indicates that roots and leaves from the initial stages of development have higher activity levels (Espunya et al. 2006). The importance of GSNOR in plant development has also been demonstrated by genetic approaches, as the over-expressing and knock-down GSNOR gene in Arabidopsis plants show an atypical phenotype with a short-root system, which correlates with a lowering of intracellular GSH levels and an alteration in its spatial distribution in the roots (Lee et al. 2008; Chen et al. 2009; Leterrier et al. 2011; Kwon et al. 2012). Moreover, new experimental data have begun to elucidate the molecular mechanism involved in the relationship between ·NO and auxin, a phytohormone that regulates growth and development processes such as lateral root formation, cell division, and elongation, as ·NO has the capacity to inhibit auxin transport through a mechanism of *S*-nitrosylation (Fernández-Marcos et al. 2011; Terrile et al. 2012; Shi et al. 2015).

·NO is also involved in the final development processes of senescence and fruit ripening. In senescent pea plants, ·NO content is down-regulated in leaves, which closely correlates with the lower L-arginine-dependent NOS activity detected as compared to that determined in the leaves of young plants (Corpas et al. 2004). However, a similar analysis in the root systems of both young and senescent plants reveals a different behavior, characterized by increased ·NO and $ONOO^-$ content and protein nitration (Begara-Morales et al. 2013), suggesting some kind of specificity in the function of ·NO and related molecules depending on the analyzed organ and stage of development, as was mentioned previously.

Nitric oxide is also involved in reproductive organs and has the capacity to repress floral transition in *Arabidopsis thaliana* by inhibiting *CONSTANS* and *GIGANTEA* gene expression (He et al. 2004) which promotes flowering and regulates photoperiodic flowering, respectively. The rate and orientation of pollen tube growth is regulated by the level of ·NO at the pollen tube tip which appears to be mediated by cGMP (Prado et al. 2004). On the other hand, ·NO is involved in pollen–pistil interactions, in which ·NO appears to influence the targeting of pollen tubes to the ovule's micropyle by modulating the action of its diffusible factors (McInnis et al. 2006; Prado et al. 2008). Analysis carried out during olive flower development shows that ·NO content is also modulated depending on the developmental stage and tissue, with an increase in ·NO production in pollen grains and tubes observed during the receptive phase in the stigma (Zafra et al. 2010).

Fruit ripening is another complex process that is regulated by ethylene production which is characterized by increased ROS production. ·NO has also been shown to interact with ethylene and the ROS metabolism (Leshem and Pinchasov 2000;

Manjunatha et al. 2010). During pepper fruit ripening, apart from the more apparent change in color from green to red, there are also significant biochemical adjustments. Thus, analysis of $^{\cdot}$NO metabolism using proteomic approaches shows that, during ripening, the nitration of proteins such as catalase, NADP-dependent glyceraldehyde-3-phosphate dehydrogenase, a transketolase 1, a 20S proteasome alpha 6 subunit, or ferredoxin-dependent glutamate synthase 1 involved in redox, oxidative, protein, and carbohydrate metabolisms changes, with the antioxidant catalase being among the most affected. However, it has been shown that the application of exogenous $^{\cdot}$NO gas can prevent protein nitration and delay fruit ripening (Chaki et al. 2015a).

5 Nitro-Oxidative Stress Under Abiotic Conditions

Adverse environmental conditions including drought, salinity, soil mineral toxicity, cold, and heat can limit agricultural production considerably. It has been well established that all these abiotic stresses may lead to oxidative stress characterized by uncontrollable overproduction of ROS that generates molecular damage in lipids, proteins, and nucleic acid. With the discovery of $^{\cdot}$NO and NO-derived molecules, many researchers set out to show that these adverse conditions are also associated with nitrosative stress (Valderrama et al. 2007; Corpas et al. 2008, 2011). Thus, it has been proposed that an increase in protein nitration could be a reliable biomarker of a specific stress similar to protein oxidation which is a marker of oxidative stress (Corpas et al. 2007; Arasimowicz-Jelonek and Floryszak-Wieczorek 2011). However, given the metabolic interplay between these two families of molecules (ROS and RNS) in which many enzymes involved in ROS metabolism are targets of PTMs mediated by $^{\cdot}$NO (see Table 2), nitro-oxidative stress would be a more appropriate term (Corpas et al. 2013).

5.1 Heavy Metals

Contamination by heavy metals such as cadmium, arsenic, lead, or mercury is an increasingly serious problem for the environment and consequently for agriculture and human health (World Health Organization 2007; Hernández et al. 2015). Although it has been well established that heavy metals usually trigger an oxidative stress response, recent analysis of the plant $^{\cdot}$NO metabolism has demonstrated that they also induce nitro-oxidative stress.

Arsenic (As) is a metalloid naturally present in the environment, with arsenate (AsV) being the main arsenic species in aerobic soils and arsenite (AsIII) in soils under anaerobic and reducing conditions. In higher plants, inorganic arsenic can be accumulated in the form of arsenite (AsIII) throughout nodulin 26-like intrinsic (NIP) aquaporin channels or in the form of arsenate (AsV) throughout the phosphate transporter system (Zhao et al. 2010). Various studies have demonstrated that arsenic triggers nitro-oxidative stress. For example, *Arabidopsis thaliana* seedlings exposed to 500 μM AsV trigger a significant increase in $^{\cdot}$NO content, GSNOR activity, and protein tyrosine nitration as well as a concomitant decrease in glutathione and GSNO content (Leterrier et al. 2012). Curiously, the exogenous application of $^{\cdot}$NO can alleviate arsenic-induced oxidative stress in different plant species by enhancing antioxidant defenses (Singh et al. 2009, 2013; Hasanuzzaman and Fujita 2013), thus corroborating the aforementioned cross talk between the families of ROS and RNS molecules.

Cadmium toxicity in plants is well established (Chmielowska-Bąk et al. 2014) and generally causes an augmentation of ROS production and consequently oxidative stress (Dixit et al. 2001). In addition, the $^{\cdot}$NO metabolism is differentially affected under cadmium stress. In pea, 50 μM $CdCl_2$ provoked a lower GSNOR activity with a decrease in $^{\cdot}$NO and GSNO content but accompanied with a rise of ROS production and an increase in salicylic acid, jasmonic acid, and ethylene (Barroso et al. 2006; Rodríguez-Serrano et al. 2006), indicating the presence of nitro-oxidative stress where $^{\cdot}$NO plays an essential role as a signaling molecule (Arasimowicz-Jelonek et al. 2011) and participates in homeostasis in order to maintain the metabolic equilibrium in the presence of cadmium (Gill et al. 2013; Liu et al. 2015). In *Arabidopsis thaliana*, cadmium induces $^{\cdot}$NO generation from NOS activity, which contributes to the inhibition of root growth partly caused by iron deprivation (Besson-Bard et al. 2009; Han et al. 2014). At the subcellular level, Cd stress in Arabidopsis has recently been shown to trigger the production of both $O_2^{\cdot -}$ and $^{\cdot}$NO in peroxisomes with a concomitant generation of $ONOO^-$, thus corroborating reports that these organelles participate in the mechanism of response to this metal (Corpas and Barroso 2014).

5.2 *Salinity*

Over 6 % of the world's land mass has been estimated to be affected by either salinity or sodicity which negatively affect plant productivity by inhibiting plant growth, ion balance, and water relations (Hasegawa et al. 2000). As mentioned previously, salinity is commonly accompanied by oxidative stress, with an increasing number of studies pointing to the involvement of RNS in these processes (Valderrama et al. 2007; Molassiotis et al. 2010). Although its effects may vary somewhat depending on the plant species and the severity of the salinity treatment, salinity generally triggers the $^{\cdot}$NO metabolism, which has been observed to cause an increase in $^{\cdot}$NO production and the number of *S*-nitrosylated and nitrated proteins as well as a modulation in redox homeostasis and the antioxidant system (Valderrama et al. 2007; Tanou et al. 2009b, 2012; Manai et al. 2014a). Some studies have also demonstrated that $^{\cdot}$NO appears to modulate and enhance the expression of Na^+/H^+ antiporter genes under high salinity conditions which contributes to mitigating the negative effects of sodium (Zhang et al. 2006; Lu et al. 2013; Chen et al. 2013).

Proteomic approaches have also identified a significant number of proteins affected by *S*-nitrosylation and nitration (Tanou et al. 2009a). Data on the ˙NO metabolism under salinity stress by the application of exogenous ˙NO appear to provide a certain level of resistance to salinity stress. Thus, in 5-month-old bitter orange (*Citrus aurantium*) trees, pretreatment of the root system with 100 μM sodium nitroprusside (SNP; a ˙NO donor) induces considerable antioxidant resistance in the form of catalase, SOD, ascorbate peroxidase, and glutathione reductase (Tanou et al. 2009a, b). Similarly, tomato (*Solanum lycopersicum*) plants exposed simultaneously to 120 mM NaCl and a ˙NO donor (100 μM or 300 μM SNP) through their root system show a decrease in NaCl-induced lipid oxidation in leaves, which was accompanied by an increase in the antioxidant system's SOD, APX, GR, and POD activities in roots and leaves and also increased ascorbate and proline content. It is also worth noting that a newly CuZnSOD is induced in roots, suggesting that the ˙NO performs a regulatory function at the protein and gene levels of this antioxidant enzyme (Manai et al. 2014b). Tomato plants have also shown an increase in the activity of some enzymes such as nitrate reductase (NR) and nitrite reductase (NiR) involved in the nitrogen metabolism. On the other hand, genetic approaches using overexpression of rat neuronal NOS (nNOS) in rice show increases in both NOS activity and ˙NO accumulation, resulting in improved tolerance of transgenic rice to salt and drought stresses (Cai et al. 2015).

5.3 Drought or Water Stress

Drought affects plants at many levels, ranging from the morphological to the molecular one. The visual symptoms of drought stress include the reduction of shoots (leaves and stem) and root proliferation which disturbs plant–water relations and reduces water-use efficiency. At the biochemical level, drought stress disturbs the balance between ROS production and antioxidant defenses, thus causing oxidative stress. As with other types of stress, ˙NO plays a prominent role in response mechanisms (Santisree et al. 2015). For example, in the legume *Lotus japonicus* exposed to water stress, the spatial distribution of nitro-oxidative stress has been described; oxidative stress levels increased in leaves while nitrosative stress levels were higher in roots in which ˙NO content increased whereas GSNO reductase activity diminished, which may explain the rise in protein tyrosine nitration (Signorelli et al. 2013). On the other hand, in white clover (*Trifolium repens*), ˙NO mediates drought tolerance through the activation of antioxidant enzymes such as SOD, APX, and catalase (Peng et al. 2015).

Abscisic acid (ABA), defined as a stress plant hormone due to its rapid accumulation in response to water stress, plays a major role in the regulation of plant growth, development, and tolerance under stress conditions. Under water deficiency conditions, plants use a stomatal closure strategy. The movement of guard cells is highly regulated, involving molecules such as ABA, H_2O_2, NO, and NADPH (Neill et al. 2008; Gayatri et al. 2013; Leterrier et al. 2016). ˙NO is known to induce stomatal closure, although the interplay between the different players is complex. A recent in vitro analysis has demonstrated that ABA receptors are targeted by tyrosine nitration which reduces receptor activity (Castillo et al. 2015). Therefore, under stress conditions, the production of both $^{\cdot}$NO and superoxide together with a concomitant generation of $ONOO^{-}$ could explain how $^{\cdot}$NO limits ABA signaling through nitration. On the other hand, $^{\cdot}$NO negatively regulates ABA signaling in guard cells by inhibiting open stomata 1 (OST1)/sucrose nonfermenting 1 (SNF1)-related protein kinase 2.6 (SnRK2.6) through *S*-nitrosylation, specifically in the Cys137 (Wang et al. 2015).

5.4 Low and High Temperature

Extreme temperatures are environmental stresses that affect crop production and quality, involving the expression of many genes as well as significant numbers of proteins and metabolites. New data have shown that $^{\cdot}$NO metabolism is affected at different levels depending on the plant species or temperature intensity among other factors (Corpas et al. 2008; Piterková et al. 2013; Puyaubert and Baudouin 2014; Sehrawat and Deswal 2014).

For example, pepper plants exposed to low temperature (LT) for several days undergo significant changes in the metabolism of RNS and ROS together with an increase in both protein tyrosine nitration (NO_2-Tyr) and lipid peroxidation, indicating that LT induces nitro-oxidative stress (Airaki et al. 2012). In *Medicago sativa* under cold stress, the interaction of $^{\cdot}$NO, H_2O_2, and ABA mediates the induction of the *S*-adenosylmethionine synthetase (SAMS), an enzyme that catalyzes the formation of *S*-adenosylmethionine (SAM), a precursor of polyamines and ethylene, which is involved in cold tolerance (Guo et al. 2014). The C-repeat binding factor (CBF) is one of the most studied cold stress-signaling pathways in plants. Recently, tomato seedlings under LT stress have been shown to undergo dual regulation of the CBF by $^{\cdot}$NO at the transcriptional and translational level through *S*-nitrosylation (Kashyap et al. 2015). Furthermore, in poplar tree, the existence of a feedback mechanism between GSNOR activity and protein *S*-nitrosylation has been shown which is regulated in response to cold stress (Cheng et al. 2015).

On the other hand, sunflower seedlings exposed to high temperature (HT) experience oxidative stress; this impairs the $^{\cdot}$NO metabolism by lowering $^{\cdot}$NO content and reducing GSNOR activity and gene expression with a concomitant accumulation of total SNOs including GSNO as well as peroxynitrite formation and increased protein nitration; ferredoxin–NADP reductase is one of these inhibited nitrated proteins that affect photosynthesis (Chaki et al. 2011). The identification and characterization of the GSNOR knock-out mutant in Arabidopsis through the use of genetic techniques demonstrate the involvement of this important gene under physiological and stress conditions including HT. For example, analysis of the mutant HOT5 (sensitive to hot temperatures) shows that GSNOR modulates the intracellular level of SNOs, resulting in thermotolerance as well as regulation of plant growth and development (Lee et al. 2008). Similarly, the mutant paraquat resistant 2 (PAR2) which encodes a GSNOR has a higher level of $^{\cdot}$NO, shows an anti-cell death phenotype (Chen et al. 2009; Xu et al. 2013).

6 Nitric Oxide in Plant–Pathogen Interactions

Systemic acquired resistance (SAR) is a cellular mechanism of disease resistance that is induced in response to initial infection and that protects uninfected areas of the plant against potential secondary infections by related or unrelated pathogens. In this process, the RNS and ROS families of molecules interact with each other to provide an adequate response to different pathogen organisms including bacteria, fungi, nematodes, and insects (Prats et al. 2005; Chaki et al. 2009; Wünsche et al. 2011; Scheler et al. 2013; Wendehenne et al. 2014; Zhou et al. 2015).

As a model plant, *Arabidopsis thaliana* has been extensively used to study the many ways in which $^{\cdot}$NO and derived molecules are involved in plant–pathogen interactions (Yu et al. 2012; Chen et al. 2014; Kovacs et al. 2015). This plant's available genomic database information combined with the use of proteomic techniques have facilitated the identification of the protein targets of *S*-nitrosylation (Romero-Puertas et al. 2008; Chaki et al. 2015b) and nitration (Cecconi et al. 2009) during pathogen infection. This information has enabled researchers to gain a deeper understanding of the $^{\cdot}$NO metabolism in this type of interaction. For example, it has been well established that plants use oxidative burst to respond to pathogen attacks, in this case, membrane-bound NADPH oxidase (NOX), also called the respiratory burst oxidase homologue (RBOH), a key element in the generation of $O_2^{-\cdot}$. Interestingly, *S*-nitrosylation of AtRBOH type D at Cys890 has been shown to abolish its ability to synthesize $O_2^{\cdot -}$ (Yun et al. 2011). However, there is complementary information on other plant species. For example, the infection of a susceptible cultivar of sunflower seedlings with the fungus *Plasmopara halstedii,* causing downy mildew, has been observed to increase protein nitration accompanied by an augmentation in SNOs; however, in the resistant sunflower cultivar, with its higher SNO content, a redistribution of these SNOs in the penetration site has been observed in the presence of the pathogen, which prevents the spread of infection (Chaki et al. 2009), thus confirming the importance of SNOs under this type of biotic stress. On the other hand, in tobacco cells exposed to the fungal elicitin cryptogein, analysis of *S*-nitrosylated proteins has identified 11 candidates for *S*-nitrosylation including the cell division cycle 48 (CDC48) protein, a member of the AAA^+ ATPase family that mediates resistance to certain pathogens. However, *S*-nitrosylation abolishes NtCDC48 ATPase activity (Astier et al. 2012). In tobacco cells exposed to cryptogein, $^{\cdot}$NO has also been observed to require NtRBOHD activity to induce cell death (Kulik et al. 2015).

7 Nitric Oxide in Plant Beneficial Interactions

Plants can also establish specific and beneficial interactions with other organisms, in which $^{\cdot}$NO and other elements have been found to act as signal molecules. In this context, the most studied interaction is the symbiosis between Legume–Rhizobium, characterized by the formation of differentiated organs called nodules, where $^{\cdot}$NO is required for the optimal establishment of the symbiotic interaction (Meilhoc et al. 2011; del Giudice et al. 2011; Hichri et al. 2015). Root nodules, enabling atmospheric N_2 to be fixed to ammonia, have two critical elements: leghemoglobin (Lb) and nitrogenase. Lb is an oxygen carrier whose function is to prevent the presence of O_2 which reduces the activity of oxygen-sensitive nitrogenase, the enzyme responsible for fixing atmospheric nitrogen to ammonia. Interestingly, nitrogenase activity is inhibited by $^{\cdot}$NO, indicating that $^{\cdot}$NO levels in rhizobia are a determining factor in efficient symbiotic processes (Cabrera et al. 2011). A rise in ROS and RNS has also been observed in senescent nodules which cause nitro-oxidative stress, leading to a reduction in the ability of symbiotic leghemoglobins to scavenge oxygen due to the modifications mediated by these ROS/RNS (Sainz et al. 2013). However, the formation of nitrated leghemoglobins during normal metabolism has been detected in functional nodules which, it has been suggested, may act as a sink for toxic peroxynitrite to protect nodule functionality (Sainz et al. 2015).

Another group of bacteria, *Azospirillum brasilense,* has the capacity to produce $^{\cdot}$NO from ammonia. When this bacterium interacts with tomato roots, the $^{\cdot}$NO produced stimulates lateral root formation (Creus et al. 2005; Molina-Favero et al. 2008). $^{\cdot}$NO is also generated in other interactions such as those between plant roots and arbuscular mycorrhizal fungi where $^{\cdot}$NO is produced in the roots of *Medicago truncatul*a when they come in contact with the exudates of the fungus *Gigaspora margarita* (Calcagno et al. 2012).

8 Conclusions and Future Perspectives

Since it was discovered that $^{\cdot}$NO could be endogenously produced in plant cells, the number of biochemical and physiological actions found to be mediated by this free radical has increased continually (Corpas and Barroso 2015a). It is now well established that $^{\cdot}$NO is responsible for a wide spectrum of actions which are based on a complex network of biochemical interactions with a diverse range of molecules, both small and large, such as metals, superoxide radicals, glutathione, proteins, lipids, and nucleic acid, that affect its structure and functions. In this context, although certain authors have begun to regard $^{\cdot}$NO as a "new phytohormone," some important issues still need to be addressed by the scientific community. For example, it is necessary to determine how and where $^{\cdot}$NO is produced in specific processes and also to identify the molecules which are targets under physiological and stress conditions, with nitro-fatty acids being a good example of these. A major effort is therefore being made to determine the way in which $^{\cdot}$NO can be sensed in order to control the concentrations of RNS. On the other hand, research into the beneficial effects of applying exogenous $^{\cdot}$NO to treat plants against certain environmental stresses has been increasing. In fact, many studies have shown that exogenous $^{\cdot}$NO can ameliorate oxidative damage caused by stress by activating a diverse range of antioxidant systems and can even modulate physiological processes such as senescence and fruit ripening which are good examples of the biotechnological applications of $^{\cdot}$NO. Nevertheless, it is important to keep in mind than production levels of $^{\cdot}$NO into cells may determine its physiological function because when it is produced at low level, NO could have signaling functions but when it is overproduced it may have toxic effects.

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