Nitric Oxide Mediated Effects on Chloroplasts

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Summary

Nitric oxide (NO) is emerging as a signaling molecule in plants. Its metabolism, site and mode of action in chloroplasts are still not clear. Chloroplasts are emerging as an alternative site for NO synthesis in plants. However, exogenous NO donors show direct evidence on the action of this molecule on chloroplasts under stress as well non-stress conditions. Nitric oxide is also implicated in the development and senescence of the organelle. The effects of NO on chloroplasts, particularly on photosynthetic and antioxidative processes are described. The target sites and probable sites of action are enumerated.

Keywords

Nitric Oxide • Chloroplast • Electron transport • Photosynthesis • Photosystems • Photophosphorylation • Greening • Senescence • Development • Abiotic stress

Contents

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Abbreviations

PSI	photosystem I
PSII	photosystem II
LHCII	light-harvesting chlorophyll *a*/*b* complex of PSII
GSNO	S-nitrosoglutathione
GSSG	glutathione disulphide
NO	nitric oxide
qL	coefficient of photochemical fluorescence quenching assuming interconnected PSII antennae
qP	coefficient of photochemical fluorescence quenching assuming non-interconnected PSII antennae
NPQ	non-photochemical quenching
Rubisco	ribulose-1,5-bisphosphate carboxylase
PTIO	2-phenyl-4,4,5,5-tetramentyl-imidazoline-1-oxyl-3-oxide
NOS	nitric oxide synthase
L-NNA	Nω-nitro-L-arginine
SNP	sodium nitropruside
OEC	oxygen-evolving complex
CPTIO	2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-l-oxyl-3-oxide

14.1 Introduction

Nitric oxide (NO) is a gaseous molecule with a signaling role in plant growth, development and responses to environmental changes (Neill et al. 2008; Palavan-Unsal and Arisan 2009; Misra et al. 2010a, b, 2011, 2012). The effects of NO in plants can be direct or through intermediate effector molecules regulating cellular metabolism (Krasylenko et al. 2010). Nitric oxide action is achieved also by modifying the redox state of the cell and can modulate the activity of proteins, through reversible reactions with functional groups such as thiols and heme. It is well known that iron is a necessary element for synthesis and development of chloroplast and NO plays an important role in the distribution of iron in the chloroplasts in plant leaves (Sun et al. 2007). Nitric oxide, a highly unstable free radical, has been described both as a cytotoxin and a cytoprotectant in plants, as well (Beligni and Lamattina 1999a, 2001a). This signal molecule appears to take part in the regulation of cellular redox homeostasis, acting either as an oxidant or as an antioxidant (Stamler et al. 1992). However, at lower concentrations, NO promotes normal plant growth and development (Beligni and Lamattina 2001b). Nitric oxide stimulates leaf expansion, prevents etiolation, retards leaf senescence and induces stomatal closure (Leshem et al. 1998; Beligni and Lamattina 2000; García-Mata and Lamattina 2001). When applied at relatively high doses to plants, NO clearly perturbs normal metabolism and reduces the net photosynthesis in leaves of oats and alfalfa (Hill and Bennett 1970). Nitric oxide in concentrations above optimal (above 10^{-6} M) inhibits the expansion of leaf lamina, increases the viscosity of simulated thylakoid lipid monolayers and potentially impairs photosynthetic electron transport (Leshem et al. 1998; Leterrier et al. 2012).

Chloroplasts are highly specialized semiautonomous photosynthesizing organelles found in green plants. There is wide diversity in chloroplast structure, function and adaptation. The chloroplasts encode a large number of their own RNAs and proteins, in addition to that synthesized by the nuclear genes, economizing the cellular energy demand for its structural organization. Chloroplast develops from a progenitor known as proplastid accompanied with the coordinated regulation of plastid and nuclear-encoded genes (Baumgartner et al. 1989; Dilnawaz et al. 2001; Joshi et al. 2013). The chloroplasts are the only organelle that supports autotrophy in plants through its role in photosynthesis and also sustains life on earth. The process involves coordination between the primary photochemical processes in the thylakoid membrane and reduction of CO_2 in the stroma of chloroplasts. The photochemical process includes solar energy trapping, photolysis of water, electron transfer and generation of

reductants for the reduction of CO_2 to carbohydrates in the stroma – the soluble fraction of chloroplasts. The thylakoid membrane has four main multi-subunit protein complexes: photosystem II (PSII), photosystem I (PSI), cytochrome b_6f and ATPase (Nelson and Yocum 2006).

Studies on the effect of NO on chloroplasts are crucial for understanding its role in green plants. In addition, chloroplasts are reported to be one of the several cellular sites for the synthesis of endogenous nitric oxide (Guo and Crawford 2005; Jasid et al. 2006; Galatro et al. 2013; Tewari et al. 2013). However, till date there is a lack of a precise report on the effect of the NO on the regulation of different physiological, biochemical and molecular processes in chloroplasts. In this review, we consolidate the up-to-date studies on the effect of NO on chloroplasts. An emphasis will be given in this chapter for the effect of NO on the photochemical efficiency in chloroplasts under physiological conditions and abiotic stress.

14.2 Sources of Nitric Oxide in Plants

The nitric oxide production in plant cells is compartmentalized and is mediated through several different pathways (Gupta et al. 2011). It has been shown to produce NO from nitrite (Desikan et al. 2002), from L – arginine by NOS like activity (Guo et al. 2003) and from S-nitrosoglutathione decomposition (Jasid et al. 2006) in chloroplasts. Non-enzymatic production of NO from nitrite involving plastid pigments such as carotenoids has also been reported (Cooney et al. 1994). Interestingly, NO synthesis in response to iron, elicitors, high temperatures, salinity or osmotic stress is first detected in chloroplasts using NO-sensitive diaminofluorescein probes (Foissner et al. 2000; Gould et al. 2003; Arnaud et al. 2006). In spite of several ifs and buts, these results corroborate the hypothesis that plastids are key players in the control of NO levels in plant cells. Nitric oxide originates in chloroplasts through the reduction of nitrite to NO and/or through nitric-oxide synthases (NOS) like activities (NOA) mediated NO biosynthetic pathway using arginine as a precursor molecule.

14.3 Effect of Nitric Oxide on Photosynthetic Pigment Dynamics

Nitric oxide improves the accumulation of chlorophylls (Chls) and even imitates red light responses in greening leaves (Beligni and Lamattina 2000). It is well known that the photosynthetic pigments, Chls in particular, are visible markers for chloroplast development and senescence in leaves (Misra and Biswal 1980, 1982; Misra and Misra 1986, 1987; Biswal et al. 2001; Dilnawaz et al. 2001). The synthesis of Chls and plastid proteins is intricately connected and is essential for the stability of Chl-protein complexes *in vivo* (Dilnawaz et al. 2001; Neill et al. 2003; Joshi et al. 2013). Seedlings grown in darkness develop etioplasts from proplastids, which ultimately transform into well organized chloroplasts in light (Misra and Misra 1987; Joshi et al. 2013). But, genes for nuclear-encoded Chl *a*/*b* – binding antennae and plastid-encoded Chl *a* – binding polypeptides are obligatorily dependent on incidence of light only. These photo-regulatory processes have several light receptors such as phytochrome and cryptochrome (Pogson and Albrecht 2011; Lepistö and Rintamäki 2012).

Nitric oxide donor sodium nitropruside (SNP) enhanced Chl synthesis and accumulation of light-harvesting chlorophyll *a*/*b* complex of PSII (LHCII) and PSIA/B, primary photochemistry of PSII and effective quantum yield of PSII of the developing chloroplasts in greening of barley leaves (Zhang et al. 2006). Nitric oxide scavenger PTIO (2-phenyl-4,4,5,5-tetramentylimidazoline-1-oxyl-3-oxide) or NOS inhibitor L-NNA (nitro-nitro-L-arginine) retarded the greening process. Moreover, sodium ferrocyanide, an analog of SNP, nitrite and nitrate etc. do not have any effect on the greening process, suggesting a positive role of NO in the greening process (Zhang et al. 2006). The endogenous NO content of greening leaves also increased in

parallel with the greening (measured by Chl accumulation) of leaves indicating a direct role of plastid NO in leaf greening (Zhang et al. 2006). Leaf senescence is associated with the symptoms of Chl degradation through various enzymatic and oxidative processes in the green cells (Biswal et al. 2001; Misra et al. 2006). Endogenous and exogenous NO at lower concentrations delayed leaf senescence, but at higher concentrations accelerated leaf senescence (Leshem et al. 1997; Guo and Crawford 2005; Mishina et al. 2007; Selcukcam and Cevahir 2008; Prochazkova and Wilhelmova 2011).

14.4 Interaction of Nitric Oxide with Oxygen Evolving Complex

Photosystem II is one of the sites of action for NO in chloroplasts (Wodala et al. 2008). At the electron donor side of PSII it acts at the oxygen-evolving complex (OEC). This complex is a part of the PSII, which is a multi-subunit chlorophyll-protein complex that uses light energy to oxidize water and form molecular oxygen, with a concomitant reduction of plastoquinone to plastoquinol (Debus 1992; Britt 1996). The functional conformation of the Mn cluster is expected to be maintained by a 33 kDa hydrophilic protein subunit of OEC attached to the luminal side of the D1/D2 heterodimer. During the oxidation of two water molecules to one oxygen molecule and protons, the OEC cycles through five intermediate redox states termed S_0–S_4 (Fig. 14.1). Dark adapted photosynthetic apparatus contains S_0 and S_1 states. The most reduced state is S_0, while S_1, S_2 and S_3 represent higher oxidation states and molecular oxygen being evolved during the transition from S_4 to S_0 states (Haumann et al. 2005; Penner-Hahn and Yocum 2005).

It is suggested that NO interacts with Mn cluster of PSII and leads to rapid destabilization of the excited states of OEC (Schansker and Petrouleas 1998). Studies with PSII and the di-manganese catalase have shown a similar mode of interaction of NO with the different oxidation states of the Mn clusters (Ioannidis et al. 2000). It is also suggested by Ioannidis et al. (2000) that one-electron reduction of the cluster occurs followed by release of NO_2^- as described below:

$$Mn^n + NO \rightarrow Mn^{n-1} + NO^+;$$
$$NO^+ + OH^- \rightarrow NO_2^- + H^+$$

Schansker et al. (2002) studied the oxygen oscillation patterns of PSII-enriched membranes and observed shift of the maximum flash-induced oxygen yield from flash 3 to flash 6/7 in the NO-treated samples. Considering these observations, the authors suggested the reduction of Mn cluster to the S_{-2} state by NO, which is assigned to the formation of Mn(II)-Mn(III) dimer. During catalysis the enzyme appears to cycle between the states Mn(II)-Mn(II) and Mn (III)-Mn(III) (Khangulov et al. 1990; Waldo and Penner-Hahn 1995).

Ioannidis et al. (2000) proposed a rapid interaction of NO with S_3 state of the OEC. This is explained by a metallo-radical characteristic of the S_3 state. A probable role of Tyr Y_D in oxidizing of Mn complex to the lower oxidizing state S_0 than the S_1 state was proposed by Styring and Rutherford (1987). Sanakis et al. (1997) proposed the formation of a Tyr-NO species which can act as an electron donor to PSII. An iminoxyl

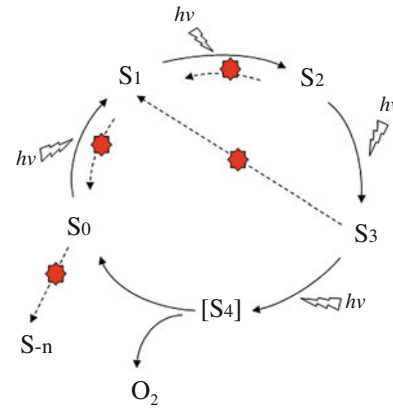

Fig. 14.1 Schematic presentation of the Kok's model of oxygen evolution, consisting of four stabile states (S_0–S_3) and one transient state (S_4). The possible sites of action of NO on the cycle are shown by *asterisks*. The back reduction of S-states by NO and possible over-reduction to S_{-n} states are shown by *dashed arrows*

radical is formed upon light-induced oxidation of this species, which is the first example of a chemical modification of one of the tyrosines of PSII to produce a photochemically active species. Our recent *in vitro* study demonstrated that the exogenous NO donor SNP (above 5 μM) has a clearly pronounced damaging effect on the primary oxygen-evolving reactions at the electron donor side of photosynthetic apparatus (Vladkova et al. 2011). In addition, our investigation for influence of exogenous NO donor SNP on isolated thylakoid membranes also revealed a dramatic increase of PSII population in the most reduced S_0 state and an increase of the turnover time of the oxygen-evolving centers, i.e. delayed the process of the electron donor capturing or S_i states turnover (Vladkova et al. 2011).

14.5 Effect of Nitric Oxide on Photosynthetic Electron Transport

One of the important reactions of NO in biology is interaction with metal complexes (Wink and Mitchell 1998). Because NO possesses an unpaired electron, it has high affinity to transition metals to form metal-nitrosyl complexes (Wink and Mitchell 1998). Due to this reason, proteins containing transition metal ions in either heme or non-heme complexes can be the potential targets for NO (Wink and Mitchell 1998). Nitric oxide is able to influence the photosynthetic electron transport chain directly by binding to such non-heme iron in the core complex of the PSII (Wodala et al. 2008). The important binding sites of NO in PSII are the non-heme iron between Q_A and Q_B binding sites (Diner and Petrouleas 1990; Petrouleas and Diner 1990) and Y_D, the Tyr residue of D2 protein (Sanakis et al. 1997). Electron paramagnetic resonance (EPR) studies confirmed the NO binding to non-heme iron and that NO competes with bicarbonate for its binding (Diner and Petrouleas 1990). Formate, an anion which also competes with bicarbonate, binds simultaneously with NO (Diner and Petrouleas 1990) besides the other anions like fluoride (Sanakis et al. 1999).

Experiments with isolated thylakoids indicated that NO binding slows down the rate of electron transfer between Q_A and Q_B (Diner and Petrouleas 1990). Binding of NO to the $Q_AFe^{2+}Q_B$ complex is facilitated in the presence of reduced Q_A acceptor, as this reduction weakens the bond between bicarbonate and iron (Goussias et al. 2002). Nitric oxide binding to PSII can also decrease the rate of electron transport on the donor side as well, since *in vitro* experiments have proven that NO interacts with the Y_D• tyrosine residue and the OEC. The latter is reduced to the S_{-2} state by NO, as shown by oxygen electrode, fluorescence and EPR measurements (Schansker et al. 2002). Measurements in the presence of DCMU demonstrated that NO induces inhibition of Q_A^- recombination with the S_2 state of the OEC. This donor side inhibition of electron transport may sufficiently be accounted by the reduction of either the OEC, or the Y_D• residue by NO. To the contrary, our recent results showed that the NO donor SNP is probably the only NO donor which stimulates the electron transport through PSII at sub-μmolar concentrations (Vladkova et al. 2011). Nitric oxide interacts with the tyrosine residue of the D2 protein (Sanakis et al. 1997) and the resulting Y_D•–NO couple has a decreased redox potential low enough to become a more efficient electron donor in isolated thylakoid membranes than the immediate redox-active tyrosine residue (Y_Z) located on the D1 protein. The probable binding sites and sites of action in thylakoid membranes are summarized in Fig. 14.2.

Chlorophyll fluorescence studies have provided contradictory effects of NO on chloroplasts *in vivo*. However, these results depend on the used NO donor. In the leaves, NO derived from S-nitroso-N-acetylpenicillinamine (SNAP) showed no effect on the maximum quantum efficiency of photosynthesis, but that from SNP and S-nitrosoglutathione (GSNO) decreased this parameter (Takahashi and Yamasaki 2002; Yang et al. 2004; Wodala 2006; Wodala et al. 2008). All the NO donors induced a decrease in effective quantum efficiency, which is related to photochemical

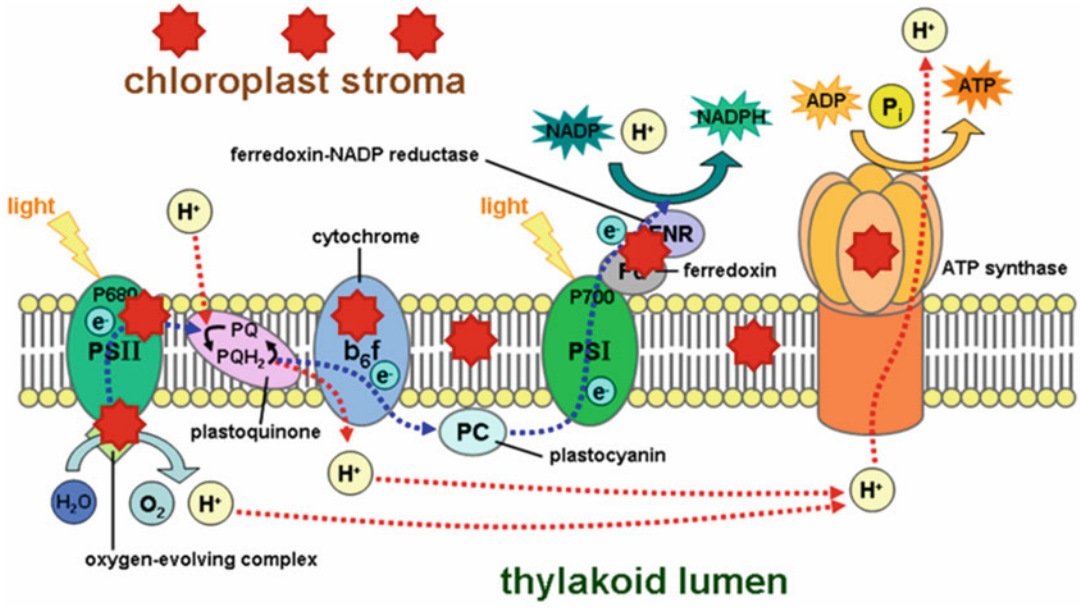

Fig. 14.2 Summary and schematic presentation of the probable binding of NO to different components of PSII, cytochrome b_6f, PSI, ATPase complexes. The nitrosylation of membrane lipids and of both thylakoid and stromal polypeptides are shown as red colored *circular asterisks*. These binding and nitrosylation affect photosynthetic processes

quenching (qP). These studies indicated that NO increases the proportion of closed PSII reaction centers in intact leaves (Wodala 2006; Wodala et al. 2008). However, all these results are not uniform and unequivocal. Wodala et al. (2008) suggested that the different chemical properties of NO donors and the different experimental conditions generate conflicting experimental results *in vivo*. Fast Chl fluorescence induction kinetics of GSNO-treated leaf disks confirmed significant donor and acceptor side inhibition of electron transport (Wodala et al. 2008).

It has been found that NO influences the non-photochemical quenching (NPQ). Besides reducing steady-state NPQ values, NO changes the amplitude and kinetics of an NPQ transient, which resembles reaction-center NPQ described by Finazzi et al. (2004). Reaction-center NPQ arises upon the onset of illumination of dark-adapted leaves and, at low light intensities, it is relaxed rapidly after a few min of illumination. On the basis of its fast relaxation and ΔpH-dependency, Finazzi et al. (2004) showed that reaction-center NPQ is caused by the rapid and transient over acidification of the thylakoid lumen, which is created by the immediate onset of the photochemistry. In addition, they suggested that the ΔpH may be further increased by cyclic and pseudo-cyclic electron transport (Mehler-reaction) and explain the relaxation of this transient form of NPQ by the activation of the carbon fixation apparatus, which decreases ΔpH and redox pressure. Although a potential effect of NO on Calvin cycle activation would account for changes in this NPQ transient, steady-state NPQ values below control values indicate that NO does not decrease the maximum rate of the Calvin cycle (Finazzi et al. 2004).

Photosynthetic studies on stomata of peeled epidermal strips respond to exogenous NO by instantly decreasing photochemical fluorescence quenching coefficients (qP and qL), the operating quantum efficiency of PSII, and NPQ to close to zero. However, NO effect *in vivo* is reversible. The reversible inhibition by NO of the electron transport rate could be restored by bicarbonate, a

compound known to compete with NO for one of the two coordination sites of the non-heme iron (II) in the $Q_AFe^{2+}Q_B$ complex (Ordog et al. 2013).

14.6 Effect of Nitric Oxide on the Photophosphorylation in Chloroplasts

Previous studies revealed that NO donor SNAP inhibits the linear electron transport rate and light-induced pH formation (ΔpH) across thylakoid membrane, and decreased the rate of ATP synthesis (Takahashi and Yamasaki 2002). The inhibitory effect of NO on the photophosphorylation can be prevented by a supplemental high concentration of bicarbonate. It has been reported that high concentrations of bicarbonate enable the bound NO to liberate from the reaction center and recover electron transport activity (Diner and Petrouleas 1990). Thus, sensitivity of photosynthesis against NO would depend on a local concentration of bicarbonate within thylakoid membranes. It is plausible that the decreased rate of electron transport, due to the NO-induced dissociation of bicarbonate from the specific sites of thylakoids, is involved in the mechanism of the inhibitory effect of NO on the photophosphorylation. The overall effect of NO on the electron transport and the photophosphorylation as well its resultant effect on the stromal enzymes is summarized and shown in Fig. 14.2.

14.7 Ameliorating Effect of Nitric Oxide on Photosynthetic Stress Responses

Plants produce substantial amounts of NO in their natural environments (Wilson et al. 2008). In recent years, there has been increasing evidence that NO is involved in regulating, if not all, many key physiological processes in plants under normal and stress conditions. NO is reported to ameliorate several stress responses in plants (García-Mata and Lamattina 2001, 2002; Arasimowicz and Floryszak 2007; Krasylenko et al. 2010; Misra et al. 2011). Abiotic stresses, such as drought, high and low temperature, salinity, heavy metals, UV-B and oxidative stress is reported to induce NO production in plants (Shi et al. 2005; Arasimowicz and Floryszak 2007; Qiao and Fan 2008; Misra et al. 2011). Stressors form free radicals and other oxidants, resulting in increased level of reactive oxygen species (ROS) in plant cells (Mittler 2002; Qiao and Fan 2008). NO eliminates the superoxide radicals and as a signal molecule interacts with plant hormones and ROS (Laxalt et al. 1997; Zhao et al. 2004; Qiao and Fan 2008). In addition to its signal roles, NO may also function as a regulator of gene expression (Kopyra and Gwozdz 2004; Qiao and Fan 2008). A large amount of NO may combine with O^{2-} to form peroxynitrite ($ONOO^-$), which has been reported to damage lipids, proteins and nucleic acids (Yamasaki et al. 1999).

14.7.1 Nitric Oxide Under Osmotic Stress

Osmotic stress is one of the major abiotic factors limiting crop productivity and natural status of the environment, affecting functions of the plants (Misra et al. 2001). Drought, high salinity and freezing impose osmotic stress on plants. Plants respond to this stress in part by modulating gene expression, which eventually leads to the restoration of cellular homeostasis, detoxification of ROS and recovery of growth (Xiong and Zhu 2002). One of the most important responses of the plants under osmotic stress is increased synthesis of abscisic acid (ABA) (Neill et al. 2008). Nitric oxide maintains leaf water content by regulating ABA-induced stomatal closure during osmotic stress. But the physiological role of NO-induced ABA accumulation remains unknown. Reactive oxygen species are one of the main damaging compounds that are produced during stress and osmotic stress in particular (Beligni and Lamattina 1999a, b). The protective action of NO against oxidative damage can be explained by two mechanisms. Firstly, NO

operates as a signaling molecule, which activates cellular antioxidant enzymes (Huang et al. 2002; Shi et al. 2005; Zhao et al. 2008). Secondly, NO might detoxify ROS directly. Mutant analysis of genetically modified *Arabidopsis* showed evidences that NO is an endogenous regulator of the tolerance of the plants to salt stress (Martinez et al. 2000; Zhao et al. 2004, 2007). These authors showed that *Atnos 1* mutant with decreased NO production due to a T-DNA insertion in *AtNOS* gene was hypersensitive to oxidative stress induced by NaCl (Martinez et al. 2000; Zhao et al. 2004, 2007).

14.7.2 Nitric Oxide Under Temperature Stress

Extreme temperatures either high or low (chilling) are stressful to plants affecting photosynthesis in plants (Misra and Misra 1986; Misra et al. 1997). Heat stress can also cause an overproduction of ROS, which could be involved in triggering defence responses against potentially damaging temperatures (Suzuki and Mittler 2006; Volkov et al. 2006; Kotak et al. 2007; Locato et al. 2008). A significant rise in NO production under heat stress in alfalfa sprouts (Leshem et al. 1998) and in tobacco leaf cells (Gould et al. 2003) are reported. Conversely, pea plants exposed at 38 °C for 4 h reduced the NO content of leaves, but it was found that the S-nitrosothiol (SNOs) content increases threefold and that the protein nitrosylation is enhanced (Corpas et al. 2008a). Protein nitrosylation can cause an inhibition of the activities of photosynthetic enzymes such as carbonic anhydrase and of ferredoxin-NADP reductase (Chaki et al. 2011). In *Arabidopsis*, several mutants have been identified to have impairment in the *GSNOR1* gene, showing the involvement of this gene in the mechanism of response against heat stress. Thus, the mutant HOT5 (sensitive to hot temperatures) showed that GSNOR modulates the intracellular level of SNOs, enabling thermo-tolerance, as well as the regulation of plant growth and development (Lee et al. 2008). In calluses of reed, the exogenous application of SNP or ABA elevated thermo-tolerance by alleviating ion leakage, lipid peroxidation and growth suppression induced by heat stress (45 °C for 2 h). On the other hand, exogenous ABA notably activated NOS activity and increased NO release, maintaining the heat tolerance (Song et al. 2008). Studies so far unequivocally report an increase in NO content and increase in thermo-tolerance of plants.

Chilling (below 4 °C) or cold (below 10 °C) stress is also detrimental for plant systems (Misra et al. 1997). A proteomic analysis showed that the chilling stress induced S-nitrosylation of Rubisco, which correlated with the inhibition of photosynthesis (Abat and Deswal 2009). Pea plants exposed to low temperature (8 °C for 48 h) showed an enhanced activity of L-arginine NOS and GSNOR, and an increase in the content of SNOs (Sharma et al. 2005). Low temperature caused an imbalance of the ROS and reactive nitrogen species metabolism in leaves, triggering a rise in the lipid oxidation and the protein tyrosine nitration, which indicates an induction of oxidative and nitrosative stress (Corpas et al. 2008b; Airaki et al. 2012). Similar responses and an increase in NO content have been reported in *Arabidopsis thaliana* exposed to chilling (4 °C for 1–4 h) stress or during cold acclimation (Zhao et al. 2009; Cantrel et al. 2011). It is most probable that temperature stress induced increase in NO and stress ameliorating effect of NO could be due to the antioxidative action of NO (Desikan et al. 2002).

14.7.3 Nitric Oxide Under High Light Stress and UV Radiation

High light causes photoinhibition of photosynthesis and generates ROS in green plants (Misra et al. 1997). Protective role of NO during photoinhibition has been reported in higher plants. Pronounced increases of NO production are found in tall fescue leaves after exposure to high-light stress (Xu et al. 2010). Nitric oxide might act as a signaling molecule to enhance antioxidant enzyme activities, further protecting

against injuries caused by high light stress (Xu et al. 2010). However, *Chlamydomonas reinhardtii* cells under very high light conditions induces $^1O_2$ (singlet oxygen) accumulation due to a decrease in the $^1O_2$ scavenging capacity caused by NO-mediated inhibition of carotenoid synthesis and PSII electron transport, which in turn leads to oxidative damage and cell death (Chang et al. 2013).

The UV-B radiation (280–320 nm) clearly affects plant growth and usually also induces oxidative stress. Moreover, UV-B triggered a rise in ROS widely distributed in chloroplasts and mesophyll cells, causing cell damage. It has been observed that apocynin reduces UV-B-induced oxidative damage because it reduces the Chl breakdown caused by H_2O_2, and this is correlated with NO production mediated by an enhanced NOS activity (Tossi et al. 2009). In the case of maize leaves, the UV-B irradiation provoked a simultaneous rise in the concentration of ABA, H_2O_2 and NO in leaves. These authors also reported that the accumulation of endogenous NO is ABA-dependent and is responsible for tolerance to high doses of UV-B radiation (Tossi et al. 2012). Exogenous NO partially alleviated the UV-B effect characterized by a decrease in Chl contents and oxidative damage to the thylakoid membrane in bean seedlings (Shi et al. 2005). Zhang et al. (2009) suggested that under UV-B stress, NO production is mediated by H_2O_2 through the enhancement of NOS activity. It is well established that H_2O_2 induces NO synthesis and accumulation and vice versa (cf. Mazid et al. 2011).

The other possible explanation of the protective action of NO on the photosynthesis under UV and temperature stress can be either due to the modification of the OEC after interaction with NO (for SNP treated thylakoid membranes), which leads to a strong increase of the most reduced S_0 state in the dark or an increase of PSII open centers (Vladkova et al. 2011). It is well established that the most sensitive component to UV and temperature stress in photosynthetic membranes is LHCII-PSII supercomplex (Ivanova et al. 2008; Dankov et al. 2009; Apostolova and Dobrikova 2010; Dobrikova et al. 2013). Apostolova et al. (2006) showed that there is a relationship between the organization of PSII complex and oxidation state of the Mn clusters of the OEC. On the other hand, it has been demonstrated that UV radiation causes increase of PSII centers in the S_0 state, as one of the reasons for the UV-induced inhibition of the oxygen evolution is the direct absorption of UV light by Mn ions in Mn(III) and Mn (IV) oxidation states (see in Ivanova et al. 2008; Dobrikova et al. 2013). Therefore, it could be assumed that modification of the oxido-reduction states (i.e. more reduced states) of the Mn cluster in OEC after NO interaction is also a possible reason for protection of photosynthetic apparatus under abiotic stress.

14.7.4 Nitric Oxide Under Heavy Metals

The sensitivity of the photosynthetic processes to heavy metals is studied extensively (Arellano et al. 1995; Barón et al. 1995; Boucher and Carpentier 1999; Prasad 2004; Rouillon et al. 2006). One of the primary sources of metal toxicity in chloroplasts is through the generation of ROS, which affects chloroplast structure and function, as in other abiotic stresses. Recently, Saxena and Shekhawat (2013) reported the role of NO in heavy metal tolerance in plants. As reported for other abiotic stresses, NO has both beneficial and harmful effects during heavy metal stress, depending on the concentration and location of NO in the plant cells. Nitric oxide decreases the harmful effects of the ROS generated by heavy metal stress, interacts with other target molecules and regulates the expression of stress responsive genes (Saxena and Shekhawat 2013).

Recently it has been shown that the metalloid arsenic (As) also triggers the NO and S-nitrosoglutathione (GSNO) metabolism in Arabidopsis (Leterrier et al. 2012). Arsenic-treated seedlings showed a significant decrease in growth and an increase in lipid oxidation due to an alteration in antioxidant enzymes with a significant increase in NO content, protein

tyrosine nitration and also the S-nitrosoglutathione reductase (GSNOR) activity, which reduced the glutathione and S-nitrosoglutathione content. Talukdar (2013) reported that the exogenous addition of NO significantly reversed the As-induced oxidative stress in *Phaseolus vulgaris* seedlings, maintaining H_2O_2 in a certain level through balanced alterations of antioxidant enzyme activities. The role of SNP donated NO in the process of amelioration has ultimately been manifested by significant decrease of the membrane damage and improvement of growth performance in plants grown on As + SNP medium. Nitric oxide synthesis inhibitor PTIO accelerates As-induced oxidative damage, which clearly demonstrates the role of NO in ameliorating metal stress in plants. Yu et al. (2013) studied the effect of Cd-induced stress in cucumber seedlings. Both leaf pigments and net photosynthesis, and antioxidant activity decreased after Cd treatment, which could be reversed by the application of exogenous NO (100 μM SNP). Similarly, Srivastava and Dubey (2012) showed ameliorating effect of NO on the ROS scavenging machinery in Mn-induced oxidative stress in rice seedlings.

14.7.5 Nitric Oxide Under Herbicides

The widespread use of herbicides in agriculture has resulted in increasing pollution of soil and water with these toxic compounds. Herbicides are one of the major abiotic stressors as that of salinity, drought, temperature extremes, flooding, toxic metals, high light intensity and UV-radiation. All of these are the major causes of yield loss in cultivated crops worldwide and pose major threats to agriculture and food security (Rodríguez et al. 2005). The primary site of action of many herbicides is chloroplast, besides the mitochondria. As many other abiotic stressors (Qiao and Fan 2008; Misra et al. 2010a, b, 2011), the herbicides also elicit the production of NO (Klepper 1979; Mallick et al. 2000; Sakihama et al. 2002). Exogenous NO has been shown to reduce herbicide toxicity by its protective effects on chloroplast membrane and by retarding herbicide induced loss of Chl (Beligni and Lamattina 1999a, b; Hung et al. 2002).

One of the most widely used herbicides is atrazine, which belongs to the triazine group of chemicals. The primary site of atrazine action is blocking the PSII electron transport via binding to the Q_B-binding site on the D1 polypeptide of PSII reaction center and inhibition of light-driven electron transport from Q_A to Q_B in PSII (Trebst 1987; Draber et al. 1991). A high sensitivity of the photosynthetic apparatus to atrazine is well documented (Qian et al. 2009; Vladkova et al. 2009; Apostolova et al. 2011; Rashkov et al. 2012). Qian et al. (2009) have shown that in unicellular green algae *Chlorella vulgaris*, atrazine (100 μg/L) or glufosinate (10 mg/L) with low concentrations of NO donor SNP (10–20 μM) significantly decreased herbicide induced ROS generation and membrane peroxidation and increased the chlorophyll content of leaves.

Other widely used herbicide in agriculture is paraquat (also known as methyl viologen), which belongs to the bipyridinium herbicides. This herbicide exerts its toxic effects by catalyzing the electron transfer from PSI to molecular oxygen, producing oxygen radicals that cause lipid peroxidation and membrane damage (Cha et al. 1982). Hung et al. (2002) have evaluated the protective effect of NO against paraquat toxicity of rice leaves. They showed that NO-donors (PBN, N-tert-butyl-α-phenylnitrone, SNP, sodium nitropruside and SIN-1, 3-morpholinosydnonimine), as well as the ascorbic acid and $NaNO_2$ are effective in reducing paraquat toxicity in rice leaves, most likely mediated through an increase in antioxidant enzyme activities and decrease in lipid peroxidation.

Recently, Sood et al. (2012) revealed the effects of the exogenous NO (donor SNP) on the paraquat treated *Azolla microphylla*. The authors results suggested that SNP released NO

can work both as cytoprotective and cytotoxic in concentration dependent manner and involvement of NO in protecting *Azolla* against paraquat toxicity. Paraquat (8 μM) alone increased the activities of antioxidant enzymes SOD, CAT, GPX, APX and the amount of H_2O_2. The supplementation of SNP (8–100 μM) suppressed the activities of antioxidant enzymes and the amount of H_2O_2 compared to paraquat alone. The addition of NO scavengers along with NO donor in paraquat treated fronds neutralized the effect of exogenously supplied NO, indicating that NO can effectively protect *Azolla* against paraquat toxicity by quenching ROS. Higher SNP concentration (200 μM) is reported to reverse the effect of NO.

Diquat, like as the paraquat is a bipyridinium herbicide and serves as an artificial electron acceptor of PSI (Beligni and Lamattina 1999a, b), influencing also the level of NO in the plants. Beligni and Lamattina (2002) reported that diquat triggered lipid peroxidation, ribulose-1,5-biphosphate carboxylase/oxygenase (Rubisco) and D1 protein loss. Supplementation of NO-donors SNP and S-nitroso-N-acetylpenicillamine greatly reduced lipid peroxidation, rapid protein turn-over and mRNA breakdown caused by the application of a high dose of diquat to potato leaf pieces or isolated chloroplasts. Moreover, diquat caused an increase in the rate of photosynthetic electron transport in isolated chloroplasts and NO restored it back to the control levels (Beligni and Lamattina 2002).

Lactofen is a diphenylether herbicide, which inhibits Chl biosynthesis by blocking the enzyme protoporphyrinogen-IX oxidase activity, which catalyses the oxidation of protoporphyrinogen-IX to protoporphyrin-IX (proto-IX) (Matringe et al. 1989). Accumulation of protoporphyrins leads to ROS generation causing oxidative stress in the plants. SNP donated NO was able to scavenge ROS generated by the lactofen action in soybean plants, avoiding the photosynthetic pigment breakdown, but the lipid peroxidation was not completely prevented (Ferreira et al. 2010). Later, Ferreira et al. (2011) demonstrated that the lactofen-induced morphological and physiological alterations in soybean leaves are reduced with NO.

14.8 Conclusion

This review clearly shows NO effects on the chloroplast structure and function under physiological and stress conditions. Many investigations revealed the role of the nitric oxide as a key signal molecule in plants. It has also been shown that NO participates under abiotic stress. Nitric oxide production increases in the plants as a response to abiotic stress (Qiao and Fan 2008). Under stress, NO enhances activities of the antioxidant enzymes (Shi et al. 2005; Neill et al. 2008) and as a signal molecule interacts with plant hormones, and affects physiological processes (Laxalt et al. 1997; Zhao et al. 2004; Misra et al. 2006; Qiao and Fan 2008; Misra et al. 2011). The other possibility of the protection of NO on the photosynthesis under abiotic stress can be due to the direct action on the thylakoid membranes, which leads to an increase of the open PSII centers and a modification of the OEC (Vladkova et al. 2011). These changes influence the structure of the LHCII-PSII supercomplex in response to stress factors (Ivanova et al. 2008; Dankov et al. 2009; Apostolova and Dobrikova 2010). On the other hand, it has been shown that there is relationship between the organization of the PSII complex and the oxidation state of the Mn cluster in the OEC (Apostolova et al. 2006). It has been proposed that the modification of the oxido-reduction state of the Mn cluster after NO interaction is a possible reason for the protection of the photosynthetic apparatus under abiotic stress.

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