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REVIEW

Effects of exogenous nitric oxide on photosynthesis

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Abstract

Nitric oxide (NO) is an important signalling molecule with diverse physiological functions in plants. In plant cell, it is synthesised in several metabolic ways either enzymatically or nonenzymatically. Due to its high reactivity, it could be also cytotoxic in dependence on concentration. Such effects could be also mediated by NO-derived compounds. However, the role of NO in photosynthetic apparatus arrangement and in photosynthetic performance is poorly understood as indicated by a number of studies in this field with often conflicting results. This review brings a short survey of the role of exogenous NO in photosynthesis under physiological and stressful conditions, particularly of its effect on parameters of chlorophyll fluorescence.

Additional key words: chlorophyll fluorescence, chloroplast, nitration, nitrotyrosine

Introduction

The molecule of NO, a gaseous free radical, has a long history in chemistry, but during the last 25 years, it has become the centre of research in many different areas of biology and medicine (Corpas *et al.* 2008, Culotta and Koshland 1992). With the finding that NO has many functions in mammalian cells, such as regulation of vascular tone, neuronal signalling or immune response to infection (Knowles and Moncada 1994), various studies have reported its presence in the plant kingdom as well. Conclusive evidence proved NO to be involved in many plant physiological and metabolic processes, such as germination (Beligni and Lamattina 2000), mitochondrial (Zottini *et al.* 2002) and chloroplast (Puntarulo *et al.* 2007) functionality, gravitropism (Hu *et al.* 2005), floral regulation (He *et al.* 2004), stomata closure (Lamattina *et al.* 2003), adaptation to environmental stresses (Uchida *et al.* 2002), and senescence (Procházková and Wilhelmová 2011).

It has been reported that photosynthesis can be affected not only by generation of reactive oxygen species (Asada 1999) but also by reaction with NO. In addition, under circumstances of a high NO steady-state concentration (*i.e.* high nitrite content in chloroplasts), generation of reactive nitrogen species (RNS) may lead to impairment of the photosynthetic machinery (Jasid *et al.* 2006). The aim of this study was to present a short survey of the role of NO and RNS in plant photosynthesis arising from studies with exogenous NO application.

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Abbreviations: Arg – arginine; DAF-2DA – diaminofluorescein diacetate; Chl – chlorophyll; F_v/F_m – maximal quantum yield of PSII photochemistry; F_v – variable fluorescence; GSNO – S-nitrosoglutathione; L-NNA – (Nω-nitro-L-arginine); NOS – nitric oxide synthase; NPQ – nonphotochemical chlorophyll fluorescence quenching; PBIT – S,S′-1,3-phenylene-bis(1,2-ethanediyl)-bis-isothiourea; PS – photosystem; q_E – energy dependent quenching of chlorophyll fluorescence; q_N – nonphotochemical quenching of F_v; q_p – photochemical quenching of F_v; RNS – reactive nitrogen species; Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; SNAP – S-nitroso-N-acetylpenicillamine; SNP – sodium nitroprusside; Φ_{PSII} – effective quantum yield of photochemical energy conversion in PSII.

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NO synthesis in chloroplasts

Biosynthesis of NO in plants is still a matter of debate and several metabolic pathways were identified. Nitrate reductase (NR, EC 1.7.1.1) is supposed to be the main NO producer in a plant cell. Activity similar to animal NO synthase (NOS, EC 1.14.13.39) was also found (Wendehenne *et al.* 2001). Concerning localization, NO production was proved to occur in root mitochondria (Planchet *et al.* 2005), peroxisomes (Barroso *et al.* 1999), and plasma membrane (Stohr *et al.* 2001). Further, nonenzymatic NO formation was proved in acidic and reducing environments, such as the apoplasm (Bethke *et al.* 2004) and plastids (Cooney *et al.* 1994).

Chloroplasts have been previously marked as NO sources based in nonquantitative studies employing fluorescence microscopy (Foissner *et al.* 2000, Gould *et al.* 2003), microscopy with immunogold labelling (Barroso *et al.* 1999), and electron paramagnetic resonance with spin trap (Puntarulo *et al.* 2007). For example, in tobacco (*Nicotiana tabaccum* L.) cells elicited with cryptogein, chloroplasts were the first organelle where NO production increased within the first 3 min after the elicitation (Foissner *et al.* 2000). Similarly, when leaves or cell suspensions of tobacco were loaded with a fluorescent probe for NO detection, diaminofluorescein diacetate (DAF-2DA), and subjected to an abiotic stressor, fluorescence appeared first in plastids (Gould *et al.* 2003).

Jasid *et al.* (2006) found two independent pathways for NO generation in soybean chloroplasts; one pathway was dependent on the activity of NOS-like enzyme employing Arg/NADPH and the other was dependent on nitrite. In addition, Tewari *et al.* (2013) proved the involvement of NOS-like activity in the generation of NO in chloroplasts of rape (*Brassica napus* L.) leaf protoplasts by the inhibition of DAF-2DA fluorescence in the presence of NOS inhibitors, *i.e.* Nω-nitro-L-arginine (L-NNA) and S,S′-1,3-phenylene-bis(1,2-ethanediyl)-bis-isothiourea (PBIT). Since NO generation in the presence of both inhibitors together did not add any further inhibition, it seems that an inducible NOS is involved in NO generation in chloroplasts (Tewari *et al.* 2013). However, neither gene nor protein with sequences similar to the large animal NOS genes or proteins have been found even in the sequenced *Arabidopsis* genome. These results suggest that the NOS activity in plants comes from a different type of enzyme (Gas *et al.* 2009, Procházková and Wilhelmová 2011). Such enzyme was demonstrated to have also GTPase activity and is targeted to plastids (Gas *et al.* 2009).

Effects of exogenous NO application on metabolism related to photosynthesis

Most experiments investigating the participation and effects of NO in photosynthesis as well as in other processes employ exogenous application of NO. It could be achieved by two ways: fumigation with NO is sometimes used for studies of NO effects on plant metabolism although NO rapidly converts to NO_2 in the air (Snyder 1992, Rodrigo *et al.* 1994, Procházková and Wilhelmová 2011). The other way is the application of various NO artificial sources (Wilhelmová *et al.* 2006). The most commonly used donors are sodium nitroprusside (SNP), S-nitrosoglutathione (GSNO), and S-nitroso-N-acetylpenicillamine (SNAP). However, the usage of artificial donors has some disadvantages as well. Primarily, the concentration of NO inside the plant tissue depends, among others, on specific chemical features of inner environment, on the kinetics of NO release from the donor, as well as the reactivity of the rest of donor molecule, the temperature, and the reducing power in the tissue (Tanno *et al.* 1996, Ramamurthi and Lewis 1997). In consequence, various NO donors have different effects on plant systems (Murgia *et al.* 2004, Wodala *et al.* 2008). For example, SNP is the only NO donor, which stimulates electron transport through photosystem (PS) II. It has been also demonstrated that GSNO is not an efficient NO generator in leaf tissue (Ederli *et al.* 2009) and that it can act also as a substrate/inhibitor for several enzymes utilizing glutathion, such as glutathione peroxidase (Hogg 2000). In animal cells, SNAP was able to increase free radical generation (Zhang *et al.* 2003).

Effects of exogenous NO on photosynthetic rate and chlorophyll (Chl) fluorescence parameters

It has been described that exogenous NO gas inhibited net photosynthetic activity of intact leaves of oat (*Avena sativa* L.) and alfalfa (*Medicago sativa* L.) at concentrations below those required to cause visible injury symptoms (Hill and Bennett 1970, Yamasaki 2000). Similarly, Saxe (1986) showed reduction of net photosynthesis in eight different kinds of pot plants. In addition, electron paramagnetic resonance and Chl fluorescence measurements using NO gas treatment of isolated thylakoid membrane complexes of pea (*Pisum sativum* L.) have clearly demonstrated that NO can reversibly bind to several sites in PSII and inhibit electron transfer (Wodala *et al.* 2008). Sanakis *et al.* (1997) and Vladkova *et al.* (2011) suggest that NO interacts with the tyrosine residue of the D2 protein (Y_D) 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 in D1 protein. NO donors were also used in studies of parameters of slow fluorescence induction curves. In intact potato (*Solanum tuberosum* L.) leaves treated with SNP, no differences in nonphotochemical Chl fluorescence quenching (NPQ) have been observed, but SNP decreased maximum quantum yield of PSII photochemistry (F_v/F_m) values in a concentration-dependent manner (Yang *et al.* 2004). In pea (*Pisum sativum* L.) leaves, F_v/F_m decreased by the increase of SNP concentration due to decline of F_v (maximum variable Chl fluorescence yield in the dark-adapted state) and increase of F_o (minimum Chl fluorescence yield in the dark-adapted state) levels, which implies a structural alteration of light harvesting complex of PSII. Furthermore, SNP abated the photochemical quenching (q_p), thus, the electron transport rate, tested under different light intensities (Wodala *et al.* 2005). Raising SNP concentrations caused an enhancement in NPQ, which, in a certain high range, decreased again. Analysis of NPQ recovery indicated that energy-dependent fluorescence quenching (q_E) followed the changes in NPQ values, while the photoinhibition component (q_I) constantly increased (Wodala *et al.* 2005). In the recent study, Ördög *et al.* (2013) showed that the rapid decreases of NPQ and the effective quantum yield of photochemical energy conversion in PSII (Φ_{PSII}) upon NO addition correlate well with each other. A reduction in Φ_{PSII} is predicted to result in a decreased proton accumulation in the lumen, which downregulates q_E, the fastest NPQ component, and thus it explains the initial drop in NPQ. However, if the NO concentration of the incubation medium is kept over 450 nM for a prolonged time, NPQ may increase mainly through its energy-dependent quenching component (Ördög *et al.* 2013).

GSNO application caused a significant decrease in F_v/F_m ratio in intact pea (*Pisum sativum* L.) leaves and decreased steady-state q_p, which indicated that NO increased the proportion of closed PSII reaction centres. Besides reducing steady-state transient NPQ values, NO changes the amplitude and kinetics of NPQ transition. These data provide the evidence that a partial inhibition of PSII by NO is the cause of impaired steady-state electron transport *in vivo* (Wodala *et al.* 2008).

Effects of exogenous NO application on metabolism related to photosynthesis

Lum *et al.* (2005) found that SNP decreased the amount of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activase and Rubisco subunit binding G-protein β-subunit, and increased the content of PSII oxygen evolving complex in mung bean (*Phaseolus aureus* L.). Abat *et al.* (2008) showed that NO slows photosynthesis *via* inhibition of Rubisco by *S*-nitrosylation in a dose dependent manner. In tomato (*Lycopersicon esculentum* L.), higher SNP concentration (1 M) decreased activity of carbonic anhydrase (EC 4.2.1.1) (Hayat *et al.* 2010), which catalyzes the interconversion of CO_2 and HCO_3^- and is a major protein constituent of chloroplasts of higher plants with C_3 carbon fixation, where it is presumed to play a role in photosynthetic carbon assimilation (Ferreira *et al.* 2008). This could be caused by the fact that elevated NO concentrations induce the closure of stomata (Garcia-Mata and Lamattina 2001). Abat *et al.* (2008) revealed nitrosylation of cysteins of Rubisco *in vivo*. Nitrosylation by GSNO inactivated Rubisco in dose-dependent manner.

SNAP inhibited light-induced ΔpH formation across the thylakoid membrane in spinach (*S. oleracea* L.) (Takahashi and Yamasaki 2002). High concentrations of nitrite or nitrate did not show such inhibitory effects, suggesting that the inhibition is not due to uncoupling effects of the oxidized products of NO but mediated by NO itself. ATP synthesis activity upon illumination was severely inhibited by NO. The inhibition was found to be temporary and the activity was completely recovered by removing NO. Bovine hemoglobin and bicarbonate were effective in preventing NO-dependent inhibition of photophosphorylation. These results indicated that NO is a reversible inhibitor of photosynthetic ATP synthesis (Takahashi and Yamasaki 2002). Ördög *et al.* (2013) showed, that NO is able to hamper the activity of the plasma membrane H^+-ATPase in bean guard cells.

Booij-James *et al.* (2009) demonstrated that NO donors, 3-morpholinosydnonimine (which is $ONOO^-$ donor as well) and S-nitrosocysteine, inhibited *in vivo* phosphorylation of the D1 protein in *Spirodella* without inhibiting degradation of the protein. Thus, the authors demonstrated that D1 phosphorylation is not highly linked to D1 degradation.

Effects of exogenous NO on photosynthesis under unfavourable conditions

NO has been shown to prevent Chl loss under stress conditions. Heavy metal contamination of the environment is currently a major global environmental problem, threatening the health of vegetation, wildlife, and humans. Photosynthesis is typically reduced by elevated contents of heavy metals, but the specific effects of a given heavy metal on photosynthesis vary among species, preventing broad generalizations about metal effects on photosynthesis (Heckathorn *et al.* 2004). Exogenous NO has important roles in protection against the deleterious effects of heavy metals. First, NO might be involved in increasing the antioxidant content and antioxidative enzyme activity (Hsu *et al.* 2004). Second, NO might increase heavy metal accumulation in root cell walls and decrease heavy metal accumulation in the soluble fraction of leaves (Xiong *et al.* 2009). Finally, NO could act as a signalling molecule in the cascade of events leading to changes in gene expression under heavy metal stresses (Wilson *et al.* 2008, Xiong *et al.* 2010).

The main symptoms of Cd-induced toxicity in plants are, beside others, chlorosis, altered chloroplast ultrastructure, photosynthesis inhibition, inactivation of enzymes in CO_2 fixation, and induced lipid peroxidation (Gill *et al.* 2013). When sunflower (*Helianthus annuus* L.) plants were pretreated with SNP, Cd-induced Chl decay was evidently reduced: Chl content remained on 88% of those shown by control plants (Laspina *et al.* 2005). Similarly, SNP treatment enhanced the contents of total Chl, Chl *a*, Chl *b*, Chl *a*/*b* ratio, and Hill reaction activity of chloroplasts in leaves of Cd-treated *Brassica napus* plants (Jhanji *et al.* 2012). One of the most common symptoms of Ni toxicity in plants is chlorosis (Kumar *et al.* 2012). Under Ni stress, SNP pretreatment enhanced Chl content in *Brassica napus* L. (Kazemi *et al.* 2010).

In mesophyll cells from Fe-deficient maize plants, SNP completely prevented leaf interveinal chlorosis, producing a 70 % increase in Chl content compared with nontreated plants. In the cells of control plants, electron micrographs revealed plastids with few photosynthetic lamellae and rudimentary grana, while mesophyll chloroplasts appeared completely developed in SNP-treated maize plants (Graziano *et al.* 2002). Similarly, NO increased the photosynthetic pigment content in leaves exposed to Fe deficiency (Ding 2008). In addition, in chinese cabbage, SNP greatly decreased thermal dissipation (Hirotsu *et al.* 2004) and increased net photosynthetic rate in leaves exposed to Fe deficiency (Ding 2008).

Treatment with SNP slowed down Chl loss, abated F_v/F_m decrease, and alleviated the increase in carbonyl contents in thylakoid membrane proteins after UV-B irradiation in bean (*Phaseolus vulgaris*) (Shi *et al.* 2005). Uchida *et al.* (2002) reported that rice seedlings treated with SNP allowed the survival of more green leaf tissue and resulted in a higher quantum yield for PSII than in nontreated controls under salinity and heat stress. SNP attenuated also the decrease in leaf Chl content, net photosynthetic rate, stomatal conductance, transpiration rate, F_v/F_m, electron transport rate, the efficiency of excitation energy capture by open PSII reaction centres (F_v'/F_m'), and q_p, and counteracted the increase in q_N in tomato seedlings under salt stress conditions (Wu *et al.* 2010). In addition, SNP enhanced photosynthesis in leaves of wheat seedlings subjected to osmotic stress (Tan *et al.* 2008). Under alkaline stress, SNP significantly alleviated the decreases of the Chl content, net photosynthetic rate, and stomatal conductance, increased F_v/F_m, photochemical efficiency, and $q_{p,}$ and decreased NPQ of PSII in ryegrass seedling leaves treated with $NaHCO_3$ (Liu *et al.* 2012).

In heat-stressed chrysanthemum, the application of SNP alleviated the decline in net photosynthetic rate, transpiration rate, and stomatal conductance (Yang *et al.* 2011). Under low temperature, SNP alleviated the decrease of Chl content and net photosynthetic rate as well (Fan *et al.* 2011). In poplar leaves, SNP increased the photosynthetic rate, photochemical efficiency of PSII (F_v/F_m), and F_m/F_o and F_v/F_o ratios, and these effects decreased with prolonging of water stress (Wang *et al.* 2005).

A protective role of NO was also reported in relation to lipid oxidation. In this sense, lipid radical content in chloroplasts was significantly reduced by GSNO exposure as compared with control chloroplasts (Radi 1998, Jasid *et al.* 2006). GSNO caused also a significant decline in the content of carbonyl groups in chloroplast proteins (Jasid *et al.* 2006). Tewari *et al.* (2009) found that application of SNP or a mixture of nitrite and ascorbic acid lead to lowered lipid peroxidation. This was attributed to limitation of ROS production through suppressed xanthine oxidase activity. Concomitantly, activities of catalase and glutathione reductase were promoted. Similarly, exposure of the isolated chloroplasts to a NO donor decreased lipid radical content in membranes (Puntarulo *et al.* 2007). SNP also enhanced antioxidant capacity, resulting in lower lipid peroxidation in cucumber chloroplasts under $NaHCO_3$ stress (Gao *et al.* 2012).

During fungal, bacterial or viral attacks, formation of NO occurs in chloroplasts and contributes to the specificity of immune reaction (Kangasjärvi *et al.* 2012). However, the final defence results from extensive cross-communication between organellar and cytosolic components, including photoperiodic and hormonal signals, which together regulate cellular functions and modulate gene expression (Fedoroff 2006, Roberts and Paul 2006, Griebel and Zeier 2008).

Peroxynitrite in photosynthesis

NO is membrane-permeable and highly diffusive (Lancaster 1996), thus, any NO produced in the cytosol could easily penetrate into the chloroplast stroma (Yamasaki 2000). This feature can reveal the adverse behaviour of NO. It could react then with superoxide radical forming peroxynitrite ($ONOO^-$), one of reactive nitrogen species, which may result in a potential source of damage, even under physiological conditions.

Nitration is a general chemical process for the introduction of $-NO_2$ group into a chemical compound. In the case of proteins, there are several amino acids, which are preferentially nitrated, such as tyrosine, tryptophan, cysteine, and methionine (Corpas 2009). This reaction is harmful as it modifies protein structure and function.

Exposure of the isolated soybean (*Glycine max*) chloroplasts to $ONOO^-$ led to an increase in lipid-derived radicals (Puntarulo *et al.* 2007). The interaction of NO or $ONOO^-$ with thiol groups in proteins causes formation of thiyl radical. The thiyl radical reacts with reduced form of thiol to produce a disulphide bond. During this reaction, superoxide radical is generated in ambient air. As chloroplast stroma contains many thiols, which are functionally important for photosynthesis, NO can inactivate the thiol-containing enzymes in the Calvin cycle (Yamasaki 2000).

González-Pérez *et al.* (2008) demonstrated the deleterious effect of $ONOO^-$ on PSII. They showed that the inhibition is caused by $ONOO^-$ interaction with the nonheme Fe^{2+}. The type of redox reaction between $ONOO^-$ and the nonheme Fe^{2+} is not known, however, the products of the one- or two-electron oxidation are suggested to oxidize or nitrate the Fe^{2+}-coordinated histidine residues or to induce Fe^{2+} release and in consequence a destruction of the magnetic coupling between quinone and the nonheme Fe^{2+} (González-Pérez *et al.* 2008).

The yield of $ONOO^-$-mediated nitration of hydrophobic tyrosine analogs is very low in liposomes, but it is substantially enhanced in the presence of transition metal complexes (Bartesaghi *et al.* 2006). Since PSII contains two Fe^{2+} ions and a cluster of four manganese ions, nitration of the tyrosine-containing PSII polypeptides is envisaged to be enhanced by the presence of these metal ions (González-Pérez *et al.* 2008).

$ONOO^-$ effects are not limited only to PSII. Mainly in PSI, PSII, cytochrome $b_{6/f}$, and ATP-synthase complex, 138 tyrosine and tryptophan nitration sites were identified indicating that protein nitration belongs to one of the prominent posttranslational protein modifications in photosynthetic apparatus of *A. thaliana* (Galetskiy *et al.* 2011a). In the thylakoid membrane of *A.thaliana* leaves adapted to growth light and subsequently exposed to high light, changes in the nitration level of 23 tyrosine residues in five PSI and nine PSII proteins were determined. The majority of them showed a lower nitration level in PSI and PSII complexes and supercomplexes under high light conditions, as compared to growth light. In contrast, the nitration level significantly increased in assembled/disassembled PSI and PSII subcomplexes under high light conditions (Galetskiy *et al.* 2011b). In addition, ferredoxin-NADP reductase activity was inhibited by $ONOO^-$ donor, 3-morpholinosydnonimine, in sunflower (*H. annuus*) (Chaki *et al.* 2011).

Conclusion

NO has a broad spectrum of regulatory functions in many physiological processes, including photosynthesis. As chloroplasts are the main site of carbon and nitrogen metabolism, as well as reactive oxygen species production, NO and related species can potentially affect and regulate a wide range of downstream signals through their effects on chloroplasts (Lum *et al.* 2005, Jasid *et al.* 2006). Besides, NO seems to be also a possible tool for photosynthesis study. Chloroplasts were proved to be the crucial player in regulation of NO concentration in a plant cell. They are not only the site of NO biosynthesis either by NR or NOS-like protein, but also NO through posttranslational modifications of proteins affects assimilatory processes of photosynthesis and thus entire growth capacity of a plant.

NO effects are mostly found to impair photosynthetic apparatus and inhibit photosynthesis. This could be attributed to posttranslation modification of particular components of PS. On the other hand, in adverse conditions, NO alleviates and diminishes stress impacts. NO probably acts as a signalling molecule in a stress response.

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