

Nitric oxide and S-nitrosylation of proteins in cyanobacteria: The story is just beginning

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Abstract

Nitric oxide (NO) acts as an important signaling molecule in green algae and higher plants, regulating many physiological processes. However, there is virtually no data on the ability of prokaryotes with oxygenic photosynthesis (cyanobacteria) to generate NO. Although the freshwater cyanobacterium *Synechococcus elongatus* PCC7942 is one of the most studied model strains, whether NO synthesis occurs in it has not yet been elucidated. Using spectrofluorometric assays and confocal microscopy with NO-sensitive fluorescence dye, we demonstrate NO synthesis by PCC7942 cells. Moreover, we found that the generated NO causes the S-nitrosylation of protein cysteine thiol groups in this cyanobacterium. Notably, *S. elongatus* PCC7942 utilizes the S-nitrosylation under nitrogen-replete conditions but not under nitrogen limitation. Together, our data argue for S-nitrosylation as an evolutionarily conserved posttranslational modification in organisms with oxygenic photosynthesis.

Keywords: cyanobacteria, nitric oxide, NO signaling, protein posttranslational modifications, S-nitrosylation, *Synechococcus elongatus*.

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Introduction

Nitric oxide (NO) was recognized as a key regulator of physiological processes in mammals and plants (Bredt and Snyder, 1992; Wendehenne, Pugin, Klessig, and Durner, 2001; Wendehenne, Durner and Klessig, 2004; Astier et al., 2021). Recently, NO biology is rapidly becoming a fascinating field in bacteriology (Chen, Liu, Wang, and Gao, 2022). Although many bacteria are unable to generate NO, some species are NO-producers, generating this redox molecule by respiratory and/or non-respiratory pathways (Guo and Gao, 2021). Various enzymes are involved in denitrification, dissimilatory nitrate reduction and ammonia oxidation, which constitute the respiratory pathway and catalyze oxidoreduction reactions to form NO (Chen, Liu, Wang, and Gao, 2022).

The non-respiratory pathway consists exclusively of bacterial nitric oxide synthases (bNOSs). NOS catalyzes NO production through oxidation of L-arginine (Arg) to L-citrulline (Cit) (Lundberg and Weitzberg, 2022). bNOSs are phylogenetically homologous to mammalian NOS and represent a simpler form from which eukaryotic NOS evolved (Crane, Sudhamsu, and Patel, 2010). Interestingly, the cyanobacterium *Synechococcus* PCC 7335 utilizes a unique NOS, SyNOS, which contains a N-terminal globin domain in addition to oxygenase and reductase domains (Correa-Aragunde, Foresi, Del Castello, and Lamattina, 2018).

To date, most of the characterized bacterial NO sensors belong to heme-nitric oxide or O₂ binding domain proteins, which are homologous to the mammalian NO sensor, soluble guanylate cyclase (Iyer, Anantharaman and Aravind, 2003; Plate and Marletta, 2013; Marletta, 2021). In contrast, in green algae and higher plants, NO can exert its biological functions mainly through protein S-nitrosylation, a redox-based posttranslational modification (PTM) (Astier et al., 2021; Mata-Perez et al., 2023; Ermilova, 2023). S-nitrosylation links the reactive cyste-

ine (Cys) thiol of target protein to form an S-nitrosothiol (SNO). In general, PTMs are widespread in bacteria and have vital roles in various physiological processes in the bacterial cell (Macek et al., 2019). PTMs are also ubiquitous in cyanobacteria and are important in maintaining the normal physiological function (Xiong, Chen, and Ge, 2015). Although protein modifications in bacteria are more diverse than in eukaryotes, S-nitrosylation has been characterized only in *Escherichia coli* (Seth, Hausladen, Wang, and Stamler, 2012; Seth et al., 2018). This PTM has not yet been reported in any cyanobacterium. Due to the apparent gap in information on NO generation and S-nitrosylation in cyanobacteria, we decided to investigate this PTM in the freshwater model cyanobacterium *Synechococcus elongatus* PCC 7942.

The present study is the first to address NO production and S-nitrosylation as an NO-dependent signaling mechanism in the representative cyanobacterium.

Materials and methods

The *S. elongatus* strain PCC7942 was provided by prof. K. Forchhammer (University of Tübingen, Germany). Cyanobacteria were grown photo-autotrophically under continuous illumination by white light (fluence rate of 45 photons $\mu\text{mol m}^{-2} \text{s}^{-1}$) in liquid BG11 medium (Rippka, 1988) at 25 °C at a constant agitation (90 rpm).

Intracellular production of NO was measured using a microplate reader CLARIOstar (BMG) as described previously (Zalutskaya, Dukhnov, Leko, and Ermilova, 2021). Excitation and emission wavelengths were 483 ± 14 and 530 ± 30 nm, respectively. Fluorescence intensity was expressed as arbitrary units per 10^6 cells. Cell autofluorescence was subtracted from the total fluorescence obtained.

Images were acquired using a Leica TCSSP5 confocal microscope (Leica-Microsystems, Germany) equipped with a HC PL APO 100 \times oil immersion objective and functioned on the base of inverted microscope Leica DMI 6000 CS. Excitation was performed with a 488-nm laser and emission was collected simultaneously on two different channels, between 500 and 544 nm and 645 and 728 nm, to separate signals arising from the DAF-FM DA and endogenous chlorophyll, respectively.

For the S-nitrosated protein labeling, 10^9 cells were collected by centrifugation (7,500 \times g, 5 min) and resuspended in 400 μL of HENS buffer (Thermo Fisher Scientific, No. 90106, Rockford, IL, USA). Cells were disrupted by glass beads (0.45 mm diameter) using Minilys disintegrator (Bertin technologies, Montigny-le-Bretonneux, France). After centrifugation (10,000 \times g, 10 min), the protein concentration was determined in the supernatant by staining with amido black, using BSA as a standard. One hundred micrograms of protein in 100 μL of HENS buffer were used per sample. To block free cysteine thi-

ols, 2 μL of 1 M sulfhydryl-reactive compound, MMTS (20 mM final concentration), was added to 100 μL of each sample and incubated for 30 min at room temperature. Proteins were precipitated by pre-chilled (-20°C) acetone and the samples were frozen at -20°C to remove unreacted MMTS. The precipitated proteins were pelleted by centrifugation (10,000 \times g, 10 min, 4°C) and resuspended in 100 μL of HENS buffer. To each 50 μL of sample, 1 μL of iodoTMT reagent (Thermo Fisher Scientific, No. 90105, Rockford, IL, USA) was added and then 2 μL of 1 M sodium ascorbate was added to the mixture. These steps were performed in the dark. For negative control reactions, 2 μL of ultrapure water instead of sodium ascorbate was added to the samples. The reaction proceeded for 2 h at room temperature.

Labeled-protein SDS-PAGE and Western blotting were performed as described (Lapina, Statinov, Puzanskiy, and Ermilova, 2022).

The values for the quantitative experiments described above were obtained from at least three independent experiments with no fewer than three technical replicates. Data are presented as means \pm standard error (SE). When necessary, statistical analyses were followed by the Student's t test ($p < 0.01$).

Results

S. elongatus PCC 7942 is usually grown on nitrate or ammonium as nitrogen sources (Kupriyanova, Sinetova, Gabrielyan, and Los, 2024; Cardoso, Azevedo, Santos, and Marins, 2025). As far as green unicellular algae are capable of synthesizing nitric oxide via an oxidative or reductive pathway in which NO is formed from arginine or nitrite, respectively (Ermilova, 2023), we explored arginine and nitrite as potential nitrogen sources. Nitrate-free medium was supplied with external arginine (1 mM, 5 mM or 20 mM) and the growth of the cyanobacterium in arginine-containing media was determined (Fig. 1A). Addition of 20 mM arginine to the medium supported the cell growth. Usual arginine concentrations (1–2 mM) for green algae (Kirk and Kirk, 1978; Foresi et al., 2010) did not support the growth of this cyanobacterium (Fig. 1A). We further monitored cell growth in the presence of nitrite instead of nitrate. 1mM nitrite supplementation resulted in faster growth compared 20 mM arginine, but with lower final yields (Fig. 1A). Nitrite concentrations above 1 mM were toxic for cells (data not shown). Taken together, these findings indicate that arginine and nitrite may be utilized as nitrogen sources for this cyanobacterium.

Next, we analyzed the potential role of nitrite in NO formation in *S. elongatus* PCC 7942. NO production was determined using the NO-specific dye DAF-FM DA. Cells incubated in nitrate-containing medium showed insignificant accumulation of NO (Fig. 1B). When the

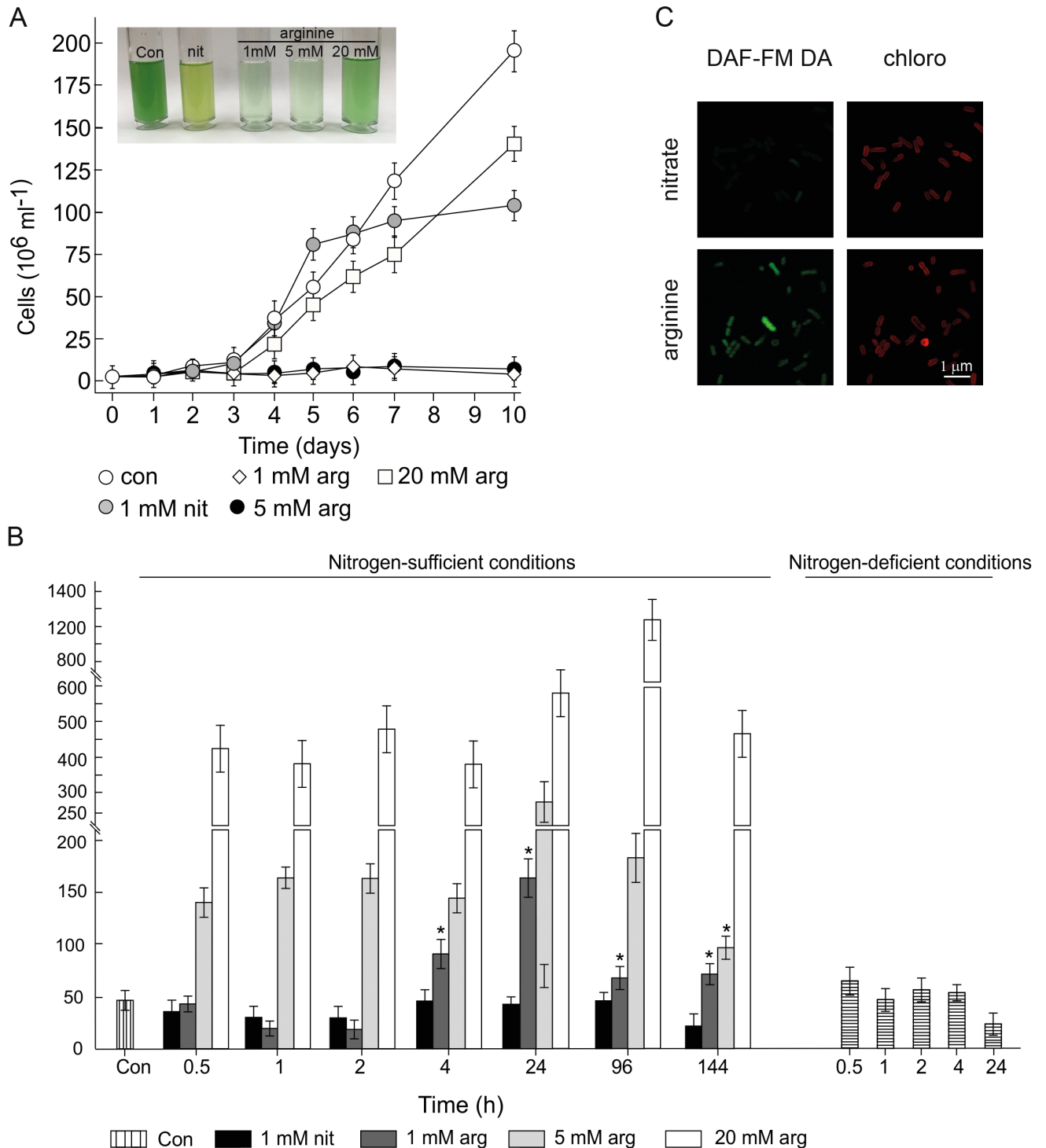


Fig. 1. Effects of arginine on growth and NO production of *S. elongatus* PCC7942. (A) The growth curves were analyzed in the presence of 1 mM nitrite or arginine (1 mM, 5 mM or 20 mM). Cells grown in a nitrate-containing medium were used as a control. Data are presented as the mean \pm SE of three independent experiments. The photographs show growth on these media after 5 days; (B) Fluorescence intensity due to intracellular NO was determined using DAF-FM DA and is expressed as arbitrary units per 10^6 cells. Cell autofluorescence was subtracted from the total fluorescence obtained. Cells were grown in nitrate-containing medium (Con) and transferred to the respective medium with 1 mM nitrite or arginine (1 mM, 5 mM or 20 mM) as a nitrogen source or in N-free medium. *denotes significant differences between the control (Con) and test variants according to the Student's t test (p value < 0.01). (C) NO visualization in cells by confocal microscopy. Images of cells grown in nitrate-containing medium and then incubated with 20 mM arginine for 1 h. The left-hand panels show DAF-FM fluorescence (green color), while the right-hand panels show chlorophyll autofluorescence (red color). Scale bar equals 1 μ m.

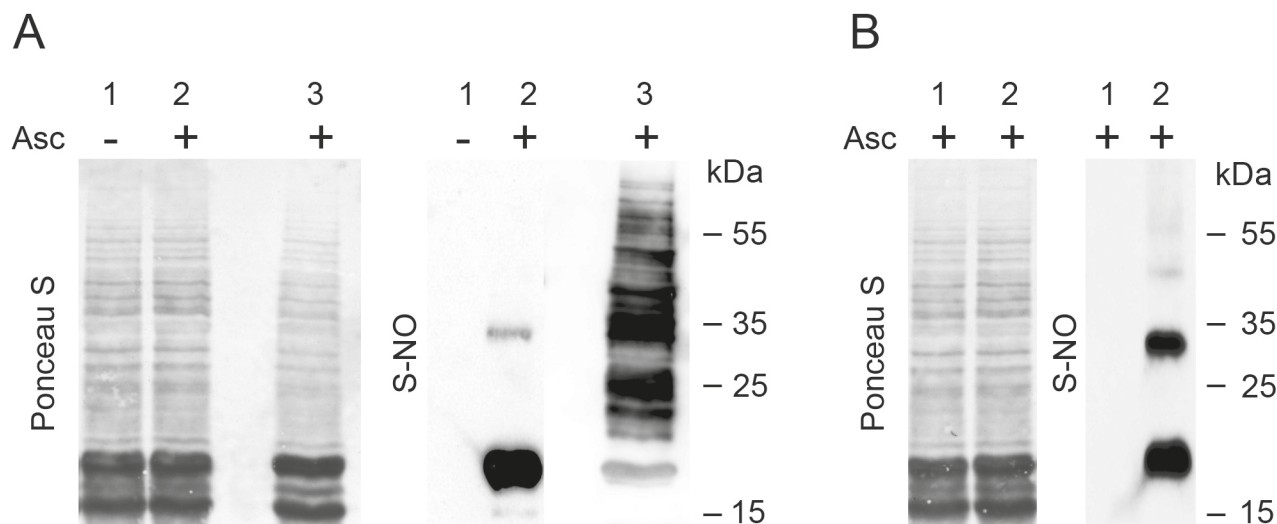


Fig. 2. Modification of proteins by S-nitrosylation in *S. elongatus* PCC7942. (A) The samples used were treated with 20 mM arginine for 1 h. The protein S-nitrosylation was analyzed by Western blotting with an anti-TMT antibody. Labeling with a non-biological iodoTMT™ reagent was performed without (lane 1) or with 5 mM ascorbate (Asc) (lane 2). Lane 3 represented the unblocked sample; the other samples were blocked with MMTS. Ponceau S staining was used to confirm the equal loading of the different samples. (B) Cells used for samples were incubated in N-free medium for 0.5 h (lane 1) or grown in nitrate-containing medium (lane 2). S-nitrosylated proteins were analyzed as described in (A).

cyanobacterium was transferred to 1 mM nitrite-containing medium, signal in the cells did not increase. Since NO is produced under nitrogen (N) starvation in some unicellular green algae (Wei et al., 2014), fluorescence levels were determined in *S. elongatus* PCC7942 under N limitation. In N-free medium, PCC7942 did not accumulate NO above the control level (Fig. 1B).

When strain PCC 7942 was treated with 20 mM arginine, signal in cells increased 9-fold after 0.5 h and reached a maximum after 96 h (Fig. 1B). In cells incubated in 5 mM arginine NO amounts were 3.4–6.0 fold higher than in cells in nitrate-containing medium (Fig. 1B). 1 mM arginine increased the fluorescence level by a maximum of 3-fold after 24 h.

These data are consistent with the images obtained by confocal microscopy (Fig. 1C). In nitrate-containing medium, *S. elongatus* PCC7942 showed a very weak signal. When the cyanobacterium was transferred to the 20 mM arginine-containing medium, a green signal appeared in cells after 1 h. The stimulation of NO production by arginine is unexpected, since the genome of *S. elongatus* PCC 7942 does not contain a gene encoding the NOS enzyme (Gupta, Srivastava, and Mishra, 2025).

It has been shown previously that S-nitrosylation of proteins represents one of the key mechanisms underlying NO-related signal transduction in plant cells (Astier et al., 2021; Lapina, Statinov, Puzanskiy, and Ermilova, 2022; Ermilova, 2023). We wondered whether the proteins undergo S-nitrosylation in *S. elongatus* PCC7942 facing arginine treatment. To test this possibility, the Pierce S-nitrosylation Western blot kit assay was employed. Since the fluorescence level was detected

at a high level after incubation with 20 mM arginine for 0.5–4 h when the cells were not yet growing, protein S-nitrosylation was surveyed upon these conditions. The probes were treated with the TMT reagent to label S-nitrosylated proteins, and were subsequently identified using anti-TMT antibody. Incubation with 20 mM arginine for 1 h produced two intense bands (about~33 and 18 kDa) (Fig. 2A). These bands were absent in control samples without ascorbate, indicating their specificity. An additional control without MMTS treatment confirmed that protein S-nitrosylation in these cells was specific. Interestingly, the same bands (about~33 and 18 kDa) and several low intense bands (between 48–60 kDa) were visualized in cells grown in nitrate (Fig. 2B). In contrast, no S-nitrosylated proteins were detected in N-deprived cells. The results indicate that S-nitrosylation is a recognizable posttranslational modification in *S. elongatus* PCC7942 and cells use this PTM under N-sufficient conditions.

Discussion

In recent years, much evidence has been accumulated supporting the idea that NO versatility exists in eukaryotic photosynthetic organisms (Qiao and Fan, 2008; Berger, Boscari, Frenedo, and Brouquisse, 2019; Zalutskaya, Dukhnov, Leko, and Ermilova, 2021). Given the profound biological role of NO in higher plants and green algae, many attempts have been made to identify the origin of NO and NO-forming enzymes (Astier et al., 2021; Lapina, Statinov, Puzanskiy, and Ermilova, 2022; Ermilova, 2023). However, the ability of bacteria

with oxygenic photosynthesis to generate NO has only been described in one representative, marine unicellular cyanobacterium *Synechococcus* PCC7335, which utilizes the NOS enzyme (Correa-Aragunde, Foresi, Del Castello, and Lamattina, 2018). Nothing was known about NO production in other cyanobacteria.

Although strains PCC7335 and PCC7942 belong to the same genus, the latter has no NOS homologs. In plants, different approaches have led to the proposal that NR is the best candidate for NO production (Rockel et al., 2002). However, we did not observe any effect of nitrite on NO production (Fig. 1B). Here, we found that only arginine induces the rapid formation of NO in *S. elongatus* PCC7942 (Fig. 1B). The subsequent question is how NO might be produced in *S. elongatus* PCC7942. It is believed that plant NOS is not a canonical type as the animal NOS enzyme (Corpas and Barroso, 2017; Lapina, Statinov, Puzanskiy, and Ermilova, 2022). The possible scenario is that some non-canonical protein(s) could generate NO from L-arginine in PCC7942. However, we cannot exclude the presence of an enzyme that generates NO from arginine as a residual by-product and/or the functioning of other arginine-dependent routes. Future research in this field may reveal actors to this scenario.

In higher plants and green algae, NO can perform its biological functions through several mechanisms, but this mainly occurs through S-nitrosylation, covalent and reversible binding of NO to cysteine thiol (Astier et al., 2021). We hypothesized that this PTM would occur in *S. elongatus* PCC7942. This does appear to be the case. We observed that after exposure to 20 mM arginine, the nitrosylation process actively developed (Fig. 2). Importantly, cyanobacterium grown on nitrate also utilizes protein S-nitrosylation, which indicates that the cells produce sufficient amounts of NO to carry out posttranslational modification. In nitrogen-depleted *S. elongatus* PCC7942, nitrosylated proteins were not detected. One possibility is that higher levels of protein targets are required for S-nitrosylation than in nitrogen-starved cells. Furthermore, in *E. coli*, S-nitrosylation by NO is essentially enzymatic (Seth et al., 2018). Therefore, we cannot rule out the use of SNO synthase, which may be non-functional in strain PCC7942 under nitrogen-deficient conditions. The proteins that are targets of this PTM, as well as the enzymatic machinery for S-nitrosylation, in *S. elongatus* PCC7942 remain to be identified.

Conclusion

We provide evidence that NO signaling in *S. elongatus* PCC7942 is mediated by S-nitrosylation of proteins. Thus, our results provide a basis for further studies to elucidate putative NO formers and NO-sensitive signaling pathways in cyanobacteria. Collectively, our finding

expands knowledge of NO generation and signaling in organisms with oxygenic photosynthesis.

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