



Editorial: Nitric oxide in plants



1. Preface

Nitric oxide (NO) is a pivotal molecule in biological systems due to its wide range of physiological and pathological functions. Despite plants being reported as the first organisms to generate NO, associated research in this life kingdom did not begin to gather momentum until the mid 1990s. In this context, the nascent European plant NO community initiated a small meeting to share new findings and interchange ideas relevant to plant NO biology. Thus, ten years ago the first Plant NO meeting was held in Verona, Italy (2006). The following NO meetings were biannually celebrated in Dijon, France (2008), Olomouc, Czech Republic (2010), Edinburgh, United Kingdom (2012), Munich, Germany (2014), with the last meeting held in Granada, Spain (2016).

The “6th Plant Nitric Oxide International Meeting” (2016) was divided into four main sessions where the participants presented their last advances in this exciting and rapidly developing field.

1.1. Session 1. Nitric oxide metabolism in plants

In higher plants, nitric oxide (NO) is a key molecule involved in a plethora of physiological and stress processes. One of the main challenges in this research area has been to identify the mechanisms responsible for NO generation. In this sense, the session was focused on different aspects of NO metabolism related to S-nitrosothiols (SNO) signaling, NO production, and its effects on the development of plant roots, and the role of nonsymbiotic hemoglobins as indirect modulators of NO levels. S-nitrosylation is a reversible redox modification consisting of the addition of a nitroso group to a particular cysteine thiol group, giving rise to S-nitrosothiols (SNOs). Furthermore, S-nitrosylation has emerged as the main redox signal through which NO transmits its bioactivity. In addition, the levels of S-nitrosoglutathione (GSNO), an endogenous NO donor and reservoir of NO bioavailability are controlled by GSNO reductase (GSNOR), which indirectly regulates total cellular levels of SNOs. In this sense, Elizabeth Vierling (University of Massachusetts Amherst, USA) presented laboratory work to elucidate the role of GSNOR in plant biology by identifying GSNOR-interacting proteins, measuring redox poise, and characterizing conserved GSNOR cysteine mutants in *Arabidopsis thaliana*. Notably, Sophie Kneeshaw et al. (University of Edinburgh, United Kingdom) indicated by selectively targeting different protein-SNO subsets, that multiple TRX family members are responsible for regulating distinct branches of SNO signaling during plant immunity, suggesting that this TRX-like enzyme might act in concert with GSNOR to control GSNO-derived protein-SNO

signaling. To determine SNO levels, Paulo T. Mioto (University of São Paulo, Brazil) presented an alternative and reliable fluorometric-based method to detect and quantify SNOs and had encouraging results. Also investigating the implication of S-nitrosylation to regulate processes such as seed maturation and germination, M.I. Sánchez-Vicente et al. (CIALE, University of Salamanca, Spain) provided evidence for the NO regulation of seed-specific bZIP transcription factors. Finally, Marília Gaspar (Institute of Botany, Brazil) presented noteworthy results about the involvement of NO in cell-wall glycome and transcriptome of the *A. thaliana* during root-hair formation. Regarding the generation of NO, two main potential pathways depend on the involvement of L-arginine (L-Arg) and nitrate/nitrite, implying the participation of a L-Arg-dependent nitric oxide synthase-like activity and a nitrate reductase (NR) activity, respectively. In this sense, Myriam Catalá (National Institute of Health Carlos III, Spain) showed that nitrate reductase and nitric oxide synthase may be involved in biosynthesis of NO during the rehydration of lichens under stress conditions. To shed light on this issue, Augustin C. Mot (Babes-Bolyai University, Romania) presented an *in vitro* mechanistic approach of nonsymbiotic plant hemoglobins as indirect NO scavengers via hydroxylamine reduction to ammonium. In addition, Jeremy Astier (Helmholtz Zentrum München, Germany) presented notable results, indicating the influence of a putative copper amine oxidase (CAO8) on arginine-dependent NO synthesis, which could constitute a new way of regulating NO production in plants. In this scenario, in relation to the hemoglobin-NO respiration (HNR) process, Renaud Brouquisse et al. (University of Nice-Sophia Antipolis, France) identified in *M. truncatula* three presumed nitrite transporters (NiRT1, 5 and 6), potentially targeted to the mitochondrial membrane, and observed that its expression is upregulated in hypoxia-treated nodules. Finally, Urszula Krasuska et al. (Warsaw University of Life Sciences) presented data concluding that the secondary mode of action of canavanine (CAN) involves serious alteration in ROS and RNS formation and metabolism.

1.2. Session 2. NO signaling and posttranslational modifications mediated by RNS

This session identified novel targets of NO signal transduction and in some cases also began to provide insights into the associated molecular mechanisms. Excitingly, Capilla Mata-Perez presented evidence for nitro-fatty acid signaling in plants, generated by the reaction of RNS and unsaturated fatty acids. Using an RNAseq approach it was demonstrated that nitro-linolenic acid was involved in the plant stress response, mainly by inducing

the chaperone network. Interestingly, nitro-linolenic acid can also function as an NO donor, both *in vitro* and *in vivo*, opening up many potential opportunities for further research. Alexandra Ageeva presented data implying an important new role for NO as an epigenetic regulator and revealed a novel regulatory mechanism of HDACs in plants. NO seems to inhibit histone deacetylase activity and in this way may modulate chromatin structure, making it accessible for the transcription machinery. Thus, by employing a ChIP-sequencing approach, genes showing NO-mediated alterations in histone acetylation could be identified. José López-Bucio presented a potential role for NO in jasmonic acid-induced changes in *Arabidopsis* root system architecture. Both jasmonic acid and the NO-donor sodium nitroprusside inhibited primary root growth and promoted lateral root development. Tamara Lechon and colleagues discussed evidence that changes in mitochondrial-dependent NO homeostasis drives root development. They performed a transcriptomic meta-analysis between PROHIBITIN3 and NO-ASSOCIATED1 and found a putative link between both proteins in root development. Moreover, they demonstrated a function for PROHIBITIN3 and NO-ASSOCIATED1 in mitochondria biogenesis and stem cell activity by regulating WUSCHEL-related homeobox5 expression. Agepati S. Raghavendra outlined insights into the function of NO in guard cells and highlighted the interaction of NO with cytoplasmic pH, ROS and calcium during stomatal closure.

Juan de Dios Alché presented an *in silico* study on the possible function of S-nitrosylation in plant reproductive tissue. The pollen and pistal transcriptome of olive was analysed with different bioinformatics tools to identify a putative S-nitrosylome of these tissues. The possible function of NO in the allergenicity of the pollen olive grain will be analysed in future work. Yasemin Tasdemir (Stöhrs lab) opened a new field in protein S-nitrosylation. They identified targets for S-nitrosylation in the plasma membranes of tomato roots, which included different aquaporin isoforms. Tyrosine nitration is another NO-dependent protein modification. Initially, thought to be a consequence of NO stress, it is now emerging as a possible signaling mechanism. Feigl and colleagues demonstrated a connection between tyrosine nitration and ascorbate metabolism. They observed higher nitration levels in both plants deficient in ascorbate (*vtc2-3*) or which are deficient in nitrate reductase activity (*nia1nia2*). Interestingly, externally applied ascorbate induced an RNS burst accompanied by intensive tyrosine nitration, suggesting a pro-nitration activity of exogenous ascorbate.

Ludidi and colleagues demonstrated that NO is an important signaling molecule for regulating the activities of antioxidative enzymes, which regulate the level of ROS in soybean. The application of NO biosynthesis inhibitors or NO scavengers changed the activities of superoxide dismutase, ascorbate peroxidase and catalase, while application of an NO donor showed the opposite effect. Treatment of tomato with the non-proteinogenic amino acid m-tyrosine results in total inhibition of root growth, but did not affect cell viability. Interestingly, Olga Andrezejczak linked the toxic function of m-tyrosine with the induction of a secondary nitro-oxidative stress displayed by formation of 3-nitrotyrosine and protein carbonylation. The differential glutathionylation of chloroplast 2-cys peroxiredoxin and mitochondrial peroxiredoxin IIF is well established, but little is known about the enzymatic systems that specifically regulate the reversal of this modification. Calderon and colleagues could show that sulfiredoxin is able to de-glutathionylate chloroplast 2-cys peroxiredoxin, but not

mitochondrial peroxiredoxin IIF. They suggested an important function of the 2-cys peroxiredoxin/sulfiredoxin system under oxidative/nitrosative stress conditions *in planta*. In aggregate, this session significantly advanced our understanding of NO signaling in plants, revealing new vistas for further exploration, for example, the potential role of NO in epigenetic control and its intersection with lipid-based signaling.

1.3. Session 3. NO and abiotic stress

Plants have to tolerate numerous abiotic stresses to be able to thrive and survive. This is of particularly importance for plants which are used for crops. Many of these stresses are natural, such as light and heat, and this may be of more significant importance as the world deals with climate change. It is also very pertinent to consider that many stresses are man-made, being generated and released from both farming and industry.

To resist abiotic stress plant cells need to both perceive that stress and then respond. Linking these two events are signal transduction pathways. These pathways recruit a multitude of components and actions, including phosphorylation modulation, with kinases and phosphatases, and the concentration of intracellular calcium ions. However, it is also known that these pathways use a range of small, reactive and transient molecules as signaling components. These include ROS such as H₂O₂. Gasotransmitters such as hydrogen sulfide are also involved, but one of the most important is the free radical gas NO. The role of NO, and how it integrates into signalling, was the focus of this session.

Studies on a variety of plant species were presented both orally and as posters. These included model organisms such as *Arabidopsis*, but also some crop species such as potato (*Solanum tuberosum* L.), soybean (*Glycine max* L.), cucumber (*Cucumis vulgaris*), barley (*Hordeum vulgare*), oat (*Avena sativa*) and even mustard (*Brassica juncea*) and sea rocket (*Cakile maritima*). Data from a variety of stresses were also shown, including metal deficiency, heavy metal tolerance, radiation, salt, wounding and drought. Linking all these plant species and stresses was the presence of NO as a central signalling molecule. Therefore, how NO is generated following abiotic stress challenge, and the downstream events of increases in NO are important to understand.

The oral session was opened by a presentation on plant hemoglobins (Hebelstrup and Møller). These are instrumental in the control of NO levels, especially class 1 and 2. Either over-expression or silencing of the genes for these proteins are powerful approaches for unravelling their action. Interestingly class 1 hemoglobins appear to be up-regulated during hypoxic stress. Furthermore, these proteins are also important in a plant's battle with biotic stress too.

Iron deficiency was the focus of the second communication (García et al.). The data presented indicated that the activity of the enzyme nitrosogluthathione reductase (GSNOR) was enhanced under those conditions. The enzyme helps to control to level of GSNO and therefore the bioavailability of NO, and it is known that genes involved in iron acquisition are partly controlled by the levels of NO and GSH. Therefore, the involvement of GSNOR in this regulation is important to be understood.

It is known that radiation is an important abiotic stress to investigate, as it is naturally present, but also levels increase due to human activity. This has been in the fore with power stations such as Chernobyl and Fukushima. Low levels of plutonium-242 were used as the stress agent for the third presentation (Gupta et al.). Using

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