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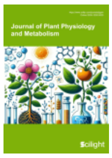

Review

A Brief History of Nitric Oxide in Plants: How We Got Here, Where We Are, and Where We Might Be Going

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Abstract: There is no doubt that nitric oxide (NO) has a range of instrumental actions in plants, from seed germination, through plant development, to flower senescence and fruit development and ripening. Over more than four decades there have been a number of seminal research papers on the generation and roles of NO in plants cells which have taken the field forward. During that time too, there has been a series of focused conferences, the PNO meetings, which have encouraged and guided the focus of plant NO research. 2025 sees the 10th such meeting. The understanding of how NO works in plants is now wide-ranging. It has often been guided by similar work on animals, although care needs to be taken with such an approach; nitric oxide synthase-dependent generation of NO in plants has not been easy to determine. Despite the difficulties, research so far has shown how NO signalling is entrenched in the rest of the complex signalling network that takes place in plant cells. There are still many future challenges to be faced in this field, including how NO may be used as a systemic signal, or even as a signal between individual organisms. However, partly guided by future PNO meetings, the future of research on NO in plant bright and likely to grow even bigger.

Keywords: germination; history; hydrogen sulfide; plant development; plant signalling; reactive oxygen species; redox; stress responses

1. Introduction

The biological effects of gases have been studied ever since they were discovered and isolated, with some of this work being carried out in the late eighteenth century [1–3]. This included work on oxygen and photosynthesis, as well as on future medical gases such as nitrous oxide. However, the work on nitric oxide (NO) in biological systems really only started in the 1980s, with the publication on the role of acetylcholine in the relaxation of arterial smooth muscle [4], with the history of the research on plants over the last forty years being highlighted in a 2019 publication [5].

The early days of work on NO in plants followed on from the work in animals, which moved on apace, and in many ways plant-based research has drawn on such work over the last four decades. In 1987, Palmer et al. [6] reported that in animals endothelial-derived relaxing factor (EDRF) was in fact the gas NO, highlighting that a small relatively reactive gas could in fact be an important signalling molecule. Work was already taking place on reactive oxygen species (ROS) and their potential signalling role. The focus on ROS research had been mainly on their roles during phagocytosis e.g., [7], but even in the 1960s the possible role of ROS in signalling events was being investigated, e.g., [8]. The work on both ROS and NO in cellular signalling events has since expanded dramatically, with other small reactive compounds being included in the mix, such as hydrogen sulfide (H_2S), including in plants, as reviewed recently [9].

It was not long before the enzymes involved in the synthesis of NO were being characterised (the three nitric oxide synthases (NOS) in humans, for example: for review on NOS see [10]), with the search for similar enzymes in plants. Roles and signalling events involving NO have since been revealed, as discussed below. With 2025 seeing the gathering of researchers in this field at the 10th Plant Nitric Oxide International Meeting (in Poland, but online [11]), it seems timely to give a brief overview of the highlights in NO plant research and to speculate on the work that should be carried out in the future.

2. Historical Highlights in NO Plant Research

Plant NO research has in many ways mirrored, or followed, the research that was taking place in animals, with the same questions being asked; how is NO made and what does it do? A timeline of the most significant reports in plant research is shown in Figure 1.

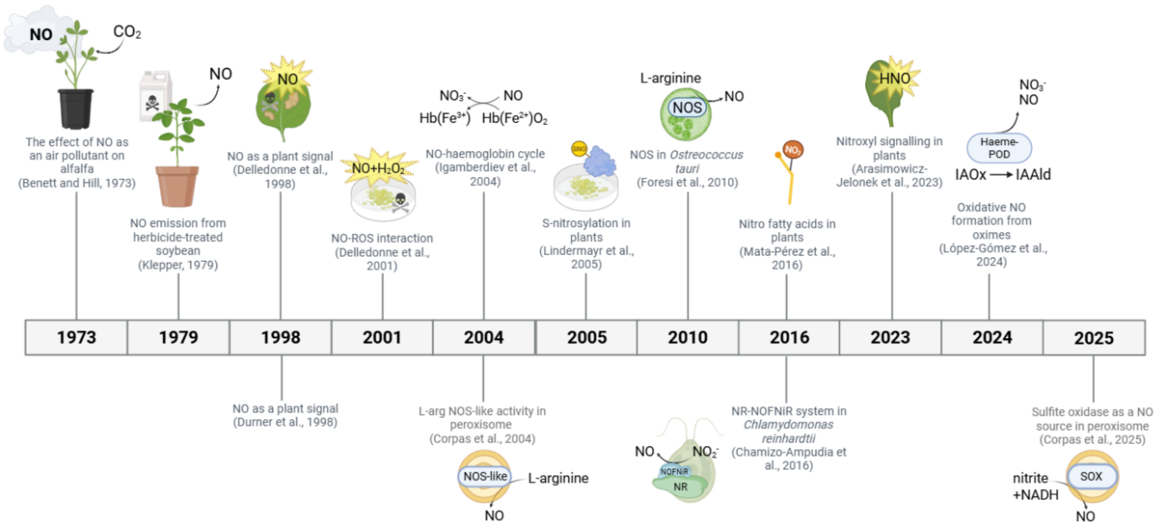

Figure 1. A timeline of some of the significant discoveries in NO research in plants [12–22].

Some of the first hints of the physiological effects of NO on plants came from the work on nitrate reduction where NO was found to be involved. This work was published in 1960 from the Long Ashton Research Station in Bristol, UK, and included the use of marrow, strawberry, cauliflower and broad bean [23]. Further suggestions of the importance of NO in biological systems came from the work on air pollution, for example, by Bennett and Hill in 1973 [12] who were looking at the net absorption rates of carbon dioxide (CO_2), in what they described as apparent photosynthesis, using alfalfa (*Medicago sativa* L.) as their model organism. This was followed by early work on NO in plants with a report from Klepper in 1979 [13], when the generation of NO was noted in soybean (*Glycine max*), and this was correlated to the levels of herbicides used. However, the NO plant field really was spurred into action with the publication of two papers in 1998, both looking at NO during plant pathogen challenge [14,24]. Here, NO was being shown to be a signalling molecule in plants, as had been found in animals, and this opened the way for the topic to expand enormously. It also suggested ways in which NO generated in plants, with inhibitors of the animal NOS having the effects on reducing the effects seen.

It was not long before NO was being found to be generated in other plant systems, with again, a plant L-Arg-dependent NOS-like enzyme being thought to be responsible. For example, in 1999 it was shown in peroxisomes. It was found that citrulline was generated in a calcium ion-dependent manner, and this was reduced by NOS inhibitors [25]. Years later, ozone chemiluminescence demonstrated that this L-Arg NOS-like activity produced NO. Furthermore, the presence of NO in peroxisomes was also confirmed by electron paramagnetic resonance (EPR) spectroscopy [26]. Interesting, it was 1999 that NO was shown to be generated by purified maize nitrate reductase (NR: EC 1.6.6.1) using nitrite as substrate and NADH as electron donor [27]. Examples of the role of NR in plant physiology includes the report in 2002 that the enzyme is used for controlling stomatal closure [28], and hence drought responses.

Of course, we know that NO does not work in plant cells in isolation, and the first evidence of this was given by Delledonne et al. in 2001 [15]. Again, looking at plant responses to pathogens, in particular, the hypersensitive response (HR) in soybean, it was found that ROS and NO interact to give the final response. Peroxynitrite was found not to be the mediator of HR cell death, and it was suggested that plants and animals use a similar signalling mechanism in host defence. A paper by Wendehenne et al. in the same year also did a comparison of the synthesis and signalling with NO in plants and animals [29]. Such comparisons have continued to guide the work taking place on plants.

In 2004, Igamberdiev et al. [16] investigated hypoxia in plants and suggested what was to become known as the haemoglobin/nitric oxide cycle (Hb-NO cycle) involved a cycling of NO(x) compounds linked to a cycle where Hb was oxygenated. This helped to maintain cellular redox and energy levels with the generation of ethanol and lactate.

2005 saw a group of important papers published. Planchet showed that NO could be generated by mitochondria [30], but it was six years later that the same was shown for chloroplasts [31]. Also in 2005, Lindermayr published a paper on the *S*-nitrosylation of proteins in plants [17]. In animals, one of the main downstream signalling pathways is that which involves cGMP [32], but even though plants have cGMP metabolism [33], this was never thought to be the main signalling pathway downstream of NO in plants. In plants, much of the NO signalling likely occurs through reversible covalent modifications of proteins, particularly at cysteine thiol groups, a process known as *S*-nitrosation or *S*-nitrosylation. In addition, irreversible tyrosine nitration may occur, and an increase in this modification is considered a marker of nitrosative stress [34,35]. Meanwhile, plant *S*-nitrosoglutathione reductase (GSNOR) was reported [36], again using plant disease resistance as a basis for the work. This showed that there was a mechanism able to reverse thiol-based covalent changes induced by NO accumulation in cells, showing how signalling in plants cells could be regulated in plants. And then a year later, in 2007, building on work that was being carried out by the same authors [37], the haemoglobin-NO cycle was reported [38], again showing how NO levels in cells could be regulated.

The evidence of the presence of a true NOS in plants has had a rocky history, with a paper being retracted and early evidence hard to repeat, as described previously [5]. However, in 2010 a NOS was found in an algal species [18], specifically the unicellular green algae *Ostreococcus tauri*. This gave hope that a similar protein would be found in higher plants, but in 2016, by interrogating the genetic data from over 1300 plant and algal species, there was no evidence found of a true NOS enzyme in higher plants [39]. Although not as thorough, others have taken a similar approach with no success in identifying a plant NOS sequence [40]. However, it has been suggested that such enzymes which have NOS characteristics (in their substrate or inhibition profiles) are referred to as NOS-like [41].

An interesting addition to the NO story in plants was made by Mata-Pérez et al. in 2016 [19], when it was reported that NO not only signalled through proteins but by the covalent modification of fatty acids too. This would also serve as a sink-sourced of NO in organisms—along with GSNO—and may help to explain systemic responses which have been discussed [42]. Also in 2016, Chamizo-Ampudia et al., looking at mutants of nitrate reductase (Nia1) and amidoxime reducing component (ARC), elucidated the NR- NOFNiR (Nitric Oxide-Forming Nitrite Reductase) system for the generation of NO in Chlamydomonas [43].

In 2023, Arasimowicz-Jelonek et al. [20] published a paper about nitroxyl (HNO). HNO, the protonated form of NO^-, was suggested to the able to react with a range of other compounds, including molecular oxygen (O_2), NO, nitrite, metalloproteins, metalloporphyrins, thiosulfate, thiols and sulfite, and therefore could be involved in signalling. A year later López-Gómez et al. proposed an oxidative generation of NO from oximes, such as indole-3-acetaldoxime (IAOx [21]). This was catalysed by peroxidases, with work being carried out both in *Medicago truncatula* and *Arabidosis thaliana.*

NO detection has had its controversies too, although EPR spectroscopy probably remains the gold standard for the measurement of radicals such as NO [44]. Using this technique, a recent study demonstrated that recombinant sulfite oxidase from pepper fruits is capable of generating nitric oxide (NO) in the presence of nitrite and NADH. This finding reveals a novel enzymatic source of NO production in higher plants. [22]. However, much of the work has relied on the interaction of NO with fluorescent dyes such as 4,5-diaminofluorescein diacetate (DAF-2DA), which is de-esterified and accumulates in cells—the non-diacetate version can be used for extracellular detection. However, even this was questioned [45]. This is only semi quantifiable, but does give spatial data, so the location of the NO accumulation can be determined, and could be used for "seeing" NO in leaves, shoots and roots. Recently this has been expanded to the use of whole plants, showing systemic signalling [46,47], opening the way for more studies on how NO may move around plants and have long-range signalling.

3. The NO Club

3.1. Its Formation

As the research on NO and plants started to grow, Delledonne in Verona, Italy, suggested that a regular meeting of researchers was formed to promote the work that was taking place. The meeting format was suggested to be ‘cheap and cheerful’. The focus of the meetings would be to encourage young and up-and-coming researchers to the field, and he was keen to make this as accessible as possible. For example, there were to be no expensive hotels used, and he wanted to host it at his home university; it was going to be done with the minimum of expenses. It was advertised as a European event, and going forward was to be hosted by NO research groups around Europe, so everyone who wished to attend would be relatively near to the meetings. This was not to exclude anyone, but to encourage those with limited finances to attend, such as doctoral students. But most importantly, the ethos of the meeting would be that all the presentations had to be given by young researchers. These would be PhD students or postdoctoral researchers. No ‘old hands’ were allowed to present, and it had to be encouraging and friendly, in other words, no nasty questioning. And of course, everyone concerned all agreed that this was a great idea to get more people interested in plant NO, and to make the current thinking accessible. And so, what was to be nicknamed ‘The NO Club’ was born.

As promised the first meeting was in Verona in Italy, at Massimo Delledonne’s university, and it was a great success. It ran as planned with excellent hosting which was cheap and convenient for all, and the coffee was amazingly strong! It was well attended, by about 60 people, many being the young researchers it was aimed at. Extramural activities in Italy are never a problem, and some even managed to see Giuseppe Verdi’s Aida at Verona’s Arena di Verona, a still-used Roman amphitheatre.

The first meeting was such a success that the organising committee decided on a two-year gap between meetings, but always to keep it relatively cheap and accessible as researchers rotated through PhDs and fixed-term contracts. The NO Club was well and truly up and running, promoting NO research on plants across Europe.

3.2. Progress of the PNO Meetings

The NO Club, now branded as the Plant NO meeting (PNO) continued to grow and thrive. It should be mentioned though, that the scientific committee has always been mindful of other meetings which overlap with PNO, and the most notable is probably the Plant Oxygen Group (POG). Of course, neither ROS, or reactive nitrogen species (RNS), such as NO, work in isolation and many researchers attend both meetings.

The PNO meetings continued in Europe and rotated around some of the research groups most active in the field. For example, in 2008, PNO moved to Dijon in France where David Wendehenne hosted about sixty guests in what was called the Second International Plant Nitric Oxide Club Workshop. The meeting followed the format of the first, and was an extremely successful event. The third then moved to be hosted by Marek Petřivalský in Olomouc, Czechia (The Czech Republic) [48]. Subsequent events occurred in various cities, including Edinburgh (2012), organized by Gary Loake; Munich (2014), organized by Christian Lindermayr; Granada (2016), organized by Francisco J. Corpas; and Nice (2018) by Renaud Brouquisse, all with great success, with locations being shown in Figure 2.

As with many other facets of life, the COVID-19 pandemic had a major effect on the organising and hosting of the PNO meetings. The Scientific Committee decided to continue the meetings, but to have them online. Therefore the 8th PNO in 2021 was hosted by Zsuzsanna Kolbert in Szeged, Hungary. Despite no face-to-face meetings, it was a very successful event [49].

With the ability to anyone to join meetings online, and with this becoming more of a norm, for the 9th meeting in 2024, it moved out of Europe for the first time, being hosted by Jagadis Gupta at the National Institute of Plant Genome Research, New Delhi, India. Online, of course, allows breakout groups and discussion fora and again this was well attended and was a very successful event, showing that the online platforms can attract people from around the world, expanding the reach of Delledonne’s original idea. Now we have reached the 10th meeting, which will be hosted back in Europe, in Poland, by Urszula Krasuska at the Instytut Biologii, Szkoła Główna Gospodarstwa Wiejskiego w Warszawie [11], where it is advertised to “create a scientific environment friendly to the exchange of ideas and knowledge,” nicely aligning with the original ethos of The NO Club. In 2027, PNO will be going to China, hosted by Shuhua Zhu at Shandong Agricultural University, so it is now truly global.

3.3. What Has PNO Achieved?

In many ways Delledonne’s original objectives are continuing to be achieved. The NO in plants topic is bigger and more wide ranging than ever; there is young and enthusiastic talent who will ensure that it has a future. But the meetings have also spurred the scientific committee to publish several overarching papers on the topic, from suggesting terminology to be used [41], discussions on the use and future of nanotechnology [50], writing a history of the topic [5], discussing relevant post-translational modifications [51], to looking at interorgan NO use in plants [42]. As themes emerge from the meetings more such papers should appear. It is hoped that they will help guide and facilitate the work of those coming into the plant NO field.

Figure 2. Geographical distribution of previous PNO meetings. Past on-site PNO events have been organized by leading researchers in plant NO field in different European countries from Spain to Scotland. Following the pandemic, PNO8, PNO9 and PNO10 meetings have been organized in online form by researchers from Hungary, India and Poland, respectively.

The other tangible outcome of the meetings has been the establishment of several Special Issues (SI) on the topic in relevant journals. For example, PNO8 had a SI in the *Journal of Experimental Botany* in 2021 [52]. This had twelve reviews and also primary research reported, as summarised in the editorial [53]. For PNO9, the SI was in *Plant Science* with a title of Current Directions in Plant Nitric Oxide Research [54] (This was still taking submissions of the time of writing, to be published during 2025). With PNO10 around the corner (July 2025), the SI will be in the journal *Nitric Oxide* to be published in 2026 (yet to be officially announced at time of writing).

4. Where is the NO Plant Field Now?

The roles of NO in plants are now well recognised and widespread, from being involved in seed germination [55] to flower senescence [56]. Nitric oxide is involved in a myriad of plant stress responses too. Many of the roles which have been accepted over the years are listed in Table 1, whereas Table 2 highlights interactions with other signaling molecules.

Table 1. Examples of roles of NO in plant function and growth.

Role or function of NO	Example Review Article(s) or Papers Highlighting Effect
Seed germination	[55,57]
Pollen and pollen tube growth	[58–60]
Plant development	[61,62]
Flower senescence	[56]
Leaf senescence	[26]
Fruit ripening	[63]
Apoptosis (programmed cell death)	[64–66]
General abiotic stress responses	[67–69]

Table 1. *Cont*.

Role or function of NO	Example Review Article(s) or Papers Highlighting Effect
Cadmium stress	[70]
Mercury stress	[71]
Aluminium stress	[72]
Nickel stress	[73]
Copper stress	[74]
Lead stress	[75]
Salinity stress	[76,77]
Cold stress	[78]
Heat stress	[79,80]
Drought and stomata	[81–83]
Hypoxia	[84]
Flooding stress	[85]
Biotic stress	[86,87]
Oxidative stress responses	[88]
Gene regulation	[89]

Table 2. Examples of where NO interacts or has effects on other cellular signalling molecules.

Interaction with NO	Example Review Article(s) or Papers Highlighting Effect
Phytohormones (in general)	[61,90,91]
Salicylic acid	[92,93]
Abscisic acid (ABA)	[94,95]
Ethylene	[96,97]
Cytokinins	[98]
Jasmonate (JA)	[99]
ROS	[100–102]
Hydrogen sulfide	[103,104]
Molecular Hydrogen	[105]
Glutathione	[106–108]
Lipids and fatty acids	[109]
Antioxidants	[75,87]
Melatonin	[110]

As can be seen in Table 2, NO interacts and therefore alters an array of other cellular components involved in signalling events. It is involved with a range of phytohormones including ones involved in stomata movements, such as abscisic acid (ABA), as well as in fruit ripening, such as ABA and ethylene. NO signalling also interacts with many of the other small relatively reactive compounds which are involved in stress responses, such as ROS, H_2S and hydrogen (H_2). The reaction of NO with superoxide leads to the formation of a new RNS, namely peroxynitrite, and this is known to have its own signalling effects [111,112]. In a similar manner, NO will react with H_2S to form nitrothiols [113,114], and again these can have their own signalling action.

Although Tables 1 and 2 are not an exhaustive list they do highlight the wide-ranging effects and roles of NO in plants, which is also reflected in animals, where NO is known to be involved in disease states [115]. It is, therefore, not surprising that mutant plants that have been developed to have reduced NO generation grow so badly and are sickly.

It is now well accepted that plants have the capacity to generate NO in their cells, with several enzymatic sources implicated. These include nitrate reductase [43], a NOS-like enzyme [27] and from mitochondrial activity [116]. It is also well recognised that downstream of NO there are modification of important cellular components. These include proteins through *S*-nitrosylation [106] (sometimes referred to as *S*-nitrosation [37) or nitration of amino acids such as tyrosine [34]. Therefore, signalling pathways from the initiation of NO generation to the cellular effects can be drawn, with these often having the alteration of amount and/or activity of enzymes. These may be involved in the modulation of other signalling pathways through crosstalk. For example, if NO alters the activity of antioxidants this will affect signalling initiated by an accumulation of ROS.

NO is known to interact with other key cellular components too. It can form *S*-nitrosoglutathione (GSNO) in a reaction with glutathione [108], and also react with fatty acids [109], and both products are thought to be able to act as sinks for NO, either prolonging the NO signalling effects or moving them through the organism, as discussed recently by Kolbert et al. [42].

There is no doubt that NO is a key regulator of plant development and growth, and instrumental in how a plant survives stress challenges. However, there is genetic variation even within the same plant species, which can complicate our understanding further. For example, genotypes with differencing drought tolerance present with different NO generation [117]. Clearly there is still much to learn about NO in plants.

Future Directions and Challenges for Plant NO: Research and Use

The field of NO research on plants has a bright future, but excellent scientists have been lost from it, either through retirement, or more sadly having passed away. Everyone who knew him will remember with fond memory Gary Loake (Edinburgh University), who did so much to contribute, amongst many other aspects, to our understanding of NO removal in plants [36]. However, partly encouraged by the regular PNO meetings, there are plenty of talented scientists moving the field forward.

However, despite over forty years of work, there are many areas of plant NO research that need to be the focus for the future. These include, but are not limited to:

- How does NO get generated and removed in specific regions of plants. What is the NOS-like activity which has remained so elusive? What is the contribution under certain conditions from the multiple sources of NO that have been suggested in plants?
- Which enzymatic source(s) are responsible for NO production in plants at the subcellular and tissue levels, and how do they contribute under different physiological and stress conditions?
- How does NO fit into the signalling where there are many interactions with other small transient molecules, such as ROS, H_2S and H_2? How do they regulate the accumulation and hence activity of each other? How does this contribute to the overall intracellular redox status? And how does this fit into all the other signalling events taking place in plant cells?
- What is the significance of the formation of 8-nitroguanine (8-NO_2-G) in RNA and mRNA [118], and how does this alter cell function in plant tissues? Other covalent modifications require further investigation too, such as tryptophan nitration [119].
- What is the significance of HNO-based signalling [20] and how does this fit into what we already know about NO metabolism and signalling?
- How is NO involved in interorgan and inter-organism signalling? How is it used between plants, or other non-plant organisms, such as fungi and animals? After all, organisms such as fungi produce NO [120] and NO has been reported during plant/fungi interactions [121,122]. Of course, animals produce NO too, and are known to release it in their breathe, including from humans [123].
- What is the intracellular pattern of NO accumulation? How does it contribute to phased signalling, or priming cells for future signalling events? Does it pass through plasmodesmata [124] and so contribute to tissue signalling in a meaningful way?
- Can NO be used to manipulate plant growth to our advantage, enhancing agricultural practice. Lei et al. [82] for example, recently did a meta-analysis on the use of NO in drought responses. Of course, others too have written on this topic. With ongoing climate change, NO may be part of an armoury of treatments which many allow plants, including those in the human food chain, to survive and thrive as their environment alters in the future.
- Finally, it is important to consider the potential environmental impacts of NO-releasing applications in plants, including their effects on organisms that interact with plants, such as insects, microorganisms, and even humans [125]. This underscores the importance of multidisciplinary and interdisciplinary research.

5. Conclusions

The history of research on NO in plants has spanned more than four decades and has seen many key research papers published. The work on NO in animal species has tracked alongside that on plants, and although there are many similarities, differences are seen, as would be expected. The plant NO field has gained from the organisation of the PNO meetings, and hopefully this will foster young researchers and new avenues of exploration in the future. There is no doubt that NO is used in a vast array of actions in plants, from interactions with other small reactive signals such as ROS or H_2S, to coordinating phytohormone signalling. 2025 sees the 10th meeting of PNO in Poland, and then in 2027 it should be in China. As the global plant NO community comes together, the research will benefit and one day NO-based agricultural treatments may mean that world food security will benefit from the decades' worth of research that has taken place on NO in plants.

Author Contributions

H.J.T.: initiated this review; F.J.C., N.M.S. and Z.K.: helped in the writing and editing of the manuscript; Z.K.: supplied both figures. All authors have read and agreed to the published version of the manuscript.

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