Nitric Oxide in Plant Physiology

Edited by
Shamsul Hayat, Masaki Mori, John Pichtel,
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Contents

Preface

The role of nitric oxide (NO) in biological systems has experienced increased prominence in the scientific literature since the 1980s, particularly after coming to light as a signaling molecule in plants in the late 1990s. The number of publications concerning the influence of nitric oxide in plants has dramatically increased since then. Nitric oxide is an easily diffused bioactive and signal-transmitting molecule that directly regulates many plant functions including germination, leaf expansion, root growth, stress physiology, and sequential cell death. This molecule also participates in the adaptation of plants to environmental stresses, working as the key signal carrier in defense response. Recent studies have shown that nitric oxide imparts synergistic effects with phytohormones in physiological regulation and signal transmission.

The purpose of this work is to present recent advances in the role on nitric oxide on plant physiology. This book, composed of 13 chapters contributed by scholars worldwide, addresses mechanisms of NO action in specific plant physiological processes and application of instrumentation for assessing such actions. Chapter 1 embodies recent discoveries in NO chemical properties and the mechanism of NO biosynthesis with special emphasis on the role of nitric oxide in physiological and biochemical changes that occur in plants under normal conditions due to exogenously applied or endogenously produced nitric oxide. Also presented is the issue of cross talk between nitric oxide and other phytohormones. In Chapter 2, electron paramagnetic resonance (EPR) is discussed as a tool to study nitric oxide generation in plants. Recent progress in nitric oxide research with respect to calcium and signaling is discussed in Chapter 3. The current knowledge of nitric oxide in plants exposed to diverse environmental stresses such as salinity, heavy metals, UV-B radiation, ozone, and mechanical wounding comprises Chapter 4. Chapter 5 deals with nitric oxide biosynthesis in relation to polyamines and cytokinins. Moreover, there are a number of similarities in cytokinin- and polyamine-mediated physiological functions such as embryogenesis, flowering, and senescence and in plant responses to abiotic and biotic stresses, which indicate overlapping functions of both these signaling substances; this is also discussed in Chapter 5.The role of nitric oxide in cadmium-induced PCD is discussed in Chapter 6, suggesting a possible regulatory role in response to heavy metal stress. Chapter 7 focuses on how research on nitrate reductase-deficient plants may contribute to the elucidation of mechanisms involved in nitric oxide production and signaling during plant–pathogen interactions. The function of nitric oxide in plant–pathogen interactions is discussed in detail in Chapter 8. In Chapter 9, various nitric oxide functions as a bioactive signaling molecule in plant abiotic stress responses are discussed. The cross talk between NO and other key signaling components under abiotic stress is also reviewed. The role of NO in the recovery from disease related to the stimulation of wound-healing processes is discussed in Chapter 10. Nitric oxide signaling by plant-associated bacteria is discussed in Chapter 11. Chapter 12 deals with nitric oxide synthase (NOS) activity in pea. The possibility of NO production from various sources in pea cells is also discussed. Chapter 13 describes posttranslational modifications of protein by nitric oxide.

This book is not intended to serve as an encyclopedic review of the subject of NO and its role in plant physiology; however, the various chapters incorporate both theoretical and practical aspects and serve as a baseline information for future research. It is hoped that this book will be useful to students, teachers, and researchers, both in universities and in research institutes, especially in the field of biological and agricultural sciences.

With great pleasure, we extend our sincere thanks to all contributors for their timely response, their excellent and up-to-date contributions, and consistent support and cooperation. We are also thankful to Dr. Zaki A. Siddiqui and Dr. Qazi Fariduddin, Department of Botany, Aligarh Muslim University, Aligarh, India for their encouragement. We are extremely thankful to Wiley-VCH, Germany, for expeditious acceptance of our proposal and completion of the review process. Subsequent cooperation from Wiley-VCH staff is also gratefully acknowledged. We express our sincere thanks to the members of our families for all the support they provided and the neglect and loss they suffered during the preparation of this book.

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1
Nitric Oxide: Chemistry, Biosynthesis, and Physiological Role

Shamsul Hayat, Syed Aiman Hasan, Masaki Mori, Qazi Fariduddin, and Aqil Ahmad

Summary

NO is recognized as a biological messenger in plants. It is a highly reactive gaseous free radical, soluble in water and lipid. It can be synthesized in plants via different enzymatic and nonenzymatic sources such as NOS, NR, XOR, and Ni-NOR. Due to its high lipophilic nature, it can easily diffuse through membrane and can act as a inter- and intracellular messenger and regulate diverse physiological and biochemical processes in plants in a concentration-dependent manner, such as seed dormancy, growth and development, senescence, respiration, photosynthesis, programmed cell death, antioxidant defense system, and so on. Moreover, NO also has an ability to act simultaneously with other molecules and signals in plants. This chapter covers the advances in chemical properties and mechanism of its biosynthesis with special emphasis on the role of NO in the physiological and biochemical changes that occur in plants under normal conditions due to the exogenously applied or endogenously produced NO, along with the cross talk between NO and other phytohormones.

1.1
Introduction

Since the past decade, nitric oxide (NO) is recognized as a novel biological messenger in plants and animals and has received special attention from most of the branches of biological sciences, including medicine, biochemistry, physiology, and genetics. The interest of biologists gained special momentum when this highly reactive radical was identified as a potent endogenous vasodilator of the endothelium [1]. Moreover, a widespread biological significance of nitric oxide was first recognized by Koshland [2] who named this free radical as "Molecule of Year." The 1998 Nobel Prize in Physiology and Medicine was awarded for the discovery of NO as a biological mediator produced in mammalian cells.

The role of NO is not confined only to the animal kingdom, but plants also have the ability to accumulate and metabolize atmospheric NO. Klepper [3] for the first time observed the production of NO in soybean plant, treated with photosynthetic inhibitor herbicides [4, 5], other chemicals [6, 7], or under anaerobic conditions [6, 8]. In plants, NO can be generated via enzymatic and nonenzymatic pathways. The enzymatic pathway is catalyzed by cytosolic nitrate reductase (cNR), NO synthase (NOS) or NOS-like enzymes, and nitrite:NO reductase (Ni-NOR). Nonenzymatic pathway is nitrite dismutation to NO and nitrate at acidic pH values [9–11].

After the discovery of the existence of NO in plant, the question arose, should NO be considered a phytohormone or not because the classical concept of hormone is based on three premises [12]: (i) localized site of biosynthesis, (ii) transport to target cells especially separated from the place of synthesis, and (iii) control of responses through changes in endogenous levels of the chemical. First, NO had been found to be formed mainly in actively growing tissues such as embryonic axes and cotyledons, and the level decreases in mature and senescing organs [13, 14]. Second, the smaller size of the molecule and its higher diffusion rate through biological membranes mean that NO fits the premise that hormones are easily transported. Third, it is the sensitivity of the target cells, rather than the concentration of the plant hormone, that defines the magnitude of a response [15]; because of this concept, some scientists decided to substitute the term hormone with a wider term, "plant growth regulator." Later on, Beligni and Lamattina [16] categorized NO as a nontraditional regulator of plant growth.

Further investigations led to the finding that NO is soluble in water and lipid. It can exist in three interchangeable forms: the radical ($NO^{\bullet}$), nitrosonium cation (NO^{+}), and nitroxyl anion (NO^{-}). Due to its high lipophilic nature, NO may diffuse through membranes [17] and acts as an inter- and intracellular messenger in many physiological functions. It plays a significant role in plant growth and development, seed germination, flowering, ripening, and senescence of organs [18]. Moreover, like other phytohormones, NO also acts in a concentration-dependent manner.

Research on NO in plants has gained a considerable attention in recent years and there is increasing evidence corroborating the role of this molecule in plants. Therefore, in this chapter, an effort has been made to cover the recent advances in chemical properties and mechanism of its biosynthesis with special emphasis on the role of NO in physiological and biochemical changes that occur in plants under normal conditions due to the exogenously applied or endogenously produced NO, along with the cross talk between NO and other phytohormones.

1.2
Nitric Oxide Chemistry

Nitric oxide is a gaseous free radical; its chemistry implicates an interplay between the three redox-related species: nitric oxide radical ($NO^{\bullet}$), nitrosonium cation (NO^{+}), and nitroxyl anion (NO^{-}). In biological systems, $NO^{\bullet}$ reacts rapidly with atmospheric oxygen (O_2), superoxide anion ($O_2^{\bullet-}$), and transition metals. The reaction of $NO^{\bullet}$ with O_2 results in the generation of NO_x compounds (including $NO_2^{\bullet}$, N_2O_3, and N_2O_4), which can either react with cellular amines and thiols or simply hydrolyze to form the end metabolites nitrite (NO_2^-) and nitrate (NO_3^-) [19]. The reaction of $NO^{\bullet}$ with $O_2^{\bullet-}$ yields peroxynitrite ($ONOO^-$), a powerful oxidant that mediates cellular injury. At physiological pH, $ONOO^-$ equilibrates rapidly with pernitrous acid (ONOOH) that, depending on its conformation, rapidly decomposes to NO_3^- or to the highly reactive hydroxyl radical $HO^{\bullet}$. $NO^{\bullet}$ also forms complexes with transition metals found in heme- or cluster-containing proteins, thus forming iron–nitrosyl complexes. This process alters the structure and function of the target proteins, as exemplified by the activation of soluble guanylate cyclase and the inhibition of aconitases.

In addition, $NO^{\bullet}$ is extremely susceptible to both oxidation and reduction. One-electron oxidation of $NO^{\bullet}$ leads to the formation of NO^+ (nitrosonium cation), while the product of one-electron reduction of $NO^{\bullet}$ is a nitroxyl anion (NO^-) [20–22]. This oxidation can be supported by Fe(III)-containing metalloproteins [20, 21]. NO^+ mediates electrophilic attack on reactive sulfur, oxygen, nitrogen, and aromatic carbon centers, with thiols being the most reactive groups. This chemical process is referred to as nitrosation. Nitrosation of sulfhydryl (*S*-nitrosation) centers of many enzymes or proteins has been described and the resulting chemical modification affects the activity in many cases. Such modifications are reversible and protein *S*-nitrosation–denitrosation could represent an important mechanism for regulating signal transduction. One-electron reduction of $NO^{\bullet}$ generates NO^-. The physiological significance of NO^- has not been clarified. Some workers [20, 23] suggest that it could act as a stabilized form of NO. NO^- is also believed to react with Fe(III) heme and to mediate sulfhydryl oxidation of target proteins.

1.3
Biosynthesis of Nitric Oxide

In biological systems, NO can be formed both enzymatically and nonenzymatically. The enzyme responsible for NO generation in animals is nitric oxide synthase. Although NOS-like activity has been detected widely in plants, animal-type NOS is still elusive. Recently, in pea seedlings, using the chemiluminescence assay, Corpas *et al.* [24] showed arginine-dependent NOS activity, which was constitutive, sensitive to an irreversible inhibitor of animal NOS, and dependent on the plant organ and its developmental stage.

A gene encoding NOS-like protein AtNOS1 was isolated from the *Arabidopsis* genome; it is involved in the process of growth and hormonal signaling [25]. It was also observed that AtNOS1 may function as NO source in the process of flowering control [26] and in defense response, induced by a lipopolysaccharide [27]. DNA sequencing analyses did not show affinity of AtNOS1 protein to any of animal-origin NOS isoforms. However, the most recent studies have raised critical questions regarding the nature of AtNOS1 [28, 29]. AtNOS1 (Q664P9) and the orthologous genes from rice (Q6YPG5) and maize (AY110367) have been cloned; however, after