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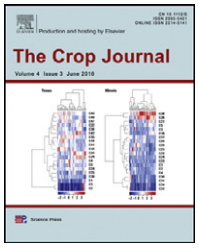

Interplay between nitric oxide and sulfur assimilation in salt tolerance in plants

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ABSTRACT

Nitric oxide (NO), a versatile molecule, plays multiple roles in plant growth and development and is a key signaling molecule in plant response to abiotic stress. Nutrient management strategy is critical for abiotic stress alleviation in plants. Sulfur (S) is important under stress conditions, as its assimilatory products neutralize the imbalances in cells created by excessive generation of reactive oxygen species (ROS). NO abates the harmful effects of ROS by enhancing antioxidant enzymes, stimulating S assimilation, and reacting with other target molecules, and regulates the expression of various stress-responsive genes under salt stress. This review focuses on the role of NO and S in responses of plants to salt stress, and describes the crosstalk between NO and S assimilation in salt tolerance. The regulation of NO and/or S assimilation using molecular biology tools may help crops to withstand salinity stress.

Contents

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1. Introduction

The exposure of plants to high salt concentration creates ionic toxicity due to the accumulation of Na^+ and Cl^- ions, which impair growth and development of plants. The accumulation of Na^+ ions in excess is largely responsible for the reductions in growth and yield under salinity. Salt stress disturbs the nutritional homeostasis of minerals [1], causes membrane damage, inhibits enzyme activity, and alters levels of growth regulators and metabolic activity [2,3]. Salt stress induces reactive oxygen species (ROS) production and causes damage to cellular components, membrane lipids, proteins, and nucleic acids [4]. To prevent the effect of excess ROS production, plants develop multiple detoxification mechanisms. The best-studied mechanism is the induction of antioxidant systems, but the mechanism of enhancement of sulfur (S)-assimilation that induces the production of S compounds via the increased activity of ascorbate–glutathione pathway (AsA–GSH) enzymes has recently been suggested as a response to salt tolerance [5–7].

S is the fourth major essential plant nutrient element after nitrogen (N), phosphorus (P), and potassium (K) [6]. S deficiency substantially limits crop productivity. S is an integral part of major metabolic compounds, such as amino acids, methionine and cysteine (Cys), GSH, Fe–S clusters, sulfolipids, glucosinolates, vitamins (biotin and thiamine), coenzyme A, and the thioredoxin system, which regulate physiological processes and raise salt tolerance [5,6]. A critical concentration of S regulates chlorophyll content, N content, activity of photosynthetic enzymes, protein synthesis, and the electron transport system [6], and appropriate availability of S determines photosynthetic function under optimal and stressful environments and potentially mitigates salt-induced oxidative stress [5,7–9]. Studies of Nazar et al. [7] and Fatma et al. [10] have shown that S supplementation improved the photosynthetic efficiency of plants under salt stress via increased GSH production and activity of enzymes of the AsA–GSH cycle. GSH is a major source of non-protein thiols and acts as an important non-enzymatic antioxidant. The antioxidant system participates in stress resistance and amino acid transport across membranes [11] along with fulfilling other roles associated with redox sensing and signaling and provides protection against salt stress.

Phytohormones are chemical messengers derived from plant biosynthetic pathways that act at the site of their synthesis or are transported to some other site in the plant to mediate growth and developmental responses under both optimal and stressful environments [12,13]. There are five groups of phytohormones: auxin, gibberellins, ethylene, cytokinin (CK), and abscisic acid (ABA). There are also other compounds that have important growth-regulating activity and function as phytohormones. These include brassinosteroids, jasmonic acid (JA), and salicylic acid (SA). Nitric oxide (NO) is considered a new member of this group [14]. It interacts with other signaling molecules to regulate physiological and molecular processes under optimal and stressful environments. NO plays an important role in resistance to abiotic stresses such as salt, drought, temperature (high and low), UV-B, and heavy metal stress by its antioxidant properties and also by acting as a signal in inducing the activity of ROS-scavenging enzymes to alleviate oxidative stress [15]. It is involved in plant resistance reactions against biotic stresses and potentiates the induction of hypersensitive cell death in soybean cells by reactive oxygen intermediates. It functions independently of such intermediates to induce genes for the synthesis of protective natural products [16] and enhances adaptive responses to drought stress by inducing stomatal closure [17]. NO mediates ABA-induced stomatal closure via regulation of Ca^{2+} fluxes [18], and closely cooperates with JA, SA, and ethylene in cell responses to different stressors in a complex network [19]. NO functions as a signaling molecule and influences several morphological processes, such as seed germination, root formation, and de-etiolation, and physiological processes through increases in superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) antioxidant enzymes in *Lupinus luteus* [20]. Zheng et al. [21] reported that NO provides signals for salt tolerance by increasing the activity of SOD and CAT, decreasing lipid peroxidation and O_2^- generation rate in the mitochondria.

Independently conducted studies of the roles of NO and S have shown their involvement in salt stress tolerance by interaction with other signaling molecules. There could be interplay between NO and S assimilation in salt tolerance. The present review explains the action of NO and S in salt resistance and describes the potential interplay between NO and S assimilation in salt tolerance.

2. Nitric oxide: Its role in salt tolerance

NO was recognized during the last decade of the 20th century as a signaling molecule with multifaceted physiological roles in plants [22]. It is converted to one of three different species: the radical (NO), the nitrosonium cation, or the nitroxyl anion, showing high reactivity and tendency to bind with reduced heme proteins [23]. Exogenous NO donors constitute a powerful way to supplement plants with NO. Most of the NO donors are organic compounds that form NO complexes such as sodium nitroprusside (SNP) [24]. SNP is the most widely studied compound of the iron nitrosyl family. Studies of Velikova et al. [25] and Courtois et al. [26] have shown a cytoprotective role of NO in photosynthesis by action as an antioxidant molecule or by regulation of stomatal closure and interaction with Ca^{2+} signals. Exogenous application of NO protected cells from oxidative damage under stress by enhancing antioxidant enzymes [27]. Plants emit NO from leaves and herbicide or NO_2 treatment enhances the release of NO [28]. *In vivo* nitrate reductase (NR) assays release NO [29]. Plant mitochondria also make NO from nitrite [30]. However, NO synthesis in plants appears more complex. Major sites of NO biosynthesis in plants are protoplasts, chloroplasts, mitochondria, and peroxisomes [31]. Fig. 1 shows different sources of NO biosynthesis in plants.

The relationship of *Arabidopsis thaliana* NITRIC OXIDE SYNTHASE 1 (*AtNOS1*) with NOS is debatable. It was previously recognized as a potential NO synthase (NOS) in *A. thaliana* and was shown to be involved in plant development and phytohormones action [32]. Based on similarity to a hypothetical snail NOS or NOS partner that cross-reacted with mammalian NOS antibody, potential NOS was identified in *A. thaliana* [32,33]. Upon knockout of the *AtNOS1* gene in *A. thaliana*, reductions in root NO accumulation and NOS activity in leaf extracts were observed. Further, overexpression of *AtNOS1* resulted in higher levels of NOS activity in leaf extracts. However, study of