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NITRIC OXIDE: FUNCTIONAL INTERACTION WITH PHYTOHORMONES AND APPLICATIONS IN CROP PRODUCTION

SUMMARY

This review considers the action of nitric oxide (NO) as a signaling molecule of plant cells, the effects of which can be modulated in crop production practice through the use of nitric oxide donors. The current understanding of nitric oxide synthesis in plants is briefly described. The characterization of synthesized and natural compounds that can be nitric oxide donors is given. The main molecular mechanisms of nitric oxide action in plant cells are characterized: post-translational modification of proteins under the action of NO, its influence on the content of other cellular mediators, in particular, reactive oxygen species and calcium ions. Considerable attention is paid to the functional interaction of nitric oxide with individual phytohormones and new groups of physiologically active substances of plants. Modern ideas on the mechanisms of nitric oxide action on seed germination and plant resistance to adverse abiotic factors are presented. Data on the effects of priming seeds with nitric oxide donors on their germination under optimal and stress conditions are discussed.

Keywords: nitric oxide, reactive oxygen species, phytohormones, seed germination, priming, abiotic stresses, plant resistance

INTRODUCTION

Nitric oxide (NO) is one of the most widely studied gasotransmitters, small gaseous molecules that are involved in signal transduction in plants, animals, and microorganisms. NO is a lipophilic radical molecule with an unpaired π-orbital electron, capable of easily penetrating cell membranes and rapidly interacting

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with its molecular targets (Mur *et al.*, 2013; Allagulova *et al.*, 2023; Khan *et al.*, 2023a). Because of its ability to enter into direct chemical reactions with specific groups of proteins, as well as functional interactions with other signaling mediators and phytohormones, nitric oxide is involved in the regulation of multiple functions of the plant organism: seed germination, cell wall lignification, flowering, pollen formation, fruit maturation and senescence, as well as different types of symbiosis and responses to biotic and abiotic stressors (Dmitriev, 2004; Turkan, 2017; Sami *et al.*, 2018; Venkatesan *et al.*, 2020; Singhal *et al.*, 2021). The accumulation of knowledge about nitric oxide functions in plants has been very intense. A Google Scholar search reveals approximately 35 000 publications in the last decade alone.

So far, the main pathways of nitric oxide synthesis in plants have been identified: oxidative (arginine-dependent) and reductive (nitrate-dependent) (Khan *et al.*, 2023a). However, enzyme systems that ensure NO synthesis in plants, especially through the oxidative pathway, remain a matter of debate (Verma *et al.*, 2020). The mechanisms of NO synthesis through minor pathways also remain unclear, as well as how these pathways contribute to NO signaling functions (Saha *et al.*, 2015; Kumar, Ohri, 2023). In recent years, much attention has been paid to the functional interaction of nitric oxide with phytohormones, which is associated with its participation in transmitting hormonal signals to the genetic apparatus, as well as its ability to induce the formation of signals that activate the synthesis of some phytohormones (Singhal *et al.*, 2021; Shang *et al.*, 2022; Kolupaev *et al.*, 2023b; Ullah *et al.*, 2024). The mechanisms of such phenomena are still poorly understood and information about them is scattered. At the same time, the widening spectrum of compounds that perform hormonal and regulatory functions in plants contributes to the search for functional relationships of NO with compounds such as melatonin, gamma-aminobutyric acid, and other "plant neurotransmitters" (Akula, Mukherjee, 2020). However, knowledge of the functions and mechanisms of action of these compounds in plants is still far from being a coherent system.

At the same time, new compounds with hormonal activity (e.g. polyamines, melatonin, strigolactones, gamma-aminobutyric acid, etc.) have already been recognized as effective for practical application in inducing plant resistance to stress factors, regulating dormancy, and other functions (Sako *et al.*, 2020; Singhal *et al.*, 2021; Kolupaev *et al.*, 2022a; Kosakivska *et al.*, 2022; Raza *et al.*, 2022). On the other hand, the efficiency of practical application of various nitric oxide donors in crop production, primarily as stress-protective agents, has already been shown (Kolupaev *et al.*, 2022b; Khan *et al.*, 2023a; Ullah *et al.*, 2024). Considering the above-mentioned functional interaction effects of nitric oxide and many compounds with hormonal activity, the question arises about the synergistic effects of these compounds and the possibility of their combination in practical use (Kolupaev *et al.*, 2018; Karpets *et al.*, 2021). However, experimental data on these questions are still insufficiently analyzed and generalized, which motivated the writing of this review.

NITRIC OXIDE SYNTHESIS IN PLANTS

The process of NO synthesis occurs in various compartments of the plant cell, including chloroplasts, mitochondria, peroxisomes, as well as apoplast and plasma membrane (Khan *et al.*, 2023a). There are two main pathways of NO synthesis in plants: reductive, based on the reduction of nitrite to NO, and oxidative, associated with the oxidation of molecules containing amino groups.

The existence of the reductive pathway of nitric oxide synthesis in plants has been convincingly proved (Figure 1). One of the key enzymes in NO synthesis is considered to be nitrate reductase (NR), a multifunctional enzyme involved in nitrogen assimilation and metabolism. It is responsible for the first limiting step of nitrate assimilation by catalyzing the reduction of nitrate to nitrite using NADH or NADPH as an electron donor. The active enzymatic homodimeric complex requires the presence of molybdopterin, heme, and FAD as cofactors (Astier *et al.*, 2018). Besides its primary activity, nitrate reductase exhibits nitrite: NO reductase activity (Mur *et al.*, 2013). Under normal conditions, this activity accounts for only 1% of the nitrate-reducing capacity of NR (Astier *et al.*, 2018). However, NO formation involving nitrate reductase is facilitated by factors such as acidic or oxygen-free environments. Despite such specific conditions, the essential contribution of NO production by nitrate reductase in plant physiology has been convincingly demonstrated using both pharmacological and genetic approaches (Mur *et al.*, 2013).
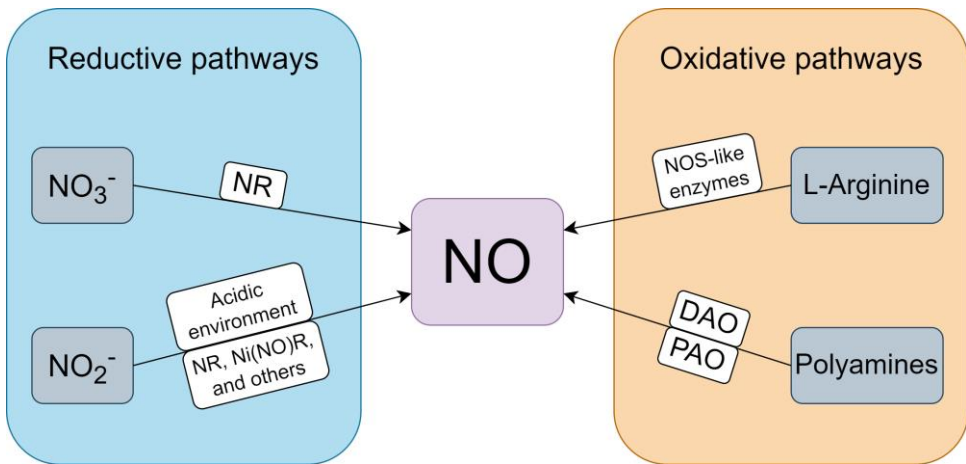

Figure 1. Nitric oxide synthesis in plants. NR – nitrate reductase; Ni(NO)R – nitrite:NO reductase; NOS – NO synthase; DAO – diamine oxidase; PAO – polyamine oxidase.

In addition to nitric oxide formation involving nitrate reductase, several minor pathways are also considered (Figure 1), which may be related to the activity of other molybdenum-containing enzymes, in particular xanthine oxidoreductase (EC: 1.17.3.2), aldehyde oxidase (EC: 1.2.3.1), and sulfite

oxidase (EC: 1.8.3.1). These enzymes perform their specific functions while having the potential ability to catalyze the formation of NO from nitrite (Allagulova *et al.*, 2023). However, their contribution to NO formation in plants and to the manifestation of its physiological functions is still very poorly understood.

The oxidative pathway of nitric oxide synthesis is considered to be as important as the reductive pathway, although the nature of the enzymatic systems that provide this pathway in higher plants has been a matter of debate for nearly three decades (Farnese *et al.*, 2016). NO synthase (NOS) proteins and NOS-producing genes have been found in prokaryotes, unicellular eukaryotes, invertebrates and vertebrates, including mammals; however, NOS enzymes have not yet been identified in higher plants (Khan *et al.*, 2023a). Nevertheless, numerous studies show that the enzymatic oxidation of L-arginine to form citrulline and NO is possible in leaf peroxisomes, and chloroplasts of green algae and vascular plants (Hancock, Neill, 2019). This enzyme activity has been called NOS-like (Figure 1) because, like its animal counterpart, it has been reported to be strictly dependent on the presence of arginine and NADPH as well as several NOS cofactors (NADPH, FAD, FMN, Ca^{2+}, and calmodulin) (Corpas, Barroso, 2014; Farnese *et al.*, 2016). However, molecular genetic evidence for the existence of the corresponding protein in higher plants is still lacking (Astier *et al.*, 2018). At present, it has been hypothesized that there are polypeptides with redox-active domains that can be combined into a single enzymatic complex that catalyzes the reactions of arginine-dependent NO formation in higher plants (Kolbert *et al.*, 2019). In this regard, the identification of specific enzymes that catalyze arginine oxidation reactions leading to NO formation remains one of the most important fundamental tasks in the field of nitric oxide biology in plants. (Allagulova *et al.*, 2023).

It is assumed that oxidative NO formation in plants can occur not only from arginine but also from polyamines and hydroxylamine with the involvement of di- and polyamine oxidases, which are predominantly localized in cell walls (Saha *et al.*, 2015) (Figure 1). However, the exact mechanism underlying this process is still unknown (Khan *et al.*, 2023a).

In addition to the enzymatic pathways of nitric oxide synthesis described above, the non-enzymatic generation of NO in plants from nitric acid is considered to be proved (Khan *et al.*, 2023a). For example, it has been shown that the aleurone layers of *Hordeum vulgare* rapidly produce NO when nitrite is added to the incubation medium (Bethke *et al.*, 2004). NO production requires apoplast acidification, which can occur through the action of gibberellin. The addition of phenolic compounds to the medium can also enhance NO production. It has been suggested that apoplastic NO production may be important for grain germination and root formation in cereals (Bethke *et al.*, 2004).

NITRIC OXIDE DONORS USED IN EXPERIMENTAL PLANT BIOLOGY AND CROP PRODUCTION PRACTICES

Nitric oxide synthesis in plants increases in response to stress factors of various nature, in particular, high and low temperatures, drought, salinity, and

heavy metals. It is also possible that nitric oxide synthesis and endogenous nitric oxide content increase at certain stages of ontogenesis, for example, during seed germination (Zhang *et al.*, 2023a) and in response to hormonal signals (Ullah *et al.*, 2023).

In experimental practices, molecules that are NO donors are used to increase nitric oxide content in plants (Venkatesan *et al.*, 2020; Ullah *et al.*, 2023). There are one and a half dozen classes including more than 300 compounds that can act as nitric oxide donors (Wang *et al.*, 2002; Oliveira *et al.*, 2018). Sodium nitroprusside (SNP), nitroglycerin, spermidine- or diethylamine-NONOate, S-nitroso-N-acetylpenicillamine, S-nitrosoglutathione (GSNO) are the most commonly used of them (Mur *et al.*, 2013; Oliveira *et al.*, 2018).

SNP is currently the most widely used NO donor for both research and practice (Plohovska *et al.*, 2019; Karpets, 2019; Kolomiiets *et al.*, 2021). The mechanisms of nitric oxide release from the SNP molecule are not yet fully understood. It is known that SNP in aqueous solution under normal conditions in a sealed container and without access to light can be preserved for years (Leeuwenkamp *et al.*, 1984), since the decomposition reaction is reversible and limited by solution saturation with its products. Intensive SNP decomposition with NO release occurs in the presence of NO acceptors and/or cyanide residue (Bates *et al.*, 1991). Also, SNP decomposition in aqueous solutions under aerobic conditions is accelerated in light and at elevated temperatures (Singh *et al.*, 1995; Karpets, 2019). On the other hand, in biological systems, NO release from SNP is known to be much faster in the presence of reducing agents (NADH, NADPH, thiols, and possibly ascorbate) (Wang *et al.*, 2002) and/or membrane-bound enzymes (probably NADPH oxidase, etc.) (Wang *et al.*, 2002; Grossi, D'Angelo, 2005; Diniz *et al.*, 2017).

In order to prove the physiological effect of SNP as a nitric oxide donor and not as a complex compound, experiments are carried out with NO scavengers that offset the physiological effects of SNP (Krasylenko *et al.*, 2012; Mur *et al.*, 2013; Plohovska *et al.*, 2019). One of the disadvantages of SNP as a nitric oxide donor is the formation of cyanide during its decomposition, which can have a significant side effect on physiological processes in plants (Mur *et al.*, 2013).

Along with SNP, the so-called NONOates, which consist of a diolate group [N(O-)N=O] linked to a primary or secondary amine or to a polyamine via a nitrogen atom, are also commercially available (Miller, Megson, 2007). NONOates spontaneously cleave at physiological pH and temperature to produce two NO molecules.

In separate studies on the induction of plant resistance to stressors, L-arginine (Barand *et al.*, 2015) and nitrate (Kumar *et al.*, 2021) are used as sources of NO formation. Thus, it was shown that 2-h incubation of wheat roots in a 5 mM L-arginine solution caused an increase in their nitric oxide content from about 50 to 80 nmol/g, while the same time exposure to 20 mM sodium nitrate increased nitric oxide content more than 3-fold (Karpets *et al.*, 2018). Both

exposures caused activation of the enzymatic antioxidant system of seedlings and increased their survival after damaging heating.

Recently, potassium and magnesium nitrates have been used for seed priming to improve germination under stress conditions (Kumar *et al.*, 2021). Their effects are at least partly associated with acting as NO sources (see below).

Polyamines can also be considered as potential nitric oxide donors, which are known as stress metabolites capable of inducing the development of plant resistance to various stress factors when applied exogenously (Kolupaev *et al.*, 2022b). Some studies have shown a causal relationship between NO formation in plants under the action of exogenous polyamines and their ability to activate plant stress-protective systems. For example, treatment of wheat seedlings with putrescine caused a diamine oxidase activity-dependent increase in nitric oxide synthesis in roots, while under the action of the diamine oxidase inhibitor guanidine, the effect of putrescine on nitric oxide content, antioxidant enzyme activity, and heat tolerance of seedlings was eliminated (Kolupaev *et al.*, 2021).

SUMMARY OF THE MOLECULAR MECHANISMS OF NITRIC OXIDE ACTION

To date, much data has accumulated indicating that nitric oxide can directly interact with many cellular proteins and alter their functional activity, as well as influence the state of other important mediators of the signaling network.

The first mechanism has sufficiently clear experimental evidence: it is the interaction of NO with certain functional groups of proteins. Three types of post-translational modification (PTM) of proteins by nitric oxide are distinguished: S-nitrosation, tyrosine nitration, and nitrosylation of metal-containing proteins (Mishra *et al.*, 2021; Kolupaev *et al.*, 2022b).

S-nitrosation is a reversible process that can alter the functional activity of target proteins. Many cellular processes in plants, including those involved in responding to environmental factors and immune function, are considered to depend on protein S-nitrosation (Corpas, Barroso, 2015; Mukherjee, Corpas, 2023). Protein S-nitrosation occurs without the involvement of enzymes (Arora *et al.*, 2016). However, this process is highly specific, as it depends not only on the proximity between NO and the target protein, but also on the amino acid sequence and protein conformation (Lamotte *et al.*, 2015). In Arabidopsis plants, a site-specific nitrosoproteomic approach identified 926 proteins as targets for S-nitrosylation (Hu *et al.*, 2015). A nitrosoproteomic study of tomato plants under medium alkalinization (sodic alkaline) stress revealed 334 S-nitrosated proteins. Among them are proteins involved in the regulation of calcium homeostasis, NO and reactive oxygen species (ROS) content (Wei *et al.*, 2022).

Another mechanism of post-translational modification of proteins under the influence of NO is tyrosine nitration. This process is mainly carried out by peroxynitrite ($ONOO^-$) and nitrogen dioxide radical ($^\bullet NO_2$) (Sánchez-Vicente *et al.*, 2019). Tyrosine nitration in proteins has traditionally been considered an irreversible mechanism and a marker of nitrosative stress (Corpas, Barroso,

2013). However, the existence of tyrosine denitrase, which reduces 3-nitrotyrosine in mammalian cells, indicates a possible role for tyrosine nitration in NO-mediated signaling processes in these cells (Valderrama *et al.*, 2019). Some proteins can undergo both S-nitrosation and tyrosine nitration. For example, the important plant antioxidant enzyme ascorbate peroxidase is activated by S-nitrosation at Cys32 (Correa-Aragunde *et al.*, 2013), but inhibited by nitration at Tyr5 and Tyr235 (Begara-Morales al., 2013).

Another NO modification of proteins – nitrosylation of metal-containing proteins – occurs when nitric oxide interacts with transition metal ions that are part of metalloproteins, leading to the formation of metal nitrosyl complexes. Such processes cause reversible conformational changes in proteins and alter their structure and/or functional activity (Arora *et al.*, 2016).

However, in general, specific proteins with known functions whose activity is regulated by various PTMs under the action of nitric oxide are still poorly understood. Although the list of plant proteins whose activity is controlled by nitric oxide is constantly expanding. Examples of such proteins that are important for plant adaptation to stress factors are given in recent reviews (Kolupaev *et al.*, 2022b; Mukherjee, Corpas, 2023).

With its ability to induce PTM of proteins, nitric oxide is at the center of the signaling network (Singhal *et al.*, 2021). In many cases, such interactions lead to the activation of signaling processes involving other mediators, primarily ROS and hydrogen sulfide. Thus, the same proteins can be targets of S-nitrosation and persulfidation (hydrogen sulfide-induced PTM) (Aroca *et al.*, 2018). These include, for example, enzymes that both degrade (catalase, ascorbate peroxidase) and generate ROS (NADPH oxidase) (Mukherjee, Corpas, 2023).

The mechanisms of functional interaction between NO, H_2S, and ROS associated with their mutual influence on each other's synthesis are extremely complex to study and interpret the results. Such effects are related both to the direct modification by active molecules of functional groups of enzyme molecules synthesizing signaling mediators and to the mediated influence of these molecules on the expression of genes encoding the corresponding enzymes. The fundamental knowledge accumulated in recent years in this area is beyond the scope of this review, but it has been analyzed in a number of recent summaries (Kolupaev *et al.*, 2022b; 2023a; Mukherjee, Corpas, 2023).

In general, ROS, nitric oxide, and hydrogen sulfide form a complex signaling network that ensures the triggering of appropriate adaptive responses. Another integral component of such a network is calcium as a universal intracellular messenger (Neill *et al.*, 2008). Calcium ions are able to activate enzymes that synthesize both nitric oxide (in particular nitrate reductase) (Gao *et al.*, 2011) and other related mediators such as ROS (NADPH oxidase) (Baxter *et al.*, 2014) and hydrogen sulfide (L-cysteine desulfhydrase) (Li *et al.*, 2012; Valivand *et al*., 2019). In turn, nitric oxide, ROS, and hydrogen sulfide can contribute to the opening of calcium channels of different types. Thus, it is known about activation of voltage-dependent calcium channels under the action

of ROS (Mori, Schroeder, 2004). Under the influence of NO, calcium channel proteins can undergo S-nitrosation, which also leads to increased calcium entry into the cytosol (Laxalt *et al.*, 2016). Hydrogen sulfide can also contribute to increased Ca^{2+} concentration in the cytosol (Jin *et al.*, 2013). Thus, nitric oxide, ROS, hydrogen sulfide, and calcium are key signaling mediators that functionally interact with each other (see reviews: Kolupaev *et al.*, 2022b; 2023; Mukherjee, Corpas, 2023). These mediators are key elements of the plant cell signaling network that ensures plant adaptation to a variety of stress factors. At the same time, this network is also involved in the realization of mechanisms of hormonal regulation of physiological processes in plants (Ullah *et al.*, 2023).

NITRIC OXIDE ROLE IN THE SIGNAL TRANSDUCTION OF STRESS PHYTOHORMONES

To date, the involvement of nitric oxide in the signal transduction of almost all known plant hormones has been established (Shang *et al.*, 2022). We briefly review the data on the functional relationships of nitric oxide with the most studied and important phytohormones for stress adaptation (abscisic acid, salicylic acid, jasmonic acid, and brassinosteroids), as well as with melatonin and γ-aminobutyric acid, compounds conventionally named plant neurotransmitters (Akula, Mukherjee, 2020). Their hormonal activity in plants has been studied only in recent years.

Abscisic acid (ABA) has long been recognized as a classical stress hormone that plays a key role in plant resistance (Wilkinson, Davies, 2002; Wang, Song, 2008). The effects of ABA are realized through a number of signaling mediators. A large amount of data has been obtained indicating the role of calcium, ROS and nitric oxide in the realization of ABA-induced physiological reactions that lead to increased plant resistance to drought, salinity, and stress temperatures (Agarwal *et al.*, 2005; Kwak *et al.*, 2006; Petrov, Breusegem, 2012; Bartoli *et al.*, 2013). Meanwhile, nitric oxide is known to be involved in the induction of ABA synthesis (Dmitriev, 2004). In particular, it was shown that NO synthase inhibitors suppressed the accumulation of ABA in leaf cells, while NO donor promoted an increase in its content (Xing *et al.*, 2004; Bajguz, 2014).

One of the most studied effects of ABA, important for plant adaptation to drought and salinity, is the closure of stomata. An increase in the content of endogenous ABA under stresses leads to the opening of anion/K^+-channels of guard cells that transport potassium to the outer side of membranes, which causes stomatal closure (Kwak *et al.*, 2006). Important signaling mediators in the induction of this process by ABA are ROS, calcium ions, and nitric oxide. The ABA-induced increase of nitric oxide content in the guard cells is believed to be a consequence of an increase in the amount of hydrogen peroxide in them (He *et al.*, 2005; Neill *et al.*, 2008) (Figure 2). It has been found that ABA-induced NO generation in Arabidopsis guard cells causes S-nitrosation of SnRK2.6/OST1

(open stomata 1) protein kinase at Cys137, leading to closure of the stomata (Wang *et al.*, 2015; Khan *et al.*, 2022).

In general, most of the accumulated experimental data testify to the synergistic action of ABA and nitric oxide in plant adaptation to abiotic stresses. This is also indicated by the results of studies of the combined effect of exogenous NO and ABA on plant resistance to extreme influences. Such an effect was shown, for example, in the study of the combined effect of NO and ABA on wheat resistance to heat stress (6-hour exposure to 40°C for 15 days). It was found that NO donor and ABA separately significantly mitigated stress-induced oxidative damage, and increased the activity and gene expression of antioxidant enzymes such as SOD, catalase, ascorbate peroxidase, and glutathione reductase (Iqbal *et al.*, 2022). However, these effects of NO and ABA were significantly stronger when used together. Nevertheless, the synergistic interaction between ABA and nitric oxide, including the mutual enhancement of their synthesis, is not evident in all objects. In particular, they have antagonistic effects on seed germination (see below).
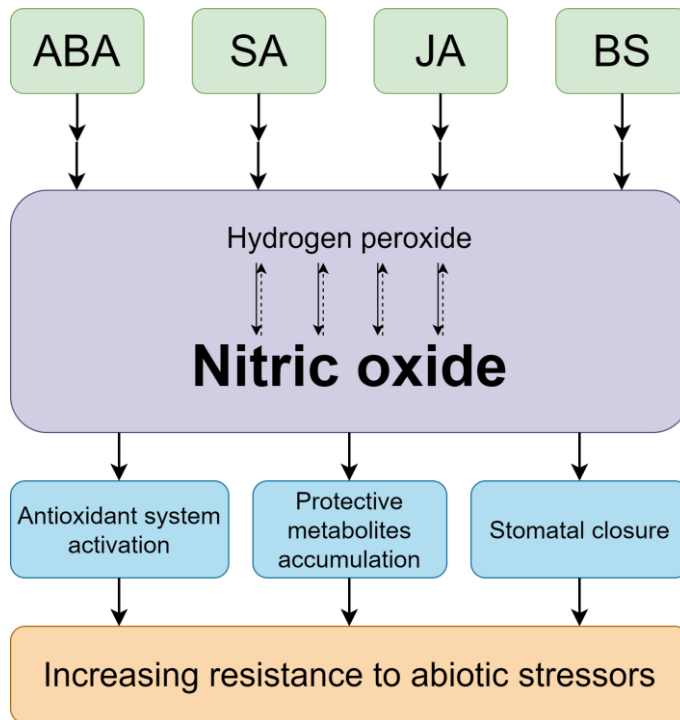

Figure 2. Involvement of nitric oxide in the realization of stress-protective effects of phytohormones. ABA – abscisic acid; SA – salicylic acid; JA – jasmonic acid; BS – brassinosteroids. Other explanations in the text.

Salicylic acid (SA) is currently considered as an endogenous polyfunctional bioregulator of phenolic nature, which participates in cell signaling, growth processes, and formation of adaptive responses of plants (Borsani et al, 2001; Kolupaev *et al.*, 2012; Isoda *et al.*, 2021; Saleem *et al.*, 2021). There are complex relationships between nitric oxide and SA as signaling molecules, the nature of which remains largely unclear. On the one hand, nitric oxide, along with ROS, is considered as a mediator in the realization of SA physiological effects (Mur *et al.*, 2006) (Figure 2). At the same time, the realization of some nitric oxide effects as a signaling molecule can also be mediated by SA. The effect of increasing SA content in tobacco cells under the influence of exogenous NO has been known for quite a long time (Durner *et al.*, 1998). It has also been shown that salicylate-deficient tobacco plants transformed with the gene of bacterial salicylate hydroxylase (*NahG*) did not develop resistance to tobacco mosaic virus under the influence of NO donor (Song, Goodman, 2001).

On the other hand, nitric oxide seems to be an important participant of SA signal transduction. An increase in NO amount in response to SA action was found in soybean (Klepper, 1991) and ginseng plants (Tewari, Paek, 2011). A convincing example of the participation of NO in the realization of physiological effects of SA is provided by the results obtained when studying the effect of stress concentrations of CO_2 on *Camellia sinensis* L. plants. It was found that this stress factor caused an increase in the content of SA, nitric oxide, and flavonoids in plants (Li *et al.*, 2019). Exogenous SA and the NO donor SNP also caused flavonoid accumulation. The SA synthesis inhibitor paclobutrazol and the NO scavenger PTIO (2-phenyl-4,4,5,5-tetramethylimidazoline-1-oxyl 3-Oxide) prevented flavonoid accumulation in response to the action of elevated carbon dioxide concentrations. At the same time, treatment of plants with paclobutrazol relieved the effect of increased NO content, whereas NO binding by PTIO had no effect on SA content. Thus, NO mediates SA-dependent flavonoid accumulation in *C. sinensis* plants (Li *et al.*, 2019).

It is possible that the SA-induced increase in nitric oxide content in plant cells is mediated by an increase in ROS. Thus, it was shown that the increase in nitric oxide content in wheat coleoptiles caused by SA treatment was eliminated by the action of the hydrogen peroxide scavenger dimethylthiourea (Karpets *et al.*, 2016). At the same time, SA increased the heat tolerance of coleoptile cells, but this effect was eliminated by antagonists of both nitric oxide and hydrogen peroxide.

The induction of salt tolerance in rice by exogenous SA was accompanied by an increase in endogenous NO content. At the same time, the nitric oxide scavenger hemoglobin eliminated the SA-induced activation of plant antioxidant system (Mostofa *et al.*, 2015). Dong *et al.* (2015) investigated the effects of SNP, SA, and their combination on salt tolerance of cotton seedlings. Both SNP and SA reduced the level of lipid peroxidation and hydrogen peroxide content in cotton leaves under salt stress. However, the stress-protective effect of SA and

SNP was more pronounced when applied together. Similar results were obtained when studying the effects of SNP and SA on salt tolerance of *Vigna angularis* (Ahanger *et al.*, 2020). When treated with these compounds separately, the manifestation of growth-inhibitory effect of salt stress was mitigated, the indices characterizing the development of oxidative stress were reduced, and at the same time, the activity of the antioxidant enzyme complex, as well as the content of sugars and glycine betaine increased. Also, nitric oxide donor and phytohormone promoted the maintenance of relative water content and photosynthetic pigments pool close to the control under stress conditions. However, when SA and SNP were applied together, all the above-mentioned protective effects were more noticeable.

In our work, we studied the combined effect of pre-sowing seed treatment with SA and foliar treatment with SNP of wheat plants on their tolerance to soil drought (Kolupaev *et al.*, 2018). It was shown that pre-sowing seed treatment with 10 or 100 µM SA solutions reduced growth inhibition and increased the activity of antioxidant enzymes in 14-day-old plants under soil drought. The same effect was induced by spraying 0.5 or 2 mM solutions of SNP before drought. The protective effect was enhanced when seed treatment with 10 µM SA was combined with spraying plants with 0.5 mM sodium nitroprusside, and was weaker when they were combined at high concentrations. Thus, exogenous nitric oxide can modify the stress-protective effect of SA on plants.

Nitric oxide, along with hydrogen peroxide and calcium ions, may be involved in SA-induced closure of stomata. It is known that NO, like SA, rapidly accumulates in plants upon infection or elicitor treatment, activating defense genes and, in some cases, inducing a hypersensitivity response (Durner *et al.*, 1998; Delledonne *et al.*, 2001). The involvement of NO in salicylate-induced closure of stomata in *Vicia faba* was demonstrated by an inhibition method. Later, using direct methods, it was found that SA caused an increase in NO in guard cells of Arabidopsis (Hao *et al.*, 2010). This effect was completely eliminated by the nitric oxide scavenger PTIO, and partially by inhibitors of animal NO synthase (L-NAME – N^G-nitro-L-arginine methyl ester) and nitrate reductase (sodium tungstate). Khokon *et al.* (2011) investigated the role of the functional interaction between ROS and nitric oxide in SA-induced closure of stomata in Arabidopsis. The authors showed that a peroxidase activity-dependent (but not NADPH oxidase activity-dependent) increase in ROS generation preceded the subsequent increase in nitric oxide content. The peroxidase inhibitor salicylhydroxamic acid relieved this effect.

Jasmonic acid (JA) is a phytohormone involved in the regulation of plant resistance to biotic (primarily necrotrophic pathogens and insect pests) and many abiotic stressors (Wasternack, 2007; Santino *et al.*, 2013; Wasternack, Hause 2013; Kolupaev *et al.*, 2023b).

There seems to be a lot of overlaps in the signaling pathways of nitric oxide and JA as one of the stresses phytohormones. A number of experimental data indicate a role of NO in JA synthesis (Sami *et al.*, 2018). It has also been

shown that the expression of key genes involved in JA synthesis was enhanced by exogenous NO (Wendehenne *et al.*, 2004; Mur *et al.*, 2013; Verma *et al.*, 2020). UV-B irradiation of *Panax quinquefolius* caused enhanced formation of nitric oxide, jasmonic acid, and the triterpene glycoside ginsenoside in roots. The UV-B-induced increase in ginsenoside content was eliminated by the NO scavenger PTIO, the NO synthase inhibitor L-NAME, and the JA synthesis inhibitor salicylhydroxamic acid. Treatment with NO antagonists inhibited the UV-B-induced accumulation of JA, suggesting that NO is upstream of the JA signaling pathway (Zhou *et al.*, 2019).

In *Sophora flavescens*, NO treatment induced an increase in lipoxygenase activity and JA level in cells. In turn, exogenous application of JA stimulated NO formation associated with the oxidation of L-arginine (Xu, Dong, 2008). Thus, a possible mutual enhancement of JA and NO synthesis in *S. flavescens* cells was shown.

Experimental data have also been obtained indicating the involvement of NO in the transduction of JA signals into the genetic apparatus (Figure 2). For example, it has been shown that JA and NO are involved in the control of allantoin synthesis in sugar beet plants, which is important for their adaptation to saline-alkaline soils (Zhang *et al.*, 2023b). Inhibition of JA biosynthesis completely abolished exogenous allantoin-induced plant tolerance to saline-alkaline and NO accumulation. Also, the NO donor-induced increase in salt tolerance was not evident upon suppression of JA synthesis. On the other hand, inhibition of NO biosynthesis attenuated allantoin-induced saline-alkaline tolerance, JA accumulation, and JA-induced saline-alkaline tolerance in plants (Zhang *et al.*, 2023b). These data provide experimental support for the assumption of different levels of functional interaction between JA and NO. They are manifested in the influence of JA and NO on each other's synthesis (the presence of a self-reinforcing feedback loop), and in the involvement of signal transduction.

Treatment of wheat coleoptiles with JA induced the development of their heat resistance (Karpets *et al.*, 2016). This effect was accompanied by an almost simultaneous and transient increase in nitric oxide and hydrogen peroxide content. Treatment of coleoptiles with nitric oxide antagonists and antioxidants eliminated the development of heat tolerance, indicating the involvement of ROS and RNS in the signal transduction inducing the development of heat tolerance of wheat coleoptile cells. Treatment of cucumber fruits with methyl jasmonate and the nitric oxide donor SNP reduced their oxidative damage during low-temperature storage (Liu *et al.*, 2016). This effect was accompanied by an increase in *CAT1* and *CAT3* genes expression, and total catalase activity, which was responsible for the reduction of hydrogen peroxide content in fruits. At the same time, inhibitors of endogenous NO accumulation L-NAME and PTIO eliminated the development of cold tolerance induced by methyl jasmonate. On the other hand, inhibitors of JA synthesis ibuprofen and salicylhydroxamic acid had no effect on SNP-activated cold tolerance of fruits. In this regard, the authors

suggest that NO mediates the methyl jasmonate signaling pathway that activates cold tolerance in cucumber (Liu *et al.*, 2016).

The effects of jasmonic acid on the state of the stomatal apparatus are mediated by calcium ions, ROS and nitric oxide (Munemasa *et al.*, 2011). The effects of increased NO and ROS content in closure cells in *Vicia faba* and *Arabidopsis thaliana* plants upon treatment with jasmonic acid or methyl jasmonate have been shown (Liu *et al.*, 2005; Munemasa *et al.*, 2007). In our experiments, we found that the reduction in the number of open stomata and in the stomatal aperture size in Arabidopsis caused by treatment with methyl jasmonate solutions was almost completely abolished by pretreatment of the epidermis with the nitric oxide scavenger PTIO and partially by the NO synthase inhibitor L-NAME and the nitrate reductase inhibitor sodium tungstate (Yastreb *et al.*, 2018). Thus, to varying degrees, jasmonate-induced closure of stomata depends on nitric oxide formation via both oxidative and reductive pathways. Nitric oxide is thought to be the final mediator of the phytohormone signal transduction that induces stomatal closure. NO by S-nitrosylation modifies the corresponding proteins and leads to changes in the activity of potassium and anion channels in guard cells (Fancy *et al.*, 2017).

Apparently, the effects of synergistic interaction between nitric oxide and jasmonic acid can also be utilized in the practical application of these compounds as inducers of plant resistance. Ahmad *et al.* (2018) investigated the combined effects of exogenous jasmonic acid and nitric oxide donor SNP on growth, antioxidant metabolism and osmolyte accumulation in tomato plants under salt stress. Treatment with both SNP and jasmonic acid promoted the preservation of relative water content and chlorophyll pool under stress conditions, reduced the manifestation of oxidative damage, increased the activity of SOD, catalase, ascorbate peroxidase and glutathione reductase, and enhanced the synthesis of flavonoids, proline and glycine betaine. At the same time, all these effects were more pronounced in the combined treatment with SNP and jasmonic acid.

Brassinosteroids (BSs) are a class of plant polyhydroxy steroids structurally related to steroid hormones of vertebrates and insects. BSs play a key role in maintaining normal plant growth both under optimal conditions and when exposed to unfavorable environmental factors (Ahammed *et al.*, 2020; Bartwal, Arora, 2020; Mohammadi *et al.*, 2021). High biological activity in plants was recorded mainly for such BSs as brassinolide, 24-epibrassinolide (24-EBL) and 28-homobrassinolide (Bajguz, 2014).

Like other phytohormones, all major signaling mediators, including ROS and NO, are involved in BSs signaling (Figure 2). It has been shown that in cucumber plants, NO antagonists relieved the effects of BS-induced increase in resistance to the oxidative stress agent paraquat, leveled the enhancement of antioxidant gene expression and an increase in their activity, which indicates the role of nitric oxide as a mediator in the realization of stress-protective effects of BSs (Cui *et al.*, 2011). Treatment of Bentham tobacco plants with brassinolide caused an increase in their salt tolerance (Zhu *et al.*, 2016). This effect was

accompanied by an increase in nitric oxide content in leaves and was leveled by treatment with the NO scavenger PTIO and the nitrate reductase inhibitor sodium tungstate.

One of the mechanisms of stress-protective action of BSs may be their induction of stomatal closure (Jiroutova *et al.*, 2018). However, it has been shown that this process is associated with an increase in ethylene synthesis, which, in turn, affects the condition of stomata by enhancing the synthesis of ROS and nitric oxide (Shi *et al.*, 2015).

It is likely that nitric oxide is also involved in the induction of heat tolerance in plants. In our experiments, it has been shown that after treatment with 24-EBL there was a transient increase in nitric oxide generation by wheat coleoptiles (Karpets, Kolupaev, 2018). At the same time, pretreatment of coleoptiles with nitrate reductase and NO synthase inhibitors partially relieved the effect of the increase in NO content caused by the action of 24-EBL. Nitric oxide antagonists also prevented the development of heat tolerance in coleoptile cells induced by 24-EBL treatment. Thus, NO appears to play a role in the transduction of the brassinosteroid signal that induces the development of heat tolerance in plant cells.

Experimental evidences for the involvement of nitric oxide in the induction of cold tolerance in *Medicago truncatula* plants by brassinolide action has also been obtained (Arfan *et al.*, 2019). Inhibitor methods showed that the NO synthesis, mediated by the increase in ROS content, is necessary for the activation of alternative oxidase gene expression under the action of brassinolide, which is important for the development of cold tolerance.

The role of nitric oxide, formed with the participation of nitrate reductase, in the realization of stress-protective effects of BSs is also indicated by the data obtained in experiments with pepper plants exposed to cadmium toxicity. It was shown that 24-EBL-induced NO formation was eliminated when plants were treated with the nitrate reductase inhibitor sodium tungstate (Kaya *et al.*, 2020a). At the same time, the nitrate reductase inhibitor also leveled the development of defense reactions induced by 24-EBL: activation of antioxidant enzymes, increase in the content of ascorbic acid and glutathione, proline accumulation.

Data have also been obtained on the enhancement of stress-protective effects of brassinosteroids and nitric oxide when applied together. Thus, it was shown on rapeseed plants that treatment with a combination of 24-EBL and SNP had a more significant positive effect on shoot growth compared to the effects of each compound separately (Gupta *et al.*, 2017). Also, under the combined effect of brassinosteroid and NO donor, higher protein and proline content was observed in plants under salt stress.

The study of the combined effect of 24-EBL and SNP on the heat tolerance of wheat seedlings showed that the nature of the effects depended on the range of concentrations of these compounds. Combined treatment with 20 nM 24-EBL and 0.2 mM SNP caused a more significant protective effects compared to the treatment with each compound separately (Karpets *et al.*, 2021). At the same

time, the combined effect of high concentrations (200 nM 24-EBL and 2 mM SNP) reduced the heat tolerance of seedlings. It was shown that the enhancement of the protective effect of 24-EBL and SNP on wheat seedlings when applied together at low concentrations was largely due to the stabilization of the pro/antioxidant balance (Karpets *et al.*, 2021).

Melatonin (N-acetyl-5-methoxytryptamine) is the major indolamine in plants. It has been described as a multifunctional stress metabolite (Fan *et al.*, 2018; Arnao, Hernández-Ruiz, 2019; Khan *et al.*, 2023b). Meanwhile, a growing body of experimental evidence suggests its involvement in the functioning of signaling and hormonal networks in plants, their stress-protective systems, including antioxidant systems (Nawaz *et al.*, 2021; Karpets *et al.*, 2023). There are emerging ideas that melatonin effects may be manifested at the level of gene expression, protein status, as well as through the involvement of other hormones and non-hormonal mediators in the signal transduction system (Zeng *et al.*, 2022).

Data on the links between melatonin and signaling mediators in the manifestation of its effects in plant cells are still insufficient, but they are dynamically accumulating. For example, there are data indicating the involvement of calcium ions and ROS in the realization of protective effects on watermelon plants under cold stress (Chang *et al.*, 2021). A number of data have also been obtained indicating the involvement of NO as a signaling mediator in the realization of physiological effects of melatonin. Thus, the induction of heat tolerance in tomato by melatonin was accompanied by a decrease in the manifestation of oxidative stress and the membrane damage index. At the same time, melatonin treatment of plants caused an increase in nitric oxide content. The authors suggest that NO is a necessary mediator for the development of heat tolerance in plants under the action of melatonin (Jahan *et al.*, 2019).

The protective effect of melatonin on wheat plants exposed to cadmium toxicity was also accompanied by an increase in NO synthesis and eliminated by the nitric oxide scavenger PTIO (Kaya *et al.* 2019). The involvement of nitric oxide as a mediator was also demonstrated in a study on the effects of melatonin on cadmium stress tolerance in Catharanthus roseus (Nabaei, Amooaghaie, 2019). Melatonin treatment of plants increased proline content and antioxidant enzymes activity in roots. These melatonin-induced responses were suppressed by the nitric oxide scavenger cPTIO. Also, nitric oxide may mediate the induction of salt tolerance in rapeseed by exogenous melatonin. Treatment of rapeseed plants with melatonin caused an increase in NO content. At the same time, the nitric oxide scavenger PTIO eliminated the stress-protective effect of melatonin (Zhao *et al.*, 2018).

In addition, it was shown that the induction of salt tolerance in rapeseed by melatonin action is mediated by nitrate reductase-dependent increase in NO synthesis. The authors believe that S-nitrosylation of target proteins is an obligatory component of the melatonin-triggered signaling pathway leading to increased salt tolerance (Zhao *et al.*, 2018).

A nitric oxide-dependent manifestation of the stress-protective effect of melatonin was also found in pepper plants subjected to salt or iron deficiency stress. The positive effect of melatonin on plants under such conditions was eliminated by treatment with the NO scavenger PTIO (Kaya *et al.*, 2020b). In general, the effects of melatonin on stress-protective systems, particularly antioxidant systems, are thought to be mediated by nitric oxide-induced post-translational modifications of target proteins (Martínez-Lorente *et al.*, 2022).

On the other hand, nitric oxide can act as a signal that induces melatonin synthesis. It has been shown that NO, mediated by cGMP, can activate the expression of genes of melatonin synthesis enzymes – *TDC*, *T5H*, *SNAT* and *COMT*, resulting in an increase in endogenous melatonin content (Wang *et al.*, 2022). The NO scavenger cPTIO disrupts Cd-induced melatonin synthesis by decreasing the expression of *TDC* and *COMT* genes in rice (He, He, 2020). Thus, it is likely that there are mechanisms for the mutual enhancement of melatonin and nitric oxide synthesis in plants.

γ-aminobutyric acid (GABA), a non-proteinogenic four-carbon amino acid found in many prokaryotic and eukaryotic organisms, has only recently been listed as an important physiologically active substance in plants (Seifikalhor *et al.*, 2019). At present, new knowledge about the regulatory functions of GABA in plants is dynamically accumulating (Suhel *et al.*, 2023), and the influence of exogenous GABA on the resistance of plants of different taxonomic groups to various types of stress factors is intensively investigated. The identified phenomena are also related to plant resistance to low and high temperatures, drought, and salinity (Kolupaev *et al.*, 2024). The relationship between GABA and nitric oxide as signal-regulatory molecules in the formation of plant adaptive responses is still poorly understood. Nevertheless, there are results that indicate the possibility of inducing GABA synthesis under the action of nitric oxide. For example, the NO donor SNP enhanced GABA biosynthesis in soybean seedlings under UV-B irradiation (Suhel *et al.*, 2023). Treatment of banana fruits with exogenous NO increased glutamate decarboxylase activity, which led to GABA accumulation (Wang *et al.*, 2016).

At the same time, the physiological effects of GABA are probably also realized with the participation of nitric oxide as a signaling mediator. Thus, it was found that the stress-protective effect of GABA on melon plants exposed to soda salinity was accompanied by an increase in the activity of the NO synthesis enzymes, such as nitrate reductase and NO synthase, as well as in nitric oxide content (Xu *et al.*, 2021). Meanwhile, treatment of plants with the nitric oxide scavenger cPTIO eliminated the increase in NO content induced by GABA treatment and its stress-protective effect on plants. The authors conclude that NO is a component of GABA signaling that is necessary for stimulation of the antioxidant system and regulation of ion homeostasis under stress conditions (Xu *et al.*, 2021).

Treatment of wheat plants with GABA increased photosynthetic productivity and reduced salt stress-induced oxidative damage by improving

ascorbate-glutathione cycle function and proline metabolism (Khanna *et al.*, 2021). Treatment with the NO scavenger cPTIO eliminated the positive effects of GABA on plant growth and photosynthesis under salt stress, indicating that the action of GABA is mediated by NO.

FUNCTIONAL INTERACTION OF NITRIC OXIDE WITH PHYTOHORMONES IN THE REGULATION OF SEED GERMINATION

It is known that the processes of seed emergence from dormancy and germination initiation are caused by an increase in the level of water content in the axial parts of the embryo and changes in the balance of phytohormones, primarily such as ABA, gibberellins, auxins, and ethylene. It has been shown that cell cycle activation, which is required for embryo germination, is induced by increased content of ethylene and gibberellins (especially gibberellic acid 3 – GA3) and decreased ABA content (Kepczynski *et al.*, 2017). According changes may be induced by signaling mediators, particularly nitric oxide, including exogenous application (Liu *et al.*, 2011). Attempts have been made to investigate the relationship between the generation of endogenous nitric oxide in seeds and their ability to germinate. Thus, it has been shown that seeds of chickpea varieties that generated more NO germinated faster than seeds of varieties with weak NO synthesis (Pandey *et al.*, 2019).

To date, the general molecular mechanisms of nitric oxide effects on the hormonal balance of germinating seeds have been elucidated (Arc *et al.*, 2013). These effects are largely related to S-nitrosation and tyrosine nitration of target proteins. Thus, an increase in the content of tyrosine nitrated proteins was recorded in sorghum germ axes during germination (Jasid *et al.*, 2008). In Arabidopsis, it has been shown that tyrosine nitration leads to the inhibition of the Mo cofactor of sulfurase, the enzyme of the last step of ABA synthesis (Lozano-Juste *et al.*, 2011). It is suggested that inactivation of ABA synthesis by this mechanism may promote seed germination (Rajjou *et al.*, 2012) (Figure 3). Also, under the influence of NO, S-nitrosation of a number of proteins involved in ABA signal reception and transduction occurs, thereby inhibiting the transmission of this signal (Signorelli, Considine, 2018). Finally, it is known that NO entails an increase in ABA catabolism, probably through induction of ABA 8'-hydroxylase gene expression (Arc *et al.*, 2013). In addition, it has been reported that nitric oxide can enhance ROS generation in plant cells through complex mechanisms involving both post-translational modifications of target proteins and influence on many components of the signaling network (Kolupaev *et al.*, 2023a). Moderate enhancement of ROS formation usually promotes seed germination. One of the reasons for this phenomenon may be the ability of ROS, primarily H_2O_2, to enhance ABA degradation processes (Bailly, 2004). Together, this eliminates the regulatory effects of ABA that condition seed dormancy (Figure 3). At the same time, nitric oxide leads to the activation of enzymes of GA3 (Signorelli, Considine, 2018) and ethylene synthesis (Kolbert *et al.*, 2019), which can activate germination. In particular, it has been shown that interruption

of apple seed dormancy by the action of exogenous NO induced ethylene production and was eliminated by inhibitors of its synthesis (Kolbert *et al.*, 2019). Induction of Amaranthus retroflexus seed germination by NO donors was also preceded by an increase in ethylene synthesis (Kepczynski *et al.*, 2017). It has been found that the treatment of seeds with NO can directly alter the activity of key enzymes in the ethylene synthesis process – S-adenosyl-L-methionine methylthioadenosine lyase (ACS) and 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) (Gniazdowska *et al.*, 2010).
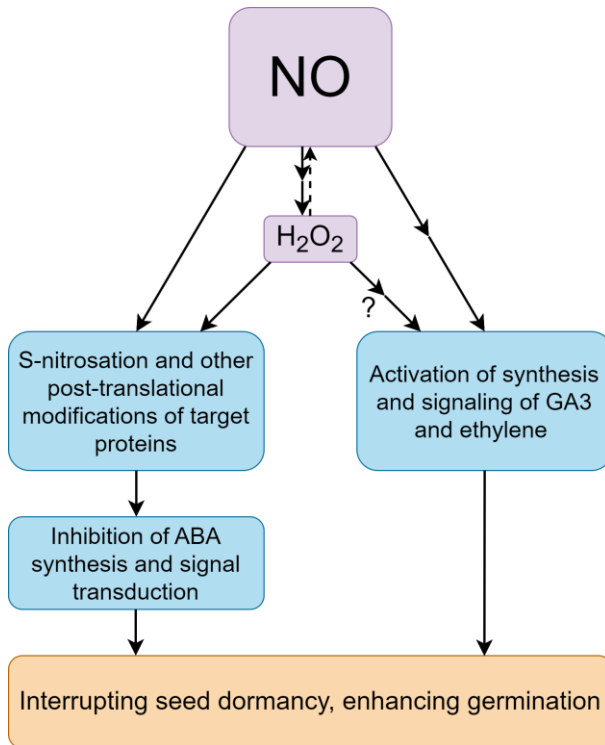

Figure 3. Mechanisms of nitric oxide effects on seed germination.

In addition to gibberellins and ethylene, two other major classes of phytohormones, auxins and cytokinins, seem to be involved in the action of nitric oxide donors. Using seed germination of different plant species as an example, it has been shown that SNP treatment promotes lateral root development and primary root elongation (Nejadalimoradi *et al.*, 2014; Ullah *et al.*, 2024). These effects are attributed to the interaction between auxin and nitric oxide, as treatment with nitric oxide donors can affect auxin content and stimulate auxin-induced root development responses (Ullah *et al.*, 2024).

At the same time, treatment of seeds with exogenous nitric oxide stimulates shoot growth in many species. This effect is attributed to the positive

interaction of NO with cytokinins, which affect cell elongation in the shoot apical meristem (Zhao *et al.*, 2020).

The effect of nitric oxide donors on seed germination is particularly pronounced under stress conditions (Ciacka *et al.*, 2022). It is well known that almost all unfavorable effects on plants lead to the disturbance of pro/antioxidant balance and the development of oxidative stress (Hasanuzzaman *et al.*, 2020). It has also been found that increased ROS formation is an indispensable attribute of seed germination process (Kranner *et al.*, 2010). At the same time, as mentioned above, ROS may be involved in stimulating seed germination, including by enhancing the degradation of ABA. However, excessive ROS generation during seed germination under stress conditions can cause oxidative damage to proteins and membrane lipids, thereby reducing germination and/or retarding seedling growth (Janmohammadi *et al.*, 2012). Thus, agents that mitigate oxidative stress by activating the antioxidant system could potentially promote seed germination. Nitric oxide, at least at physiological concentrations, activates many antioxidant enzymes both by PTM of protein molecules and by affecting gene expression of antioxidant enzymes (Kolupaev *et al.*, 2023a). In this regard, it is believed that one of the components of the potentially positive effect of nitric oxide donors on seed germination under stress may be the activation of their antioxidant system (Ciacka *et al.*, 2022). This component of NO action may explain the described phenomena of more effective influence of nitric oxide donors on seed germination under stress conditions compared to normal conditions (Shams *et al.*, 2018).

A number of studies have reported the enhancement of seed germination of various crops at reduced temperatures by nitric oxide donors. Such effects were observed, for example, in wheat (Bibi *et al.*, 2020) and tomato seeds (Amooaghaie, Nikzad, 2013). Soaking rapeseed seeds in SNP solutions also increased seed germination indicators under low temperature and drought conditions (Zhu *et al.*, 2021). At the same time, under the influence of SNP treatment, a change in the hormonal balance and an increase in the activity of antioxidant enzymes in seedlings under stress conditions were observed.

Priming of maize seeds with NO donor also enhanced antioxidant defense of seedlings under heat stress conditions. Increase in SOD, catalase and peroxidase activities and decrease in content of hydrogen peroxide and LPO product (MDA) were observed in seedlings of seeds primed with SNP (Kaur, Kaur, 2018). Similarly, priming of *Arachis hypogaea* L. seeds with SNP enhanced their germination under model drought conditions. It increased the activity of antioxidant enzymes, sugar and soluble protein content, and decreased MDA content (Sepehri, Rouhi, 2016).

It has also been shown that NO mitigates the decrease in germination percentage, germination index, viability index and water absorption rate in wheat seeds subjected to salt stress (Duan *et al.*, 2007). According to the authors, this effect is largely due to an increase in β-amylase activity. Treatment of quinoa (*Chenopodium quinoa*) seeds with SNP also reduced the adverse effects of salt

stress on α-amylase and β-amylase activity and seed germination rate (Hajihashemi *et al.*, 2020). A similar effect of SNP was also shown in the germination of *Brassica chinensis* L. under salt stress (Ren *et al.*, 2020). The authors showed an increase in the indicators of seed germination and vigor under the influence of the NO donor, as well as an increase in the activity of antioxidant enzymes. Moreover, SNP pretreatment significantly increased K^+ content and decreased Na^+ content in roots and shoots, resulting in an increase in the K^+/Na^+ ratio (Ren *et al.*, 2020).

A number of studies have reported the enhancement of seed germination by nitric oxide donors in the presence of heavy metals. Thus, it was shown that SNP treatment attenuated Cd-induced inhibition of seed germination and growth of rice seedlings (He *et al.*, 2014). The authors attributed this effect to the stimulation of antioxidant enzyme complex activity and proline accumulation by the nitric oxide donor. Soaking lettuce (*Lactuca sativa* L.) seeds in SNP solutions reduced the toxic effect of copper, although in the absence of stress the NO donor did not affect the germination of seeds of this species (Shams *et al.*, 2018). SNP pretreatment of Indian mustard (*Brassica junea* L.) seeds also improved their germination against the toxic effect of copper (Rather *et al.*, 2020). Under the influence of NO, the antioxidant defense system was enhanced (SOD, glutathione reductase and ascorbate peroxidase activities increased) and lipid peroxidation decreased in seeds exposed to copper. Seeds pretreated with NO donor also retained higher amylase activity (Rather *et al.*, 2020).

CONCLUSIONS

Nitric oxide is a key regulatory molecule of plant cells. Its diverse effects on almost all functions of the plant organism are due to its ability to selectively interact with many protein targets, and thus influencing the formation or inactivation of other signaling molecules, as well as the synthesis and degradation of phytohormones. Many of the effects of nitric oxide are associated with its involvement in the subtle processes of redox regulation of cellular functions and are related to both the enhancement of ROS generation and the activation of the antioxidant system. These processes are very important for plant resistance to stress factors. At the same time, these processes together with the hormonal system are also involved in the regulation of seed germination. Thus, nitric oxide can be considered as a subtle tool in the regulation of plant resistance to stress factors and seed germination processes. The availability of relatively non-toxic and cheap nitric oxide donors (e.g., the most popular sodium nitroprusside) makes such a tool available for practical application. However, the effects of nitric oxide donors are dose-dependent. The range between concentrations that have stress-protective or stimulating effects and concentrations that cause toxic or inhibitory effects is not so wide. In this regard, for the practical application of nitric oxide donors, special studies are needed to select optimal concentrations and treatment methods for each new object, taking into account its species and even varietal characteristics. The practical

application of nitric oxide donors in crop production is also hampered by the fact that the currently accumulated knowledge is mainly in the field of physiology and biochemistry and is largely empirical in nature. It is hoped that the use of molecular genetic tools, as well as proteomics and metabolomics, will make it possible to develop theoretical models that more thoroughly explain the mechanisms of nitric oxide influence on growth and stress-protective processes in plants. This, in turn, should allow for a clearer prediction of the effects of exogenous nitric oxide, which is necessary for its application in crop production technologies.

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