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Polyamines and nitric oxide crosstalk in plant development and abiotic stress tolerance

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ABSTRACT

Polyamines (PAs) and nitric oxide (NO) are crucial signalling molecules that exhibit a promising role in improving stress tolerance in plants, maintaining their growth and development. They act as protecting agents for plants through activation of stress adaptation strategies such as membrane stabilisation, acid neutralisation and suppression of ROS generation. NO interacts with PAs during several developmental processes and stress responses. External supplementation of PAs to plants is also reported to cause an increase in NO content. However, it is unclear whether PAs promote synthesis of NO by either as substrates, cofactors, or signals. Impact of NO on synthesis of PAs has been also reported in some studies, yet the exact governing mechanisms of the interrelation between NO and PAs is currently obscure. Understanding the crosstalk between PAs and NO during growth and stress condition in plants can aid in providing better tolerance to plants against stressful environment.

Keywords: abiotic, biotic, chlorophyll, hydrogen peroxide, lipid peroxidation, nitric oxide, oxidative stress, polyamines, ROS, spermidine, spermine.

Polyamines and nitric oxide: signalling molecules for plant growth regulation and stress resistance

Polyamines (PAs) are aliphatic amines found either in free, conjugated or bound forms in the plant cells and their contents vary on the basis of species and developmental stage of the plants (Mustafavi *et al.* 2018; Chen *et al.* 2019). PAs show direct protective effect in plant cells owing to their cationic nature that enables them to interact with macromolecules having negative charge for stabilising their structure during normal as well as stressful situations (Takahashi 2020). They also play the role of signalling molecules for regulation of several cellular processes in plants, especially during exposure to abiotic stresses (Pál *et al.* 2015; Paul *et al.* 2018; Allakhverdiev 2020). Nitric oxide (NO), a gaseous free radical, regulates plant growth and development and varies in concentration in different tissues depending on plant species and environmental conditions (Domingos *et al.* 2015; Kolbert *et al.* 2019). NO is a crucial signalling molecule in plants surviving under stressful conditions by interacting with other signalling molecules including phytohormones and reactive oxygen species (ROS) along with regulating the protein activity and expression of genes (Simontacchi *et al.* 2015; Sahay and Gupta 2017; Nabi *et al.* 2019).

Collectively, PAs and NO are crucial signalling molecules acting as regulators of plant growth and development (Krasuska *et al.* 2017). Both interact with phytohormones to perform various biological functions under normal as well as stressful situations responses (Nahar *et al.* 2016). Scavenging of ROS through antioxidant activation, protecting biomolecules and bio-membranes are common mechanisms of action of PAs and NO (Choudhary *et al.* 2022). The biosynthesis pathways of PAs and NO overlap as PAs either induce generation of NO or directly convert to NO (Nahar *et al.* 2016). Inter-relation between PAs and NO can provide improved resistance to plants under challenging environment; however, the studies are limited in this context (Nahar *et al.* 2016; Choudhary *et al.* 2022). This special issue brings latest researches evaluating the crosstalk between PAs and NO into light for better understanding by the scientific community.

Latest insights into polyamine and nitric oxide interaction in plants

Maize (*Zea mays* L.) is a major staple crop that is extremely prone to yield losses due to adverse environmental constraints. PAs are known to regulate plant responses to environmental perturbations including abiotic and biotic stresses to maintain the viability of the living cells under such unfavourable conditions. The relative production of higher PAs such as spermidine (Spd), spermine (Spm) with respect to the diamine putrescine (Put) and PA catabolism regulates the stress tolerance in plants. Understanding the regulatory role of PAs in response to stresses in maize can aid in development of novel stress tolerance strategies to cope up with the escalating demands for maize production. In this volume, Ramazan *et al.* (2023) critically reviewed and summarised the up-to-date reports on the role of PAs in enhancing stress resistance in maize. The accumulation, metabolism and mechanism PAs action, their role as signalling molecules, and a connection with other metabolic pathways, and genetic manipulation studies conducted in relation to PAs have been discussed (Ramazan *et al.* 2023).

Sodium nitroprusside (SNP), an exogenous donor of NO, is known to curtail the postharvest losses caused in the cut flowers in the form of a postharvest vase preservative. A study by Ul Haq *et al.* (2023) explores the potential of SNP to ameliorate the senescence at postharvest stage in cut spikes of *Consolida ajacis* (L.) Schur. The *C. ajacis* spikes treated with SNP (20–80 μM range) depicted improved vase life and quality of flowers in comparison to the control spikes held in distilled water. SNP treatments also caused a prominent increase in sugars, phenols and soluble proteins as well as improved the membrane stability as indicated by decrease in the lipoxygenase activity. These results were accompanied by upregulation of activity of antioxidant enzymes, namely catalase (CAT), superoxide dismutase (SOD) and ascorbate peroxidase (APX). This research suggests 40 μM SNP to be an adequate concentration to preserve the quality of flowers and extend the display period of spikes of *C. ajacis*. Overall, SNP can modulate various physiological and biochemical processes related to senescence to mitigate the adverse postharvest alterations. SNP aids in preserving the quality of flowers through improvement of membrane stability, vase life, flower quality, content of sugars, soluble proteins and phenols, and antioxidant activity (Ul Haq *et al.* 2023).

Plants reallocate the resources from mature and old tissues of leaves to new tissues and organs towards the end of the growing season via a process termed as leaf senescence. At present, optimising the senescence for particular species is a major objective of the crop breeding initiatives. The work by Altaf *et al.* (2023) examined the effectiveness of PAs in delaying the leaf senescence in *Berginia ciliata* (Haw.) *sternb* leaf discs via regulation of several biochemical and physiological processes to delay the process of senescence in *B. ciliata* leaf discs. Leaf discs exposed to exogenously supplied Put (20 μM), Spd (20 μM) and Spm (15 μM) remained green and fresh by almost 4 days in comparison to the control, thereby showed delay in the senescence. PAs application also resulted in an increase in chlorophyll content, soluble protein content, membrane stability and reduction in ROS by enhancing the activity of antioxidant enzymes such as SOD, APX and CAT. This was accompanied by reduced lipid peroxidation as indicated by the low levels of malondialdehyde (MDA) level and improved membrane stability measured in terms of membrane stability index (see Altaf *et al.* 2023).

Various anthropogenic activities, for instance the combustion of fossil fuels, mining, agrochemical usage in agricultural sector, and industrial pollution have led to elevated arsenic (As) content in environment. A paper by Kapoor *et al.* (2023) studied the mitigation of arsenate (AsV)-incited stress in chickpea (*Cicer arietinum* L.) plants via supplementation of NO and SPD. AsV treatment caused reduction in length of *C. arietinum* seedlings, their biomass and relative water content along with other biochemical parameters. Addition of SPD or SNP, either alone or together with AsV, improved these parameters. Also, As + SNP + SPD treatment decreased the AsV-induced enhancement in electrolyte leakage and MDA content in chickpea seedlings, while stimulated the contents of sugar, proline and glycine betaine by 89, 249 and 333%, respectively, compared to control. SNP and SPD also regulated the detoxification of methylglyoxal (MG) by regulating the activity of glyoxalase enzymes. Overall, NO and SPD, when supplied synergistically, protected the chickpea plants from AsV stress by activation of antioxidant machinery and glyoxalase system (Kapoor *et al.* 2023).

Chromium (Cr), a toxic heavy metal, significantly limits the growth and productivity of crops. As NO and Spm play a significant role in enhancing the plant resistance against abiotic stresses, Basit *et al.* (2023) investigated the protective potential of seed priming of rice (*Oryza sativa* L.) plants with NO (100 μM) and/or Spm (0.01 mM) in alleviating the toxic impacts of Cr. Their results showed that application of Cr alone (100 μM) prominently reduced the rate of seed germination rate, as well as had negative impact on plant photosynthetic parameters, nutrients uptake and activity of antioxidant enzymes, but enhanced the generation of ROS. NO + Spm treatment significantly rescued rice seedlings from Cr-stress by reducing the accumulation of Cr and improving the nutrient uptake, germination indices, photosynthetic pigment level and total soluble sugar content. By improving antioxidative enzyme activities, NO + Spm treatment declined the content of oxidative markers, namely superoxide radical, $O_2^{\cdot-}$, hydrogen peroxide, H_2O_2 and MDA, along with the electrolyte leakage. Their results suggest that simultaneous application of NO and Spm can be used for fostering resistance against Cr stress in rice as the combined treatments (NO + Spm) displayed more efficacy in mitigating Cr-induced adverse effects than NO and Spm alone.

The HAK (High-affinity K^+) transporters are essential for plant growth and stress tolerance. In this volume, Saha *et al.* (2023) have elucidated the evolutionary aspects, overall structural and functional characterisation along with the global expression pattern of rice HAK transporters under the influence of exogenous spermidine and salt stress. They clustered the rice transporters phylogenetically with various members from dicot and monocot family and studied the structural patterns of exon–intron, substitution matrix based on evolutionary divergence and analysed the conserved motifs and orthologous–paralogous relationships. Besides structural characterisation of *OsHAK* gene members, their global expression patterns were studied under salt stress and their profile depicted a clade-specific expression pattern. The authors also selected five *OsHAK* genes for expression analysis in root and shoot of two varieties of rice under short-term salt exposure in the presence and absence of exogenous spermidine. The data collected by this study can be used for dissecting the regulatory role of HAK transporters in rice under different abiotic stresses.

In another study, Shah *et al.* (2023) showed that combined application of zinc oxide nanoparticles (ZnONPs) and potassium (K^+) regulated the NO content in the seedlings of faba bean (*Vicia faba* L.) to alleviate As stress. The increase in NO content was accompanied by an increment in chlorophyll content, rate of photosynthesis, and antioxidant activity resulting in improved plant growth. Arsenic stress caused reduction in lengths of root and shoot, chlorophyll content and net photosynthetic rate in soil grown faba bean seedlings. However, ZnONPs and K^+ ameliorated the As stress by decreasing the accumulation of $O_2^{\cdot-}$ and H_2O_2 through increased antioxidant activity of SOD, APX, CAT and peroxidase (POD) enzymes in faba bean seedling. Also, ZnONPs and K^+ prominently increased the NO content, cysteine content and serine acetyltransferase activity, while decreased the uptake of As in the As-stressed faba bean seedlings. Thus, this study opens new doors for research to explore the molecular mechanisms of interaction between K^+ interaction and nanoparticles involved in providing abiotic stress tolerance to faba bean seedlings.

Singh *et al.* (2023) also investigated the amelioration efficacy of NO against copper (Cu) and copper nanoparticles (CuONPs) toxicity in sorghum (*Sorghum bicolor* L.) seedlings. Cu and CuONPs application resulted in a reduced growth, decreased contents of chlorophyll, carotenoids and proteins, and enhanced Cr accumulation in the seedlings. in root and shoot which was coincided with increased accumulation of Cu. However, supplementation with SNP as a source of NO reversed the toxic impacts of Cu and CuONPs on these parameters. Also, SNP positively regulated the antioxidant activity to reduce the stress-induced increase in H_2O_2, $O_2^{\cdot-}$, and MDA content, thereby mitigated the Cu and CuONP-induced oxidative stress. Furthermore, SNP addition regulated the proline metabolism in the seedlings under stress condition by increasing free proline accumulation. Overall, this study demonstrated that NO can mitigate the toxicity of Cu and CuONPs in sorghum seedlings and the results can be used in developing new resistant varieties of sorghum with high tolerance to Cu or CuONP stress (Singh *et al.* 2023).

Concluding remarks and future outlooks

Altogether, the recent research in this field provides advanced knowledge on understanding the crosstalk between two endogenous signalling molecules of plants, PAs and NO, for regulation of growth and enhancement of stress tolerance. The roles of different PAs and NO in physiological processes inside plants have been delineated in the latest studies. Some studies also elaborate on their synergistic action for improved plant growth under stressed condition. These reports affirm the potential of PAs and NO to act as a shielding agent for plants during stress exposure and the decoding the underlying mechanisms can help in developing stress-resistant varieties with improved productivity.

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