

Signaling Molecules in Plants: Exogenous Application

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Signaling molecules (hormones, growth regulators, proteins, amino acids, nucleotides, etc.) are essential for the growth, development and adaptation of plants, as well as for the activation of their antioxidant responses to a number of environmental stress factors such as extreme temperatures, light, drought, salinity, heavy metals, herbicides, pathogens and others [1-3]. The study of their impact on plants is becoming more relevant in view of progressive climate changes and increasing pollution worldwide. Recognition of the stress stimulus by cell membrane receptors induces in the cell a signaling cascade leading to the triggering of specific defense responses. In recent years, there has been an increasing interest in clarifying the role of signaling molecules in plant adaptation and protection mechanisms against environmental stress. As agriculture needs to produce more and be environmentally friendly, crop models are used to support agronomists and to overcome current and future challenges for agriculture.

In response to changing normal environmental conditions, various compounds such as signaling intermediates, phytohormones, osmolytes (amino acids, sugar alcohols, tertiary amines) and some other metabolites in plant cells and tissues are accumulated and interact with one another [1,4,5]. Recently, nitric oxide (NO) has emerged as a key signalling molecule in plants and attracted a great attention of researchers [5-7]. NO is a small, water and lipid soluble gas with ubiquitous importance: it plays a diverse role in plants including plant growth, stomatal movement, iron homeostasis, protection against biotic and abiotic stresses, senescence, etc. In the case of environmental stress caused by both abiotic and biotic factors, enhanced NO generation is observed in different plant species and organs. NO can provoke both beneficial and harmful effects on plant cells depending on its local concentration. The essential role of NO in plant signaling network has been associated with the expression of defense

response genes under various stress conditions, as well as with its ability to directly interact with other molecules and signals [5]. In some cases, NO mediates the biological effects of primary signaling molecules such as hormones [5-7].

Reactive oxygen species (ROS) have been also shown to play an important role in plant defense mechanisms [4,8]. It has been proposed that ROS participate as signaling molecules in the transduction of stress signals from chloroplasts to the nuclear genome and also the interactions between ROS and other signaling systems within the cell [8]. In addition to the damaging effects of ROS, new roles for ROS such as control and regulation of cell growth, cell cycle, programmed cell death, hormone signaling, plant responses to biotic and abiotic stress, and development of tissues have been reported [4]. Depending on the concentration, ROS induce different effects: low concentrations induce the synthesis of antioxidant enzymes. An increase of both ROS and NO has been reported to take place under high temperature, osmotic stress, salinity and mechanical stress [5,7]. There are several lines of evidence suggesting strongly that hydrogen peroxide (H_2O_2) initiates a signal transduction process for acquisition of tolerance to abiotic and biotic stresses [4]. Plant treatment with H_2O_2 induces the expression of chloroplast and nuclear genes related to plant protective responses to stress [4]. The regulatory role of H_2O_2 has been proposed in both functioning of the photosynthetic apparatus and the development of its stress protective systems.

Furthermore, it has been identified peptides as a new class of plant signalling molecules which play crucial roles in plant growth and development, including defense mechanisms [9].

Salicylic acid (SA) has long been known as a signal molecule in the induction of plant defense responses against biotic or abiotic stresses in plants [10-12]. Pre-treatment of plants with SA might have an acclimation-like effect causing enhanced tolerance towards most kinds of abiotic stresses, primarily by enhanced antioxidative capacity or

by inducing various signal transduction pathways [11,13,14]. Exogenous application of SA influences plant growth, transpiration rates, stomatal regulation and photosynthesis, as well as ion uptake and transport [13,15]. The concentration of exogenous SA appears to be important in regulation of plant growth and responses to changes in the environmental conditions.

Brassinosteroids (BRs) are a class of plant steroid hormones involved in several physiological and morphological processes, as well as in the responses to environmental stresses via activation of different protective mechanisms [16]. The potential application of BRs in agriculture is based on their ability to increase crop yield and ameliorate stress. Exogenous application of very low BRs concentrations influences multiple plant growth and development processes. Many studies have demonstrated that exogenously applied BRs enhances plant tolerance to abiotic stresses such as drought, salinity, heavy metals, extreme temperatures, oxidative stress, etc [1,16-18].

Plant phytohormones such as abscisic acid (ABA), jasmonic acid (JA), gibberellin (GB), auxin, cytokinin, ethylene, etc. also act as dedicated signalling molecules involved in several physiological processes, including photosynthesis, plant growth, biotic and abiotic stress responses and senescence [1]. A number of literature exists describing experiments involving the effects of exogenous application of hormones (foliar sprays or root applications) to different plant species, tissues, developmental stages, and so on [1,2,19,20]. One of the major factors that limit researchers from elucidating the precise roles of phytohormones is the highly complex nature of hormonal crosstalk in plants.

Crosstalk of the signaling pathways

In order to combat oxidative stress, plants induce several strategies of which hormone crosstalk is an imperative strategy. Crosstalk between the plant hormones was well studied for their roles in plant development and stress tolerance [1,2]. For example, the accumulation of GB has been associated with the signaling network of major phytohormones such as ABA, SA and ethylene under various abiotic stress conditions [1]. Several phytohormone signaling cascades are also reported to interplay during abiotic stresses, which include GB, ABA, SA, BRs, JA and ethylene [1,21]. Gururani, *et al.* [1] reviewed the current understanding on the role of various phytohormones in the expression of photosynthetic genes and in the regulation of photosynthetic machinery under various abiotic stresses, which is important for

acclimation of the photosynthetic apparatus under environmental conditions. Moreover, the over-accumulation and exogenous application of hormones may exhibit entirely different dose-dependent effects on the photosynthetic machinery. On the other hand, different species, tissues, developmental stages and so on, may respond very differently to the same concentration of hormone.

In plants, NO is known to maintain a diverse network with other growth regulators. For instance, the cellular NO level is affected by ABA, JA, SA, BRs, cytokinin, auxin, polyamine and interplay with these molecules modulates cellular and whole-plant responses to various environmental factors [2,5,22]. It has been also demonstrated that the exogenous NO induced expression of resistance genes and this expression depended on the accumulation of SA [23,24]. NO, ROS and SA attracted a special attention as components of the signaling pathways that can affect the functioning of other signaling pathways. ROS and NO stimulate the synthesis of SA, which in turn accelerates ROS- and NO-dependent responses [1,2,24,25]. Close functional cooperation between signal molecules of ABA, H₂O₂ and NO was also confirmed [5]. In addition, ABA synthesis in wheat roots in response to water deficit was much higher in the presence of NO donors and ROS, suggesting the synergistic action of ROS and NO [26]. Additionally, JA is supposed to function as a second messenger of NO and its biosynthesis is regulated by NO [22]. It has been also demonstrated that BRs-induced NO production and NO-activated ABA biosynthesis are important mechanisms for enhanced stress tolerance in leaves of maize plants [27]. This allows an assumption that a coordinated signaling network functions in plant cells.

Therefore, investigations of the interactions between various signaling pathways are of considerable interest and also of practical use. They would allow us to understand the physiological significance of phytohormones and how the signal integration is related to the best defense strategy. A high immune status of plants is especially crucial at the present time when plants are subjected to numerous biotic and abiotic stresses.

Conflict of Interest

The author declares that there are no financial interest and conflict of interest.

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