Chapter 1

Introductory Chapter: Hormonal Regulation in Plant Development and Stress Tolerance

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1. Introduction

Phytohormones are regulatory compounds produced in low concentrations and serve as chemical messengers to regulate various plant physiological and developmental processes. They also play essential roles in signal transduction pathways during stress response and regulate internal and external stimuli [1]. Phytohormones comprise five main groups, namely auxins (IAAs), cytokinins (CKs), abscisic acid (ABA), gibberellins (GAs) and ethylene (ET). Salicylates (SAs), jasmonates (JAs), brassinosteroids (BRs), strigolactones (SLs), polyamines, and some peptides represent new families of phytohormones.

Hormone actions form a signaling network and regulate various systems in plants. The interacting actions among hormone signal transduction cascades are called crosstalk [2, 3]. Phytohormones interact by activating a phosphorylation cascade or a common second messenger. Furthermore, several phytohormones interact together, forming a defense network against environmental stresses such as JA, SA, and ABA which play a crucial role in regulating signaling pathways [3]. Understanding the crosstalk between these phytohormones and defense signaling pathways helps reveal new important targets for developing host resistance mechanisms [3, 4]. Here, the current work presents an overview and discusses recent progresses of phytohormone roles and their crosstalk in plant development and stress tolerance.

2. Phytohormones signaling roles

2.1. Abscisic acid

Abscisic acid (ABA), termed stress hormone, plays an important role in plant leaves abscission and abiotic stresses tolerance [3]. ABA also has important roles in various plant developmental and physiological processes such as seed dormancy, embryo morphogenesis, stomatal opening, cell turgor maintenance, and biosynthesis of lipids and storage proteins [3, 5]. ABA regulates protein-encoding genes [6]. ABA enables plants to survive under severe environmental factors [7] and water-deficit conditions [8]. ABA is also important for root growth and architectural modifications under nitrogen deficiency [9] and drought stress [10]. Furthermore, ABA is involved in the biosynthesis of dehydrins, osmoprotectants and protective proteins [3, 11, 12].

2.2. Auxins

Some pathways for auxin (IAA) biosynthesis in plants have been reported so far including one tryptophan-independent and four tryptophan-dependent pathways [3, 13]. IAA plays an important role in plant growth and development as well as in regulating growth under stress factors [14]. IAA plays essential roles in plant adaptation to salinity [15] and heavy metal stresses [16]. Furthermore, auxins induce the transcription of the primary auxin response genes which are identified in various plants such as rice, *Arabidopsis* and soybean [3, 17]. Auxin also regulates crosstalk between biotic sand abiotic stresses [18].

2.3. Cytokinins

Cytokinins (CKs) regulate plant growth and development [3, 19]. They are also involved in abiotic stresses [20] such as salinity [21] and drought [19]. They are also important for various crop traits such as productivity and enhanced stress tolerance [3, 22]. CKs also release seeds from dormancy [18] and are considered as abscisic acid antagonists [23]. Decreased CK content promotes apical dominance, which assists in the adaptation to drought stress [3, 20].

2.4. Ethylene

Ethylene (ET) is a gaseous phytohormone regulating plant growth and developmental processes, including flower senescence, fruit ripening, and petal and leaf abscission, as well as regulating stress responses [3, 24, 25]. Ethylene biosynthesis begins from methionine via S-adenosyl-L-methionine and the cyclic amino acid ACC. ACC synthase converts S-adenosyl-L-methionine to ACC, whereas ACC oxidase catalyzes the conversion of ACC to ET. Various abiotic stresses affect endogenous ethylene levels in plant species. Higher ET concentrations promote stress tolerance [26]. Ethylene may combine with other hormones such as jasmonates and salicylic acid and plays crucial roles in regulating plant defense against biotic stress factors [3, 1]. Ethylene and abscisic acid may act together to regulate plant growth and development [3].

2.5. Gibberellins

Gibberellins (GAs) are carboxylic acids that may regulate plant growth and development [27]. They positively regulate leaf expansion, seed germination, stem elongation, flower development and trichome initiation [3, 28]. They also play important role in abiotic stress tolerance [29] such as osmotic stress. GAs may interact with other hormones and regulate various developmental processes [30]. These interactions may involve both negative and positive regulatory roles [3, 30].

2.6. Brassinosteroids

Brassinosteroids (BRs) comprise polyhydroxy steroidal phytohormones which regulate plant growth and developmental processes including root and stem growth, and flower initiation and development [3]. BRs were first isolated from *Brassica napus*. Brassinolide, 24-epibrassinolide, and 28-homobrassinolide are the most bioactive BRs widely used in physiological studies [31]. They are found in flower buds, pollen, fruits, vascular cambium, seeds, leaves, roots, and shoots [32]. BRs also play important roles in abiotic stress responses such as chilling, high temperature, soil salinity, drought, light, flooding, and organic pollutants [3].

2.7. Jasmonates

Jasmonates (JAs) are multifunctional phytohormones derived from the membrane fatty acids metabolism and are widely distributed in several plant species [3]. JAs play crucial roles in growth and developmental processes such as fruiting, flowering, senescence and secondary metabolism [3, 33]. JAs are also involved in biotic and abiotic stress responses such as salinity, drought, irradiation and low temperature [3, 34]. Exogenous concentrations of methyl jasmonate (MeJA) minimize salinity stress symptoms [35]. Additionally, endogenous levels of JA are induced in roots under salinity stress [36]. JA levels also reduce heavy metal stress through inducing the antioxidant machinery [3, 37]. MeJA accumulates phytochelatins, conferring tolerance against Cu and Cd stress [38].

2.8. Salicylic acid

Salicylic acid (SA) is a phenolic compound which regulates the expression of pathogenesis-associated proteins [39]. SA plays an important role in plant growth and development, as well as in biotic and abiotic stress responses [3, 40]. SA has two biosynthesis pathways: the major isochorismate (IC) pathway and the phenylalanine ammonia-lyase (PAL) pathway. Low levels of SA promote the plant antioxidant capacity [3]. However, the high SA levels may result in cell death [41]. SA comprises genes encoding chaperones, antioxidants, heat shock proteins, and secondary metabolite biosynthetic genes such as cinnamyl alcohol dehydrogenase, sinapyl alcohol dehydrogenase and cytochrome P450 [3, 41]. SA may also combine with ABA to regulate drought response [39]. However, the SA mechanism in abiotic stress tolerance remains mainly unknown and still needs more investigations.

2.9. Strigolactones

Strigolactones (SLs) are carotenoid-derived compounds, produced in small quantities in roots, or synthesized in several plant species [3, 42]. SLs play an important role in root architecture and development [43]. They induce nodulation during interaction processes [44] and may be used for inducing the parasitic plants seed germination [45]. SLs are also involved in biotic and abiotic responses [3].

3. Phytohormones crosstalk

Sessile plants should maintain growth plasticity and adaptation ability to severe environmental conditions. Stress-responsive hormones assist in the alteration of cellular dynamics and thus regulating plant growth under stress conditions [3, 46]. The interacting actions among hormone signal transduction cascades are called crosstalk and form a signaling network [2, 3]. In this case, hormones interact by activating a phosphorylation cascade or a common second messenger. Several phytohormones interact together forming a defense network against environmental stresses such as JA, SA, and ABA which play a crucial role in regulating signaling pathways [3]. Understanding the crosstalk between these phytohormones and defense signaling pathways helps reveal new important targets for developing host resistance mechanisms [3, 4].

A complex signaling network regulates stomatal closure. ABA regulates gene expression which mediates root growth maintenance and water uptake. ABA interacts with signaling molecules and other phytohormones such as nitric oxide and JA to induce stomatal closure, as well as to induce genes controlling response to cytokinin, ethylene or auxin [2, 3]. Furthermore, exogenous treatment of ABA down-regulated the key cytokinin biosynthetic pathway gene, termed isopentenyltransferase, but up-regulated genes encoding cytokinin dehydrogenases and oxidases [3, 21]. GA is also included in the hormonal crosstalk in environmental signals [47]. In conclusion, like the potential use of molecular and genetic markers in crop improvement [48–57], phytohormones play crucial roles in development and stress tolerance of crops.

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