Plant Hormones

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This article is a revision of the previous edition article by M Estelle, volume 3, pp 1480–1481, © 2001, Elsevier Inc.

Glossary

β-Carotene Carotene that has two β-rings and serves as provitamin A in animals.
Climacteric fruit Fruits that can ripen after harvest and their ripening is characterized by a high respiration rate.
F-box protein Proteins contain an F-box domain that interacts directly with the Skp1 protein, a component of the SCF complex involved in the ubiquitination of proteins targeted for degradation.
Leucine-rich repeat (LRR) A protein structural motif composed of 20–30 amino acid repeats rich in the hydrophobic leucine residue. The LRR motif serves as a part of the ligand-binding domain in several hormone receptors.
Parasitic plants These plants obtain water and nutrients from the host plant to sustain their life.
Stomata Stoma (plural stomata) is a pore existing on the plant surface that plays an essential role in gas exchange and transpiration in plants.
Terpene These are a diverse class of naturally occurring hydrocarbons that are synthesized by assembly of C_5-compound isoprene, 2-methyl-1,3-butadiene. Terpenes composed of two isoprene units are called monoterpenes (C_{10} compounds), and those with three and four isoprenes are called sesquiterpenes (C_{15} compounds) and diterpenes (C_{20} compounds), respectively.

Plant hormones are a group of small, unrelated molecules that have profound effects on diverse aspects of plant development and physiology. For many years there were only five known plant hormones: auxins, cytokinins, gibberellins (GAs), abscisic acid (ABA), and ethylene. To date, jasmonic acid (JA) derivatives, salicylic acid (SA), brassinosteroids (BRs), peptide hormones, and strigolactones have been added to the list. Plant hormones are made by plants themselves and their chemical structures and functions are largely conserved among higher plants. These compounds are signal molecules; therefore, their cellular concentrations are tightly regulated at the level of biosynthesis, catabolism, and transport in response to developmental and environmental cues. All of these compounds are active at extremely low concentrations through specific binding to their receptors.

In animals, hormones typically act at sites distant from their site of synthesis. This is also true for some plant hormones. For example, auxin moves through plant tissues via a specialized polar transport mechanism. This process involves movement of the hormone through files of cells by successive cellular influx and efflux events. However, unlike animal hormones, plant hormones may be active at both the site of synthesis and at distant sites.

The most abundant naturally occurring auxin is indole-3-acetic acid (IAA). This hormone is involved in diverse aspects of plant growth and development, ranging from embryogenesis to floral development. IAA is primarily synthesized from tryptophan (Trp). Recent genetic analysis of *Arabidopsis* showed that conversion of Trp to indole-3-pyruvic acid is a primary route for IAA biosynthesis, which is most likely conserved in other plant species. IAA is also synthesized via indole-3-acetaldoxime in *Arabidopsis*, but this pathway may be an additional pathway found in a limited species such as crucifers. Polar IAA transport is involved in the accumulation of IAA in particular cells (called auxin maxima) in response to developmental and environmental cues, which elicit plant tropic responses to gravity and to light. Auxin exerts these effects by regulating both cell elongation and cell division. Genetic studies have revealed that auxin perception and early signaling events occur in the nuclei. In the absence of auxin, early auxin-induced genes are repressed by Aux/IAA transcriptional repressors. Auxin receptors are the TIR1 F-box proteins that contain a leucine-rich repeat (LRR) domain. Auxin binds to the LRR domain of these receptors that enhances the recruitment of Aux/IAA repressors to the ubiquitin–proteasome pathway for degradation. For many years, synthetic auxins such as 2,4-dichlorophenoxyacetic acid (2,4-D) have been used as herbicides.

Cytokinins are N^6-prenylated adenine derivatives. The name cytokinin is derived from cytokinesis, and this is not related to cytokine, one of many regulatory proteins that function in animal immune systems. N^6-(Δ^2-isopentenyl)adenine (2iP) and *trans*-zeatin (*t*Z) are naturally occurring cytokinins that are widespread among plant species. These are synthesized from dimethylallyl diphosphate (DMAPP), originating from the methylerythritol phosphate (MEP) pathway via *N*-prenylation of adenosine 5′-phosphates and deribosylation. *Cis*-zeatin, another cytokinin, is synthesized via prenylation of tRNA in which DMAPP from the mevalonate (MVA) pathway is utilized. *Agrobacterium tumefaciens*, a soil-borne bacterium, hijacks cytokinin biosynthesis (and auxin biosynthesis) by integrating its T-DNA into plant genomes. The T-DNA region includes a gene for the enzyme responsible for *N*-prenylation of ATP using 1-hydroxy-2-methyl-2-(*E*)-butenyl 4-diphosphate, the precursor of DMAPP, which bypasses *t*Z biosynthesis. This newly made biosynthesis pathway disturbs endogenous levels of plant hormones, which causes disease symptoms such as tumorigenesis. Cytokinins were originally defined by their ability to stimulate plant cell division in culture. The balance between auxin and cytokinin in culture media is a determinant of *in vitro* shoot regeneration from undifferentiated callus cells. Cytokinins also release bud dormancy, enhance sink strength, promote chloroplast development, and delay leaf senescence. Cytokinin

 doi:10.1016/B978-0-12-374984-0.01170-0

biosynthesis is stimulated by nitrate in the roots and is critical for coordinated shoot–root growth. Cytokinin receptors are membrane-localized two-component histidine kinases that phosphorylate response regulators, transcription factors responsible for cytokinin-mediated transcription.

The gaseous hormone ethylene is synthesized from *S*-adenosylmethionine via two reactions catalyzed by 1-amino-cyclopropane-1-carboxylic acid (ACC) synthase and ACC oxidase. Ethylene regulates cell growth in a number of contexts. This hormone is particularly important for fruit ripening in many plants that show so-called climacteric fruit ripening such as tomato and banana. Ethylene also plays a prominent role in the growth response of submerged plants. The major quantitative trait loci of rice that influence submergence tolerance and growth encode components of ethylene signaling. Largely determined through genetic studies, ethylene receptors and signaling pathways are well known. Ethylene receptors are the two-component type histidine kinases localized at the endoplasmic reticulum membrane. In the absence of ethylene, the ethylene receptors activate a Raf-like protein kinase CTR1, a negative regulator of ethylene signaling. Ethylene inhibits receptor function, which, in turn, inactivates CTR1. The ethylene signal is transduced via a mitogen-activated protein (MAP) kinase cascade and negatively regulates the degradation of the EIN3 transcription factor triggering ethylene-regulated gene expression.

ABA is a sesquiterpene synthesized from a group of xanthophylls derived from β-carotene. This name is derived from its role in promoting leaf abscission in cotton. Genetic analysis using ABA auxotrophs has shown its extremely important roles in water stress and the establishment of dormancy during seed development. The hormone acts rapidly to induce stomatal closure during conditions of water deficit. ABA biosynthesis is stimulated by drought in vascular tissues and is thought to spread throughout the entire plant to induce a large number of drought-inducible genes. ABA is perceived by PYR1/PYL/RCAR soluble receptors in the nuclei. The ABA-bound receptors inhibit the function of a subset of type 2C protein phosphatases (PP2Cs), the negative regulators of ABA signaling. This releases SnRK2 kinases from PP2C inhibition and allows them to activate downstream regulators including ABA-responsive element binding bZIP proteins.

GAs are diterpenes and are synthesized from geranylgeranyl diphosphate. More than 100 GAs are identified as plant products but there are only a few biologically active forms such as GA_4 and GA_1. GA was originally identified as a fungal toxin produced by *Gibberella fujikuroi*, a pathogen of rice. Rice plants that become infected with this fungus grow tall and spindly because of fungal production of GA. As evidenced by this behavior, and by the phenotype of mutants deficient in GA biosynthesis, these hormones are important regulators of stem elongation. GA-deficient or -insensitive semidwarf varieties of rice and wheat were utilized as the high-yield varieties in 1950s to 1970s during the Green Revolution. In addition, GA is essential for seed germination of many plant species and often plays an important role in flowering and fruit development. Genetic studies in maize and *Arabidopsis* have led to a detailed understanding of GA biosynthesis. GA is perceived by the GID1 soluble receptor. The binding of GA to the receptor accelerates the recruitment of DELLA transcriptional repressors that form a complex with GID2/SLY F-box proteins, which, in turn, promote degradation of DELLA repressors by the proteasome pathway.

JA derivatives are a group of oxylipins, the oxygenated hydrocarbons derived from fatty acids, and regulate biotic and abiotic stress responses in plants. JA is synthesized from linoleic acid. A biologically active form of JA is the JA conjugate to the amino acid isoleucine (JA-Ile). JA-Ile binds to the COI1 receptor, an F-box protein that contains an LRR domain. The mechanism of JA-Ile signaling resembles that of auxin, as the transcriptional repressor JAZ is recruited to the proteasome system by the JA-Ile-bound COI1 complex. A volatile derivative, JA methyl ester and other oxylipins such as oxophytodienoic acid (OPDA) may also have biological activity. JA and its derivatives appear to be particularly important for defense responses. JA is synthesized after wounding or some other insult and induces the synthesis of defense-related proteins, including proteinase inhibitors that inhibit insect feeding. In *Arabidopsis*, JA action depends on regulated protein degradation in a manner similar to auxin.

SA is a plant-derived phenolic compound that has an important role in plant defense responses. SA is also known to relieve aches and pains and reduce fever in human, and its derivative acetylsalicylic acid (aspirin) is often used as a drug. SA is synthesized from chorismate via isochorismate, and another pathway via phenylalanine ammonia lyase. SA methyl ester is a volatile compound and is also thought to have biological activity. Infection results in an increase in SA levels, which, in turn, results in the expression of a number of pathogenesis-related (PR) proteins. SA is also associated with a nonspecific persistent defense syndrome called systemic acquired resistance. Plants that are locally exposed to a pathogen develop a systemic and long-lasting resistance to a variety of pathogens. Unlike many other plant hormones, perception mechanisms of SA are largely unknown.

BRs are closely related to animal steroid hormones. This class of plant hormone is required for cell elongation and may play a special role in light regulation of plant growth. Brassinolide is primarily the active form and castarsterone is also bioactive. Unlike other hormones, BRs are not thought to move between cells. Genetic studies have revealed an important difference between the action of plant and animal steroid hormones. In animals, steroid hormones interact with cytoplasmic receptors. Hormone binding results in translocation of the receptor into the cell nucleus where it stimulates specific gene transcription. In contrast, the BR receptor is an LRR domain-containing protein kinase located on the cell surface.

Peptide hormones are secreted small peptides that act as signals for cell–cell communication in plants. There is no clear definition as to the size of peptide hormones, but peptides composed of ~100 amino acids or less are generally categorized into this group. The *Arabidopsis* genome predicts there are ~1000 orphan peptide hormones. The known peptide hormones play essential roles in the regulation of many processes including meristem maintenance, positioning and density of the stomata, vascular development, and plant defense responses. One major group of the peptide hormones is characterized by their small size (<20 amino acids); they are synthesized by proteolysis of pre-propeptides consisting of 70–110 amino acid residues. These peptides are often posttranslationally modified by tyrosine sulfation, proline hydroxylation, and by hydroxyproline arabinosylation. Another group of these secreted peptides is the small cysteine-rich proteins, in which cysteine residues form intramolecular disulfide bonds. Some of these peptides require proteolysis to be biologically active. The identified receptors for these peptide hormones are membrane-localized LRR domain-containing proteins either with or without functional protein kinase domains. For example, in stomatal development, the ERECTA receptor family members activate the downstream MAP kinase cascade.

Strigolactones are recently identified hormones that regulate shoot branching. This class of plant hormones had been known as plant-derived stimulators of parasitic plant seed germination such as *Striga* and of symbiosis of mycorrhizal fungi. Strigolactones are secreted to the rhizosphere from roots of host plants. Genetic analysis has revealed that strigolactones inhibit shoot branching. Recent genetic analysis showed that strigolactones promote seed germination in *Arabidopsis*. Strigolactones are produced via carotenoid cleavage, but its biological active form and mode of action remain unknown.

Most plant processes are regulated by multiple plant hormones; therefore, hormone balance is a key determinant for the biological output. Indeed, most plant hormones influence metabolism, signaling, and transport of other plant hormones. This crosstalk allows a biological response to be coordinated within an entire plant body plan and its physiology. Systems biology approaches are suitable to address the complex interactions of hormone signaling and their effect on plant processes.

See also: Brassinosteroids; Plant-Growth-Promoting Rhizobacteria.

Further Reading

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Relevant Websites

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http://www.plantcell.org – Teaching tools in plant biology.