

## TEACHING TOOLS IN PLANT BIOLOGY™: LECTURE NOTES

# INTRODUCTION TO PHYTOHORMONES

Hormones are chemical messengers that coordinate the cellular functions of multicellular organisms. Animals produce many chemical hormones, each of which usually targets a small number of cells and triggers a specific response. By contrast, plant hormones (phytohormones) are fewer in number, usually affect most if not all cells, and trigger diverse responses. Furthermore, the accumulation and effects of each phytohormone are modulated by environmental and developmental influences as well as the activities of other phytohormones. Unraveling the complex networks of hormonal action and signaling pathways in plants is ongoing; several hormone receptors have only recently been identified, and many signaling components are still unidentified. This lecture provides a brief introduction to the phytohormones and their functions throughout the plant life cycle, their cellular effects and signaling pathways, and some of their interactions with other hormones. Other articles in this series examine individual plant hormones in greater depth.

### WHAT ARE HORMONES AND PHYTOHORMONES?

In their 1937 book *Phytohormones*, Frits Went and Kenneth Thimann define a hormone as “a substance which, being produced in any one part of the organism, is transferred to another part and there influences a specific physiological process.” They emphasize the functional aspect of hormones, stating that “these hormones are characterized by the property of serving as chemical messengers, by which the activity of certain organs is coordinated with that of others.”

The use of the term hormone to describe small chemical messengers in plants has been contentious. Some argue that the differences between hormone action in animals and plants are too great for a common term. Animal hormones are produced within a specific tissue (e.g., an endocrine gland such as the pituitary), are transported through the blood, and act at another distant tissue. By contrast, most plant cells appear able to produce most hormones, their mechanisms of transport are diverse, and the hormones can affect their cell of origin as well as more distant cells. Nevertheless, there are important similarities in the functions of hormones in animals and plants, including that they are active in very small quantities and function as chemical signals (as opposed to having nutritional or catalytic functions), and so the term hormone has become a widely accepted to describe these molecules in plants. In this article, we will again follow the lead of Went and Thimann, who state, “To avoid the possibility of confusion with animal mechanisms the term phytohormones has been introduced for such substances in plants. However, since in this book we shall deal only with the plant kingdom, the prefix can suitably be dropped.”

We often refer to the five classical plant hormones, which were identified in the early to mid 20th century. They are auxin (isolated in 1926 by F. Went), cytokinins (1950s, F. Skoog), ethylene (1901, D. Neljubow), gibberellins (1926, E. Kurosawa), and abscisic acid (ABA; 1950s, T. Bennett-Clark and N. Kefford). Within the past 50 years or so, several other compounds have been identified that meet the criteria of hormones. We will include in this discussion four of the more recently identified types of hormones: brassinosteroids (BRs), jasmonates, salicylates, and strigolactones. Their incorporation into the family of plant hormones is largely but not universal accepted. We won't include other compounds that have signaling roles in plant development, such as the many signaling peptides, polyamines, reactive oxygen species, or nitrous oxide. Like Thimann and Went, we will drop the prefix “phyto” and refer to these compounds simply as hormones.

The functions of plant hormones are diverse, but all have profound effects on growth and development. Hormones affect all phases of the plant lifecycle from seed to seed, and their responses to environmental stresses, both biotic (from a living organism) and abiotic (from the physical environment). Because of their pleiotropic effects, unraveling the functions of plant hormones has been challenging and continues to be one of the most active areas of plant biology research. Because of their fundamental roles as integrators and regulators, the study of plant hormones and the genes that control their synthesis, transport, and downstream effects has identified many new tools for agricultural improvements.

In this article, we will briefly describe the functions of plant hormones (focusing on angiosperms) throughout a plant's life, starting with seedling germination. We will introduce each hormone in the context of one of its roles, without overlooking the fact that most hormones function throughout the plant's life. Other articles will examine in greater depth the molecular pathways and proteins underlying the synthesis and action of each of the major hormones as well as the synergistic and antagonistic interactions between hormones.

### OVERVIEW OF HORMONE ACTION

To understand the function of a hormone, we need to know how it is synthesized and accumulates, how it is transported, how it is perceived, and how its perception is transduced into a response.

#### Synthesis and Accumulation

The synthesis of a plant hormone is tightly regulated, usually subject to positive or negative feedback control depending on the context, and often affected by crosstalk by other hormones and environmental inputs. Once synthesized, many hormones are subject to chemical modifications affecting their activity; in

some cases, the inactive hormone can be stored and readily released in active form through reversing these modifications. Hormone levels are further controlled by their rate of catabolism. The enzymes of the anabolic and catabolic pathways of most hormones are encoded by families of independently regulated genes, allowing the plant to finely tune metabolic control of hormone accumulation. As an example, the enzyme that catalyzes the rate-limiting step of ABA synthesis is highly expressed in maturing seeds and drought-stressed roots via separate organ-specific genes.

### Transport

Hormones can exert their influence at their site of action, move throughout the plant body via the xylem or phloem transport stream, move short distances between cells by regulated transport proteins, or in some cases by freely diffusing across membranes. The proteins involved in hormone transport are generally not well characterized with the exception of the sophisticated auxin transport system.

### Perception

Hormones exert their influence on target cells by binding to receptor proteins. Some hormones bind transmembrane receptors located at the plasma membrane or endoplasmic reticulum. These receptors bind the hormone ligand at one site and transduce information to another site and often involve activation of a receptor kinase activity. Transmembrane receptors can be thought of as information relays; the presence of the hormone initiates a course of action at a site removed from the hormone itself, through allosteric changes in the protein. Other hormones interact with intracellular receptors, in which the hormone forms part of a protein–protein interaction domain. Binding of the hormone to the receptor or coreceptor changes the binding affinity of the receptor for other proteins, with the hormone itself participating in the binding domain interaction. The receptors for some hormones (e.g., strigolactones and salicylic acid [SA]) remain to be elucidated.

### Signal Transduction

The downstream effects of hormonal signaling include alterations in gene expression patterns and in some cases nongenomic responses. In most cases, many of the transcription factors (TFs) whose activities respond to hormonal signaling have been identified. The steps between hormone binding to receptor and TF activation can be simple or convoluted, and when known usually incorporate signaling via protein kinases and phosphatases, a phosphorelay system, or regulated proteolysis of target proteins via the ubiquitin 26S proteolysis system.

Protein kinases covalently add phosphate groups to proteins. The addition of the phosphate group (phosphorylation) can activate or inactivate a protein, which is reversed by the removal of the phosphate group by a protein phosphatase. Targets of kinases and phosphatases include the receptor proteins themselves (autophosphorylation), other protein kinases and

phosphatases, ion channels, TFs, and other proteins. This rapid and reversible form of protein regulation is ancient in origin and pervasive. The phosphorelay system is similar except the phosphoryl group itself moves from protein to protein, and it is reversible; the phosphoryl group can move backward, and up the phosphorelay system as well as down it.

Some hormonal signals are transduced by regulated proteolytic destruction of a target protein, through the ubiquitination of the target protein and its destruction by the 26S proteasome. Ubiquitin is a small protein that is covalently attached to other proteins by the action of an ubiquitin ligase complex. Upon ubiquitination, the tagged protein is transferred to the large 26S proteasome complex that specifically degrades ubiquitinated proteins. Proteolytic degradation of inhibitory proteins is central to several hormonal signaling pathways, including those of auxin, gibberellins, and jasmonates.

## HORMONE ACTION IN GROWTH AND VEGETATIVE DEVELOPMENT

When it germinates, a new plant is little more than two generative tissues: the shoot and root apical meristems. For the first part of its life, it will grow vegetatively, accumulating the resources it needs prior to reproduction. Growth in plants includes linear growth, through cell division and expansion in the primary axis defined by the shoot and root apical meristems; branching growth, through the action of secondary branch meristems in the shoot and root; radial growth, through cell division activities in the vascular meristem or cambium; and organogenesis, the production of leaves, lateral roots, and flowers. Vegetative growth patterns are regulated largely by the combined actions of auxin, cytokinin, strigolactones, gibberellins, and BRs.

### Auxins

Auxins are a family of related compounds that were originally identified as promoters of growth; their name derives from the Greek word *auxein*, meaning “to grow.” Auxin promotes growth and cell elongation but also has critical roles in embryonic pattern formation, promoting and specifying the positions of vascular tissues and leaf and lateral root initiation, and maintaining stem cell populations. Auxin synthesis is tightly regulated and contributes to the auxin gradients that underlie developmental patterning. The most abundant naturally occurring auxin is indole-3-acetic acid (IAA). IAA is chemically similar to the amino acid Trp from which it is synthesized via several different enzymatic pathways. (There is also a Trp-independent pathway that isn’t well characterized.) Diverse pathways contribute to auxin accumulation in different cell types and even in different plant families, with some functional redundancies between the pathways and the genes encoding various enzymatic steps.

One of the effects of what we now know to be auxin was described by Charles Darwin and his son Francis in their book *The Power of Movement in Plants* (1881). Through a series of elegant experiments on the effects of unidirectional light on plant growth, they recognized that although the tip of a seedling

perceives light, the bending movement occurs more basally. They summarized their experiments by saying, "We must therefore conclude that when seedlings are freely exposed to a lateral light some influence is transmitted from the upper to the lower part, causing the latter to bend." We now recognize that this influence is auxin. When a seedling is illuminated from one side, auxin redistributes to the shaded side, stimulating cell elongation and causing curvature toward the light source. Auxin's redistribution in a horizontally oriented root or shoot forms the basis for their positive and negative gravitropic responses too.

The regulated transcellular movement of auxin between cells is critical to its action. Auxin is transported into and out of cells by families of auxin influx and efflux carriers, setting up auxin gradients and local auxin maxima or minima. These gradients and maxima/minima are sufficient to trigger morphogenetic events, including leaf initiation and lateral root initiation. Auxin distribution plays a key role in embryonic pattern formation, including specifying the cells that will form the root stem cell population.

Many of auxin's effects are mediated through its transcriptional regulation of genes that control growth and other signaling pathways. Auxin binds to a small family of intracellular receptors, of which the best characterized is TIR1. When TIR1 binds auxin, the complex then binds to any of several Aux/IAA coreceptor proteins. In the absence of auxin, Aux/IAA proteins are bound to auxin-regulated transcription factors and prevent them from functioning. As well as functioning as an auxin receptor, TIR1 is a component of an ubiquitin ligase complex that transfers ubiquitin molecules to the Aux/IAA proteins, targeting them for proteolysis by the 26S proteasome. The auxin-initiated removal of the corepressors clears the way for transcriptional control by auxin-regulated transcription factors.

Auxin also acts through its interaction with another receptor protein, Auxin Binding Protein1 (ABP1). ABP1 is associated with auxin responses at the plasma membrane, including activation of a proton pump and cell wall acidification, and contributes to auxin-regulated gene expression. At this point, we don't know how signaling downstream of ABP1 is transduced; this is an unfinished chapter in the auxin story.

### Cytokinins

Cytokinins (CKs) are a family of related compounds that are derived from adenine. CK biosynthesis and catabolism are strongly regulated by hormones and inorganic nutrients. Most plants make multiple CKs that interact with differing specificities with different CK receptors, which may fine-tune CK signaling. CK transport mechanisms are not well understood, but there is evidence that they are translocated from root to shoot.

CKs are perceived by a family of membrane-localized receptors that form part of a two-component system that closely resembles bacterial two-component systems. The receptors are His kinases that upon CK binding autophosphorylate and then transfer the phosphoryl group ultimately to other proteins, the response regulators. Type A response regulators are negative regulators of CK signaling, whereas type B response regulators are positive regulators.

In many of its actions, CK acts antagonistically to auxin. This was shown elegantly in the work of F. Skoog and colleagues in the 1950s, in which they observed that ratio of auxin to cytokinin in tobacco (*Nicotiana tabacum*) pith explant culture medium determines whether the explant produces roots or shoots. More recent experiments have identified a similar antagonistic function for auxin and CK at the shoot and root apical meristems. At the shoot apex, auxin promotes lateral organ initiation, whereas CK maintains the cells in an undifferentiated, proliferating stem cell state. At the root apex, auxin maintains the stem cell population and CK induces differentiation. Experiments have revealed a simple signaling network through which auxin and cytokinin coordinate these activities at the root apical meristem. A high auxin level in the stem cells (as a consequence in part of polar auxin transport to the root tip) promotes cell division and directly represses the expression of CK biosynthetic enzymes. Just above the meristem, in the transition zone, CK promotes cell differentiation and represses auxin movement from the tip and auxin action. Thus, the two hormones establish two mutually exclusive domains that collectively ensure that cell division and differentiation are kept in coordination.

Antagonistic effects of auxin and CK similarly control the outgrowth of branches in the shoot and root. A localized auxin maximum is sufficient to initiate the outgrowth of a lateral root, whereas CK represses lateral root initiation. In the shoot, axillary bud meristems are formed in association with a leaf. The outgrowth of these buds is controlled in part by auxin; early experiments showed that the decapitation of a plant allowed them to grow out, whereas decapitation followed by auxin application to the cut site prevented them from growing out (referred to as the apical dominance effect). Studies in intact plants showed that CK antagonizes auxin's effects, promoting bud outgrowth, and that auxin derived from the apex represses cytokinin biosynthesis at the bud. A third hormone that inhibits bud outgrowth was later identified as a strigolactone (see below).

CKs also have important roles in controlling plant nutrient uptake and allocation, nitrogen-fixing root nodule development, root and shoot architecture and seed yields, and leaf senescence. Recently, drought-tolerant plants were produced by introduction of a drought-induced CK biosynthesis gene, providing a new and exciting approach for enhancing plant growth under suboptimal conditions.

### Strigolactones

Strigolactones are exuded by plant roots into the soil and are recognized and responded to by mutualistic mycorrhizal fungi. However, parasitic plants of the *Striga* genus (for which the compound is named) eavesdrop on this communication and respond to the presence of strigolactones by germinating, penetrating the roots of the host, and withdrawing nutrients. In many parts of the world, parasitic *Striga* are a major cause of reduced crop yields. Recently, strigolactones were found to participate in the control of shoot branching, demonstrating that these compounds serve as intraorganismal signaling hormones as well as interorganismal signals. Auxin transported from shoot

to root induces the synthesis of strigolactones, which are ultimately translocated into the shoot, where they interfere with bud outgrowth. Decapitation of the apex reduces auxin flow into the root and strigolactone synthesis, facilitating bud outgrowth, and mutant plants that don't make strigolactones produce extra branches. In some plants, strigolactone synthesis is induced upon nutrient limitation. By promoting root growth and mycorrhizal symbiosis while limiting shoot growth, strigolactones help optimize growth patterns for nutrient acquisition under nutrient-limited conditions. The full details of how this newly identified hormone is synthesized and functions are still being elucidated.

### Gibberellins

Gregor Mendel studied genes whose allelic variants were easily recognized. One of the traits he studied affects the height of the plant, which he called *Le*, for length. The dominant *Le* allele causes plants to be tall, whereas those individuals homozygous for *le* are short. Much later, the *Le* gene was found to encode an enzyme involved in the biosynthesis of gibberellic acid (GA); plants with only the recessive *le* allele produce less GA and are genetic dwarfs.

Gibberellins are a family of compounds, only some of which have biological activities in plants; gibberellic acid (GA<sub>3</sub>) is the most active and the most well characterized. GA accumulation is tightly regulated by the control of key enzymes in its synthesis and degradation. Gibberellins were first identified biochemically through investigations of the strange effect that a fungal pathogen, *Gibberella fujikuroi*, has on its host plant. Infected plants grow extremely tall, aren't able to support themselves, and fall over to rot. Because of this odd effect, the disease caused by the fungus was called bakanae, which translates to foolish seedling. Later, gibberellins were identified as endogenous plant hormones that control diverse aspects of plant development. The biosynthetic pathway for gibberellins was deduced by analyzing GA-deficient mutants. Early steps occur in plastids, but subsequent steps occur in the endoplasmic reticulum and cytoplasm.

GA dwarfism is an extremely valuable agricultural trait, especially in grasses, because shorter, sturdier stems are better able to support the large, heavy seeds that well-fertilized crop plants produce; dwarf varieties produce higher grain yields due to increased resource allocation into the seed as well as fewer plants falling over and rotting. In the green revolution of the 1960s, crop yields doubled as a result of increased fertilizer use in combination with semidwarf varieties. Although their value in grain production was recognized more than 50 years ago, the gene products of the green revolution semidwarf genes were only recently identified. The rice (*Oryza sativa*) green revolution gene *semi-dwarf1* encodes an enzyme in the GA biosynthetic pathway, GA 20-oxidase.

Other genes that confer the desirable semidwarf phenotype include genes in the GA response pathway. Like auxin, GA binds to an intracellular receptor protein. Binding of GA to the receptor causes the receptor to bind to and target for proteolysis any of several proteins that are negative regulators of growth and GA response. These proteins have a conserved DELLA (Asp-Glu-Leu-Leu-Ala) sequence at their N-terminal end that is critical for their

function. The wheat (*Triticum aestivum*) *Reduced height1* gene encodes a DELLA protein; the semidwarf allele has the DELLA domain deleted, making it insensitive to GA. Because this mutant protein acts in a dominant fashion, genes encoding it can be readily introduced into plants to generate dwarf varieties when a naturally occurring loss-of-function dwarfing allele is not available.

Gibberellins have several other functions in plant growth and development, only some of which are understood at the molecular level. Many if not all of these are mediated through the interaction of gibberellins with the DELLA proteins. For example, gibberellins promote flowering, by destabilizing the DELLA proteins that interfere with the transcription of genes that promote flowering, promote root growth by destabilizing the growth inhibitory effects of DELLA proteins in the root, and promote seed germination by inactivation of DELLA proteins that promote the action of the dormancy-promoting hormone ABA (see below). It appears that gibberellins do much more than control stem elongation; rather, they may be a key node in many of the cross-regulatory interactions among the plant hormones.

### Brassinosteroids

In 1979, a growth-promoting compound previously identified in pollen extracts from *Brassica* was purified and shown to be a steroid, now called brassinolide. Brassinolide and its related plant steroid hormones are collectively called brassinosteroids (BRs) to reflect their initial characterization in *Brassica*, although they are present in all plants and some algal species as well. BRs are synthesized from campesterol, a sterol. The identity of many of the biosynthetic genes was determined from the study of dwarf mutants that don't produce BRs. As yet, little is known about the regulation of BR biosynthesis.

BRs are perceived by membrane-localized Leu-rich repeat receptor-like kinases. Hormone binding initiates a protein kinase cascade, ultimately leading to changes in gene expression. BRs participate in diverse processes, including vascular and reproductive development, control of plant architecture, light responses, and stress responses.

BRs promote cell elongation. BR-induced genes include genes that loosen cell walls to permit cell expansion by the internal turgor pressure within plant cells. In part because of their growth-promoting effects, some BR-overproducing (or BR-hypersensitive) plants can produce higher yields. On the other hand, the *uzu* mutant of barley (*Hordeum vulgare*) has a mutation in the BR receptor that makes it semidwarfed, resistant to blowing over in the wind, and also higher yielding. Thus, understanding the role of BR in cell elongation opens up several opportunities for crop yield improvements.

### HORMONE ACTION IN REPRODUCTIVE DEVELOPMENT

Several hormones influence the time at which a plant flowers, but their relative roles in this timing vary considerably. How hormonal signals affect flowering time is dependent upon environmental signals, particularly daylength, and whether the plants flowers only once and then dies, as do annual plants, or continues to flower year after year, as do perennial plants like shrubs and trees. The molecular control of the decision to flower

has been most thoroughly studied in short-lived annual plants, including *Arabidopsis thaliana*, pea (*Pisum sativum*), maize (*Zea mays*), rice, and *Lolium temulentum*, a temperate grain plant. In most plants studied, the protein product of the *FT* gene is a mobile signal that moves from the leaves to the shoot meristem and initiates the expression of genes controlling reproductive development. In some of these plants, the gibberellins augment this signal, whereas in others it has little to no effect except under unusual circumstances. *Lolium* (and some other temperate grasses) seem to use gibberellins as the sole or primary signal to induce reproductive growth. In *Arabidopsis* grown in noninductive short days, gibberellins can promote flowering, whereas in perennial plants, gibberellin application either has no effect or restricts flowering. In bromeliads, including pineapple (*Ananas comosus*), flowering is strongly induced by ethylene, which is used commercially to synchronize flower and fruit production. Most other hormones can influence the time of flowering indirectly through effects on growth rate and nutrient assimilation.

Many hormones have been shown to contribute to proper flower development and function. For example, auxin contributes to organogenesis, jasmonates are necessary for pollen viability and anther filament elongation, and in some plants, gibberellins and ethylene have roles in sex determination.

Hormones also participate in fruit development and ripening. A fruit is an enlarged ovary that contains the developing seed. Fruits assist in the successful propagation of the enclosed seed by providing an extra nutrient supply or by enticing consumption and thus dispersal by an animal. Pollination and seed development trigger auxin and gibberellin accumulation, which promote cell division and expansion in the ovary; these hormones have to be applied exogenously in the production of seedless fruit varieties. Commercially, many fruits are routinely sprayed with gibberellins to increase their size.

## Ethylene

Ethylene promotes ripening in many fruits. Fruit ripening is a complex process that includes changes in color, flavor through the breakdown of starches into sugars, and texture through changes in cell wall structures. The important role of ethylene is vividly seen in mutants affected in ethylene production or response. In ethylene-ripened fruits (called climacteric fruits), such as tomato (*Solanum lycopersicum*), a rapid increase in ethylene synthesis promotes a rapid ripening response across the entire fruit. Because ripening occurs very quickly and includes softening, ripe fruits are notoriously difficult to transport and store. Many fruits are picked green and subsequently treated with exogenous ethylene once they are ready to be consumed. To prevent overripening, ethylene can be absorbed by commercial products that react with and degrade ethylene.

Ethylene also causes the senescence of leaves and flowers. In the 19th century, many homes used coal gas, a complex mixture of gases including ethylene, as a source of gas lighting, making 19th century homes a hostile environment for houseplants. *Aspidistra* spp are unusually tolerant to ethylene, making them most popular plants in those days and giving them their

nickname of the “cast-iron plant.” Ethylene production accelerates senescence in cut flowers as well. Some powders that florists pack with their cut flowers contain compounds that degrade or interfere with ethylene production and so extend the life of the flowers.

Ethylene is synthesized from the amino acid Met by the sequential action of two hormones, ACC synthase (which produces 1-amino carboxylic acid) and ACC oxidase. Because of the importance of controlling ripening commercially, several plants have been engineered to reduce expression of these enzymes and ethylene production. Ethylene is perceived by a small family of membrane-bound receptors found on the endoplasmic reticulum; as a gas, ethylene is freely permeable through the plasma membrane. When the receptors bind ethylene, they dissociate from and inactivate CONSTITUTIVE TRIPLE RESPONSE1 (CTR1), a negative regulator of ethylene signaling. In the absence of ethylene, CTR1 indirectly inactivates ethylene-responsive TFs, which, when CTR1 is inactivated, are free to initiate gene expression.

Ethylene also contributes to vegetative growth and has an important, although not well understood, role in plant stress responses. Mutants affected in ethylene production or signaling are less stress tolerant. Ethylene contributes to the extremely rapid elongation in deep-water rice and is produced in response to wounding, various abiotic stresses, and pathogen attack. Ethylene induces genes that generally stabilize the stressed cells through detoxification of reactive oxygen species and physical stabilization of proteins and membranes. Ethylene also functions synergistically with jasmonates in plant defense responses (see below).

## HORMONE ACTION IN SEED MATURATION, DORMANCY, AND GERMINATION

Seeds are exceptionally important contributors to the successes of seed-bearing plants because they allow for a period of dormancy between generations. The final step of seed development is a period of dehydration and the initiation of dormancy. Dehydration makes the dry seeds resistant to microbial degradation. Cells in the embryo can dehydrate to ~5% water content or less, an extreme dehydration that is lethal to most cells. To survive desiccation, the embryo produces seed-specific proteins that stabilize cellular structures. The hormone ABA induces the transcriptional activation of these cryoprotectants. Plants deficient in ABA production or response fail to initiate embryonic dormancy. For example, in the maize *vp1* mutant, embryos sometimes germinate from seeds that are still attached to the cob, in a process called vivipary (live birth). Similarly, *Arabidopsis* embryos with mutations in several partially redundant protein kinases required for ABA responses fail to become dry and dormant; they sprout within the seedpod.

Once dormant, seeds can be incredibly stable, in some cases maintaining living embryos for hundreds of years, awaiting appropriate conditions to sustain a germinating seedling. Many seeds need only water to break dormancy, whereas others have requirements for seed coat scarification, fire, light, or temperature. Sometimes the seed needs to remain dormant long enough for the ABA it accumulated in preparation for dormancy

to degrade, as ABA is a potent inhibitor of seed germination. When a seed receives water or other stimulation, it begins to produce GA. GA promotes germination in part by suppressing ABA-induced dormancy but also directly by promoting cell elongation in the embryo to facilitate its emergence from the seed coat. In some seeds, GA contributes to the mobilization of the nutrients stored in the endosperm; this process has been thoroughly studied in barley, a key ingredient in beer production. Brewers soak barley seeds in water to promote germination and GA production; sometimes they add additional GA to encourage germination. GA triggers the barley aleurone cells to produce enzymes, including amylase that digests stored starches and releases sugars, which are then fermented into ethanol by yeast.

### HORMONE ACTION IN RESPONSES TO ABIOTIC STRESS

Once a seed germinates, it is anchored into the soil for better or for worse. A spot that was ideal for germination can rapidly become a hostile environment with changing conditions or seasons. Abiotic stresses are the primary cause of crop losses and include extremes of heat and cold, drought and flooding, and excessive soil salinity or toxic ions. Often plants are able to survive extreme environmental fluctuations through the expression of diverse stress-responsive genes. Many of these genes also affect growth rate or reproductive success, so they are generally inactive until needed. The hormone ABA is produced in response to several types of stress and induces appropriate stress-responsive genes. Some of the ABA-induced genes in vegetative tissues are similar to those expressed in seeds that help cells survive osmotic challenges.

### ABA

During seed development or in response to abiotic stress ABA synthesis is strongly induced by transcriptional activation of genes encoding biosynthetic enzymes. ABA accumulation initiates the transcription of genes whose products confer protection against dehydration or osmotic challenge. Among these are proteins that stabilize other proteins or membranes to prevent their rupture or denaturation during osmotic challenge, enzymes that produce small molecules that confer osmotic balance, enzymes that detoxify reaction oxygen species, and aquaporins and membrane channels that facilitate the movement of water and ions across membranes. These ABA-induced genes are regulated by the action of several TFs that bind to conserved DNA regulatory elements in the promoters of ABA-responsive genes. The TFs are activated by phosphorylation by conserved protein kinases (SnRKs in *Arabidopsis*) and inactivated by dephosphorylation by conserved protein phosphatases (PP2Cs).

Upstream events in ABA signaling are not fully resolved. Several proteins have been identified as putative ABA receptors, but most of these reports have been subsequently called into question or retracted. At the moment, the strongest candidates for ABA receptors are intracellular proteins referred to as PYR, PYR-like, and RCARs. When bound to ABA, these receptors interact with PP2Cs, sequestering and inactivating them to permit TF phosphorylation and activation.

ABA has a critical role in the regulation of rate of water loss through stomatal transpiration. The stomatal ABA response is much more rapid than responses that require de novo transcriptional changes and is affected primarily through changes in membrane permeability of the guard cells that overlie the stomatal pores. Within a few minutes of ABA treatment, guard cell ion channel activities cause a decrease in solute concentration and concomitant loss of water by osmosis. As the guard cells shrink, they collapse together and cover the stomata. ABA also prevents stomata from reopening. The ABA signaling events that control guard cell turgor occur largely at the plasma membrane and include an increase in cytoplasmic calcium and reactive oxygen levels, which act as cellular signals, membrane depolarization and cytoplasmic alkalinization, and activation of anion and potassium channels. Several studies have shown that modifications to guard cell ABA signaling can enhance plant drought tolerance.

### HORMONE ACTION IN RESPONSES TO BIOTIC STRESS

As sessile organisms, plants seem to be easy targets for herbivores and pathogenic microorganisms. Not surprisingly, plants produce numerous physical and chemical defenses, such as thorns and toxic or foul-tasting compounds. Some defenses are constitutive (produced all the time), whereas others are induced by the presence of a pathogen through pathways that include hormonal signaling. The hormonal response depends on the type of pathogen or herbivore attacking the plant. Biotrophic pathogens live within living tissues and don't immediately kill the plant cells; *Pseudomonas* is a bacterium that is widely studied as a model for plant responses to biotrophic pathogens. Plant defenses against biotrophic pathogens are mediated in part through SA signaling pathways. Necrotrophic pathogens, such as many fungi, kill their plant hosts directly through the production of toxins or hydrolytic enzymes. Responses to necrotrophic pathogens and many herbivores are mediated in part by jasmonates and synergistic effects of ethylene. The salicylate and jasmonate/ethylene pathways are sometimes antagonistic; one response dampens the other. Activation of either pathway interferes with GA or auxin-induced growth pathways, and both defense pathways are reduced by elevated ABA levels (suggesting that a stressed plant puts its resources into combating the abiotic challenge before the biotic challenge). Other hormone signaling pathways also affect stress responses; for example, reducing the auxin response increases resistance to some pathogens. These interactions are sometimes exploited by pathogens that produce phytohormones or affect hormone signaling in other ways.

### Jasmonates

Jasmonates are derivatives of jasmonic acid (JA), which is derived from membrane lipids in a series of steps occurring in the chloroplast and peroxisome. Herbivore damage (wounding and/or herbivore oral secretions) induces JA accumulation within 30 min. In the cytoplasm, JA is conjugated to isoleucine to form the active compound JA-Ile. Jasmonate accumulation leads to an induction of the expression of genes that have an antiherbivory function, including several that interfere with insect digestive

capabilities, as well as defensin proteins with broad antimicrobial functions. Mutant plants that don't produce or respond to jasmonates are far more susceptible to insect or necrotrophic pathogen attack. Jasmonates can also induce systemic defense responses and the production of herbivore-induced plant volatiles that attract carnivorous or parasitoid arthropods, to eat or lay their eggs on or in the herbivore. Other volatile signals are perceived by nearby plants or other branches of the same plant, priming them to produce defensive compounds in case of an attack. The signaling pathway for jasmonate response is very similar to that of auxin. Like TIR1, the JA-Ile coreceptor COI1 is an F-box protein; binding of JA-Ile to COI1 causes the complex to bind to and ubiquitinate JAZ coreceptor repressor proteins, thereby promoting transcription via MYC2 TFs. Besides their role in defense, jasmonates participate in reproductive and vegetative developmental functions.

### Salicylates

Salicylates include salicylic acid (SA) and its derivatives. SA is named for willow trees in the genus *Salix*; willow bark has long been known for its pain-relieving properties. In the 19th century, the active ingredient was purified, and in 1899, a derivative of SA, acetylsalicylic acid, was given the trade name aspirin. In the 20th century, aspirin and SA were recognized as promoting disease resistance in plants.

SA synthesis is induced by pathogen infection, and mutants affected in SA synthesis are less resistant to pathogens. SA can be methylated to produce a mobile signal, methyl salicylate, which is thought to move through phloem to uninfected cells and, after demethylation to SA, prime them to a heightened resistance, a phenomenon called systemic acquired resistance. Although SA's role in mediating plant defense responses, including systemic acquired resistance, has been recognized for 20 years, its receptor has not yet been identified, and many gaps remain in our understanding of its signal transduction pathway. It is clear, however, that SA has a central role in the plant response to many pathogenic microorganisms.

Plant cells perceive molecules that are commonly found on microbial pathogens, referred to as pathogenesis-associated molecular patterns (PAMPs). The cellular response to PAMPs is referred to as PAMP-triggered immunity. Recognition of a pathogen initiates the production of SA, which leads to the induction of several genes that contribute to pathogen defenses; some of these are pathogenesis-related proteins. Pathogenesis-related proteins include enzymes that directly attack bacteria or fungi, such as chitinases or proteases, as well as those that synthesize compounds with antimicrobial activities. Some pathogens produce effectors that induce a more vigorous defense response called effector-triggered immunity. These stronger responses are conferred by plant resistance genes, which have a very narrow specificity. The effector-triggered immunity response is more vigorous than the PAMP-triggered immunity response and ensures that the recognized pathogen is quickly killed off. This response, called a hypersensitive response, includes the production of sticky cell wall materials called lignin to seal off the infected cell and a burst of reactive oxygen species to kill the infected cell and the pathogen.

### HORMONE RESPONSE NETWORKS AND CROSSTALK

The hottest topic in plant hormone biology is the interconnectedness of the hormones in their effects, referred to as crosstalk or cross-regulation. These interactions can be positive (additive or synergistic) or negative and can occur at any point in hormone signaling pathways. There are countless examples of these interactions, only a few of which will be described by way of introduction; see other articles in this series for additional examples.

Ethylene enhances plant stress responses in diverse ways; this is evident by the increased stress sensitivities of ethylene mutants. Most of these effects are not well understood yet, but a synergistic effect with JA has been characterized at the molecular level. The TF ERF1 is required for increased transcription of several defense genes. Loss-of-function mutants in JA or ethylene signaling interfere with *ERF1* gene expression, and activation of both pathways is necessary for high-level expression. *ERF1* is a member of a multigene family of which several other members are similarly responsive to both JA and ethylene.

Defense signaling is also characterized by an interesting antagonistic interaction between the SA-mediated responses and JA-mediated responses. In some circumstances, induction of one pathway strongly suppresses the other. Some of the downstream players in this antagonism have been identified, including a redox-sensitive protein NPR1 that shuttles between the nucleus and cytoplasm and the WRKY70 TF. Some herbivores and pathogens exploit this antagonism to suppress the plants immune responses. Interestingly, the antagonism between these pathways is strongly localized and doesn't affect systemic signaling nearly as much.

GA is emerging as central to just about every aspect of plant hormonal and environmental signaling, largely due to its regulation of the DELLA proteins. DELLA proteins contribute to the regulation of root growth by auxin and ethylene, seed dormancy and germination by ABA, flooding responses by ethylene, and flowering time controls. It will be very exciting to see how these diverse pathways coordinate their effects through this small set of proteins.

### FUTURE PROSPECTS

Whether you call them plant growth regulators, phytohormones, or hormones, the collection of molecules introduced here clearly have profound roles in regulating all aspects of plant growth, development, and responses to their external environment. Understanding how these molecules function is of tremendous importance for augmenting agricultural productivities, as demonstrated by the enormous impacts of the semidwarf varieties introduced in the mid 20th century. The insights gained from biochemical, physiological, and genetic studies have been enhanced by genomic approaches, revealing not only the identities of some of the major genes controlling these signaling pathways but also their extensive interdependence. Frits Went and Kenneth Thimann's words, written in 1937, are certainly now more true than ever, "The field of plant hormones is perhaps now at the stage of its most rapid development." With the powerful tools we have available, we are beginning to appreciate the

sophistication of plant hormone networks and the insights of the pioneers in this discipline.

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## SUGGESTED READING

(This is a representative list of review articles intended to help the reader access a huge body of primary literature. We apologize in advance to those whose work is not included.)

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