**PHYTOHORMONES**

THE FORM AND FUNCTION of multicellular organism would not be possible without efficient communication among cells, tissues, and organs. In higher plants, regulation and coordination of metabolism, growth, and morphogenesis often depend on chemical signals from one part of the plant to another. This idea originated in the nineteenth century with the German botanist Julius von Sachs (1832–1897). Sachs proposed that chemical messengers are responsible for the formation and growth of different plant organs. He also suggested that external factors such as gravity could affect the distribution of these substances within a plant. Although Sachs did not know the identity of these chemical messengers, his ideas led to their eventual discovery.

Plants also produce signaling molecules, called *hormones*, that have profound effects on development at vanishingly low concentrations. Until quite recently, plant development was thought to be regulated by only five types of hormones: auxins, gibberellins, cytokinins, ethylene, and abscisic acid. However, there is now compelling evidence for the existence of plant steroid hormones, the brassinosteroids, that have a wide range of morphological effects on plant development. A variety of other signaling molecules that play roles in resistance to pathogens and defense against herbivores have also been identified, including jasmonic acid, salicylic acid, and the polypeptide systemin. Thus the number and types of hormones and hormone like signaling agents in plants keep expanding.

**AUXINS**

During the latter part of the nineteenth century, Charles Darwin and his son Francis studied plant growth phenomena involving tropisms. One of their interests was the bending of plants toward light. This phenomenon, which is caused by differential growth, is called **phototropism**. In some experiments the Darwins used seedlings of canary grass (*Phalaris canariensis*), in which, as in many other grasses, the youngest leaves are sheathed in a protective organ called the **coleoptiles.** The experiments done during the course of identification of auxins are summarized as follows:



**Physiological effects of auxins:**

**Auxin induced cell elongation**:

How does auxin cause a five- to tenfold increase in the growth rate in only 10 minutes? To understand the mechanism, we must first review the process of cell enlargement in plants. Plant cells expand in three steps:

1. Osmotic uptake of water across the plasma membrane is driven by the gradient in water potential (Δ*Y*w).
2. Turgor pressure builds up because of the rigidity of the cell wall.
3. Biochemical wall loosening occurs, allowing the cell to expand in response to turgor pressure.

According to the widely accepted **acid growth hypothesis**, hydrogen ions act as the intermediate between auxin and cell wall loosening. The source of the hydrogen ions is the plasma membrane H+-ATPase, whose activity is thought to increase in response to auxin. The acid growth hypothesis allows five main predictions:

1. Acid buffers alone should promote short-term growth, provided the cuticle has been abraded to allow the protons access to the cell wall.
2. Auxin should increase the rate of proton extrusion (wall acidification), and the kinetics of proton extrusion should closely match those of auxin-induced growth.
3. Neutral buffers should inhibit auxin-induced growth.
4. Compounds (other than auxin) that promote proton extrusion should stimulate growth.
5. Cell walls should contain a “wall loosening factor” with an acidic pH optimum.

In theory, auxin could increase the rate of proton extrusion by two possible mechanisms:

1. Activation of preexisting plasma membrane H+-ATPases

2. Synthesis of new H+-ATPases on the plasma membrane

**Other effects of auxins**:

1. Auxins stimulate the plant so sense and respond to the photoperiodic stimulus.
2. Auxins sense the gravity and provides the ability to the root to grow towards the gravity or away from the light.
3. Auxins stimulate apical dominance i.e. it promotes the apical bud to grow and blocks the lateral buds hence giving the plant a conical appearance.
4. Auxins help in initiation of roots and also the formation of lateral and adventitious roots on the plants.
5. Auxins delay onset of leaf senescence.
6. Auxins regulate the development of floral bud and
7. They help in the differentiation of floral elements.

**GIBBERELLINS**

1. **Gibberellins stimulate stem growth in dwarf plants**: Applied gibberellin promotes internodal elongation in a wide range of species. However, the most dramatic stimulations are seen in dwarf and rosette species, as well as members of the grass family. Exogenous GA3 causes such extreme stem elongation in dwarf plants that they resemble the tallest varieties of the same species. Accompanying this effect are a decrease in stem thickness, a decrease in leaf size, and a pale green color of the leaves.
2. **Gibberellins regulate the transition from juvenile to adult phase**: Many woody perennials do not flower until they reach a certain stage of maturity; up to that stage they are said to be juvenile. The juvenile and mature stages often have different leaf forms, as in English ivy
3. (*Hedera helix*). Applied gibberellins can regulate this juvenility in both directions, depending on the species. Thus, in English ivy GA3 can cause a reversion from a mature to a juvenile state, and many juvenile conifers can be induced to enter the reproductive phase by applications of nonpolar gibberellins such as GA4 + GA7.
4. **Gibberellins influence floral initiation and sex determination**: In plants where flowers are unisexual rather than hermaphroditic, floral sex determination is genetically regulated. However, it is also influenced by environmental factors, such as photoperiod and nutritional status, and these environmental effects may be mediated by gibberellin. In maize, for example, the staminate flowers (male) are restricted to the tassel, and the pistillate flowers (female) are contained in the ear. Exposure to short days and cool nights increases the endogenous gibberellin levels in the tassels 100-fold and simultaneously causes feminization of the tassel flowers. Application of exogenous gibberellic acid to the tassels can also induce pistillate flowers.
5. **Gibberellins Promote Fruit Set:** Applications of gibberellins can cause *fruit set* (the initiation of fruit growth following pollination) and growth of some fruits, in cases where auxin may have no effect. For example, stimulation of fruit set by gibberellin has been observed in apple (*Malus sylvestris*).
6. **Gibberellins Promote Seed Germination:** Seed germination may require gibberellins for one of several possible steps: the activation of vegetative growth of the embryo, the weakening of a growth-constraining endosperm layer surrounding the embryo, and the mobilization of stored food reserves of the endosperm. Some seeds, particularly those of wild plants, require light or cold to induce germination.
7. **Gibberellins have commercial application:** The major uses of gibberellins (GA3, unless noted otherwise), applied as a spray or dip, are to manage fruit crops, to malt barley, and to increase sugar yield in sugarcane. In some crops a reduction in height is desirable, and this can be accomplished by the use of gibberellin synthesis inhibitors.

**CYTOKININS**

Although discovered as a cell division factor, cytokinins can stimulate or inhibit a variety of physiological, metabolic, biochemical, and developmental processes when they are applied to higher plants, and it is increasingly clear that endogenous cytokinins play an important role in the regulation of these events in the intact plant.

**Biological roles**:

1. **Cytokinins Regulate Cell Division in Shoots and Roots:** Much of the cell division in an adult plant occurs in the meristems evidence linking cytokinin to the regulation of cell division in vivo came from analyses of mutations in the cytokinin receptor. Mutations in the cytokinin receptor disrupt the development of the root vasculature. Known as *cre1*, these mutants have no phloem in their roots; the root vascular system is composed almost entirely of xylem
2. **Cytokinins Regulate Specific Components of the Cell Cycle** Cytokinins regulate cell division by affecting the controls that govern the passage of the cell through the cell division cycle. Zeatin levels were found to peak in synchronized culture tobacco cells at the end of S phase, mitosis, and G1 phase.
3. **The Auxin: Cytokinin Ratio Regulates Morphogenesis in Cultured Tissues:** Shortly after the discovery of kinetin, it was observed that the differentiation of cultured callus tissue derived from tobacco pith segments into either roots or shoots depends on the ratio of auxin to cytokinin in the culture medium. Whereas high auxin:cytokinin ratios stimulated the formation of roots, low auxin:cytokinin ratios led to the formation of shoots. At intermediate levels the tissue grew as an undifferentiated callus.
4. **Cytokinins Modify Apical Dominance and Promote Lateral Bud Growth:** Although apical dominance may be determined primarily by auxin, physiological studies indicate that cytokinins play a role in initiating the growth of lateral buds. For example, direct applications of cytokinins to the axillary buds of many species stimulate cell division activity and growth of the buds.
5. **Cytokinins Delay Leaf Senescence:** Leaves detached from the plant slowly lose chlorophyll, RNA, lipids, and protein, even if they are kept moist and provided with minerals. This programmed aging process leading to death is termed **senescence**. Leaf senescence is more rapid in the dark than in the light. Treating isolated leaves of many species with cytokinins will delay their senescence. Although applied cytokinins do not prevent senescence completely, their effects can be dramatic, particularly when the cytokinin is sprayed directly on the intact plant. If only one leaf is treated, it remains green after other leaves of similar developmental age have yellowed and dropped off the plant.
6. **Cytokinins Promote Movement of Nutrients:** Cytokinins influence the movement of nutrients into leaves from other parts of the plant, a phenomenon known as *cytokinin-induced nutrient mobilization*. This process is revealed when nutrients (sugars, amino acids, and so on) radiolabeled with 14C or 3H are fed to plants after one leaf or part of a leaf is treated with a cytokinin. Later the whole plant is subjected to autoradiography to reveal the pattern of movement and the sites at which the labeled nutrients accumulate.

**ETHYLENE**

During the nineteenth century, when coal gas was used for street illumination, it was observed that trees in the vicinity of streetlamps defoliated more extensively than other trees. Eventually it became apparent that coal gas and air pollutants affect plant growth and development, and ethylene was identified as the active component of coal gas. In 1901, Dimitry Neljubov, a graduate student at the Botanical Institute of St. Petersburg in Russia, observed that dark-grown pea seedlings growing in the laboratory exhibited symptoms that were later termed the *triple response*: reduced stem elongation, increased lateral growth (swelling), and abnormal, horizontal growth*.* When the plants were allowed to grow in fresh air, they regained their normal morphology and rate of growth. Neljubov identified ethylene, which was present in the laboratory air from coal gas, as the molecule causing the response.

The first indication that ethylene is a natural product of plant tissues was published by H. H. Cousins in 1910. Cousins reported that “emanations” from oranges stored in a chamber caused the premature ripening of bananas when these gases were passed through a chamber containing the fruit. However, given that oranges synthesize relatively little ethylene compared to other fruits, such as apples, it is likely that the oranges used by Cousins were infected with the fungus *Penicillium*, which produces copious amounts of ethylene. In 1934, R. Gane and others identified ethylene chemically as a natural product of plant metabolism, and because of its dramatic effects on the plant it was classified as a hormone.

**Physiological effects of ethylene:**

1. **Ethylene Promotes the Ripening of Some Fruits:** Ethylene has long been recognized as the hormone that accelerates the ripening of edible fruits. Exposure of such fruits to ethylene hastens the processes associated with ripening, and a dramatic increase in ethylene production accompanies the initiation of ripening. However, surveys of a wide range of fruits have shown that not all of them respond to ethylene.
2. **Ethylene Induces Lateral Cell Expansion:** At concentrations above 0.1 μL L–1, ethylene changes the growth pattern of seedlings by reducing the rate of elongation and increasing lateral expansion, leading to swelling of the region below the hook. These effects of ethylene are common to growing shoots of most dicots, forming part of the **triple response**. In *Arabidopsis*, the triple response consists of inhibition and swelling of the hypocotyl, inhibition of root elongation, and exaggeration of the apical hook.
3. **Ethylene Breaks Seed and Bud Dormancy in Some Species:** Seeds that fail to germinate under normal conditions (water, oxygen, temperature suitable for growth) are said to be dormant. Ethylene has the ability to break dormancy and initiate germination in certain seeds, such as cereals. In addition to its effect on dormancy, ethylene increases the rate of seed germination of several species. In peanuts (*Arachis hypogaea*), ethylene production and seed germination are closely correlated. Ethylene can also break bud dormancy, and ethylene treatment is sometimes used to promote bud sprouting in potato and other tubers.
4. **Ethylene Promotes the Elongation Growth of Submerged Aquatic Species:** Although usually thought of as an inhibitor of stem elongation, ethylene is able to promote stem and petiole elongation in various submerged or partially submerged aquatic plants. These include the dicots *Ranunculus sceleratus*, *Nymphoides peltata*, and *Callitriche platycarpa*, and the fern *Regnellidium diphyllum*. Another agriculturally important example is the cereal deepwater rice.
5. **Ethylene Induces the Formation of Roots and Root Hairs:** Ethylene is capable of inducing adventitious root formation in leaves, stems, flower stems, and even other roots. Ethylene has also been shown to act as a positive regulator of root hair formation in several species.
6. **Ethylene Induces Flowering in the Pineapple Family:** Although ethylene inhibits flowering in many species, it induces flowering in pineapple and its relatives, and it is used commercially in pineapple for synchronization of fruit set. Flowering of other species, such as mango, is also initiated by ethylene. On plants that have separate male and female flowers (monoecious species), ethylene may change the sex of developing flowers (see Chapter 24). The promotion of female flower formation in cucumber is one example of this effect.
7. **Commercial uses of ethylene**: Ethephon is sprayed in aqueous solution and is readily absorbed and transported within the plant. It releases ethylene slowly by a chemical reaction, allowing the hormone to exert its effects: Ethephon hastens fruit ripening of apple and tomato and degreening of citrus, synchronizes flowering and fruit set in pineapple, and accelerates abscission of flowers and fruits. It can be used to induce fruit thinning or fruit drop in cotton, cherry, and walnut. It is also used to promote female sex expression in cucumber, to prevent self-pollination and increase yield, and to inhibit terminal growth of some plants in order to promote lateral growth and compact flowering stems.

**ABSCISSIC ACID**

The extent and timing of plant growth are controlled by the coordinated actions of positive and negative regulators. Some of the most obvious examples of regulated nongrowth are seed and bud dormancy, adaptive features that delay growth until environmental conditions are favorable. For many years, plant physiologists suspected that the phenomena of seed and bud dormancy were caused by inhibitory compounds, and they attempted to extract and isolate such compounds from a variety of plant tissues, especially dormant buds.

Early experiments used paper chromatography for the separation of plant extracts, as well as bioassays based on oat coleoptile growth. These early experiments led to the identification of a group of growth-inhibiting compounds, including a substance known as *dormin* purified from sycamore leaves collected in early autumn, when the trees were entering dormancy. Upon discovery that dormin was chemically identical to a substance that promotes the abscission of cotton fruits, *abscisin II*, the compound was renamed abscisic acid (ABA), to reflect its supposed involvement in the abscission process.

**PHYSIOLOGICAL EFFECTS OF ABA**

Abscisic acid plays primary regulatory roles in the initiation and maintenance of seed and bud dormancy and in the plant’s response to stress, particularly water stress. In addition, ABA influences many other aspects of plant development by interacting, usually as an antagonist, with auxin, cytokinin, gibberellin, ethylene, and brassinosteroids. In this section we will explore the diverse physiological effects of ABA, beginning with its role in seed development.

1. ABA Levels in Seeds Peak during Embryogenesis
2. ABA Promotes Desiccation Tolerance in the Embryo
3. ABA Promotes the Accumulation of Seed Storage Protein during Embryogenesis
4. ABA Inhibits Precocious Germination and Vivipary
5. ABA Accumulates in Dormant Buds
6. ABA Inhibits GA-Induced Enzyme Production
7. ABA Closes Stomata in Response to Water Stress
8. ABA Promotes Root Growth and Inhibits Shoot Growth at Low Water Potentials

**BRASSINOSTEROIDS**

**Brassinosteroids** (BRs) are a class of polyhydroxysteroids that have been recognized as a sixth class of [plant hormones](https://en.wikipedia.org/wiki/Plant_hormones). These were first explored nearly 40 years ago, when Mitchell et al. reported promotion in stem elongation and cell division by the treatment of organic extracts of rapeseed (*[Brassica napus](https://en.wikipedia.org/wiki/Brassica_napus" \o "Brassica napus)*) pollen. [Brassinolide](https://en.wikipedia.org/wiki/Brassinolide" \o "Brassinolide) was the first isolated brassinosteroid in 1979, when pollen from *[Brassica napus](https://en.wikipedia.org/wiki/Brassica_napus" \o "Brassica napus)* was shown to promote stem elongation and cell divisions, and the biologically active molecule was isolated. The yield of brassinosteroids from 230 kg of *Brassica napus* pollen was only 10 mg. Since their discovery, over 70 BR compounds have been isolated from plants.

The BR is biosynthesised from [campesterol](https://en.wikipedia.org/wiki/Campesterol" \o "Campesterol). The biosynthetic pathway was elucidated by Japanese researchers and later shown to be correct through the analysis of BR biosynthesis mutants in [*Arabidopsis thaliana*](https://en.wikipedia.org/wiki/Arabidopsis_thaliana), tomatoes, and peas. The sites for BR synthesis in plants have not been experimentally demonstrated. One well-supported hypothesis is that all tissues produce BRs, since BR biosynthetic and signal transduction genes are expressed in a wide range of plant organs, and short distance activity of the hormones also supports this.[[5]](https://en.wikipedia.org/wiki/Brassinosteroid#cite_note-Clouse-5)[[6]](https://en.wikipedia.org/wiki/Brassinosteroid#cite_note-6) Experiments have shown that long distance transport is possible and that flow is in an [acropetal](https://en.wikipedia.org/w/index.php?title=Acropetal&action=edit&redlink=1" \o "Acropetal (page does not exist)) direction, but it is not known if this movement is biologically relevant. Brassinosteroids are recognized at the cell membrane, although they are membrane-soluble.

**Physiological roles**:

BRs have been shown to be involved in numerous plant processes:

* Promotion of cell expansion and cell elongation; works with [auxin](https://en.wikipedia.org/wiki/Auxin" \o "Auxin) to do so.
* It has an unclear role in cell division and cell wall regeneration.
* Promotion of [vascular](https://en.wikipedia.org/wiki/Vascular_bundle) differentiation; BR [signal transduction](https://en.wikipedia.org/wiki/Signal_transduction) has been studied during vascular differentiation.
* Is necessary for pollen elongation for pollen tube formation.
* Acceleration of [senescence](https://en.wikipedia.org/wiki/Senescence) in dying [tissue](https://en.wikipedia.org/wiki/Tissue_(biology)) [cultured cells](https://en.wikipedia.org/wiki/Cell_culture); delayed senescence in BR mutants supports that this action may be biologically relevant.
* Can provide some protection to plants during chilling and drought stress.

Extract from the plant *Lychnis viscaria* contains a relatively high amount of Brassinosteroids. *[Lychnis viscaria](https://en.wikipedia.org/wiki/Lychnis_viscaria" \o "Lychnis viscaria)* increases the disease resistance of surrounding plants.

[24-Epibrassinolide](https://en.wikipedia.org/w/index.php?title=24-Epibrassinolide&action=edit&redlink=1) (EBL), a brassinosteroid isolated from *Aegle marmelos* Correa (Rutaceae), was further evaluated for the antigenotoxicity against maleic hydrazide (MH)-induced genotoxicity in *Allium cepa* chromosomal aberration assay. It was shown that the percentage of chromosomal aberrations induced by maleic hydrazide (0.01%) declined significantly with 24-epibrassinolide treatment.

BRs have been reported to counteract both abiotic and biotic stress in plants.Application of brassinosteroids to cucumbers was demonstrated to increase the [metabolism](https://en.wikipedia.org/wiki/Metabolism) and removal of pesticides, which could be beneficial for reducing the human ingestion of residual pesticides from non-organically grown vegetables.In all Type of brassinosteroids 28-homoBL is the most effective type of brassinosteroids. Brassinosteroids increased tolerance to high temperature in *Brassica juncea* L. The ability of 28-homobrassinolide to confer resistance to stress in *Brassica juncea* L. has also established. Application of 24-epiBL have any protective role on shoot, root length, soluble protein, proline content and peroxidases along with proline content PPO and IAA in seedlings of *B. juncea* L. under seasonal stress.

**Agricultural uses:**

BR might reveal to have a prominent interest in the role of horticultural crops. Based on extensive research BR has the ability to improve the quantity and quality of horticultural crops and protect plants against many stresses that can be present in the local environment.With the many advances in technology dealing with the synthesis of more stable synthetic analogues and the genetic manipulation of cellular BR activity, using BR in the production of horticultural crops has become a more practical and hopeful strategy for improving crop yields and success.

BR could also help bridge the gap of the consumers' health concerns and the producers need for growth. A major benefit of using BR is that it does not interfere with the environment because they act in natural doses in a natural way.Since it is a “plant strengthening substance” and it is natural, BR application would be more favorable than pesticides and does not contribute to the co-evolution of pests.

**JASMONIC ACID**

**Jasmonic acid** (JA) is derived from the fatty acid [linolenic acid](https://en.wikipedia.org/wiki/%CE%91-Linolenic_acid" \o "Α-Linolenic acid). It is a member of the [jasmonate](https://en.wikipedia.org/wiki/Jasmonate" \o "Jasmonate) class of [plant hormones](https://en.wikipedia.org/wiki/Plant_hormone). It is biosynthesized from linolenic acid by the [octadecanoid pathway](https://en.wikipedia.org/wiki/Octadecanoid_pathway" \o "Octadecanoid pathway).

The major function of JA and its various metabolites is regulating plant responses to abiotic and biotic stresses as well as plant growth and development. Regulated plant growth and development processes include growth inhibition, [senescence](https://en.wikipedia.org/wiki/Senescence), [tendril](https://en.wikipedia.org/wiki/Tendril" \o "Tendril)coiling, flower development and leaf abscission. JA is also responsible for [tuber](https://en.wikipedia.org/wiki/Tuber) formation in potatoes and yams. It has an important role in response to [wounding](https://en.wikipedia.org/wiki/Wounding) of plants and [systemic acquired resistance](https://en.wikipedia.org/wiki/Systemic_acquired_resistance). The Dgl gene is responsible for maintaining levels of JA during usual conditions in *[Zea mays](https://en.wikipedia.org/wiki/Zea_mays" \o "Zea mays)* as well as the preliminary release of jasmonic acid shortly after being fed upon. When plants are attacked by insects, they respond by releasing JA, which activates the expression of [protease inhibitors](https://en.wikipedia.org/wiki/Protease_inhibitor_(biology)), among many other anti-herbivore defense compounds. These protease inhibitors prevent proteolytic activity of the insects' digestive proteases or "salivary proteins", thereby stopping them from acquiring the needed nitrogen in the [protein](https://en.wikipedia.org/wiki/Protein) for their own growth.

Jasmonic acid is also converted to a variety of derivatives including [esters](https://en.wikipedia.org/wiki/Ester) such as [methyl jasmonate](https://en.wikipedia.org/wiki/Methyl_jasmonate); it may also be conjugated to amino acids.

This chemical may have a role in pest control, according to an October 2008 BBC News report. Researchers at the UK's Lancaster University have signed a licensing deal with an American company to market jasmonic acid as a seed treatment. JA seed treatment stimulates the natural anti-pest defenses of the plants that germinate from the treated seeds, without harming plant growth as happens when jasmonates are sprayed onto plants that have already started growing. However, due to its antagonistic relationship with [salicylic acid](https://en.wikipedia.org/wiki/Salicylic_acid) (an important chemical signal in pathogen defense) in some plant species, it may result in an increased susceptibility to viral agents and other pathogens. In *[Zea mays](https://en.wikipedia.org/wiki/Zea_mays" \o "Zea mays)*, [salicylic acid](https://en.wikipedia.org/wiki/Salicylic_acid) and JA are mediated by [NPR1](https://en.wikipedia.org/wiki/NPR1) (nonexpressor of pathogenesis-related genes1), which is essential in preventing herbivores from exploiting this antagonistic system.[[8]](https://en.wikipedia.org/wiki/Jasmonic_acid#cite_note-Ballar.C3.A92011-8) An [Armyworm](https://en.wikipedia.org/wiki/Fall_armyworm" \o "Fall armyworm)like the [Spodoptera](https://en.wikipedia.org/wiki/Spodoptera" \o "Spodoptera) spp., through unknown mechanisms, are able to increase the activity of the [salicylic acid](https://en.wikipedia.org/wiki/Salicylic_acid) pathway in maize, resulting in the depression of JA synthesis, but thanks to [NPR1](https://en.wikipedia.org/wiki/NPR1) mediation, JA levels aren't decreased by a significant amount.

JA FUNCTION AND RESPONSIVE GENES

Jasmonate modulates the expression of numerous genes and influences specific aspects of plant growth, development, and responses to abiotic and biotic stresses. Many of these responses were identified by application of jasmonate to plants, sometimes at nonphysiological levels. Interactions between JA and other plant growth regulators make assignment of physiological roles for JA even more complicated. In the section below, proposed actions of JA in plants are related to the level of JA in plant tissues, the activity of JA responsive genes, and insights provided by JA insensitive and JA deficient plants.

*Seed Germination and Growth:* JA and MeJA inhibit the germination of nondormant seeds and stimulate the germination of dormant seeds.

*Vegetative Sinks and Storage Proteins*

*Photosynthesis, Senescence, and Abiotic Stress:* Application of JA to leaves decreases expression of nuclear and chloroplast genes involved in photosynthesis. JA treatments also cause a loss of chlorophyll from leaves or cell cultures. Jasmonate’s ability to cause chlorosis led to the suggestion that this compound plays a role in plant senescence.

*Flower and Fruit Development:* Jasmonate might be expected to play a role in formation of flowers, fruit, and seed because of the relatively high levels of this compound in developing plant reproductive tissues. The presence of jasmonate and related volatile fatty acid derivatives may be involved in insect attraction related to pollen dispersal. Other aspects of flower, fruit, and seed development that can be modulated by jasmonate include fruit ripening, fruit carotenoid composition, and expression of genes encoding seed and vegetative storage proteins. Jasmonate-stimulated tomato and apple fruit ripening most likely occurs through activation of EFE and production of ethylene.

*Insect and Disease Resistance:* JA plays an important role in plant insect and disease resistance. Several lines of evidence support this conclusion. First, JA accumulates in wounded plants and in plants or cell cultures treated with elicitors of pathogen defense. Second, JA activates genes encoding protease inhibitors that help protect plants from insect damage. JA also activates expression of genes encoding antifungal proteins such as thionin, osmotin, PDF, and the ribosome-inactivating protein RIP60. JA modulates expression of cell wall proteins such as PRP that may be involved in synthesis of barriers to infection. Furthermore, JA induces genes involved in phytoalexin biosynthesis (*Chs, Pal,* HMGR) and phenolics (polyphenol oxidase) that are involved in plant defense. The oxylipin pathway that leads to JA is also the source of other volatile aldehydes and alcohols that function in plant defense and wound healing. For example, the C6-aldehyde 2-hexenal completely inhibited growth of *Pseudomonas syringae* and *E. coli*, and C6-aldehydes and alcohols reduced aphid fecundity. These compounds are synthesized from 13-hydroperoxylinolenic acid via the action of hydroperoxy lyase. Jasmonate, wounding, and elicitors increase the expression of lipoxygenase and stimulate hydroperoxy lyase activity. This response enhances the ability of plants to produce the six carbon compounds that contribute to plant protection.