

What is a Plant Hormone?

Material taken from many sources, but in particular: Botany online: Plant Hormones (Phytohormones) by Peter V. Sengbusch (www.biologie.uni-hamburg.de/b-online/e31/31.htm); plant-hormones.info, sponsored by Mendipweb (www.plant-hormones.info)

I. Concepts From the Animal Kingdom

In animals, hormones are chemicals produced in and secreted by cells that control the activity of other cells at distant parts of the organism (usually, see below). They regulate metabolism, integrate different functions within the organism, and control growth. The activities of the hormones are themselves controlled by the central nervous system, which coordinates all functions within the organism.

Classically, hormones are produced by glands, and reach the tissue or cells they affect via the blood stream. They are then recognized and cause a specific reaction, so they are also called effectors. Hormone induced reactions can be reversible or irreversible. For example, insulin functions in adjusting blood sugar levels, i.e. cellular metabolism is adjusted to the prevailing need of the organism. On the other hand, insufficient amounts of growth hormone lead irreversibly to dwarfism.

Some hormones are targeted to specific cells that have the proper **receptor**. Hormone receptors are usually proteins on the cell surface that change their conformation and activity according to their binding state. When a receptor binds a hormone, a signal cascade is elicited within the cell that controls the cell's metabolism. Other hormones enter the cell where they are recognized by an intracellular receptor and transported into the nucleus. There they selectively control the expression of a group of genes.

The classical definition of a hormone involved the separation between place of synthesis and target organ. Now it is known that some hormones act at their place of synthesis. Neurohormones, for example, are both produced by neurons and affect neurons.

II. Plant Hormones

It is difficult to transfer the concept of hormones as defined in animals to plants. First, although plants have phloem and xylem, they do not have glands or a circulatory system as such; also plants do not have the equivalent of a central nervous system that integrates and co-ordinates all physiological activities.

However, plants do have regulated growth, plainly determined steps of differentiation, specialized cell types, and communication between cells. And, it has been found that

compounds classically termed **plant hormones** play an integral role in controlling the growth and development of plants.

A plant hormone can be defined as a small organic molecule that elicits a physiological response at very low concentrations (e.g., <1mM and often <1uM). As in animals, the definition classically includes synthesis at one site and transport to and action at a different site, but also as in animals, plant hormones are not necessarily translocated. For example, ethylene may bring about changes in the same tissue or even the same cell in which it is synthesized.

It is now clear that what we refer to as plant hormones differ from mammalian hormones in a number of ways. Animal hormones are generally compounds like proteins, that have a high information content, or steroids, while plant hormones are low-molecular-weight chemicals that only provide an on/off signal, although they do stimulate a cascade of events in the cell leading to a response. Therefore, although the term plant hormone or **phytohormone** has been used for many years, it is an inaccurate term and it is better to refer to these substances as **plant growth regulators (PGRs)** (some say plant growth substances), which have the following characteristics:

- Synthesized by plants and broadly distributed within the plant kingdom.
- Show specific biological activity at very low concentrations.
- Display multiple functions in plants.
- Play a fundamental role in regulating physiological phenomena in vivo in a dose-dependent manner, which may change due to changes in the sensitivity of the plant tissue during development or due to environment.
- Unlike mammalian hormones, different PGRs may interact, either synergistically or antagonistically, to produce a particular effect.

It has been well documented that extremely low concentrations of PGRs have the ability to regulate many aspects of plant growth and development from seed germination through senescence and death of the plant. A large and growing body of research indicates that PGRs enter cells and regulate intracellular processes.

Unlike animal hormones, which tend to be very specific in their actions, PGRs generally display a very broad and complex action spectrum. In some cases, effects are observed immediately after the application of a PGR, while in other cases, it may take much longer to observe a change. It is presumed that the activities of existing enzymes or membrane properties are modified in fast reactions, while in the slower reactions it is likely that gene expression (transcription or translation) is affected.

In plants, five substances have been classically defined as plant hormones for many years. However, some other substances are being studied that are currently considered to be PGRs, or that are likely PGRs.

The five classical hormones:

- Auxin
- Cytokinin
- Gibberelin
- Abscisic acid
- Ethylene

These are all small molecules ranging from 28 Da (ethylene) to 346 Da (GA), all synthesized by the plant, and all active at 10^{-6} to 10^{-8} M. They are distributed within tissues from cell to cell, as in the case of auxin, *via* vascular bundles (as in the case of cytokinin), or via the intercellular space (ethylene).

Additional substances gaining recognition as PGRs:

- Polyamines
- Jasmonates
- Salicylic acid
- Brassinosteroids
- Others

What a PGR is not:

- Inorganic compounds such as Ca^{2+} and K^{+} even though these compounds cause physiological responses and can be moved throughout the plant, because they are not synthesized by the plant.
- Sucrose is not a hormone even though it is synthesized, translocated, and stimulates a response (growth) because it is only effective at high concentrations. This is also true for other sugars, amino acids, organic acids, and other metabolites that are usually present in concentrations ranging from >1 mM up to 50 mM or higher.
- Technically, synthetic growth regulatory substances such as 2,4-D even though its structure is similar to that of auxin.

III. How PGRs Have Been Identified and Characterized

The presence of PGRs in plants was first detected or inferred by observed plant behavior under various conditions. However, much of what was known about PGRs until recent years was largely determined empirically because they were very difficult to study.

Why?

- Compartmentalization of PGRs in cells or organelles.

- PGR levels are by definition very low. This has historically made endogenous detection difficult, although detection methods have vastly improved over the past 15 years due to improved instrumentation, e.g. GC/MS-detection, use of immunological methods.
- The site of biosynthesis and the site of action of a plant growth regulator may be different. Because the site of action may be in specialized cells, located physically within a variety of other cells and tissues, it may be difficult to correlate levels of PGRs with particular physiological responses.
- A potential PGR may have an effect when applied exogenously, however, this does not mean that the compound normally acts to elicit the same effect in the plant.
- A PGR may be applied but may not penetrate or be transported like the endogenous PGR, so it does not get to the site of action.
- High concentrations of PGRs may cause non-physiological effects.
- Different tissues, cells, respond differently to the same PGR.
- Different processes are sensitive to different levels of PGR, even in the same cell.
- Changes in environment or development alter responses to a PGR.

Thus, the problems of working with biosynthetic pathways for hormones, which represent a minor portion of carbon flux throughout plant, are distinct. Reactions involving intermediates must be detected using radioisotopes or immunological techniques to get sufficient sensitivity.

When hormones control gene expression, it is likely that gene regulation is affected by certain enzymes after initial hormone binding. Genes may be altered by secondary and tertiary messengers of a cellular cascade as well. Hormones may indirectly control gene expression through these enzymes and messengers by acting during transcription, during mRNA processing, on mRNA stability, at translation, and/or post-translationally. A single aspect of growth and development can be influenced by several hormones: a particular response probably results from a changing ratio of hormones rather than from the presence or absence of an individual hormone. Further, physiological responses elicited by hormones are strongly influenced by nonhormonal factors like light of a certain wave length, temperature, etc. PGR actions may be synergistic or antagonistic. However, it should be emphasized that there is still much to learn about PGRs and their actions.

IV. Auxins

Auxin was the first plant hormone to be discovered.

In early plant physiological studies, some by Charles and Francis Darwin (1880), it was found that a growing grass coleoptile that was illuminated on one side grew towards the source of illumination. Anatomical studies showed that this was due to an elongation of the cells on the side away from the light. This phenomenon was termed "phototropism". The phototropic reaction does not happen if the coleoptile's tip is removed, though it can be induced again by replacement of the tip. This indicates the existence of a substance that moves from tip to bottom (in a basipetal direction) and that causes the elongation.

In 1913 Salkowski discovered IAA in fermentation media. It would be almost 50 years before the same compound was identified in plant tissue. The Danish botanist P. Boysen-Jensen in 1913 inserted a mica sheet into the shielded side of a coleoptile, thus separating the coleoptile's tip from the tissue below. This interrupted the phototropic reaction. The bending occurred when the mica sheet was inserted into the illuminated side or along the coleoptile's vertical axis.

In 1926, a graduate student from Holland by the name of Fritz Went published a report describing how he isolated a plant growth substance by placing agar blocks under coleoptile tips for a period of time then removing them and placing them on decapitated *Avena* stems (Went, 1926). After placement of the agar, the stems resumed growth (see below). In 1928, Went developed a method of quantifying this plant growth substance. His results suggested that the curvatures of stems were proportional to the amount of growth substance in the agar (Went, 1928). This test was called the *avena* curvature test.

Went called the effector **auxin**, derived from the Greek word *auxein*, which means to grow. We now know this hormone as indole-3-acetic acid (IAA). Compounds are generally characterized as auxins if they are synthesized by the plant, they induce cell elongation in stems, and they otherwise resemble IAA in physiological activity. Auxins typically affect other processes in addition to elongation of stem cells but this characteristic is considered integral to all auxins and thus helps "define" the hormone. IAA is chemically similar to the amino acid tryptophan, which is generally accepted to be the molecule from which IAA is derived, although there are apparent exceptions.

It is now known that auxin is a collective name for several similar compounds. To be active, an auxin compound has to have three structural properties:

- The molecule has to contain a ring system with at least one double bond.
- The double bond has to be adjacent to a side chain.
- A carboxyl group that is separated by one or two C-atoms is required.

These conditions led to several clues about the structure of the binding site(s); the receptor must have two separate contact sites.

Transport of auxin within the plant is an active and polar process. There are at least 6 pieces of evidence for this:

- Transport always occurs in a polar direction, e.g. unidirectionally down the plant stem through parenchyma cells (apparently auxin does not move through vascular tissue).
- The transport velocity is higher than is expected from simple diffusion.
- Transport can occur against a concentration gradient.
- Transport is energy-consuming and is drastically reduced in the absence of oxygen.
- The transport system is substrate-specific. It transports certain auxin molecules like IAA or naphthylacetic acid faster than 2,4-dichlorophenoxy acetic acid, for example.
- The transport system can be blocked by specific inhibitors.

Auxins are believed to affect several different primary processes of the cell, i.e. to:

- Increase the rate of transcription (RNA synthesis).
- Control the activity of certain enzymes.
- Influence ion pumps within the membrane.

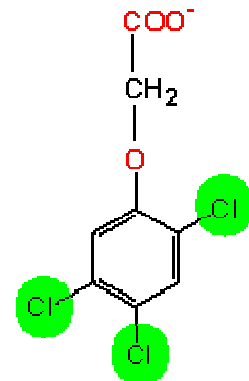
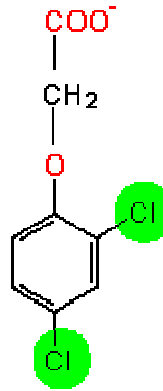
Auxin is produced primarily in apical and root meristems, young leaves, and seeds in developing fruits.

Auxin

- Stimulates cell elongation.
- The auxin supply from the apical bud suppresses growth of lateral buds. **Apical dominance** is the inhibiting influence of the shoot apex on the growth of axillary buds. Removal of the apical bud results in growth of the axillary buds. Replacing the apical bud with a lanolin paste containing IAA restores the apical dominance. The mechanism involves another hormone - ethylene. Auxin (IAA) causes lateral buds to make ethylene, which inhibits growth of the lateral buds.
- Differentiation of vascular tissue (xylem and phloem) is stimulated by IAA.
- Auxin stimulates root initiation on stem cuttings and lateral root development in tissue culture (adventitious rooting).
- Auxin mediates the tropistic response of bending in response to gravity and light (this is how auxin was first discovered).
- Auxin has various effects on leaf and fruit abscission, fruit set, development, and ripening, and flowering, depending on the circumstances.

Many synthetic auxins have been developed that are used for a variety of purposes, e.g. indole-3-butyric acid (IBA)(root initiation) and naphthaleneacetic acid (NAA)(apple fruit thinning). 2,4 dichloro-phenoxy acetic acid (2,4-D) and 2,4,5-trichlorophenoxy acetic acid (2,4,5-T) proved to be herbicides selectively affecting dicots.

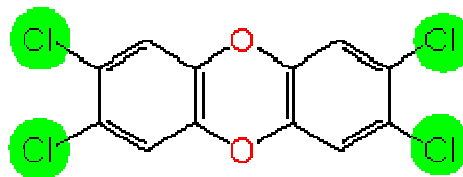
herbicides
 2,4 - dichlorophenoxy-acetic acid
 (2,4 - D)
 2,4,5 - trichlorophenoxy-acetic acid
 (2,4,5 - T)



2,4-D increases the rate of DNA, RNA and protein synthesis, so that susceptible plants literally grow themselves to death. Treated plants display abnormal growth of shoots, breakdown of chlorophyll (bleaching), and dying of roots. 2,4,5-T is especially toxic to perennial woody plants and is therefore most often used in forestry. Its is less easily degraded than 2,4-D. IAA, in contrast, is very easily degraded and is consequently of no use as a herbicide. When these compounds are used in tissue culture, they are used in very small amounts.

Although it has not been clearly shown that these chemicals cause injury to humans or animals, there is no doubt that a by-product of the synthesis of 2,4,5-T, tetrachlorodibenzoparadioxin (TCDD) (also called dioxin), is highly toxic. The Agent Orange used in the Vietnam war as a defoliation agent was about 50% 2,4-D, but it was the dioxin in the agent that was subsequently shown to cause the illnesses of individuals exposed.

dioxin



Auxins are frequently used in tissue culture, for a variety of purposes. We will cover specifics when we discuss the various tissue culture procedures.

V. Cytokinins

Researchers tried for many years to culture plant tissue on artificial nutrient medium. The first approaches go back to the Austrian plant anatomist G. Haberlandt (1854-1945, professor at Graz, later at Berlin). At first, determining the composition of a suitable nutrient medium posed large problems. The Dutch plant physiologist van Overbeek discovered in 1941 that plant embryos grow faster when given coconut milk (the endosperm of the coconut seed). Then, Skoog and Miller, while working with tissue culture methods for plants, used coconut milk in media formulations. While trying to determine what substance in the milk was necessary for growth, they added various chemicals they had available in the lab to media. Herring-sperm DNA appeared to stimulate growth when they first tried it, but on a second attempt, it produced no effect. They discovered a breakdown product similar to adenine in the first bottle, which was responsible for the stimulation.

Kinetin was the first cytokinin discovered and was so named because of its ability to promote cytokinesis (cell division). However, kinetin is not made in plants, and is therefore considered a synthetic PGR. The most common form of naturally occurring cytokinin in plants is zeatin, which was isolated from maize (*Zea mays*) in 1961 (Miller, Letham).

Besides increasing the rate of DNA replication, cytokinins also increase the general rate of RNA and protein synthesis (binds to ribosomes, regulates protein synthesis). Cytokinins are made via the same pathway that leads to gibberellin production: the mevalonate pathway. These compounds have a structure resembling that of adenine. Like auxins, cytokinins can glycosylated or bound to an amino acid or a protein, thereby being at least temporarily inactive. Cytokinins have been found in almost all higher plants as well as mosses, fungi (Witch's broom), and bacteria (*Agrobacterium*). Today there are more than 200 natural and synthetic cytokinins that have been identified.

Effects of cytokinins

- Stimulate cell division (cytokinesis).
- Stimulate morphogenesis (shoot initiation/bud formation) in tissue culture.
- Stimulate the growth of lateral (or adventitious) buds - release of apical dominance.
- Stimulate leaf expansion resulting from cell enlargement.
- May enhance stomatal opening in some species.

- Promotes the conversion of etioplasts into chloroplasts via stimulation of chlorophyll synthesis.
- Stimulate the dark-germination of light-dependent seeds.
- Delays senescence.
- Promotes some stages of root development.

Cytokinins are produced mainly in root meristems, young leaves, young fruits, and seeds. They enter the shoot organs via the xylem, translocated from the roots. Organs that are cut off from a continuous cytokinin supply like cut shoots age faster than those that are connected to their roots. The addition of kinetin can stop senescence, as can the development of adventitious roots and thus a new supply of cytokinins.

Thus, cytokinins like auxins have many modes of action. The variety of hormonally induced phenomena points to the existence of different receptors.

Commercial uses: applied as Kinetin, BA, or zeatin conjugates

- axillary bud growth in orchids, day lilies
- antioxidant (browning preventer) in cut salads
- mixed with GA as a fruit size simulator

VI. Gibberellins

Unlike auxins, which are classified on the basis of function, gibberellins are classified on the basis of structure as well as function. Gibberellins are diterpenes synthesized from acetyl CoA via the mevalonic acid pathway. They all have either 19 or 20 carbon units grouped into either four or five ring systems. All gibberellins are acidic compounds and are therefore also called gibberellic acids (GA) with a different subscript to distinguish between them. GA₃ has historically been called gibberellic acid but the term is also often used in describing all gibberellins.

In 1926, the Japanese scientist E. Kurosawa was studying a rice disease that is known as 'foolish seedling'. The affected plants grow extremely fast, look spindly and pale, and break off easily. Kurosawa determined that the reason for this abnormal growth was a substance that is secreted by a parasitic fungus (*Fusarium moniliforme* = *Gibberella fujikuroi*). The compound was termed gibberellin.

During the thirties was gibberellin isolated and crystallized by Japanese scientists from Tokyo (Yabuta and Sumiki), and then was almost forgotten in the following years. In 1956, C. A. West and B. O. Phinney isolated gibberellins from *Phaseolus vulgaris* and other plants, showing that these compounds are wide-spread in the plant kingdom.

Today are more than 110 (125?) different gibberellins known (GA_1 , GA_2 , ..., GA_3 , GA_4 , ..., GA_{110}) that differ little chemically but very much in their biological effects.

Roughly 30 percent of all known gibberellins are biologically active. All higher plants contain presumably at least one, but usually several active and inactive gibberellins that exist in different concentrations depending on the respective tissue. They have also been isolated from lower plants such as mosses and algae, at least two fungal species and most recently from two bacterial species.

Effects of Gibberellic Acid

Young, growing meristematic tissue, embryos, apical root cells, young fruits, as well as unripe or germinating seeds are all rich in gibberellins.

- Stimulates stem elongation by stimulating cell division and elongation. GA controls internode elongation in the mature regions of plants. Dwarf plants do not make enough active forms of GA.
- Flowering in biennial plants is controlled by GA. Biennials grow one year as a rosette and after the winter, they bolt (rapid expansion of internodes and formation of flowers).
- Breaks seed dormancy in some plants that require stratification or light to induce germination.
- Stimulates α -amylase production in germinating cereal grains for mobilization of seed reserves.
- Juvenility refers to the different stages that plants may exist in. GA may help determine whether a particular plant part is juvenile or adult.
- Stimulates germination of pollen and growth of pollen tubes.
- Induces maleness in dioecious flowers (sex expression).
- Can cause parthenocarpic (seedless) fruit development or increase the size of seedless fruit (grapes).
- Can delay senescence in leaves and citrus fruits.
- May be involved in phytochrome responses.

Certain commercial chemicals that are used to stunt growth do so in part because they block the synthesis of gibberellins. Some of these chemicals are Phosphon D, Amo-1618, Cycocel (CCC), ancymidol, and paclobutrazol.

VII. Abscisic Acid

The phytohormone abscisic acid (ABA) plays regulatory roles in a host of physiological processes in all higher as well as lower plants. Abscisic acid mediates stress tolerance responses in higher plants, is a key signal compound that regulates stomatal aperture and, in concert with other plant signaling compounds, is implicated in mediating responses to pathogens and wounding. It has therefore been called the stress hormone.

In 1963, abscisic acid was first identified and characterized by Frederick Addicott and his associates. They were studying compounds responsible for the abscission of fruits (cotton). Two compounds were isolated and called abscisin I and abscisin II. Abscisin II is presently called abscisic acid (ABA)(Addicot, 1963). Two other groups at about the same time discovered the same compound. One group headed by Philip Wareing was studying bud dormancy in woody plants. The other group led by Van Steveninck was studying abscission of flowers and fruits from lupine. Plant physiologists agreed to call the compound abscisic acid.

ABA is a sesquiterpenoid (15-carbon) compound. It is believed that biosynthesis occurs indirectly through the production of carotenoids in plastids. Carotenoids are pigments produced by plastids that have 40 carbons. Biosynthesis of ABA is believed to occur as follows: The 40 carbon carotenoid violaxanthin is isomerized and then split via an isomerase reaction followed by an oxidation reaction. One molecule of xanthonin is produced from one molecule of violaxanthin and it is uncertain what happens to the remaining biproduct. The one molecule of xanthonin produced is unstable and spontaneously changed to ABA aldehyde. Further oxidation results in ABA.

The transport of ABA can occur in both xylem and phloem tissues. It can also be translocated through parenchyma cells. The movement of abscisic acid in plants does not exhibit polarity like that of auxins. ABA is capable of moving both up and down the stem.

Effects of ABA

- Involved in abscission of buds, leaves, petals, flowers, and fruits in many, if not all, instances, as well as in dehiscence of fruits.
- Production is accentuated by stresses such as water loss and freezing temperatures.
- Involved in bud dormancy
- Prolongs seed dormancy and delays germination (vivipary).
- Inhibits elongation.
- Promotes stomatal closure.
- ABA is implicated in the control of elongation, lateral root development, and geotropism, as well as in water uptake and ion transport by roots.

- ABA coming from the plastids promotes the metabolism of ripening.
- Promotes senescence.
- Can reverse the effects of growth stimulating hormones.

VIII. Ethylene

Unlike the rest of the plant hormone compounds, ethylene is a gas. Like abscisic acid, it is the only member of its class.

Ethylene has been used in practice since the ancient Egyptians, who would gas figs in order to stimulate ripening. The ancient Chinese would burn incense in closed rooms to enhance the ripening of pears. In 1864, leaks of gas from street lights were discovered to cause stunting of growth, twisting of plants, and abnormal thickening of stems (termed the triple response) In 1901, a Russian scientist named Dimitry Neljubow showed that the active component was ethylene. Ethylene is produced in all higher plants.

In higher plants, ethylene is produced from L-methionine. Methionine is activated by ATP to form S-adenosylmethionine through the catalytic activity of S-adenosylmethionine synthetase. The next step produces the non-protein amino acid 1-aminocyclopropane-1-carboxylic acid (ACC). It is catalyzed by ACC synthase with pyridoxal phosphate acting as a co-factor. Formation of ACC is the rate-limiting step in ethylene biosynthesis. ACC synthase is encoded by a medium-size multigene family. Various signals, which influence ethylene synthesis, result in increased expression of single members of the ACC synthase gene family. Production of ethylene from ACC is catalyzed by ACC oxidase. This reaction is oxygen-dependent. At anaerobic conditions ethylene formation is completely suppressed. Fe^{2+} is a co-factor and ascorbate a cosubstrate; CO_2 was shown to activate ACC oxidase. ACC oxidases are encoded by small gene families in plants.

The concentration of ethylene in a plant tissue is dependent on the rate of biosynthesis and on diffusion of the gas. Ethylene is neither actively transported nor degraded. Induction of ethylene synthesis by signals such as auxin or wounding usually occurs through activation of ACC synthase. ACC oxidase activity on the other hand is constitutively present in most vegetative plant tissues. In some cases, further induction of ACC oxidase by ethylene is observed.

Ethylene is produced in many plant tissues. In maturing fruits, ethylene synthesis is autocatalytically enhanced, i.e., ethylene induces its own biosynthesis. The self-enhancing synthesis and diffusion of the gaseous hormone throughout the fruit accelerate ripening and contribute to a synchronized ripening process.

Ethylene binds to a protein in the endoplasmic reticulum?

Ethylene action very often involves transcriptional activation. In recent years, much has been learned about the transduction pathway from ethylene perception to gene activation. Ethylene is bound by a receptor that is membrane-localized. The N-terminal domain of the receptor protein is responsible for binding of ethylene. The intracellular portion of the protein is a protein kinase which is activated upon binding of ethylene. Such receptor protein kinases are termed two-component-systems because they are generally composed of a sensor, in this case the ethylene binding site, and a response regulator. Two-component-receptors have first been characterized in bacteria, but are now also known in plants. The first two-component-receptor to be discovered in plants was the ethylene receptor ETR1 (ethylene resistant 1) from *Arabidopsis thaliana* L. Transduction of the ethylene signal is thought to be achieved through a series of phosphorylations that are carried out by a cascade of protein kinases similar to the MAP (mitogen activated protein kinase) kinase pathway and probably through other, as yet less well defined, steps. Finally, a transcription factor that is present in the cell is activated, leading to induction of one or more early gene(s). One such early gene is itself a transcriptional activator that induces late genes. These late-induced genes may encode enzymes that degrade the middle lamellae or the cell wall during fruit ripening and abscission. They may encode for proteins involved in pathogen defense. Or they may encode for proteins required for other ethylene responses.

Ethylene acts as a negative regulator of the signaling pathway. This means that the signal pathway is turned on in the absence of ethylene and is shut down when ethylene is present. Shutting down of the pathway induces an ethylene response. As a result of this negative regulation, mutations in the ethylene receptor are perceived as dominant gain-of-function mutations.

Components of the ethylene signal transduction pathway have been identified by a mutational approach with *Arabidopsis*. The initial steps in ethylene signal transduction are shared for all these responses. Cloning of these genes has started to reveal how ethylene is perceived in plants. ETR1 (along with ERS1, ETR2, ERS2, and EIN4) are all related to the two-component signaling proteins from bacteria. CTR1 is related to the Raf-like serine/threonine protein kinases from mammals. EIN2 is related to the Nramp family of metal transporters. EIN3, EIL1, EIL2, and ERF1 are transcription factors.

Effects of ethylene

- Production stimulated during ripening, flooding, stress, senescence, mechanical damage, infection.
- Entral regulator of cell death programs in plants (apoptosis).
- Stimulates the release of dormancy.
- Stimulates shoot and root growth and differentiation (triple response)
- Regulates ripening of climacteric fruits.

- May have a role in adventitious root formation.
- Stimulates leaf and fruit abscission.
- Flowering in most plants is inhibited by ethylene. Mangos, pineapples and some ornamentals are stimulated by ethylene.
- Induction of femaleness in dioecious flowers.
- Stimulates flower opening.
- Stimulates flower and leaf senescence.

Commercial Uses - Ethylene Application (applied as ethylene gas or ethephon or ethrel sprays)

- flower initiation (pineapples)
- stimulation of ripening (bananas, tomatoes)
- degreening of citrus
- abscission induction prior to mechanical harvesting (cherries)

Commercial Uses - Ethylene Inhibition (chemical removal or low atmosphere)

- long term CA apple storage
- cut flower maintenance (silver thiosulfate)
- hypobaric storage of many fruits, vegetables, flowers

Silver thiosulfate (0.02 M) is commonly used to block the action of ethylene in plant cell cultures, where it has been shown to increase due to wounding or the presence of auxins.

IX. Other Potential PGRs

A. Brassinosteroids

There are approximately 60 naturally occurring polyhydroxy steroids known as brassinosteroids (BRs). They are named after the first one identified, brassinolide, which was isolated from rape in 1979. They appear to be widely distributed in the plant kingdom.

Biological Effects of BRs

- Promote shoot elongation at low concentrations
- Strongly inhibit root growth and development
- Promote ethylene biosynthesis and epinasty
- Interfere with ecdysteroids (moulting hormones) in insects

- Have had contradictory effects in tissue culture. 24-Epibrassinolide has been shown to mimic culture conditioning factors and to be synergistic with these factors in promoting carrot cell growth. However, in transformed tobacco cells brassinosteroids in low concentrations significantly inhibited cell growth.
- Enhance xylem differentiation
- Decrease fruit abortion and drop
- Enhance resistance to chilling, disease, herbicide, and salt stress
- Promotion of germination
- Promote changes in plasmalemma energization and transport, assimilate uptake
- Increase RNA and DNA polymerase activities and synthesis of RNA, DNA, and protein

In the early 1980s USDA scientists showed that BR could increase yields of radishes, lettuce, beans, peppers and potatoes. However, subsequent results under field conditions were disappointing because inconsistent results were obtained. For this reason testing was phased out in the United States. More recently large-scale field trials in China and Japan over a six-year period have shown that 24-epibrassinolide, an alternative to brassinolide, increased the production of agronomic and horticultural crops (including wheat, corn, tobacco, watermelon, and cucumber). However, once again depending on cultural conditions, method of application, and other factors, the results sometimes were striking while other times they were marginal. Further improvements in the formulation, application method, timing, effects of environmental conditions, and other factors need to be investigated further in order to identify the reason for these variable results.

Brassinosteroids may be a new class of plant growth substances. They are widely distributed within the plant kingdom, they have an effect at extremely low concentrations, both in bioassays and whole plants, and they have a range of effects that are different from the other classes of plant substances. Finally, they can be applied to one part of the plant and transported to another location where, in very low amounts, they elicit a biological response.

B. Salicylic Acid

Salicylic acid has been known to be present in some plant tissues for quite some time, but has only recently been recognized as a potential PGR. Salicylic acid is synthesized from the amino acid phenylalanine.

SA has numerous effects including:

- Promotes flowering
- Stimulates thermogenesis in *Arum* flowers
- Stimulates plant pathogenesis protein production (systemic acquired resistance)
- May enhance longevity of flowers

- May inhibit ethylene biosynthesis
- May inhibit seed germination
- Blocks the wound response
- Reverses the effects of ABA

SA is thought by some to be a new class of plant growth regulator. It is a chemically characterized compound, ubiquitously found in the plant kingdom and has an effect on many physiological processes in plants at low concentrations. Further molecular studies on SA signal transduction should yield insights into the mechanism of action of this important regulatory compound.

C. Jasmonates

Jasmonates are represented by jasmonic acid and its methyl ester. They were first isolated from the jasmine plant in which the methyl ester is an important product in the perfume industry. Jasmonic acid is synthesized from linolenic acid, which is an important fatty acid.

Jasmonates have important effects in plants, including:

- Inhibition of many processes such as seedling longitudinal growth, root length growth, mycorrhizial fungi growth, tissue culture growth, embryogenesis, seed germination, pollen germination, flower bud formation, carotenoid biosynthesis, chlorophyll formation, rubisco biosynthesis, and photosynthetic activities
- Promotion of senescence, abscission, tuber formation, fruit ripening, pigment formation, tendril coiling, differentiation in plant tissue culture, adventitious root formation, breaking of seed dormancy, pollen germination, stomatal closure, microtubule disruption, chlorophyll degradation, respiration, ethylene biosynthesis, and protein synthesis
- They play an important role in plant defense by inducing proteinase synthesis (and in other ways?).

Jasmonic acid is considered by some to be a new class of plant growth regulator. It is a chemically characterized compound and has been identified in many plant species. It has physiological effects at very low concentrations and indirect evidence suggests that it is transported throughout the plant.

D. Polyamines

There is some controversy as to whether these compounds should be classified with PGRs. They are widespread in all cells and exert regulatory control over growth and development at very low levels. Polyamines have a wide range of effects on plants. They appear to be essential in growth and cell division.

E. Others

- dehydrodiconiferyl alcohol glycosides (cytokinin-like)
- chlorogenic acid (protects IAA from oxidation)
- flavonoids (inhibit auxin transport)
- various ethylene inhibitors
- various GA biosynthesis inhibitors