Plant hormones

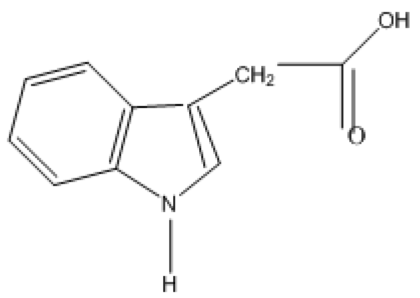
Plant hormones are physiological intercellular messengers which are needed to control the complete plant lifecycle, including growth, germination, rooting, fruit ripening, flowering, foliage and death. They are secreted in response to environmental factors such as light, temperature, abundance of nutrients, drought conditions, chemical or physical stress. Every aspect of plant growth and development is under hormonal control to some degree. A single hormone can regulate a diverse array of cellular and developmental processes, while at the same time multiple hormones often influence a single process. The application of growth factors allows synchronization of plant development to occur. For example, ripening bananas can be regulated by using desired atmospheric ethylene levels. Other applications include rooting of seedlings or the suppression of rooting with the simultaneous promotion of cell division.

Five major classes of plant hormones are known in plants. With progressing research, more active molecules are being found and new families of regulators are emerging, one example being polyamines such as putrescine or spermidine.

1. Auxin
2. Gibberellin
3. Cytokinin
4. Abscisic acid
5. Ethylene

1. Auxin:

The term auxin is derived from the Greek word ‘auxein’ which means to grow. They are a class of plant hormones which has a cardinal role in coordination of many growth and behavioral processes in the plant's life cycle essential for development of plant. Auxin is the first plant hormone to be identified. They have the ability to induce cell elongation in stems and resemble indoleacetic acid (the first auxin to be isolated) in physiological activity.



Auxin

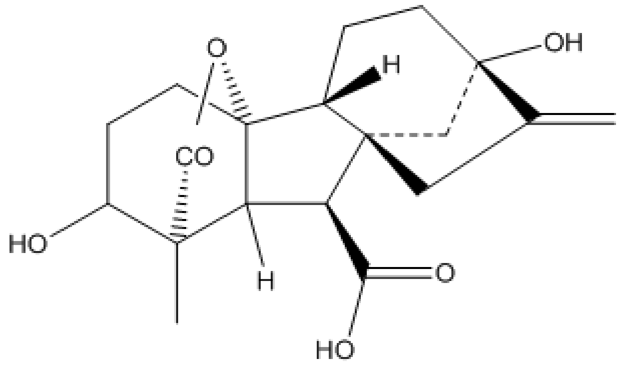
Indole-3-acetic acid (IAA) is the main auxin in most plants. IAA is transported is cell to cell.

Sites of biosynthesis of auxin: IAA is synthesized primarily in actively growing tissue in leaf primordia and young leaves, fruits, shoot apex and in developing seeds. It is made in the cytosol of cells.

Tryptophan-dependent Pathways for auxin synthesis: Tryptophan, one of the protein amino acids, is the precursor of auxin biosynthesis. The conversion of tryptophan to Indole Acetic Acid can occur by either transamination followed by a decarboxylation or decarboxylation followed by a transamination. Formation of IAA via an oxime (C=NOH) and nitrile (CN) is shown in Figure 3.

Auxin signaling: Auxin binds to a receptor with ubiquitin ligase activity. This stimulates ubiquitination and degradation of a specific transcriptional repressor further leading to transcription of auxin-induced genes

Functions of Auxin: Indole acetic acid regulates many responses: Cell elongation and wall relaxation and cell differentiation. It promotes differentiation of vascular tissue (i.e., xylem & phloem). IAA apparently stimulates the production of ethylene. IAA at more than 10^{-6} M concentration inhibits root elongation. However, very low concentration ($>10^{-8}$ M) favor root elongation. It stimulate root initiation both lateral roots and adventitious roots. Most plants do not initiate the production of flowers after auxin treatment except pineapple and its relatives belonging to Bromeliaceae. Once flowers are initiated, in many species, IAA promotes the formation of female flowers, especially in cucurbits (gourd family). Parthenocarpic fruit development is regulated by auxins. The apical meristem (apex) controls or dominates the development of the lateral buds. Apical dominance also occurs in roots. Auxin mediates the tropistic (bending) response of shoots and roots to gravity and light. It delays leaf senescence. Auxin may inhibit or promote (via ethylene) leaf and fruit abscission.



Gibberlin:

Gibberellins (GAs) are a group of diterpenoid acids that function as plant growth regulators inflencing a range of developmental processes in higher plants including stem elongation, germination, dormancy, flowering, sex expression, enzyme induction and leaf and fruit senescence.

Discovery of Gibberellin: Kurusawa, a Japanese plant pathologist, discovered gibberellin in 1926. When he was working in the rice fields, he observed that some of the rice seedlings grew much taller than the others which were found to be infected by a fungus, *Gibberella fujikuroi*, about 62 different gibberellins are known out of which 25 have been isolated from the fungus *Gibberella fujikuroi.*

Chemical structure of Gibberellins:

All gibberellins are derived from the ent-gibberellane skeleton. 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. The fifth ring is a lactone ring. They have been depicted in Figure 7.

Transport of Gibberellin in plants is non-polar. It moves from one part to another in the phloem. Due to the lateral movements between the two vascular bundles, gibberellins are translocated in the xylem.

Functions of Gibberellin: Gibberellins are involved in stem elongation. Many seedlings (eg. radish, lettuce, tomatoes etc.) when grown in petri dishes containing GA3 solution, show elongation of hypocotyl. GA1 also causes hyperelongation of stems by stimulating both cell division and cell elongation. GAs cause stem elongation in response to long days GAs can cause seed germination in some seeds that normally require cold (stratification) or light to induce germination as shown in Figure 7. Barley is one such example. Gibberellins are known to stimulate the de-novo synthesis of numerous hydrolases, notably α-amylase in the aleurone cells that surround the starchy endosperm in barley. In seed germination in lettuce, the main signal stimulating gene expression of amylase and other germination-initiating enzymes is light. Thus the photoactivation is achieved by phytochrome in its Pfr form. GA stimulates the production of numerous enzymes, notably a-amylase, in germinating cereal grains.

3. Cytokinin:

Cytokinins are a class of phytohormones with a structure resembling adenine which promote cell division and have other similar functions to kinetin. This hormone is termed as "cytokinin" because they stimulate cell division (cytokinesis). Cytokinins promote cell division or cytokinesis, in plant roots and shoots. They are involved primarily in cell growth and differentiation, but also affect axillary bud growth, apical dominance and leaf senescence. Kinetin was the first cytokinin to be discovered and it is so named because of the compounds' ability to promote cytokinesis (cell division). Though it is a natural compound, it is not made in plants and therefore it is usually considered a "synthetic" cytokinin. The most common form of naturally occurring cytokinin in plants today is called zeatin which was isolated from corn (*Zea mays*). Cambium and other actively dividing tissues also synthesize cytokinins. Approximately 40 different structures of cytokinin are known. Other naturally occurring cytokinins include dihydrozeatin (DHZ) and isopentenyladenosine (IPA). Cytokinin concentrations are highest in meristematic regions and areas of continuous growth potential such as roots, young leaves, developing fruits, and seeds. Cytokinins have been found in almost all higher plants as well as mosses, fungi, bacteria and also in tRNA of many prokaryotic and eukaryotic organisms. Today there are more than 200 natural and synthetic cytokinins combined.

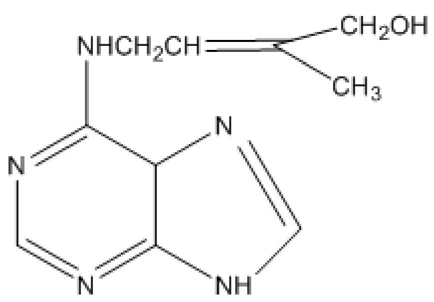


Figure 6: Cytokinin

Chemical nature of cytokinin:

Chemical nature of cytokinins is based on two types:

1. Adenine-type cytokinins
2. Phenylurea-type cytokinins

Adenine-type: These cytokinins are represented by kinetin, zeatin and 6-benzylaminopurine. Majority of the adenine-type cytokinins are synthesized in the roots. Cytokinin biosynthesis also takes place in the cambium and other actively dividing tissues.

Phenylurea-type: These cytokinins are represented by diphenylurea and thidiazuron (TDZ). Till now there is no evidence that the phenylurea cytokinins occur naturally in plant tissues.

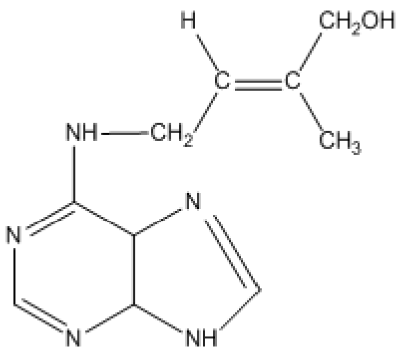
Cytokinins are involved in both local and long distance signaling. Cytokinins are transported within the xylem.

Classes of cytokinin:
There are two classes of cytokinin hormone**:** They are as follows:}

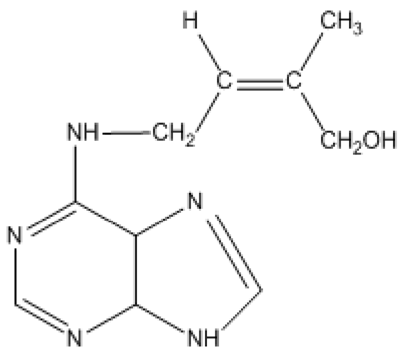
(i) Natural cytokinin
(ii) Synthetic cytokinins

(i) Natural Cytokinin:

The most common form of naturally occurring cytokinin in plants today is called zeatin which was isolated from corn (*Zea mays*). Approximately 40 different structures of cytokinin are known. Other naturally occurring cytokinins include dihydrozeatin (DHZ) and isopentenyladenosine (IPA). Figure 7depicts some cytokinins.



Trans-zeatin



Cis-zeatin

(ii) Synthetic Cytokinin:

Kinetin is also known as synthetic cytokinin.

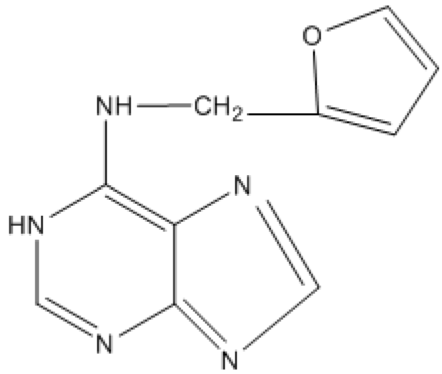


Figure 8: Kinetin

Function of Cytokinin:

Stimulates cell division: Especially by controlling the transition from G2 mitosis. This effect is moderated by cyclin-dependent protein kinases (CDK's) and cyclins. Stimulates morphogenesis (shoot initiation/bud formation) in tissue culture: In plant tissue cultures, cytokinin is required for the growth of a callus. Stimulates the growth of lateral buds- Cytokinin application to dormant buds causes them to develop. Witches' broom is caused by a pathogen *Corynebacterium fascians* (or *Agrobacterium tumefaciens*) that produces cytokinin which, in turn, stimulates lateral bud development. Thus apical dominance may be related to cytokinin too. Stimulates leaf expansion resulting from cell enlargement: Cytokinins stimulate the expansion of cotyledons. The mechanism is associated with increased plasticity of the cell wall. May enhance stomatal opening in some species. Promotes the conversion of etioplasts into chloroplasts via stimulation of chlorophyll synthesis.

4. Abscicic acid:

Abscisic acid (ABA) is the major phytohormone that controls plant’s ability to survive in harsh, changing environment. ABA promotes abscission of leaves and fruits; hence it is this action that gave rise to the name of this hormone ‘abscisic acid’. ABA is a naturally occurring compound in plants. The ABA signaling pathway is conserved across all plants, including mosses, and it is considered as an early adaptation to the terrestrial environment. ABA is found in leaves (where it is partially synthesized), stems, and green fruits. It is generally associated with negative-feedback interactions or stress-related environmental signals such as drought, freezing temperatures and environmental pollutants

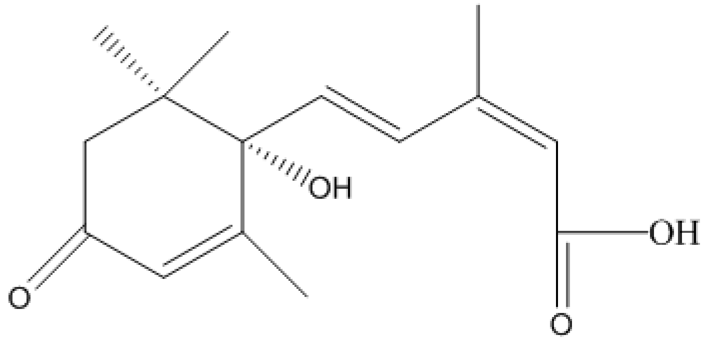


Figure 9: Abscisic acid

Chemical nature of abscisic acid:

Abscisic acid is a naturally occurring compound in plants. Abscisic acid (ABA) is an isoprenoid plant hormone, which is synthesized in the plastids by the 2-*C*-methyl-D-erythritol-4-phosphate (MEP) pathway; It is a sesquiterpenoid (15-carbon) which is produced partially via the mevalonic pathway in chloroplasts and other plastids. Since it is sythesized partially in the chloroplasts, biosynthesis of ABA primarily occurs in the leaves. The production of ABA is accentuated by stresses such as water loss and freezing temperatures.

Functions of Abscisic acid:

Some of the physiological responses of Abscisic acid are listed below:

(1) Antitranspirant: Stimulates the closure of stomata by decreasing transpiration to prevent water loss (water stress brings about an increase in ABA synthesis). In angiosperms and gymnosperms (but not in ferns and lycopsids), ABA triggers closing of stomata when soil water is insufficient to keep up with transpiration.

Mechanism: ABA binds to receptors at the surface of the plasma membrane of the guard cells.
The receptors activate several interconnecting pathways which converge to produce a rise in pH in the cytosol. Transfer of Ca^{2+} from the vacuole to the cytosol. These changes stimulate the loss of negatively-charged ions (anions), especially NO_3^{-}– and Cl–$^{-}$– , from the cell and also the loss of K^+ from the cell. The loss of these solutes in the cytosol reduces the osmotic pressure of the cell and thus turgor. The stomata close. ABA also promotes abscission of leaves and fruits (in contrast to auxin, which inhibits abscission). It is, in fact, this action that gave rise to the name abscisic acid. The dropping of leaves in the autumn is a vital response to the onset of winter when ground water is frozen — and thus cannot support transpiration — and snow load would threaten to break any branches still in leaf. Inhibits shoot growth but will not have as much affect on roots or may even promote growth of roots, induces seeds to synthesize storage proteins. It inhibits the affect of

gibberellins on stimulating de novo synthesis of alpha-amylase. It also has some effect on induction and maintanance of dormancy. ABA inhibits seed germination in antagonism with gibberellins and induces gene transcription especially for proteinase inhibitors in response to wounding which may explain an apparent role in pathogen defense. Inhibits fruit ripening and is responsible for seed dormancy by inhibiting cell growth. It downregulates enzymes needed for photosynthesis.

5. Ethylene:

Ethylene (IUPAC name: ethene), unlike the rest of the plant hormone compounds is a gaseous hormone. Of all the known plant growth substance, ethylene has the simplest structure. It contains a carbon-carbon double bond, ethylene is classified as an unsaturated hydrocarbon. It is produced in all higher plants and is usually associated with fruit ripening. Ethylene which is also known as the 'death hormone' or 'ripening hormone' plays a regulatory role in many processes of plant growth, development and eventually death. Fruits and vegetables contain receptors which serve as bonding sites to absorb free atmospheric ethylene molecules. The overall effect is to hasten ripening, aging and eventually spoilage.

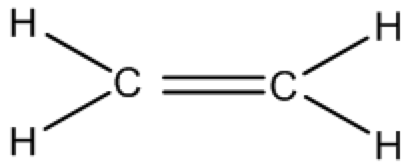


Figure 10: Ethylene

Biosynthesis of ethylene:

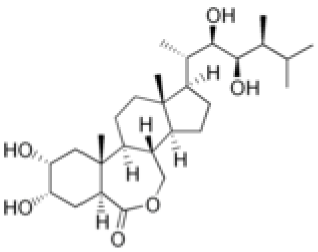
Methionine is the precursor of ethylene, and 1- aminocyclopropane-1-carboxylic acid serves as an intermediate in the conversion of methionine to ethylene. Ethylene is produced by almost all parts of higher plants but the rate of production of ethylene depends on the type of tissue and the stage of development. Meristematic regions and the nodal regions of plants are the most active in ethylene biosynthesis. Ethylene production increases during fruit ripening, leaf abscission and flower senescence. Any type of wounding and physiological stresses such as flooding, chilling, disease, and temperature or drought stress can induce ethylene biosynthesis.

Functions of ethylene:

Ethylene has various physiological responses which are listed below:

Ethylene plays vital role in fruit ripening: The changes which typically takes place due to the stimulating effect of ethylene includes softening of the fruit due to the enzymatic breakdown of the cell walls, sugar accumulation, starch hydrolysis and disappearance of organic acids and phenolic compounds including tannins. Ethylene has the ability to initiate germination in certain seeds, such as cereals and break the dormancy. Ethylene increases the rate of seed germination of several species. Ethylene can also break bud dormancy and ethylene treatment is used to promote bud sprouting in tubers such as potatoes etc. It stimulates shoot and root growth along with differentiation. Ethylene induces abscission. Abscission takes place in specific layers of cells, called abscission layers, which become morphologically and biochemically differentiated during organ development. Weakening of the cell walls at the abscission layer depends on cell wall–degrading enzymes such as polygalacturonase and cellulase. Ethylene induces flowering in Bromeliaceae family plants which includes pineapple and its relatives. Flowering of other species of plants, such as mango, is also initiated by ethylene. Ethylene may change the sex of developing flowers on monoecious plants (plants which have separate male and female flowers).
The femaleness of diocious flowers in plants is stimulated by the production of ethylene. The promotion of female flower formation in cucumber is one example of this effect.Flower and leaf senescence stimulation is caused by ethylene. Exogenous applications of ethylene accelerate leaf and flower senescence. Enhanced ethylene production in plants is associated with the loss of chlorophyll and the fading of colours.

Brassinosteroids



Brassinosteroids are a class of polyhydroxysteroids, the only example of steroid-based hormones in plants. Brassinolide was the first identified brassinosteroid and was isolated from extracts of rapeseed (*Brassica napus*) pollen in 1979.

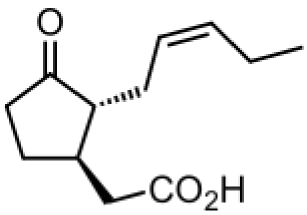
Brassinosteroids are a class of steroidal phytohormones in plants that regulate numerous physiological processes. This plant hormone was identified by Mitchell et al. who extracted ingredients from Brassica pollen only to find that the extracted ingredients' main active component was Brassinolide.

Brassinosteroids control cell elongation and division, gravitropism, resistance to stress, and xylem differentiation. They inhibit root growth and leaf abscission.

. In plants these steroidal hormones play an important role in cell elongation via BR signaling.

Brassinosteroids receptor- brassinosteroid insensitive 1 (BRI1) is the main receptor for this signaling pathway. The BRI1 mutant displayed several problems associated with growth and development such as dwarfism, reduced cell elongation and other physical alterations. These findings mean that plants properly expressing brassinosteroids grow more than their mutant counterparts. Brassinosteroids bind to BRI1 localized at the plasma membrane which leads to a signal cascade that further regulates cell elongation. This signal cascade however is not entirely understood at this time. What is believed to be happening is that BR binds to the BAK1 complex which leads to a phosphorylation cascade. This phosphorylation cascade then causes BIN2 to be deactivated which causes the release of transcription factors. These released transcription factors then bind to DNA that leads to growth and developmental processes and allows plants to respond to abiotic stressors.

Jasmonates



Jasmonates (JAs) are lipid-based hormones that were originally isolated from jasmine oil. JAs are especially important in the plant response to attack from herbivores and necrotrophic pathogens. The most active JA in plants is jasmonic acid. Jasmonic acid can be further metabolized into methyl jasmonate (MeJA), which is a volatile organic compound. This unusual property means that MeJA can act as an airborne signal to communicate herbivore attack to other distant leaves within one plant and even as a signal to neighboring plants. In addition to their role in defense, JAs are also believed to play roles in seed germination, the storage of protein in seeds, and root growth.

JAs have been shown to interact in the signalling pathway of other hormones in a mechanism described as “crosstalk.” The hormone classes can have both negative and positive effects on each other's signal processes.

They act in signalling pathways in response to herbivory, and upregulate expression of defense genes.