

Plant Hormones (Lecture 10)

...plant hormones are endogenous organic compounds active at very low concentration, produced in one tissue, and translocated to another point in the plant where their effects on growth and development are manifested.

•Plant "hormones" are sometimes preferentially referred to as plant growth regulators (PGR) because they differ from animal hormones in the following ways:

- Plant hormones are not made in specialized tissues
- Plant hormones do not have specific target tissues
- Plant hormones usually do not have specific effects

•auxin (indoleacetic acid)

•cytokinins (zeatin, zeatin riboside, isopentenyl adenine)

•gibberellins ($GA_{x...80}$)

•abscisic acid (ABA)

•ethylene

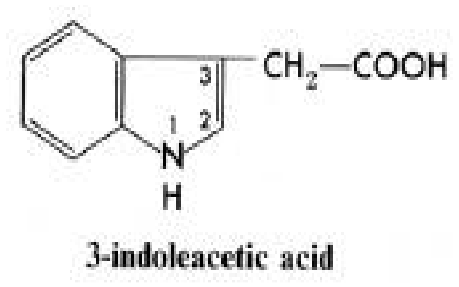
•others (real and fabled; jasmonic acid, brassinolide, florigen, juvenone)

Class	Endogenous Hormone	Growth Regulators
auxin	indoleacetic acid	IBA, NAA, 2,4-D, others
cytokinin	zeatin, zeatin riboside	kinetin, BA, 2iP, TDZ
gibberellin	$GA_{x...80}$	GA_3 , GA_{4+7}
abscisic acid	abscisic acid (ABA)	
ethylene	ethylene	Ethephon, Ethrel

Auxin (*indoleacetic acid*)...

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

- cell elongation and expansion
- suppression of lateral bud growth
- initiation of adventitious roots
- stimulation of abscission (young fruits) or delay of abscission
- hormone implicated in tropisms (photo-, gravi-, thigmo-)



•Transport

While other plant hormones are transported in the xylem or phloem, IAA is actively transported (faster than just by diffusion) through parenchyma tissue such as the cortex, the pith, or the parenchyma cells associated with the vascular tissue.

- IAA moves down through the plant.

Therefore, it moves toward the base in shoots and toward the root tips in roots. (Movement like this in a specific direction is termed "polar" movement).

• Effects

Cell elongation: IAA contributes to the growth of cells by loosening the cell wall.

- In general, growth occurs by water uptake.
- In order for the cell to enlarge, the cell wall has to expand.
- IAA increases the extensibility of the cell wall, but its role in this process is not completely clear.
- It is likely that IAA turns on genes for the synthesis of new cell wall materials.

• The fact that cell elongation was influenced by a transported substance, which later turned out to be auxin, was investigated as long ago as the 1870's by Charles Darwin and his son Francis.

• Plants will grow toward a source of light (phototropism), and these scientists found that the tip of the coleoptile of oat seedlings sensed the light, but that growth toward the light occurred below the tip of the coleoptile.

• If the tip of the coleoptile was covered or removed, the coleoptile did not grow toward the light. However, if the growing region was covered while the tip was still exposed to light, growth toward the light did occur.

• The growth-stimulating substance was shown to be a water-soluble compound in 1913 by Boysen-Jensen, a Danish plant physiologist.

He placed a slice of agar between the excised tip and the rest of the coleoptile, and found that the substance causing the response could move through the agar.

However, he also showed that if water movement was prevented, the coleoptile no longer responded to light.

• A Hungarian, Paál, showed that the substance stimulating growth was driven away from light, by removing coleoptile tips and replacing them to one side of the coleoptile.

This resulted in growth on the side in contact with the tip.

• In 1926, Frits Went extracted the substance by placing coleoptile tips on agar for an hour, then discarding the tips and using the agar to produce growth in the decapitated coleoptiles.

• Went also named the substance "auxin" which comes from the Greek work for growth.

• Other Effects of Auxins:

• Apical Dominance:

• The inhibiting effect of the shoot apical meristem on the growth of axillary buds is termed apical dominance.

• It is thought that the optimal concentration of IAA for axillary bud growth is much lower than what is produced by the apical meristem; concentrations both greater than or less than the optimal result in less growth.

• Therefore, when the apical meristem is removed and production of IAA is reduced, a lower or more optimal concentration of IAA permits axillary bud growth.

• Formation of Adventitious Roots:

When a leaf is excised from a plant and placed in a moist environment, the auxins produced by the leaf accumulate above the wound site.

These relatively high levels of auxin, especially in the absence of another hormone, cytokinin, which normally comes from the root, causes the plant to form roots at this location.

IAA is often applied to shoot cuttings in the form of compounds such as RooTone to encourage rooting.

•Leaf Abscission:

- Growing leaves produce IAA, but stresses such as drought, cold, or nutrient deficiencies cause the production of IAA to decrease.
- This decrease in IAA production causes ethylene production at the base of the petiole.
- In response, walls of cells in the "abscission zone" become suberized and the middle lamella breaks down.
- Synthetic auxins are sometimes sprayed on apple or orange trees to inhibit preharvest fruit drop.

Herbicides:

- The synthetic auxin 2,4-D (Weed-B-Gon) is a cheap and relatively non-toxic herbicide that selectively kills broadleaf dicots (e.g., killing dandelions in a lawn without killing the grass).

Auxin-like growth regulators

- indolebutyric acid (IBA)
- 2, 4 dichlorophenoxyacetic acid (2,4D)
- 2, 4, 5 trichlorophenoxyacetic acid (2, 4, 5 T)
- picloram

Commercial uses - auxins

applied as IBA, NAA, auxin-conjugates or mixes

- stimulation of adventitious rooting
- 2,4-D as a herbicide for dicots
- sprout prevention in pruned trees
- fruit thinning or fruit holding depending on stage of development

Cytokinin (*zeatin*, ZR, IPA)...

...produced in root meristems, young leaves, fruits, seeds.

- cell division factor
- stimulates adventitious bud formation
- delays senescence
- promotes some stages of root development



- The chemical structure of cytokinins is related to adenine**, to one of the four "bases" that are the key components of DNA.

It was originally thought that cytokinins were breakdown products of DNA, because their effect was associated with coconut milk, which is rich in nucleic acids.

Coconut milk is the liquid endosperm of coconut seeds, and was used to artificially culture other plant embryos.

The naturally occurring cytokinin **zeatin** was isolated from corn (*Zea mays*) in 1964.

Several additional cytokinins have now been isolated from plants.

Location of Synthesis

In angiosperms or flowering plants, most cytokinins are made in the roots.

•Effects

Cell division:

•Cytokinins speed up the process of cell division, but this effect depends on the presence of auxins, which are necessary for cell elongation.

•Organogenesis:

- Individual plant cells are capable of generating new plants when cultured in the proper medium.
- The balance of cytokinin and auxin in the growth medium of cultured cells has a profound effect on whether root formation or shoot formation takes place.
- If the ratio of cytokinin to auxin is high, shoots will form, and if it is low, roots will form.
- Varying these ratios allows the formation of complete plants.
- The techniques of "micropropagation" allow the selective production of plants with desirable traits.

Commercial uses - cytokinins

applied as kinetin, benzyladenine, or zeatin conjugates

- axillary bud growth in orchids, daylilies
- antioxidant (browning preventer) in cut salads
- mix with GAs as fruit size stimulator

Gibberellins (1 -- 80)...

..role in many functions associated with tissue elongation and phytochrome-mediated responses.

- cell elongation and expansion
- stimulation of amylase activity
- elongation of flower stalks of chilled bulbs
- reversal of "physiological dwarfism"

•Although more than 80 different gibberellins or gibberellic acids (GAs) have been isolated from plants, most are inactive.

Only GA₁ is thought to control stem elongation in higher plants.

•Location of Synthesis

Gibberellic acids are synthesized in immature seeds, the root and shoot apical meristems, and in young leaves.

•Transport

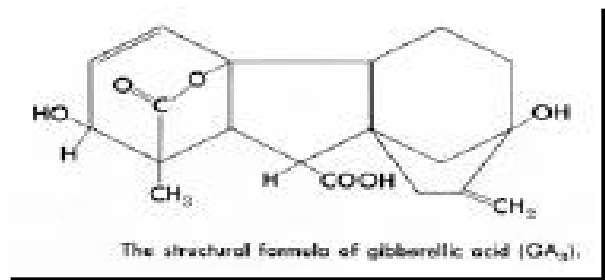
Only auxins are transported in a polar fashion.

GAs and other plant hormones (except ethylene, which is a gas) are transported in the xylem and phloem.

Effects

Cell division and elongation:

- Gibberellic acid increases plant height by increasing internode length.
- It can be applied to dwarf plants and cause them to attain normal height.
- Dwarf plants are not deficient in GA, but they don't make enough of the active form of the hormone (GA₁).
- GA differs from auxins in stimulating cell division as well as elongation.



•GA was discovered by botanists in Japan in the 1920's studying rice infected with the fungus *Gibberella fujikuroi*.

• *These plants were pale and spindly, falling over before they could be harvested.*

•By 1939, the substance had been isolated from the fungus and named gibberellin.

•Seed germination:

•In the cereal grain barley, the cotyledon produces gibberellic acid when germination begins.

•The GA is transported to the aleurone layer, a layer of living cells surrounding the non-living endosperm cells that store starch.

•The GA causes cells in the aleurone layer to produce the enzyme amylase, which is secreted (in vesicles from dictyosomes) into the endosperm.

•The amylase breaks the starch down to glucose, which can be used by the germinating seedling for growth.

•This process is well-studied in barley because the malting step of brewing is the breakdown of starch in germinating barley seeds.

•Commercial breweries add gibberellic acid to ensure complete starch breakdown.

•[In oats and corn, the scutellum itself is the source of the enzymes that break down the starch, and in the seeds of dicots and gymnosperms, cytokinins (another growth hormone) may stimulate the breakdown of food reserves].

•Flowering:

•Biennial plants may have short stem internodes their first year (rosette form), then undergo internode elongation (bolting) and flowering in year two.

•Gibberellic acid will substitute for a daylength response and probably also for a cold temperature requirement, and induce bolting if it is applied to the rosette form of plants.

•This permits seed production to be completed within one year.

Commercial uses - GA inhibitors

cycocel, Bonsai, Sumagic

•height control in flowering pot plants (lilies, orchids)

•height control in bedding plants

apply as GA₃, or GA₄₊₇

•increase flower size on certain ornamentals (eg, “gibbing” camellias)

•increase berry separation and size in bunch grapes

•overcome shallow dormancies in vegetative buds

•stimulate seed germination

Ethylene...

...gaseous hormone produced in many plant tissues.

•autocatalytic (stimulates its own production.

•volatile gas.

•production stimulated during ripening, flooding, stress, senescence, mechanical damage, infection.

•product of combustion of petrochemicals.

• Fruit Ripening (with GA)

•Abscission (dropping): leaf, flower, and fruits (with auxin)

- Induces epinasty (down turning of leaves) (with auxin)
- Triple Responses (with auxin)
- Triple Res. is well characterized in pea and *Arabidopsis*• Maintaining hook closure (with auxin)
- Promotes root hair elongation
- Initiates germination in grains (corn) (with GA)
- Activates dormant buds (peanuts, and potatoes in storage) (with CK?)
- Stem elongation in deep-water rice
- Induces flowering in pineapple (with GA?)
- Promotes female expression in flowers
- Promotes flower and leaf senescence (with CK), Ag⁺ added to prevent death of flowers

• The effects of ethylene on plants were first noticed in German cities in the 1800's, when gas street lamps were associated with stunted growth and leaf loss of nearby trees.

• Ethylene was identified in 1901 as a by-product of combustion, which caused defoliation and inhibited plant growth.

• The fruit-ripening effects of some fruits on others were noted in 1910 in a Jamaican Dept. of Agriculture report, and the causative agent was later identified as ethylene.

• The dark spots on the peel of ripe bananas are areas of high ethylene production.

• Effects

Fruit ripening:

• Ethylene causes chlorophyll to break down and other pigments to form (e.g., the change in apple skin color with ripening).

• It also causes fruit softening by causing the production of the enzymes cellulase and pectinase, which break down cellulose and pectin, structural components of the cell wall.

• Ethylene also causes starches to be converted to sugars.

Fruits such as apples, bananas, kiwi, avocado, and tomatoes can be stored under ethylene-free, low oxygen conditions for months without ripening.

When they are needed for market, about 1 ppm ethylene is added to the air.

These fruits experience a **climateric**, which is an increase in respiration caused by production of ethylene by the plant itself.

• *Abscission:*

• Ethylene production following a drop in IAA production by leaves causes the breakdown of the middle lamella and

the suberization of cells in the abscission zone, which is followed by leaf drop.

• Some fruits are sprayed with **ethephon**, which breaks down to ethylene, to synchronize abscission and allow a shorter harvesting period.

Phases: leaf maintenance, shedding induction, and shedding

Evidence...

1. exogenous application increase leaf senescence
2. Increased ethylene is associated with chlorophyll loss (yellowing)
3. Inhibitors retard leaf senescence
4. Mutants defective in ethylene signaling (*etr1* and *ein2* in *Arabidopsis*) live longer, lose chlorophyll later, leaves senescence later.
5. Transgenic plants that express anti-sense mRNA for ACC synthase show delayed senescence.

Commercial uses - ethylene inhibition removed by chemical “scrubbing” or low atmosphere

- long term storage of apples in CA storages
- treatment of cut flowers with silver thiosulfate
- long-keeper (delayed ripening) mutants (or rDNA) of tomato
- hypobaric storage of many fruits, vegetables, flowers

applied as ethylene gas or Ethephon or Ethrel sprays

- flower initiation (bromeliads, pineapples)
- stimulation of ripening (bananas, tomatoes)
- degreening of citrus
- abscission induction prior to mechanical harvest (cherries)
- increased color development in once-over harvested processor type tomatoes

Abscisic acid (ABA.)...

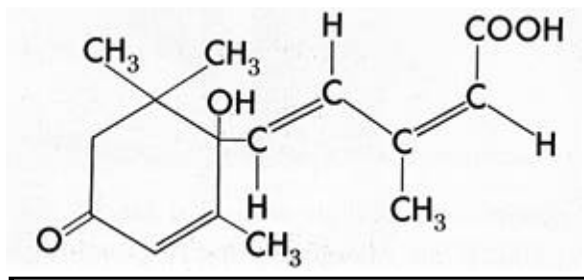
...found in stressed leaves, dormant seeds, dormant buds.

Absciscic acid (ABA) was discovered as a contaminant and inhibitor of IAA from plant extracts.

It was also present in high amounts in dormant buds. It was, therefore, at first named "dormin".

ABA is high in dormant buds, and purified ABA will cause dormancy when applied to other buds.

Another scientist discovered a compound that stimulated the abscission of cotton fruits, and named it "abscisin".



•stomatal closure

ABA is used as a signal by plants under drought stress. Drought-stressed leaves make large amounts of ABA, which causes the stomata to close.

•inhibits germination of some seeds (seed dormancy)

ABA appears to play an important role in seed maturation and maturity.

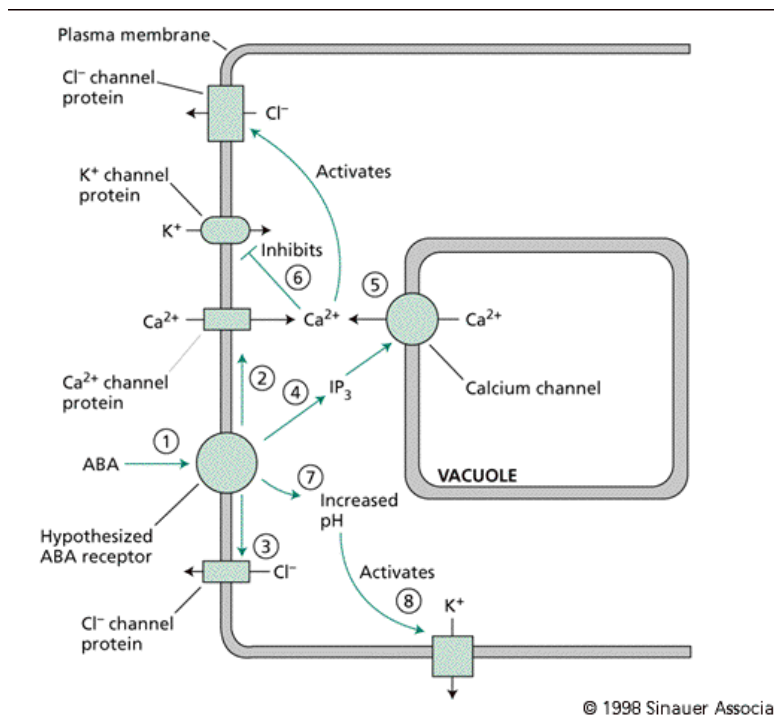
As seeds mature, premature growth of the embryo is prevented by relatively high levels of ABA.

When ABA is deliberately reduced or is unusually low due to a mutation, the result is vivipary, or the germination of seeds on the seedhead.

ABA also opposes the action of gibberellic acid in the stimulation of amylase activity that occurs during seed germination.

•inhibits active growth of axillary buds

- 1.ABA binds to receptor (none identified yet),
- 2.ABA causes Ca^{2+} to open depolarizing membrane,
- 3.opening Cl^- channels
- 4.ABA increase inositol triphosphate (IP_3) levels, which
- 5.causes Ca^{2+} channels to open on the Vac membrane,
- 6.increases Ca^{2+} intracellular levels inhibit K^+ influx and promotes Cl^- efflux, and inhibit H^+ -ATPase activity,
- 7.which result in increases in pH
- 8.which can activate K^+ efflux.



Apical dominance...

inhibition of growth of lateral buds by the apical meristem

- varies with plant species (vines are strong; shrubs weak)
- varies with plant age (younger plants - stronger apical dominance)
- decreases in basipetal direction
- readily altered by pinching or chemical treatment

Production of the roots and shoots is dependent on the ratio of auxin to cytokinin in the culture medium.

High level of auxin relative to kinetin stimulates roots formation, whereas high levels of cytokinin relative to auxin led to the formation of shoots
An intermediate levels the tissue grew as an undifferentiated callus

Part of the material was adapted from

<http://www.hos.ufl.edu/mooreweb/TissueCulture/tcclass.html>

Images from Purves et al., Life: The Science of Biology

From

http://wiscinfo.wisc.edu:2070/I9/.image/.bot/.130/Angiosperm/Lilium/Flower_dissection/Flower.html
<http://www.plant.uoguelph.ca/research/biotech/haploid/haploids.htm>