Charles Darwin

*The Power of Movement in Plants* “marks the beginning of the modern study of plant growth”, including signals and growth stimuli, later shown to be plant hormones.
References
Plant Physiology. Sinauer Associates, Inc., Taiz and Zeiger, 2nd Ed, 1998 (has chapters on hormones), and Taiz, Zeiger, Moller and Murphy, 6th Ed. 2015

Definitions

Hormone - an endogenous or naturally-occurring compound that is produced or synthesized in one part of the plant and causes a change in physiology, growth or development in another part of the plant; usually present in very small quantities.

Elicitors Signaling molecules that may be involved in morphological changes, resistance to pests, and defense against herbivores, and other hormone-like activity.

Growth Substance - all naturally-occurring or synthetically produced compounds that affect the physiology, growth and development of plants.

Plant Hormones, Elicitors and Photoreceptors
Classically, plants have been known to contain five hormones, which are auxin, cytokinin, gibberellic acid, ethylene and abscisic acid. Recently, other endogenous compounds have been shown to elicit hormone-like reactions, which are brassinosteroids, salicylic acid, strigolactone, and jasmonic acid. Some do not elevate these to the status of one of the five classical hormones, so often they are called elicitors. In addition, there are photoreceptors (red/far red light, blue light) that are involved in causing plant responses. All the classical hormones have application in horticultural practices. The elicitors and photoreceptions have little horticultural application, but they do explain many very important development processes.

Five Classical Hormones
- Auxin
- Cytokinin
- Gibberellin
- Ethylene
- Abscisic Acid

Elicitors
- Brassinosteroid
- Salicylic Acid
- Strigolactone
- Jasmonic Acid
- Polyamine

Photoreceptors
- Phytochrome
- Blue-Light Responses
Common Scheme for Hormonal Regulation

*(Plant Physiology and Development, 6th Ed., Taiz, Zeigler, Moller and Murphy)*
AUXIN

<table>
<thead>
<tr>
<th>Naturally-Occurring</th>
<th>Synthetic</th>
<th>Structure</th>
<th>Site of Production</th>
</tr>
</thead>
<tbody>
<tr>
<td>• indoleacetic acid (IAA)</td>
<td>• indolebutyric acid (IBA)</td>
<td></td>
<td>Rapidly dividing tissue:</td>
</tr>
<tr>
<td>• 4-chloro-IAA</td>
<td>• naphthaleneacetic acid (NAA)</td>
<td></td>
<td>• shoot tips</td>
</tr>
<tr>
<td></td>
<td>• 2,4-dichlorophenoxyacetic acid (2,4-D)</td>
<td></td>
<td>• young leaves</td>
</tr>
<tr>
<td></td>
<td></td>
<td><img src="IAA.png" alt="IAA Structure" /></td>
<td>• developing fruit</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>• embryos</td>
</tr>
</tbody>
</table>

DISCOVERY and HISTORY
- **Charles Darwin** – *The Power of Movement in Plants* 1881 – proposed existence of hormones in plants.
- **Frits Went** – demonstrated presence, 1929
- Named auxin, from Greek auxein – to increase or to grow
- 1930s auxin isolated and identified by K.V. Thimann in U.S. (and Kogl, Haagen-Smit Holland).
- Immediately, chemists began synthesizing similar structures and testing for auxin activity.
- Synthetic versions that have stood the test of time are listed in the above table.
  - Synthetic version almost always more effective – Why?

SYNTHESIS
tryptophan → via multiple pathways → indoleacetic acid

![Synthesis Diagram](Synthesis.png)

Synthesis if in the young developing leaves of the shoot tip and just below the apical meristem.

TRANSPORT
- 3:1 basipetal transport – creates a gradient top to bottom
- only hormone with polar transport
- primarily in phloem parenchyma

AUXIN TRANSPORT INHIBITORS
- **NPA** (naphthylphthalamic acid)
- **TIBA** (2,3,5-triiodobenzoic acid)
- Primarily used to alter auxin transport to elucidate mode of action of auxin
EFFECTS AND APPLICATIONS

Cellular Effects
1) **Cell elongation**
   - this is the effect Darwin studied in phototropism
   - causes acid induced cell wall growth

2) **Cell division** - stimulates

Whole Plant/Organ Effects
3) **Tropism** - response of plants to environmental or physical stimuli.
   - **phototropism** - response to light
     - auxin transport switches from basipetal to laterally to the dark side.
   - **geotropism** or **gravitropism** - response to gravity
   - **thigmotropism** - response to touch

4) **Apical dominance** –
   - determined by **correlative inhibition** of apical bud, high auxin produced by shoot tip.
   - dormancy of lateral buds may be a balance between high auxin/low cytokinin
   - removal of apical dominance is the bases of pruning and lateral branching

5) **Branch angle**
   - high auxin causes wide branch angles
   - pruning produces narrow branch angle

6) **Zn Deficiency in pecan** - **Witches Broom or Little Leaf**
   - Zn required for synthesis of auxin from tryptophan

7) **Sprout Inhibitors**
   - retard basal branching.

8) **Fruit set**
   - low concentrations stimulate fruit set without pollination or low rates of pollination
   - may lead to parthenocarpic (seedless) fruit or fruit with fewer seeds
   - common in greenhouse production of tomato

9) **Fruit or flower thinning**
   - high concentrations cause flower and/or fruit abortion

10) **Herbicides** –
    - 2,4-D at high concentrations acts as a herbicide.
    - Broad-leaved plants only, e.g. dicots
    - Monocots – maize and other monocots quickly conjugate and inactivate synthetic auxin

10) **Adventitious root formation**
    - stem and leaf cuttings
    - tissue culture - high auxin/low cytokinin stimulates
Cytokinin

<table>
<thead>
<tr>
<th>Naturally-Occurring</th>
<th>Synthetic</th>
<th>Structure</th>
<th>Site of Production</th>
</tr>
</thead>
<tbody>
<tr>
<td>zeatin</td>
<td>benzyladenine (BA)</td>
<td></td>
<td>root tips, embryos, young leaves?</td>
</tr>
<tr>
<td>kinetin (not in plants)</td>
<td>pyranylbenzyldenine (PBA)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Discovery and History**

- Second hormone isolated and identified.
- Discovered investigating factors that trigger cell division.
- 1913 Haberlandt found that phloem tissue contained a diffusate that would trigger cell division in potato parenchyma.
- 1942 VanOverbeek demonstrated that extracts from coconut milk promoted growth of embryos in tissue culture.
- 1954 Skoog’s showed vascular tissue could do the same in tissue culture. Skoog was a pioneer in tissue culture. Cytokinin was named after cytokinesis. They screened many compounds and found adenine stimulated cell division.
- 1955 Miller isolated from herring sperm DNA and adenine type compound that stimulated cell division. It was named **kinetin**. Kinetin is an adenine derivative.
- 1964 Letham identified the first natural plant cytokinin in corn endosperm, and named it **zeatin**.
- Since its discovery, zeatin has been found in many plants.
- Steward later found the cytokinins effected more than cell division, including tissue differentiation, dormancy, phases of flowering/fruiting and senescence.

**Synthesis**

$\text{adenine} \rightarrow \text{zeatin}$

Synthesis largely is in the root tips. But, cytokinin is also synthesized in embryos and young developing leaves.

**Transport**

- xylem transported, found in root exudates
- primarily acropetally in the xylem, but not necessarily polar
- cytokinin exists in free and bound forms.
EFFECTS

Cellular Effects
1) Cell division
   • stimulates cell division; named after cytokinesis

2) Protein synthesis -
   • stimulates

3) Chlorophyll breakdown –
   • decreases chlorophyll breakdown; promotes chloroplast development in etiolated tissue.

Whole Plant/Organ Effects
4) Adventitious shoot formation -
   • leaf and root cuttings


• tissue culture – high cytokine/low auxin stimulates 4)

http://irrecenvhort.ifas.ufl.edu/plant-prop-glossary/09-tissue-culture/01-types/04-tctypes-micropropagation.html
Summary

https://www.semanticscholar.org/paper/Plant-Growth-Regulators-II%3A-Cytokinins%2C-George-Hall/0c3bcebcd3f46d613e62abd5f8dc6c13d86923e0

5) Apical dominance
   • high cytokinin/low auxin may overcome apical dominance

https://plantcellbiology.masters.grkraj.org/html/Plant_Growth_And_Development5-Plant_Hormones-Cytokinins.htm

6) Seed germination –
   • may overcome dormancy or stimulate germination

7) Nutrient mobilization
   • nutrients transported towards high cytokinin concentration.

8) Leaf Aging or abscission –
   • may delay

9) Root growth –
   • may be inhibitory to root growth

HORT 604, DW Reed
GIBBERELLIC ACID (GA)

<table>
<thead>
<tr>
<th>Naturally-Occurring</th>
<th>Synthetic</th>
<th>Structure</th>
<th>Site of Production</th>
</tr>
</thead>
<tbody>
<tr>
<td>Well over 100</td>
<td>None</td>
<td>GA backbone</td>
<td>shoot tips, root tips, embryos</td>
</tr>
<tr>
<td>(a “bewildering number”, named by consecutive numbers; not all have biological activity)</td>
<td>(all in use are isolated from fungal cultures)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

DISCOVERY AND HISTORY

- Existence of a stem elongation factor was known to Japanese rice farmers for many years. Observed certain seedlings grew very tall, and this caused “lodging”. It was thought to be cause be a disease causing organism. The phenomenon was called “bakanae” or “foolish seedling disease”. Plants were shown to be infected by the fungus Gibberella fujikuroi. A compound that caused the elongation was isolated from the filtrates of fungal culture.
- 1930s isolated crystals of the compound and termed it gibberellin, after the generic name of the fungus.
- 1950s Japanese, US and Britain identified the structure. Termed Gibberellin $A_2$ and $A_3$. They all have in common a 3 ring structure common to kaurene and sometimes termed the “gibbane backbone”.
- 1958 MacMillin identified GA in plants.
- Many gibberellins were subsequently identified and they were named in numerical sequence. Well of a hundred have been identified. It appears as though each fungus and/or plant may synthesize its own unique GA.

TRANSPORT

- no polarity
- in phloem or xylem

GA INHIBITORS

growth retardants - chemicals that block synthesis of GA.

Commercial GA Inhibitors

<table>
<thead>
<tr>
<th>Product Name</th>
<th>Active Ingredient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cycocel, Citade</td>
<td>chlormequat chloride</td>
</tr>
<tr>
<td>A-Rest, Abide</td>
<td>ancydrol</td>
</tr>
<tr>
<td>B-Nine, Daminozide</td>
<td>daminozide</td>
</tr>
<tr>
<td>Topflor</td>
<td>flurprimidol</td>
</tr>
<tr>
<td>Bonzi, Piccolo</td>
<td>paclobutrazol</td>
</tr>
<tr>
<td>Sumagic, Concise</td>
<td>uniconazole</td>
</tr>
</tbody>
</table>
SYNTHESIS (from Moore, 1979)

Mode of Action of Growth Retardants
- block ring closure between geranylgeranyl pyrophosphate and copalyl pyrophosphate
- block ring closure between copalyl pyrophosphate and kaurene

Biosynthetic Pathway of Gibberellic Acid

<table>
<thead>
<tr>
<th>Type compound</th>
<th>Chemical Name</th>
<th>Blocks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Onium compounds</td>
<td>Chloromequat chloride, mepiquat chloride, chlorphonium, and AMO-1618</td>
<td>cyclases copalyl-diphosphate synthase and ent-kaurene synthase</td>
</tr>
<tr>
<td>2) N-containing heterocycle</td>
<td>ancymidol, flurprimidol, tetcyclacis, paclobutrazol, uniconazole-P, and inabenfide</td>
<td>cytochrome P450-dependent monoxygenases, thereby inhibiting oxidation of ent-kaurene into ent-kaurenoic acid</td>
</tr>
<tr>
<td>3) Structural mimics of 2-oxoglutaric acid that co-substrate of dioxygenases that catalyze late steps of GA formation</td>
<td>prohexadione-Ca and trinexapac-ethyl and daminozide, block particularly 3ss-hydroxylation</td>
<td>inhibiting the formation of highly active GAs from inactive precursors,</td>
</tr>
<tr>
<td>4) 16,17-Dihydro-GA5 and related structures</td>
<td>mimicking the GA precursor substrate of the same dioxygenases</td>
<td></td>
</tr>
</tbody>
</table>

Cellular Effects

1) **Protein synthesis** - triggers *de novo* synthesis of some proteins, ex. α-amylase.

2) **Cell elongation** - primary stimulus for cell elongation

Whole Plant/Organ Effects

3) **Rosette or dwarf plants** - lack of endogenous GA often contributes to decreased height.

5) **Height control**

   a. **Increase height** – treat with GA.

   ![GA spray as Fresco](https://gpnmag.com/article/increasing-height-of-chrysanthemum-with-pgr-drenches/)

   b. **Decrease height** – apply growth retardants (see previous table).
5) **Flowering** - may cause bolting in biennials

6) **Fruit size** - increases size of seedless grapes


‘Crimson’ table grapes. The cluster on the left was sprayed with gibberellic acid (GA).


7) **Bud dormancy** - may overcome and substitute for cold treatment; greenhouse Azalea?

8) **Seed germination** - may increase or speed up

![Graph showing seed germination](Penstemon seeds 24 hour GA soak)

9) **Sex expression** - favors staminate flower formation on monoecious plants
ETHYLENE

<table>
<thead>
<tr>
<th>Naturally-Ocurring</th>
<th>Synthetic</th>
<th>Structure</th>
<th>Site of Production</th>
</tr>
</thead>
<tbody>
<tr>
<td>ethylene</td>
<td>ethephon or ethrel (release ethylene inside plant)</td>
<td>H₂C=CH₂ ethylene</td>
<td>ripening fruits, aging flowers, germinating seeds, wounded tissue; thus can be made in almost all parts of the plant.</td>
</tr>
</tbody>
</table>

Other sources of ethylene
- Auxin can induce ethylene synthesis
- Natural component of natural gas
- Incomplete combustion of any hydrocarbon; any yellow or orange flame, e.g. non-blue flame

DISCOVERY AND HISTORY
- Turn of the century, it was first noticed that trees in the vicinity of coal gas powered street lamps defoliated more, and that the presence of fruit may cause other fruit to ripen, and ethylene gas was involved.
- 1930s it was determined that plants produce ethylene. At that time, ethylene was not considered a hormone. Many thought ethylene effects might actually be auxin effects.
- 1959 Thimann’s lab demonstrated that ethylene did regulate growth. The advent of gas chromatography to detect ethylene was critical in these studies.
- 1960s to 1980s the biosynthetic pathway was elucidated.

SYNTHESIS

methionine → s-adenosylmethionine → 1-aminocyclopropane-1-carboxylic acid → ethylene (SAM) (ACC) action

TRANSPORT
- diffusion as a gas throughout plant (in and out)
ETHYLENE INHIBITORS

ethylene inhibitors - chemicals that inhibit the synthesis or action of ethylene

Synthesis Inhibitors (block synthesis of SAM → ACC)
• AVG - aminoethoxyvinyl glycine
• MVG - methoxyvinyl glycine
• AOA - aminoacetic acid

Action Blockers (block ethylene → action)
• STS - silver thiosulfate
• CO₂ - carbon dioxide
• Ni - nickel
• Co – cobalt
• MCP – 1-methylcyclopropane
  o it is a gas that can saturate the receptor sites, and block action for several days
  o EthylBloc – commercial compound

EFFECTS

Cellular Effects

1) Auxin – ethylene interaction
   • ethylene alters basipetal transport of auxin; causing abnormalities in growth
   • auxin induces ethylene production
     o therefore, some auxin effects may be ethylene effects

2) Membrane permeability - increases

3) Respiration - increases

4) Cell elongation – decreases

5) Aerenchyma formation
   • naturally occurring in stems and roots on aquatic plants and halophytes

https://en.wikipedia.org/wiki/Aerenchyma
- induces aerenchyma formation in stems and roots under anaerobic or hypoxic conditions (i.e. under low oxygen or flooded conditions)

Sesbania javanica flooded – stem bursting open with aerenchyma

https://www.researchgate.net/figure/Sesbania-javanica-growing-successfully-in-deep-water-illustrates-the-contribution-of-stem_fig10_308165999

Whole Plant/Organ Effects

6) Fruit ripening
- stimulates climacteric fruits to ripen, ex. banana, pear, avocado, mango, tomato

- gas fruits in warehouses with ethylene using catalytic converters.
7) **Flowering** - triggers flowering in some bromeliads, ex. pineapple
   - Old time method. Bromeliad and apple in plastic bag. See YouTube video [https://www.youtube.com/watch?v=wJeI57TXh5U](https://www.youtube.com/watch?v=wJeI57TXh5U)
   - Old time method – beat pineapple plants with sticks – cannot document
   - Ethylene applied as ethrel to rosette leaves of pineapple
   - FYI, there are many chemicals that can be used to cause pineapple to flower. Calcium carbide, NAA, BOH, acetylene

8) **Flower fading** –
   - Pollination often triggers ethylene production, and the first sign is flower fading
   - Ethylene application causes flower fading

9) **Fruit color** - decreases green, increases other colors
   - Ripening of fleshy fruit often triggers coloration to attract seed dispersal animals.
   - Ethylene can induce coloration of many fruit
     - Can be used to induce **degreening fruit** – example citrus

10) **Flower longevity**
    - Ethylene triggers the climacteric rise and senescence (death) of cut flowers
    - Can be stopped by ethylene inhibitors
      - **Synthesis inhibitors** protects the flower from itself.
      - **Block inhibitors** make the plant “immune” to its ethylene and all other/external sources of ethylene
11) **Seed germination**
   - increases germination of some seeds

12) **Sex expression**
   - favors pistillate flower formation on monoecious plants

13) **Leaf epinasty** (curling and contortion or leaves)
   - causes in herbaceous plants

14) **Flower drop**
   - ethylene will trigger flower drop
   - can be caused by malfunctioning heater

15) **Leaf abscission** (leaf drop) - causes in some plants
- ethylene and abscisic acid are both involved in defoliation of deciduous trees in the fall.
- External sources of ethylene can cause leaf abscission.
  - Such as a malfunctioning heater in greenhouses

**Malfunctioning heater**
- color of flame is orange to yellow
- properly adjusted, the flame is blue
- must be properly vented
- Can you heat a greenhouse with a wood burning stove?

  - can be caused by malfunctioning heater

  ![Improper venting](improper_venting.jpg)

  - yellow flame – beware

  ![Yellow flame](yellow_flame.jpg)
ABSCISIC ACID (ABA)

<table>
<thead>
<tr>
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<th>Synthetic</th>
<th>Structure</th>
<th>Site of Production</th>
</tr>
</thead>
<tbody>
<tr>
<td>abscisic acid</td>
<td>none</td>
<td><img src="image" alt="ABA Structure" /></td>
<td>plastids, especially chloroplast</td>
</tr>
</tbody>
</table>

DISCOVERY AND HISTORY

Historically also called:
- **abscisin** - because early investigators found it caused leaf abscission
- **dormin** - because early investigators found it caused dormancy

SYNTHESIS

mevalonate $\rightarrow$ farnesyl pyrophosphate $\rightarrow$ ABA

EFFECTS

1) **Dormancy** - causes bud or seed dormancy
2) **Leaf abscission** (leaf drop) - may cause in some plants
3) **Stoma** - causes stoma to close (a response to drought stress)

Whole Plant/Organ Effects – Practical uses? really none.
**Brassinosteroid**

**Effects:**
- pollen tube growth
- stem elongation
- unrolling/bending grass leaves
- orientation of cellulose microfibrils
- enhanced ethylene production

**Jasmonic Acid**

**Effects:**
- defense mechanisms, promotes antifungal proteins
- growth inhibitor
- inhibit seed and pollen germination
- promotes curling of tendrils
- induces fruit ripening

**Salicylic Acid**

**Effects:**
- blocks ethylene synthesis
- induces flowering in some long day plants
- induces thermogenesis in voodoo lily
- defense mechanisms, promotes antifungal proteins

**Polyamines**

**Effects:**
- elicit cell division, tuber formation, root initiation, embryogenesis, flower development and fruit ripening
- may not have a truly hormonal role; rather participate in key metabolic pathways essential for cellular functioning.
Light Responses and Light Signalling

Phytochrome – Red and Far Red Light Responses

**Two Forms of Phytochrome (interconvertible by light)**

- **Pr**
  - red light - 660 nm
  - far red light - 730 nm
  - dark reversion ≈ 3 hr
  - decay

**Effects:**
- Germination of light requiring seeds
- Photoperiodic plants sense the time of sunrise and sunset.
  - Allows regulation of daily rhythms, called circadian rhythms
  - Nyctinasty events, e.g. nights
    - leaf rolling/folding
    - photoperiodic nighttime events/processes.

Blue-Light Responses

**Effects:**
- Chloroplast movement
- Stomatal opening and guard cell functioning.
- Regulates some gene expression.
- Sun tracking of leaves
- Phototropism and asymmetrical bending
- Inhibits stem elongation – especially right after a seedling emerges from the soil.