Plant Hormones & cell signal transduction

Chemical Signals Regulating Plant Growth, Development, and Stress Responses

1. **Concepts and Classification of Plant Hormones**
   Definitions, characteristics, biosynthesis, transport, and signaling principles
2. **Physiological Functions of Major Plant Hormones**
   Auxin, gibberellins, cytokinins, abscisic acid, ethylene, and brassinosteroids
3. **Plant Growth Regulators and Agricultural Applications**
   Hormone analogs, biosynthesis inhibitors, growth retardants, ripening regulators, and stress-management applications

Plant Growth Substances

Plant growth substances (植物生长物质) are physiologically active compounds that regulate plant growth, development, reproduction, senescence, and stress responses.

Plant growth substances

- **Plant hormones / phytohormones 植物激素**
- **Plant growth regulators, PGRs 植物生长调节剂**

What Are Plant Hormones?

Plant hormones, also called **phytohormones** (植物激素), are naturally occurring signaling molecules produced by plants that regulate growth, development, reproduction, and stress responses, usually at very low concentrations.

- **Produced by plant cells or tissues**
- **Active at low concentrations**
- **May act locally or after transport**
- **Effects are concentration-dependent and tissue-specific**
- **Interact through hormone crosstalk (激素互作)**
- **Regulate gene expression, enzyme activity, membrane transport, cell division, elongation, differentiation, and senescence**

What Are Plant Hormones?

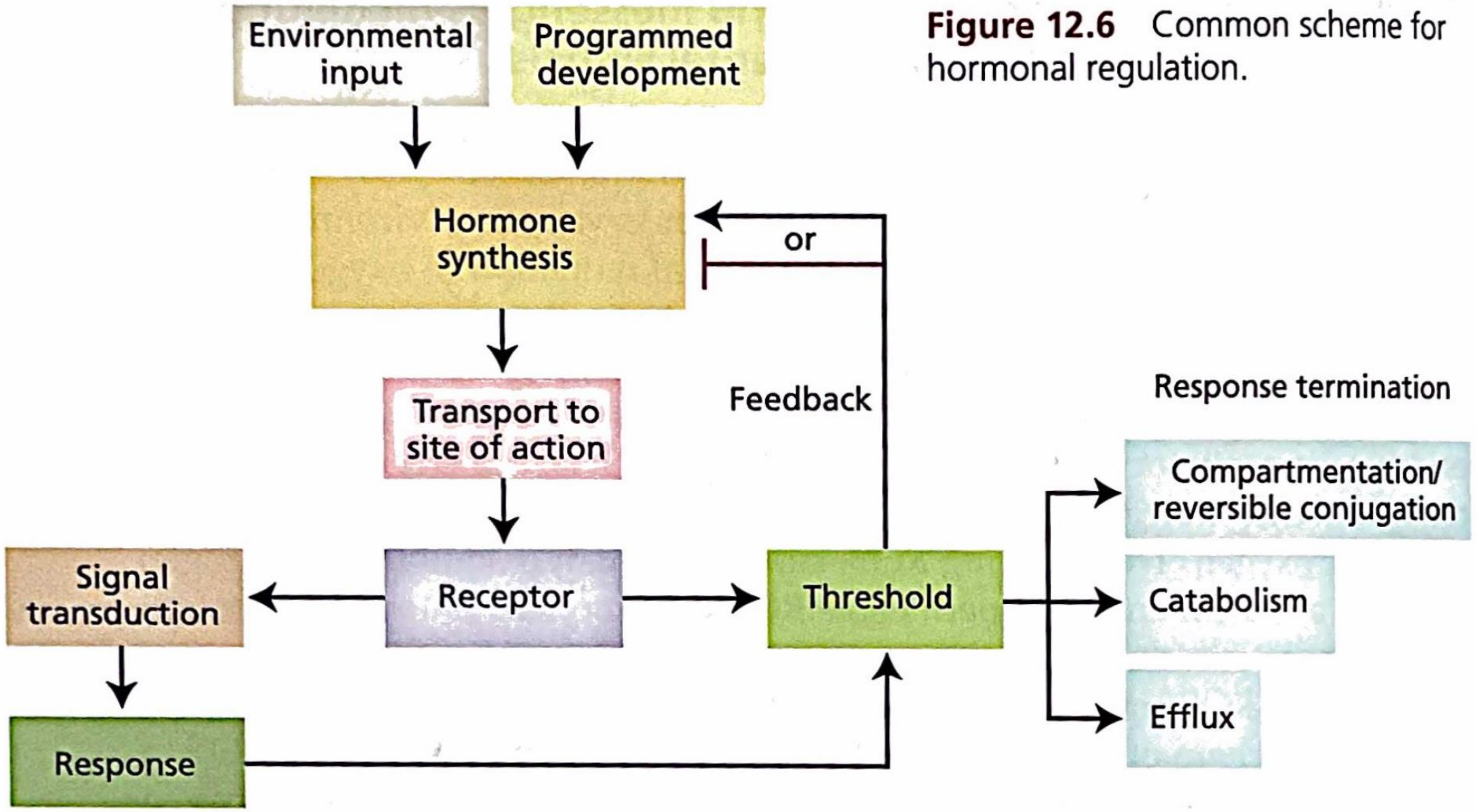


Figure 12.6 Common scheme for hormonal regulation.

What Are Plant Hormones?

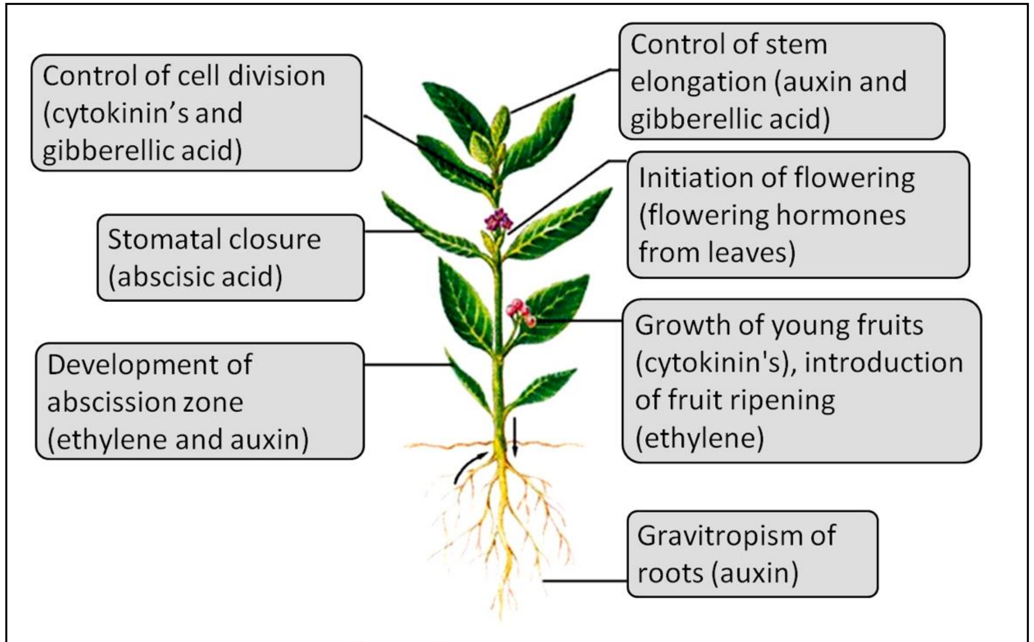
Major hormone

- ❖ Auxins (生长素类)
- ❖ Gibberellins, GAs (赤霉素类)
- ❖ Cytokinins, CKs (细胞分裂素类)
- ❖ Abscisic acid, ABA (脱落酸)
- ❖ Ethylene, ET (乙烯)
- ❖ Brassinosteroids, BRs (油菜素甾醇类)

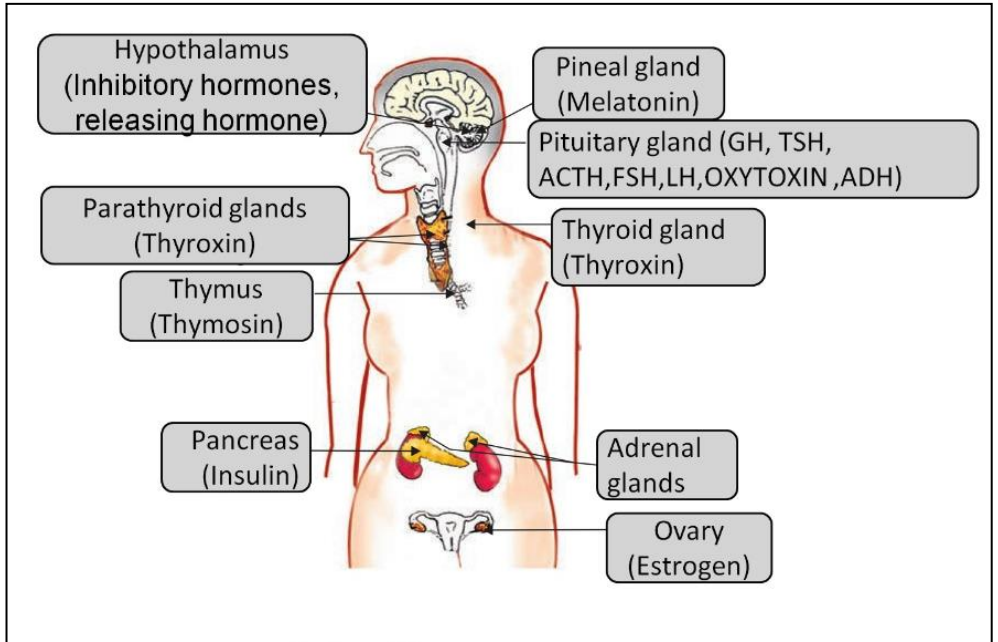
Other plant signaling hormones

- ❖ Jasmonates, JAs (茉莉酸类)
- ❖ Salicylic acid, SA (水杨酸)
- ❖ Strigolactones, SLs (独脚金内酯类)
- ❖ Peptide hormones (肽类激素)

Plant Hormones vs Animal Hormones



Plant hormones



Animal hormones

Plant hormones generally lack dedicated endocrine glands, but their biosynthesis can be enriched in specific tissues or developmental zones.

Plant growth regulators

Natural or synthetic compounds applied externally to regulate plant growth and development.

- **Hormone analogs (激素类似物)**
- **Biosynthesis inhibitors (生物合成抑制剂)**
- **Transport inhibitors (运输抑制剂)**
- **Growth retardants (生长延缓剂)**
- **Ripening and senescence regulators (成熟与衰老调节剂)**

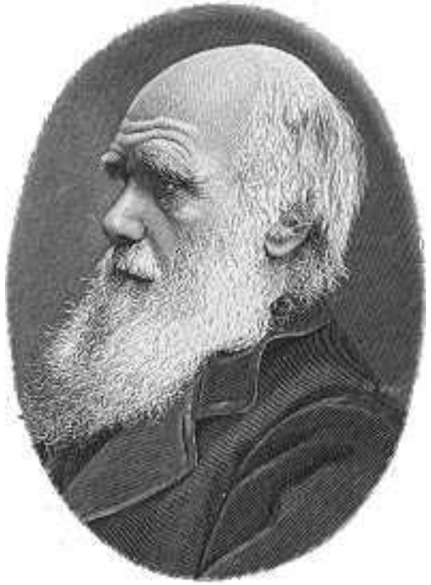
Plant Hormones vs Plant Growth Regulators

Feature	Plant hormones	Plant growth regulators
Origin	Endogenous	Usually applied externally
Chemical nature	Natural signaling molecules	Natural or synthetic compounds
Function	Regulate internal developmental and stress programs	Modify growth or development for research or agricultural purposes
Examples	IAA, GA_3, zeatin, ABA, ethylene, brassinolide	NAA, IBA, 2,4-D, ethephon, paclobutrazol, chlormequat chloride, 1-MCP

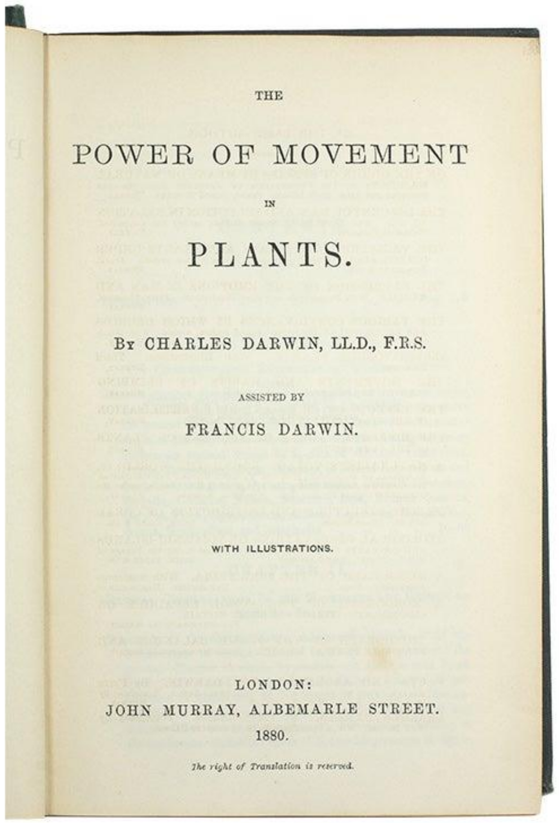
Auxins (生长素类)

1. Overview of Auxins
2. Biosynthesis, Catabolism, Transport, and Distribution
3. Physiological Effects
4. Mechanisms of Action

Discover of Auxins



C. Darwin



THE

POWER OF MOVEMENT

IN

PLANTS.

By CHARLES DARWIN, LL.D., F.R.S.

ASSISTED BY

FRANCIS DARWIN.

WITH ILLUSTRATIONS.

LONDON:

JOHN MURRAY, ALBEMARLE STREET.

1880.

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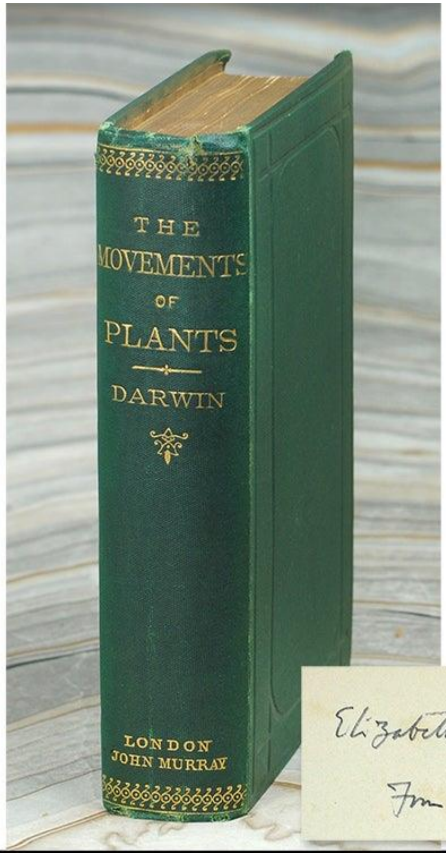
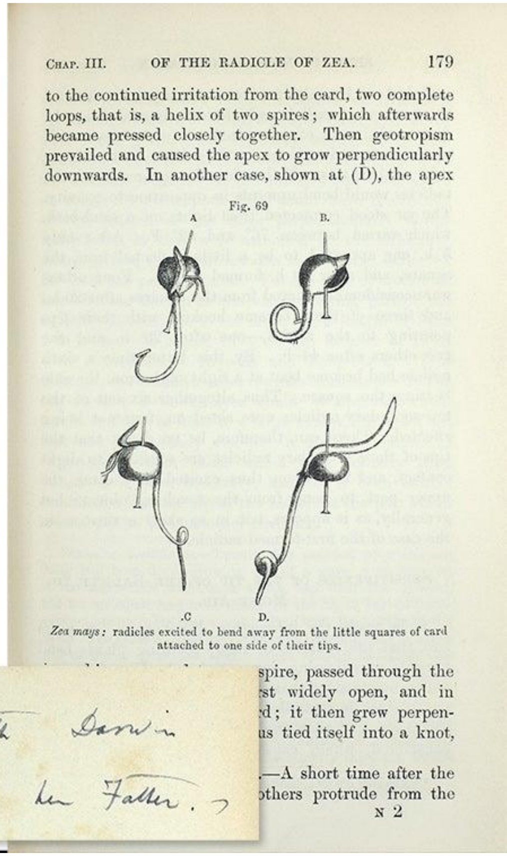




CHAP. III. OF THE RADICLE OF ZEA. 179

to the continued irritation from the card, two complete loops, that is, a helix of two spires; which afterwards became pressed closely together. Then geotropism prevailed and caused the apex to grow perpendicularly downwards. In another case, shown at (D), the apex

Fig. 69

A. B.

C. D.

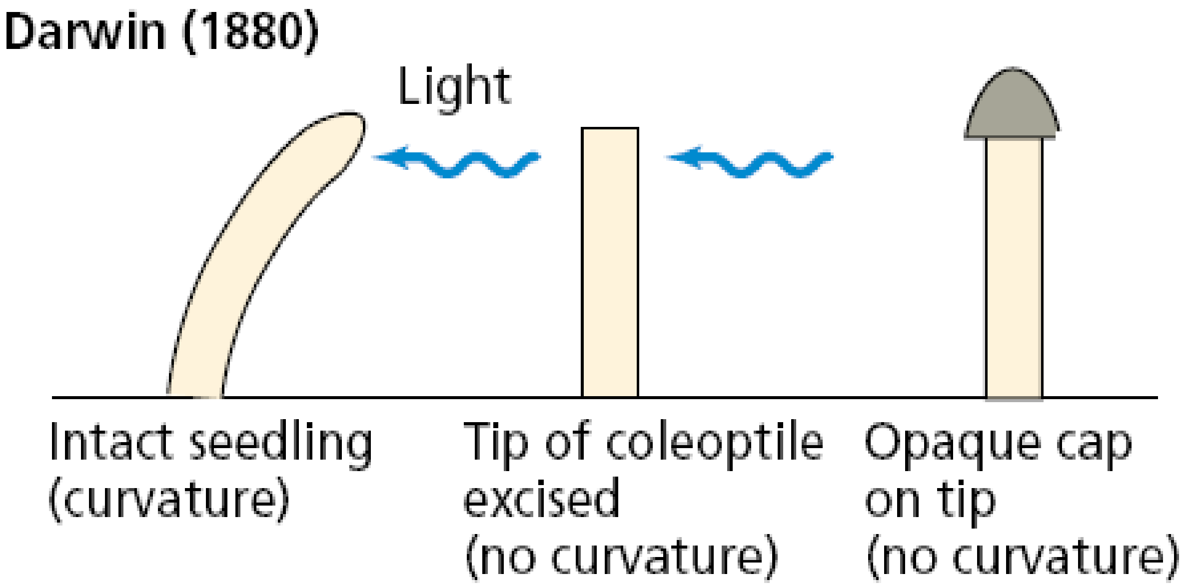
Zea mays: radicles excited to bend away from the little squares of card attached to one side of their tips.

spire, passed through the
st widely open, and in
d; it then grew perpen-
us tied itself into a knot,

—A short time after the
others protrude from the
N 2

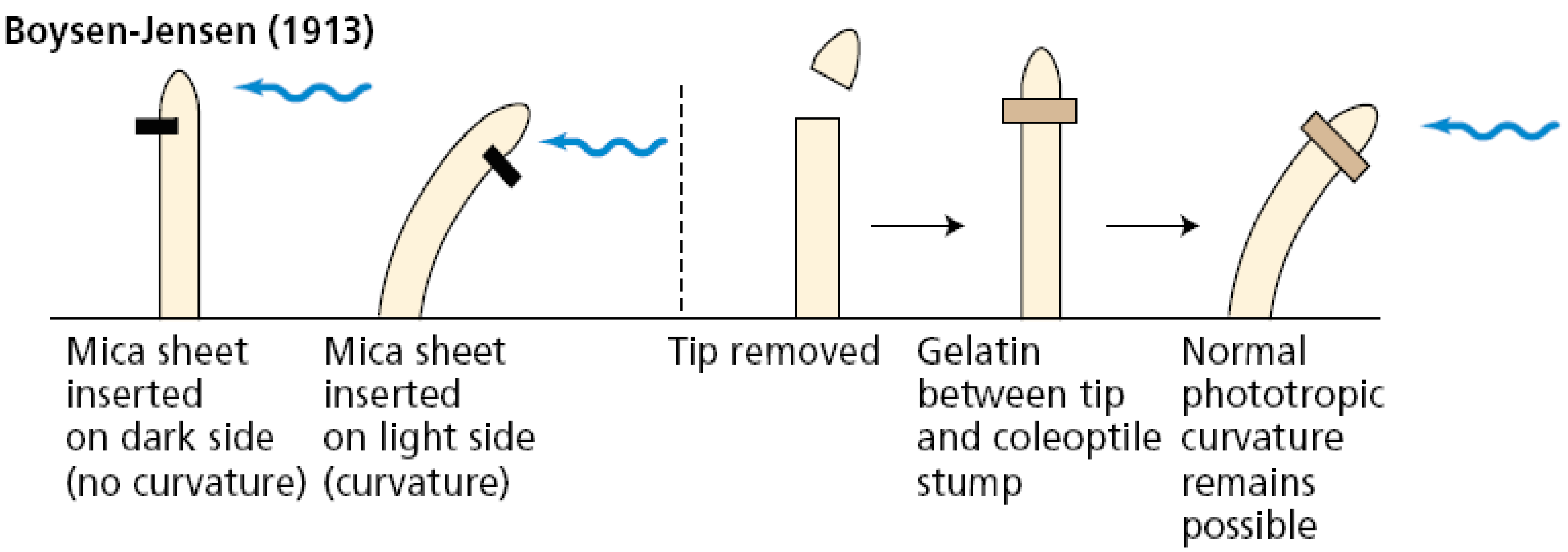
Discover of Auxins

Charles Darwin and Francis Darwin showed that coleoptiles of canary grass (金丝雀虉草) bend toward unilateral light only when the tip is intact and exposed to light.



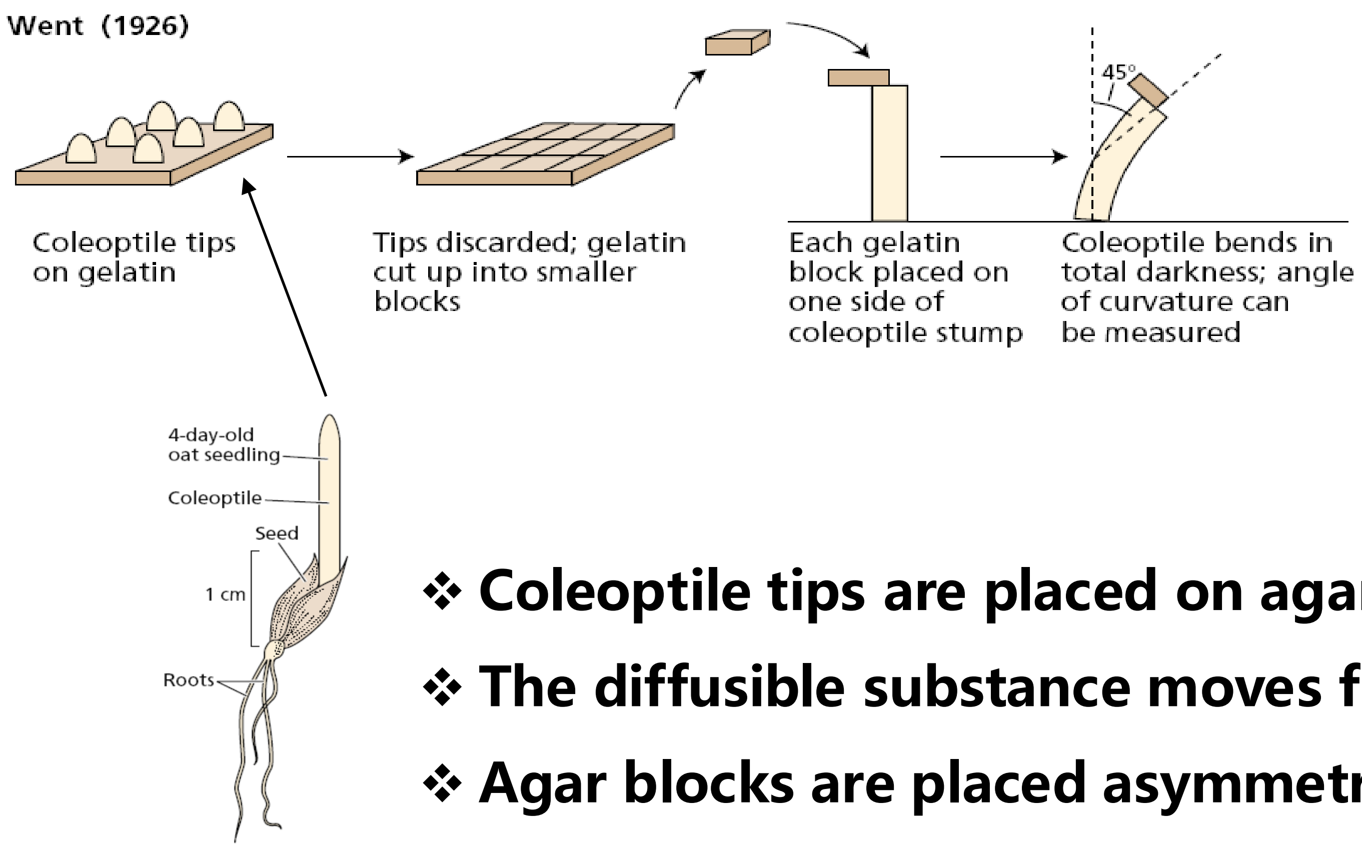
The light-perception site is located in the coleoptile tip (胚芽鞘尖端), but growth curvature occurs in the elongation zone below the tip.

Discover of Auxins



Boysen-Jensen demonstrated that the coleoptile tip produces a mobile chemical signal (可移动化学信号) that travels from the tip to the elongation zone.

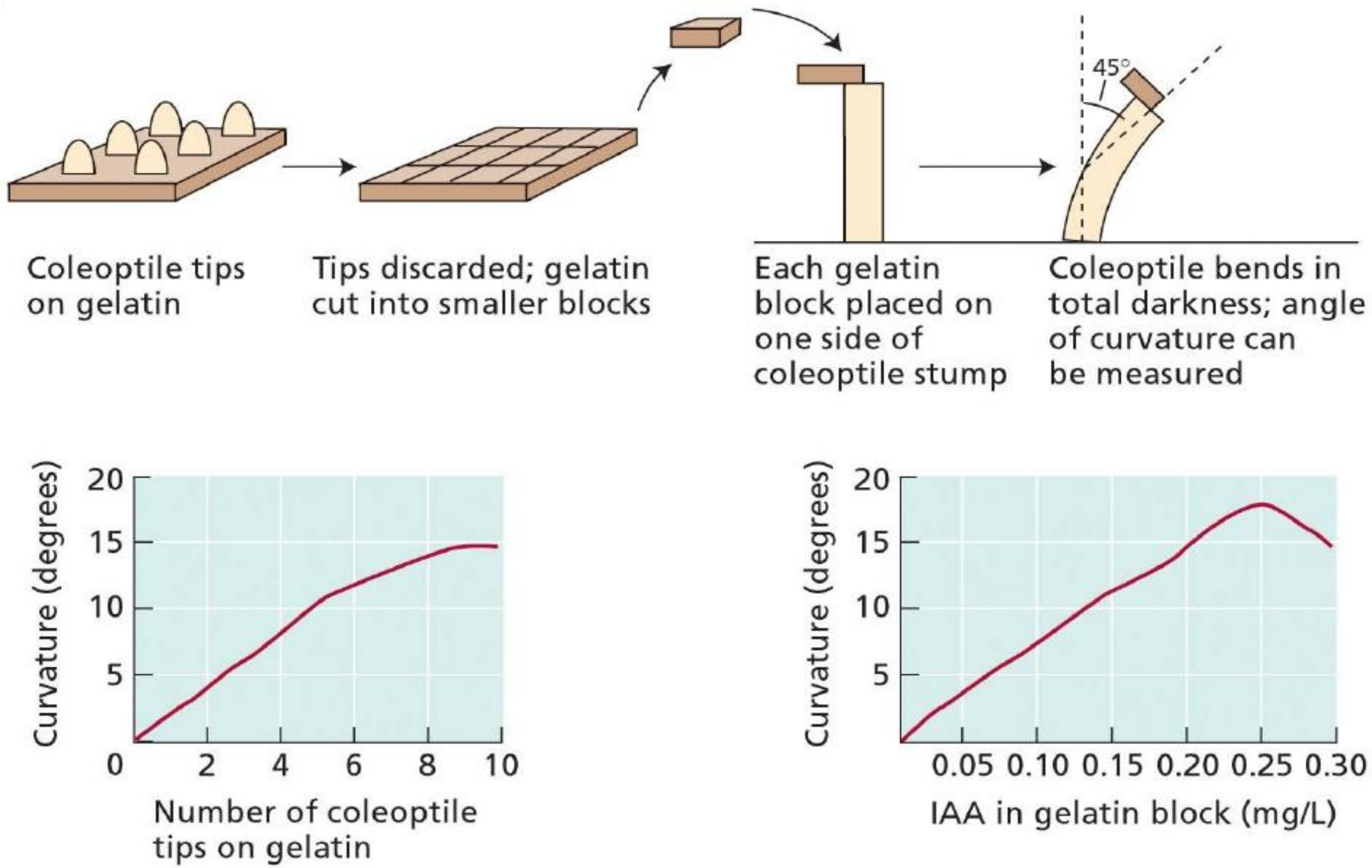
Discover of Auxins



The growth-promoting substance was named auxin (生长素), from Greek auxein, meaning “to increase” or “to grow.”

- Coleoptile tips are placed on agar blocks.
- The diffusible substance moves from the tips into the agar.
- Agar blocks are placed asymmetrically on decapitated coleoptile stumps.
- Unequal growth causes curvature.
- Curvature angle provides a bioassay for hormone activity.

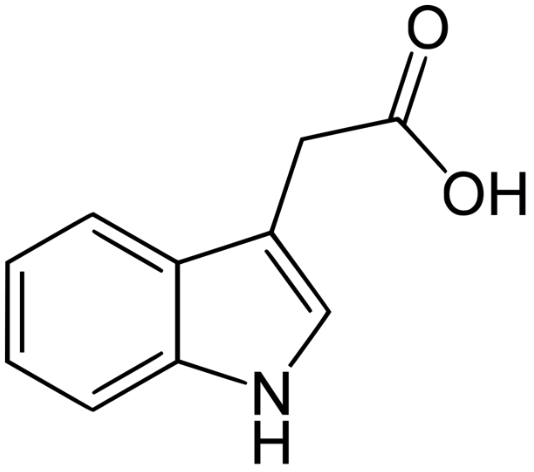
Chemical Identification of Auxin: Indole-3-Acetic Acid

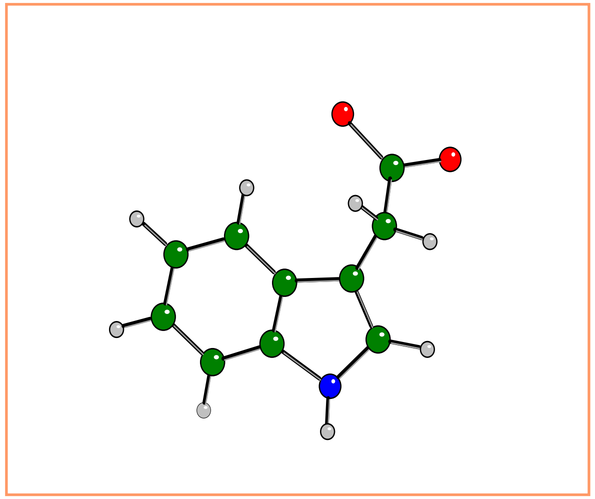


PLANT PHYSIOLOGY, Third Edition, Figure 19.1 (Part 3) © 2002 Sinauer Associates, Inc.

Chemical Identification of Auxin: Indole-3-Acetic Acid

- ❖ In 1934, Kögl and co-workers isolated auxin-like active compounds from human urine, including indole-3-acetic acid, IAA (吲哚-3-乙酸).
- ❖ In 1942, IAA was isolated from plant materials, supporting its status as a naturally occurring plant auxin.

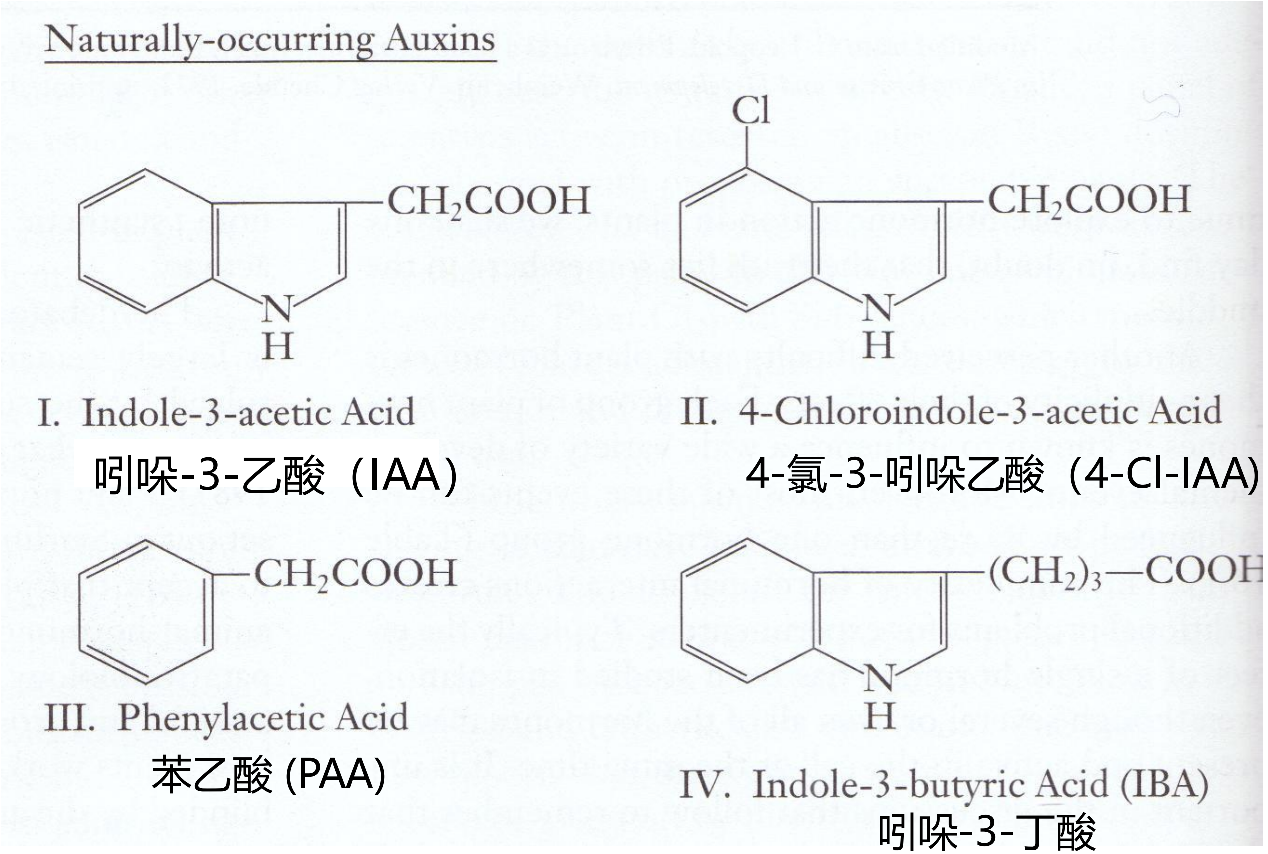




- ❖ **Indole-3-acetic acid, IAA (吲哚-3-乙酸)**
- ❖ **$C_{10}H_9NO_2$**
- ❖ **175.18 g mol^{-1}**

Naturally Occurring Auxins

IAA is usually the dominant endogenous auxin, but multiple naturally occurring auxin-like compounds contribute to auxin biology in specific taxa, tissues, or developmental contexts.



吲哚-3-乙酸（IAA）

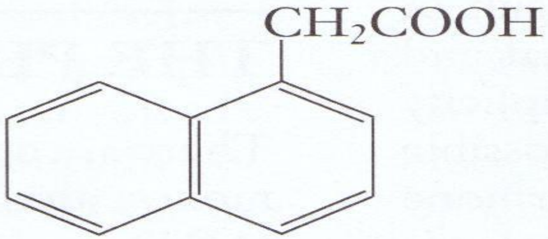
4-氯-3-吲哚乙酸（4-Cl-IAA)

苯乙酸 (PAA)

吲哚-3-丁酸

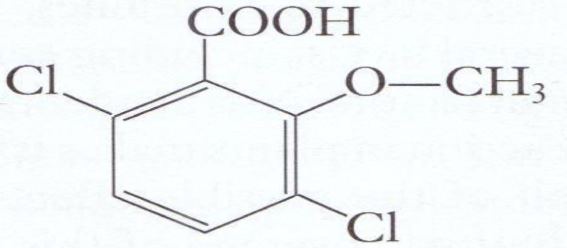
Synthetic Auxins and Auxin-Type Growth Regulators

Synthetic Auxins



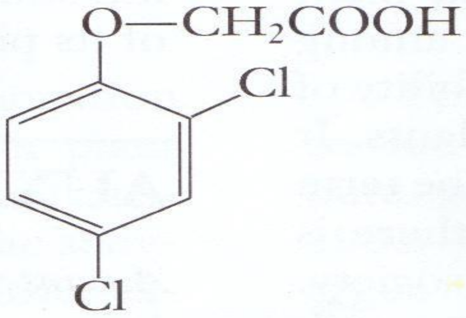
V. Naphthalene acetic Acid

奈乙酸

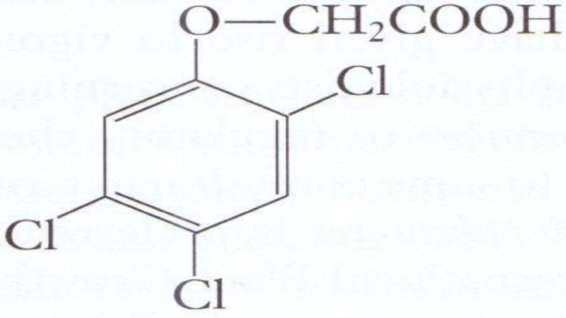


VI. 2-Methoxy-3,6-dichloro-benozic Acid (dicamba)

2-甲基氧-3，6-二氯苯甲酸



VII. 2,4-Dichlorophenoxyacetic Acid (2,4-D)



VIII. 2,4,5-Trichlorophenoxy-acetic Acid (2,4,5-T)

2，4-二氯苯氧乙酸

2，4，5 –三氯苯氧乙酸

Synthetic Auxins and Auxin-Type Growth Regulators

Synthetic auxins (人工合成生长素) are auxin-like compounds designed or used to mimic, enhance, or perturb auxin responses.

1. **Indole-ring auxins (吲哚环类)**
   Examples: IAA, IBA
   Common feature: indole ring with an acidic side chain.

2. **Naphthalene-ring auxins (萘环类)**
   Examples: NAA, naphthoxyacetic acid
   Widely used for rooting, fruit thinning, and fruit set regulation.

3. **Phenoxyacetic acid auxins (苯氧乙酸类)**
   Examples: 2,4-D; 2,4,5-T
   Strong synthetic auxins; some are used as herbicides.

4. **Benzoic acid auxins (苯甲酸类)**
   Examples: dicamba
   Often used as selective herbicides.

Auxins (生长素类)

1. Overview of Auxins
2. Biosynthesis, Catabolism, Transport, and Distribution
3. Physiological Functions
4. Mechanisms of Action

Auxin Biosynthesis, Metabolism, Transport, and Distribution

- **Biosynthesis (生物合成):** production of IAA
- **Metabolism (代谢):** conjugation, deconjugation, and degradation of IAA
- **Transport (运输):** directional auxin movement between cells and tissues
- **Distribution (分布):** formation of local auxin maxima and gradients

These processes together determine where, when, and how auxin regulates plant growth.

Sources and Fates of Endogenous Auxin

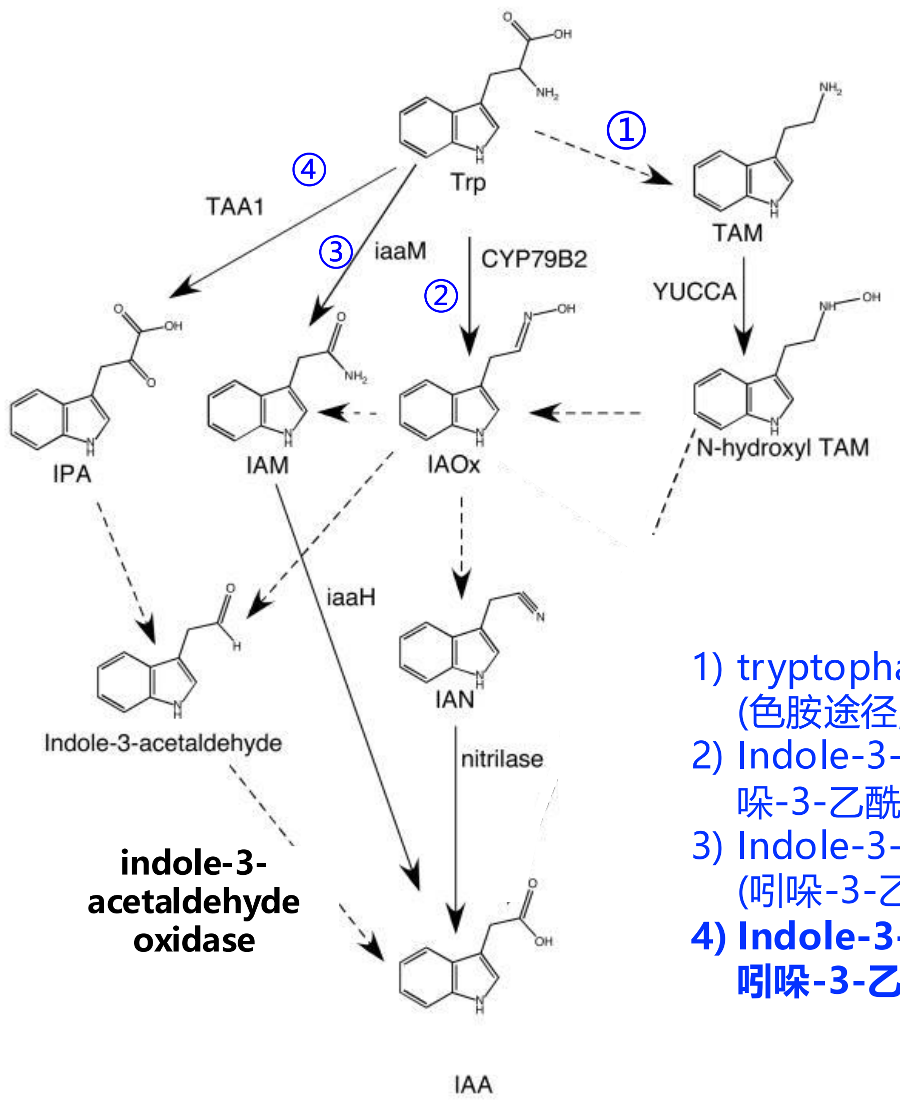
Free active auxin, mainly IAA, comes from:

- ❖ **De novo biosynthesis (从头合成) from precursor molecules**
- ❖ **Deconjugation (解偶联) of stored IAA conjugates**
- ❖ **Transport (运输) from auxin-producing tissues**

Major Sites of Auxin Biosynthesis

- ❖ **Auxin is synthesized mainly in actively growing tissues:**
  - ✓ Shoot apical meristems (茎端分生组织)
  - ✓ Young expanding leaves (幼嫩叶片)
  - ✓ Developing seeds and fruits (发育中的种子和果实)
  - ✓ Root tips (根尖)
- ❖ **Mature leaves generally have much lower rates of auxin biosynthesis.**
- ❖ **Local IAA synthesis contributes to organ initiation, vascular development, root growth, and embryo patterning.**

IAA Biosynthesis Pathway



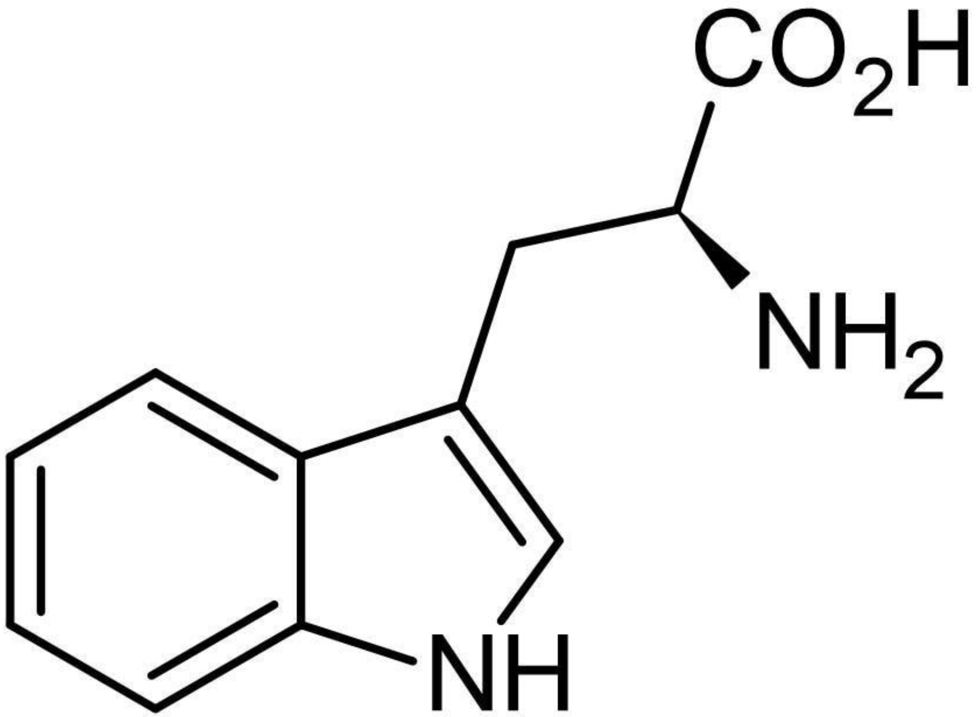
1) tryptophan-dependent pathway (色胺途径, TAA/YUC)
2) Indole-3-acetamide pathway (吲哚-3-乙酰胺途径, IAM)
3) Indole-3-acetaldoxime pathway (吲哚-3-乙醛肟途径, IAOx)
4) **Indole-3-acetonitrile pathway (吲哚-3-乙腈途径, IAN)**

Trp: 色氨酸
TAM: 色胺
YUCCA: 类黄素单加氧酶
N-hydroxyl TAM: N-羟基色胺
IAOx: 吲哚-3-乙醛肟
IAN: 吲哚-3-乙腈
nitrilase: 腈水解酶
IAA: 吲哚-3-乙酸
iaaM: 色氨酸单加氧酶
IAM: 吲哚-3-乙酰胺
iaaH: 吲哚乙酰胺水解酶
TAA1: 色氨酸氨基转移酶
IPA: 吲哚-3-丙酮酸
indole-3-acetaldehyde: 吲哚-3-乙醛
indole-3-acetaldehyde oxidase: 吲哚乙醛氧化酶

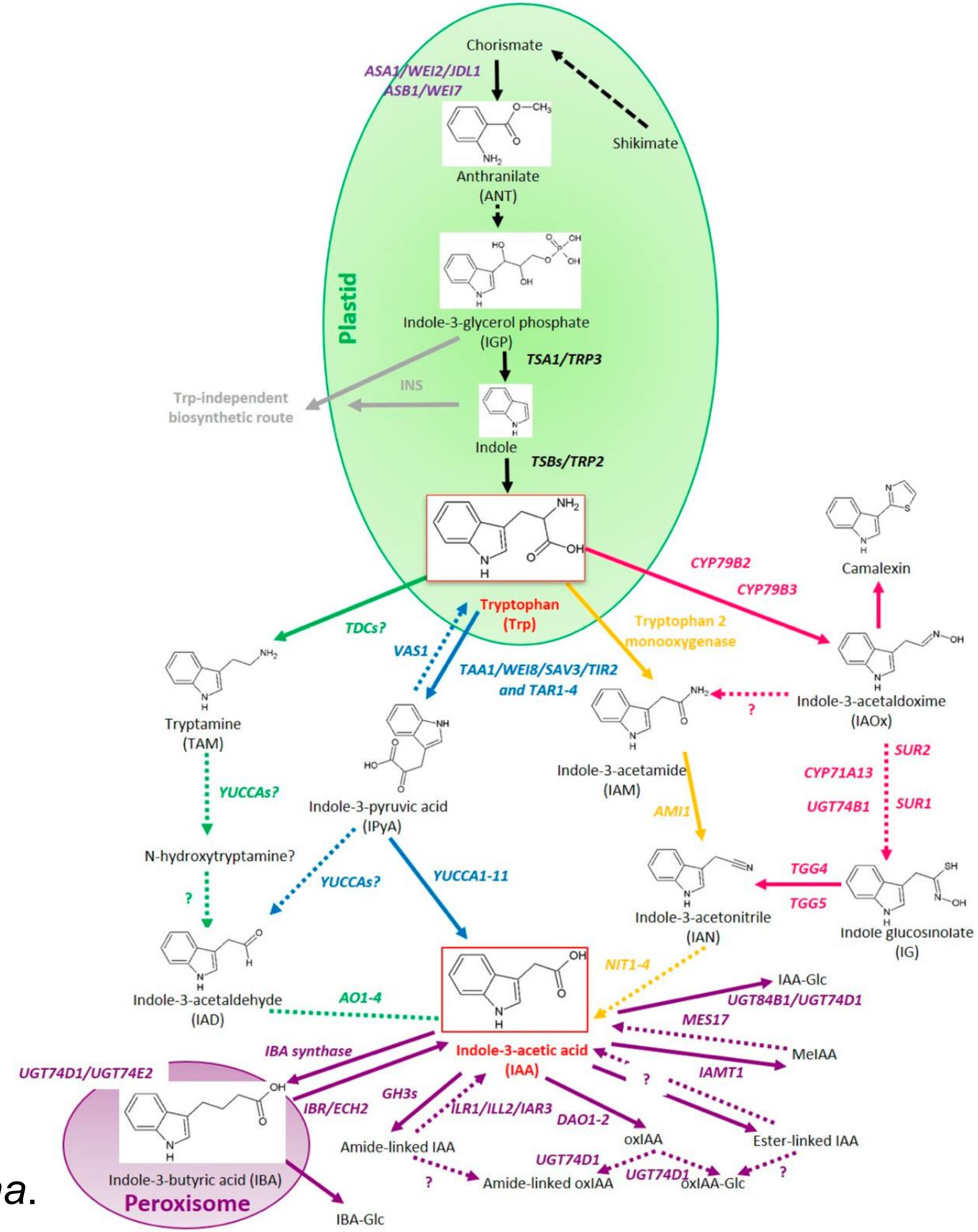
Zhao , 2010

Tryptophan-Dependent IAA Biosynthesis Pathway

- IAA contains an indole ring (吲哚环) and an acetic acid side chain (乙酸侧链).
- The most important precursor for IAA biosynthesis is tryptophan (色氨酸, Trp).
- Some plants also contain tryptophan-independent routes, but these are less well defined.



IAA Biosynthesis Pathway



Auxin biosynthetic pathways in *Arabidopsis thaliana*.

Auxin Degradation and Inactivation

❖IAA can be inactivated by oxidation (氧化)

- **Oxidative degradation (氧化降解)**: DAO dioxygenases (DAO双加氧酶) convert IAA to inactive oxIAA (氧化IAA).
- IAA is also chemically light-sensitive, but **photooxidation (光氧化)** is not the main physiological degradation pathway in intact plants.

Auxin Degradation and Inactivation

Plant cells contain an internal pool of IAA, mainly in the cytosol and chloroplasts.

IAA exists in two major forms:

- **Free IAA (游离IAA):** biologically active auxin.
- **Conjugated IAA (结合IAA):** IAA linked to amino acids, sugars, or peptides.

Conjugated IAA can function as a storage form, transport form, or inactive/degradation-associated form. Some conjugates can be hydrolyzed to release free IAA.

Auxin Degradation and Inactivation

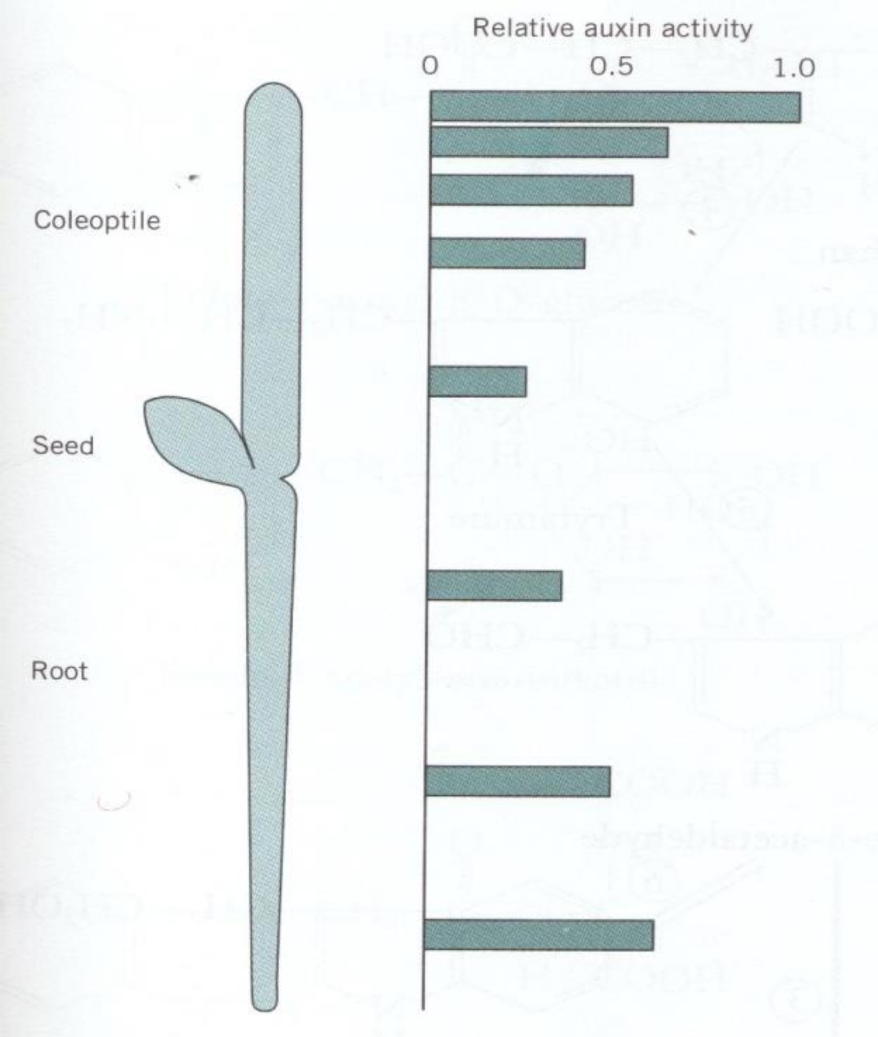
Functions of Auxin Conjugation

- ❖ Storage form (贮藏形式): maintains an inactive reserve of IAA.
- ❖ Transport form (运输形式): some conjugates may move between tissues.
- ❖ Regeneration of free IAA (释放游离IAA): hydrolysis can release active IAA.
- ❖ Detoxification / inactivation (解毒/失活): reduces excess free IAA.
- ❖ Homeostatic control (稳态调控): adjusts the amount of free active auxin.

Auxin Distribution in Plant Tissues

- **Higher auxin activity is often found in:**
  - Shoot apical meristem (茎端分生组织)
  - Young leaves (幼叶)
  - Developing seeds and fruits (发育中的种子和果实)
  - Root tips (根尖)

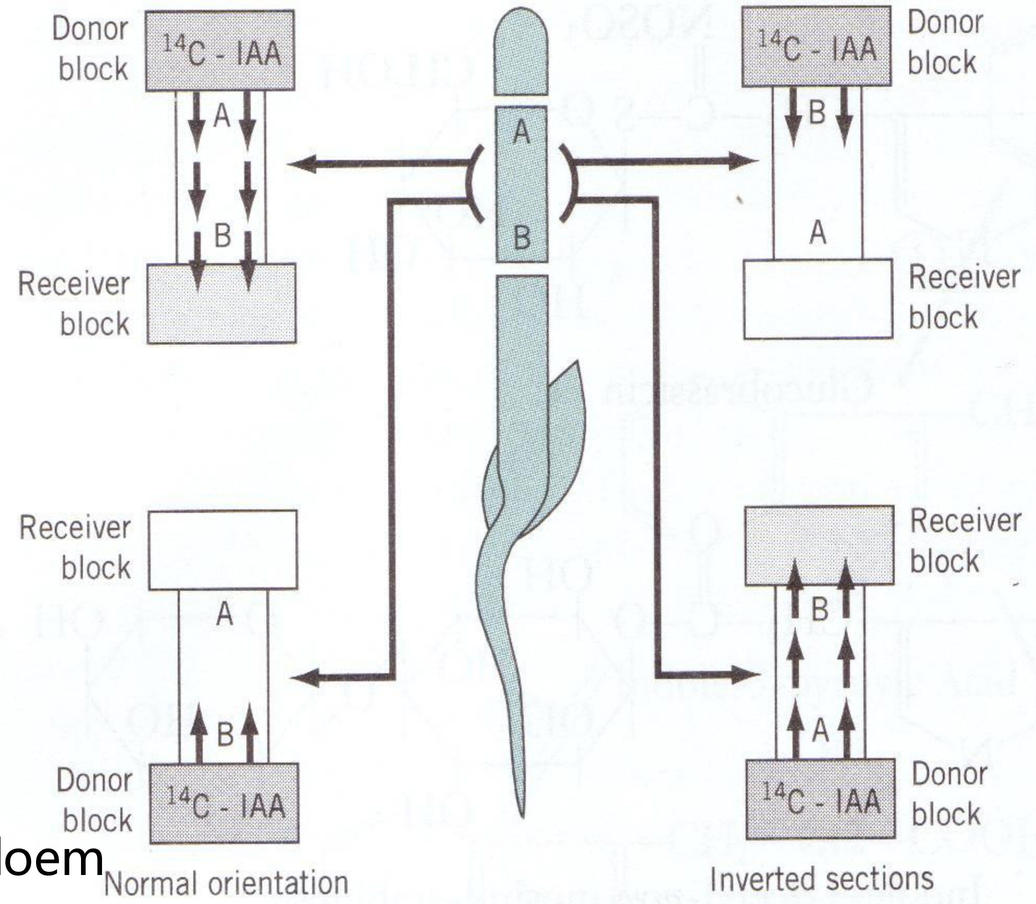
- **Mature or senescing organs generally show lower auxin activity.**
- **Typical IAA levels are low and variable; 10–100 ng/g fresh weight is only an approximate range.**



Auxin Transport

IAA moves through plants by two major transport systems:

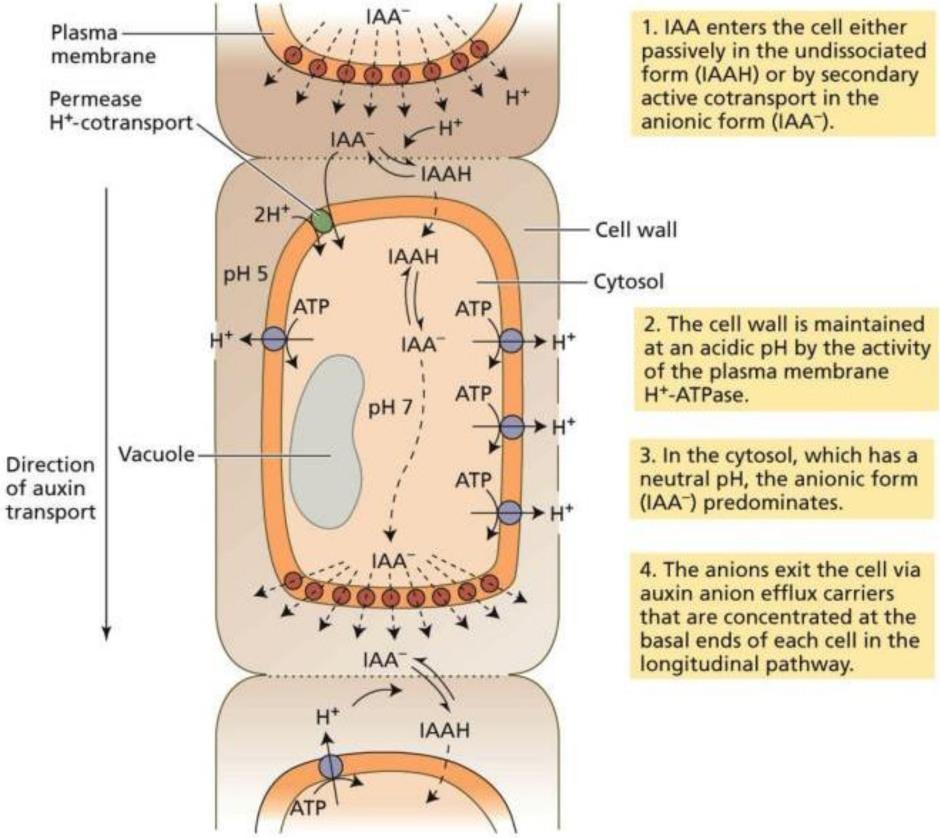
- ❑ **Polar auxin transport (极性生长素运输):**
  - ❖ Directional cell-to-cell movement.
  - ❖ Usually basipetal in shoots, from the shoot apex toward lower tissues.
  - ❖ Depends on asymmetric localization of transport proteins.
- ❑ **Non-polar / long-distance transport (非极性/长距离运输):**
  - ❖ Occurs mainly through vascular tissues, especially phloem (韧皮部).
  - ❖ Can move auxin and auxin-related compounds over longer distances.



Auxin Transport

Chemiosmotic Model of Polar Auxin Transport(化学渗透学说)

- The apoplast (质外体) is acidic, about pH 5.
- Some IAA⁻ becomes protonated IAAH, which can diffuse into the cell.
- In the cytosol (细胞质), near-neutral pH convert IAAH back to IAA⁻.
- IAA⁻ exits mainly through auxin transporters, especially PIN proteins (PIN蛋白).

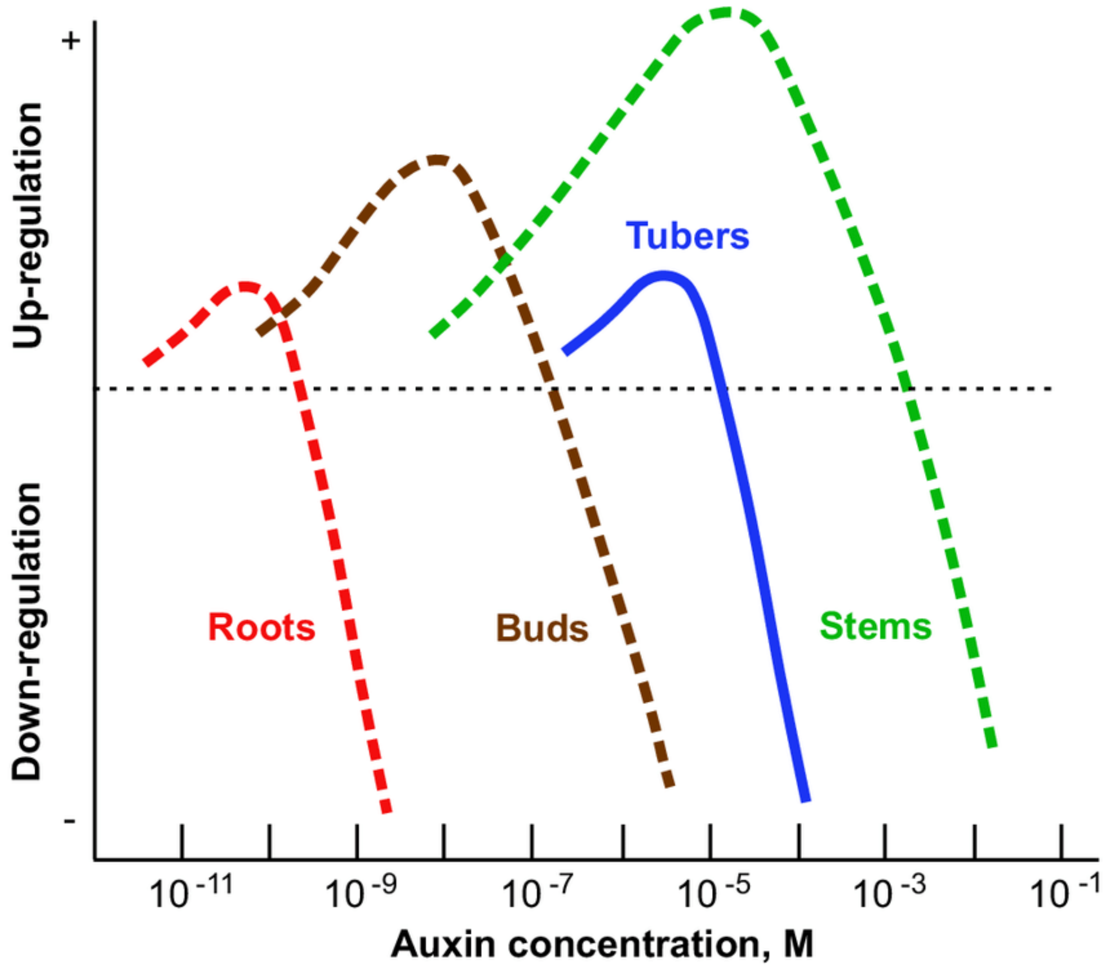


PLANT PHYSIOLOGY, 5e, Figure 19.8

Auxins (生长素类)

1. Overview of Auxins
2. Biosynthesis, Catabolism, Transport, and Distribution
3. **Physiological Functions**
4. **Mechanisms of Action**

1. Regulates Elongation Growth



❖ **Auxin responses are dose-dependent :**

- ✓ Low to moderate auxin promotes elongation.
- ✓ Excess auxin inhibits growth.

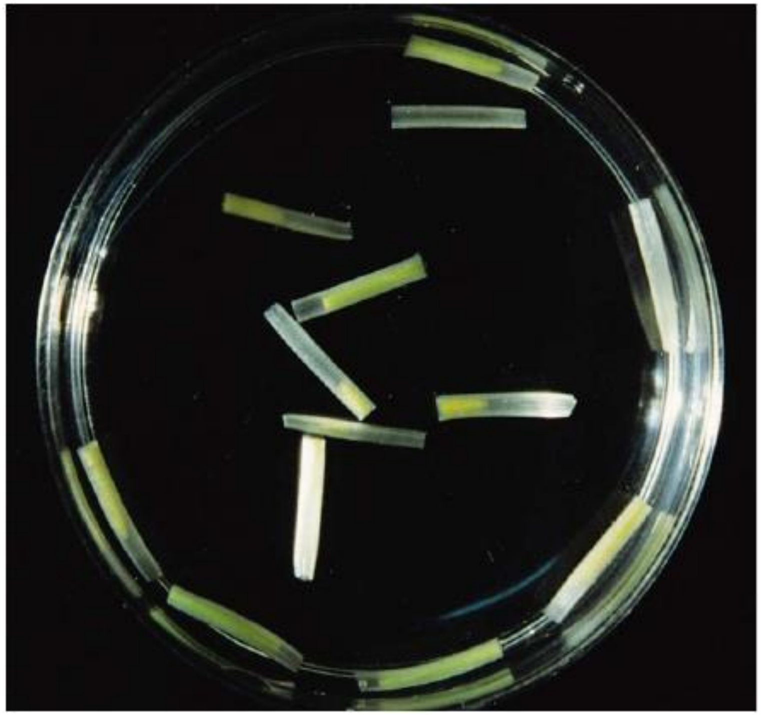
❖ **Different organs have different auxin sensitivity:**

- ✓ Roots (根) are usually the most sensitive.
- ✓ Shoots and coleoptiles (胚芽鞘) often require higher auxin levels.

1. Regulates Elongation Growth

Coleoptile Elongation

Coleoptile segments incubated with IAA elongate more strongly than in water.

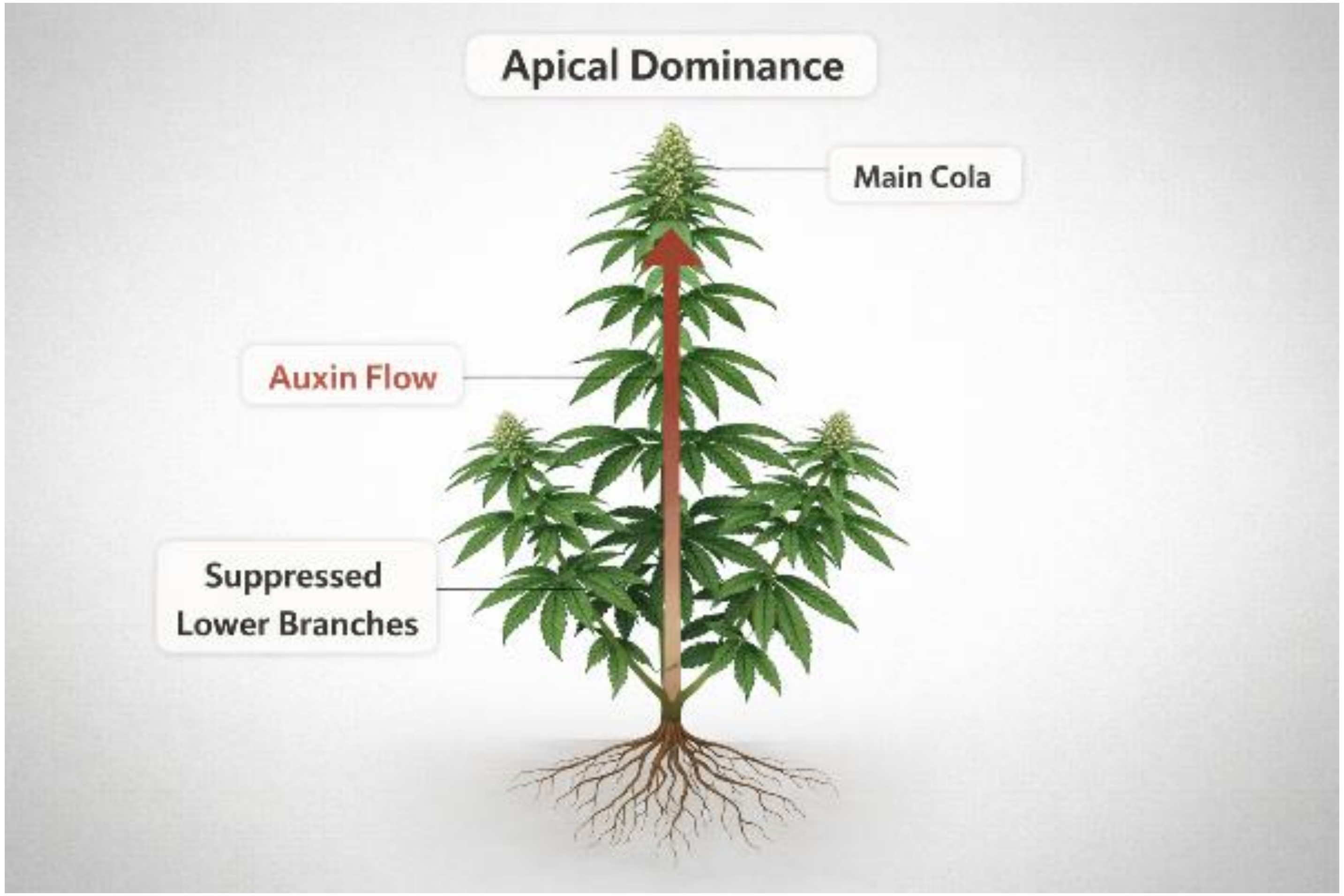


water for 18 hours

+IAA for 18 hours

2. Auxin and Apical Dominance

Apical dominance (顶端优势) is the suppression of axillary bud (腋芽) outgrowth by the shoot apex.

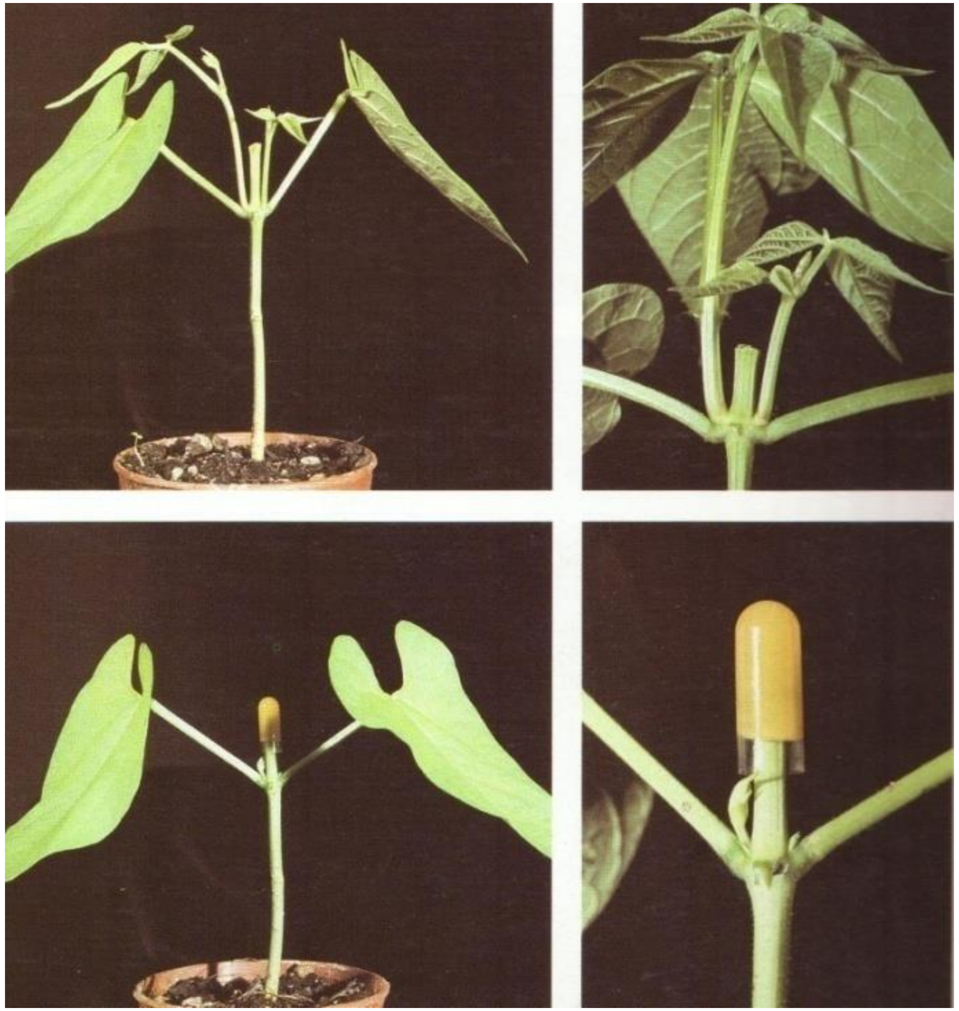


2. Auxin and Apical Dominance

❖ Removing the shoot apex reduces the main source of auxin.

❖ Lateral buds begin to grow after decapitation.

❖ Applying IAA to the cut stump can restore inhibition of bud outgrowth.



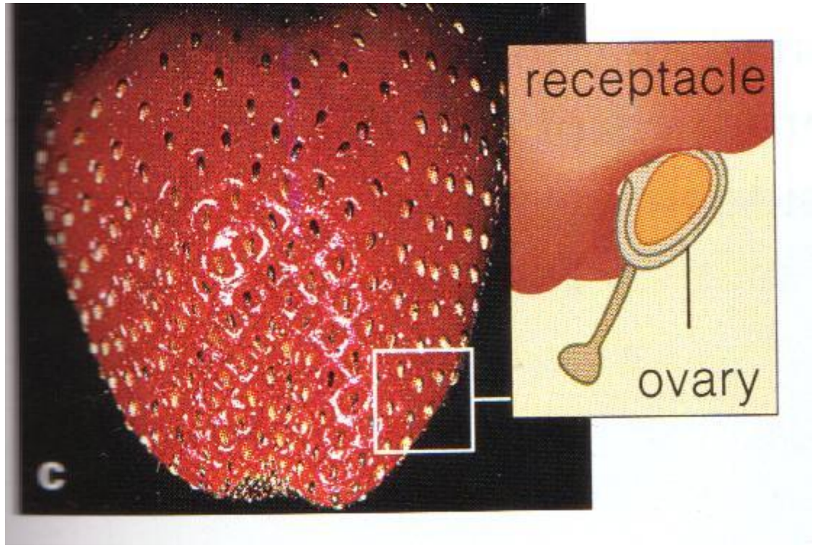
3. Auxin Induces Root Formation

Auxin promotes adventitious root formation (不定根形成) in cuttings.

Auxin: − + − +

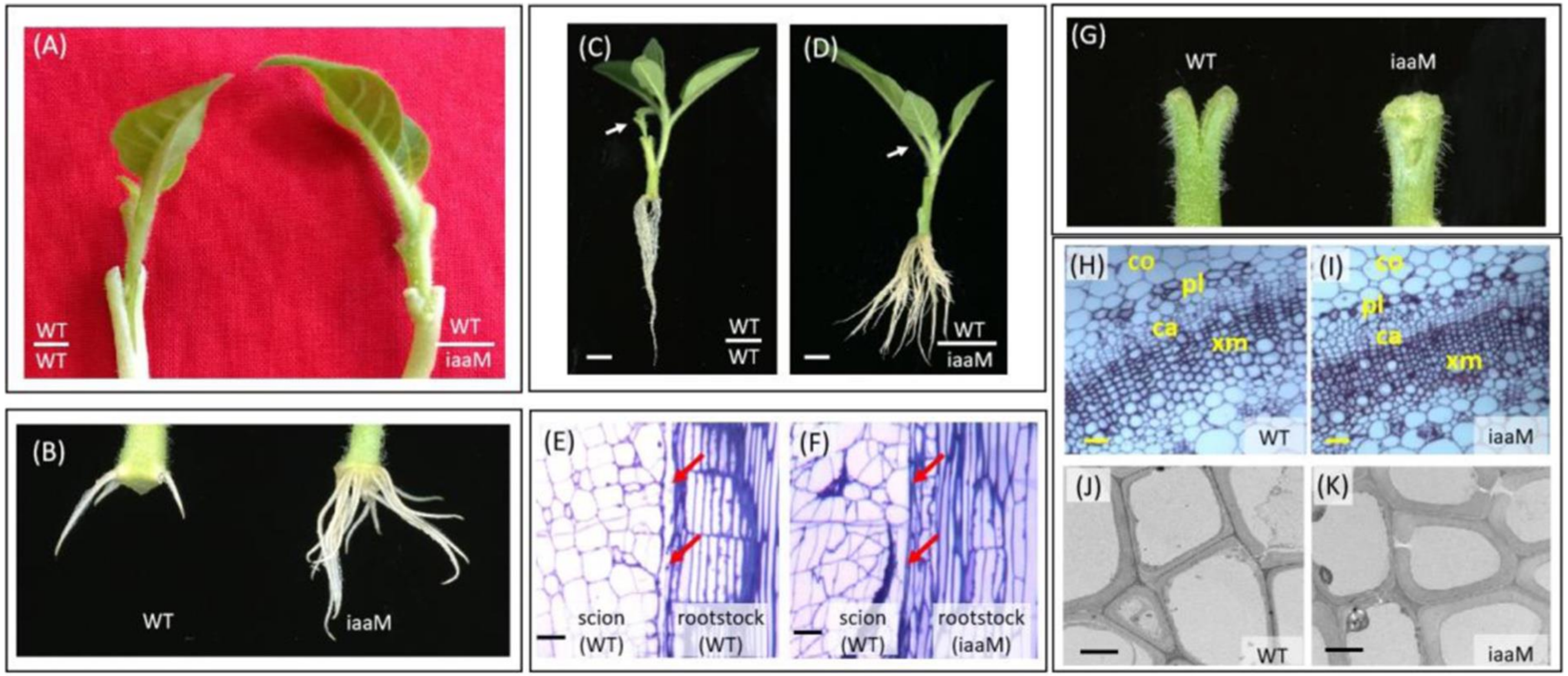
4. Auxin Promotes Fruit Development

+Seeds – Seeds – Seeds+ Auxin



- Developing seeds are major sources of auxin
- Applying auxin can sometimes induce seedless fruit development, called parthenocarpy (单性结实).

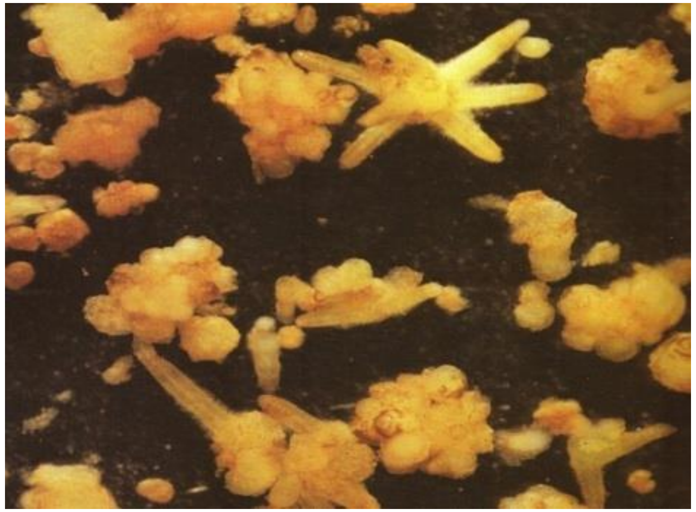
5. Auxin and Cell Differentiation



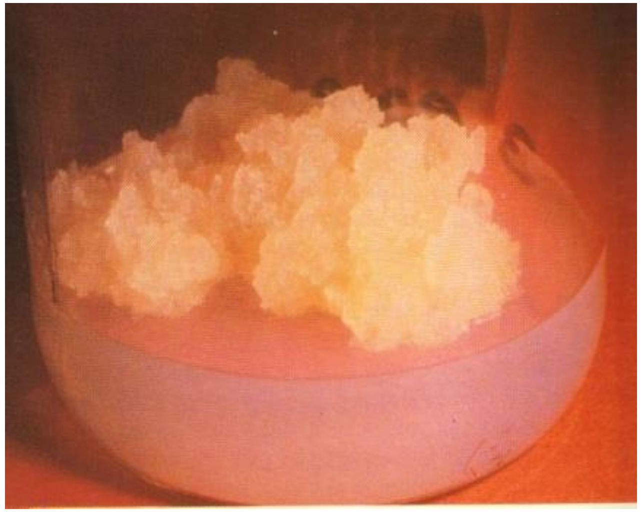
- ❖ **During wound repair, auxin accumulation and polar auxin transport (极性生长素运输) contribute to vascular regeneration (维管组织再生).**
- ❖ **Auxin gradients help guide the formation of xylem (木质部) and phloem (韧皮部).**
- ❖ **Vascular differentiation depends on auxin together with cytokinin (细胞分裂素) and wound-induced signals.**

5. Auxin and Cell Differentiation

CTKs/ Auxins ratio:



High cytokinin / low auxin promotes shoot formation.



Intermediate auxin–cytokinin balance promotes callus (愈伤组织) proliferation.

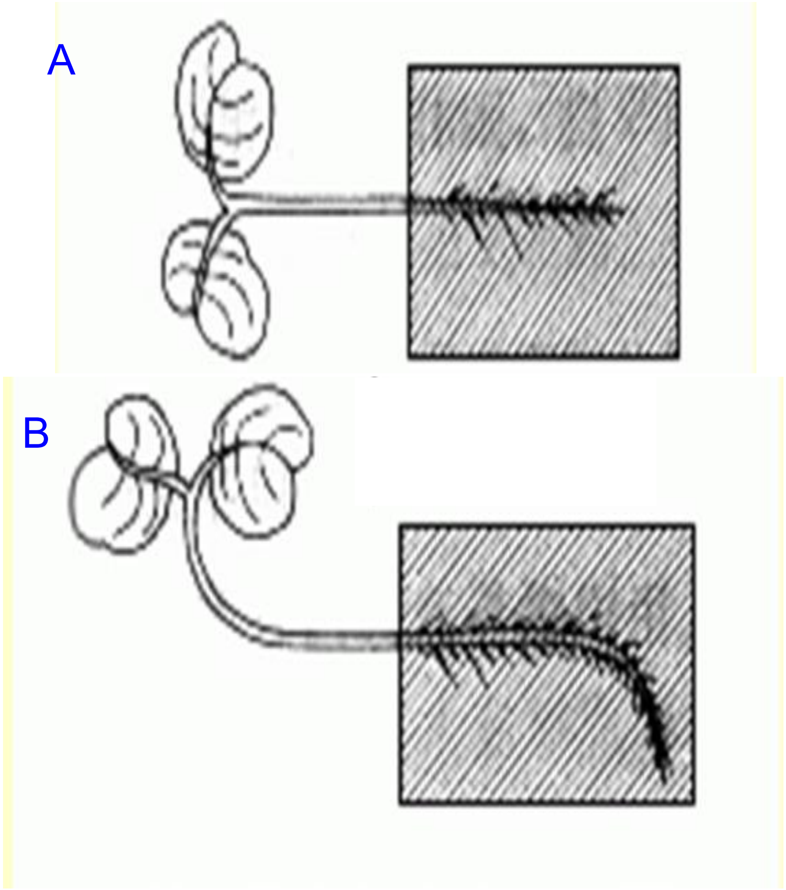
High auxin / low cytokinin promotes root formation.

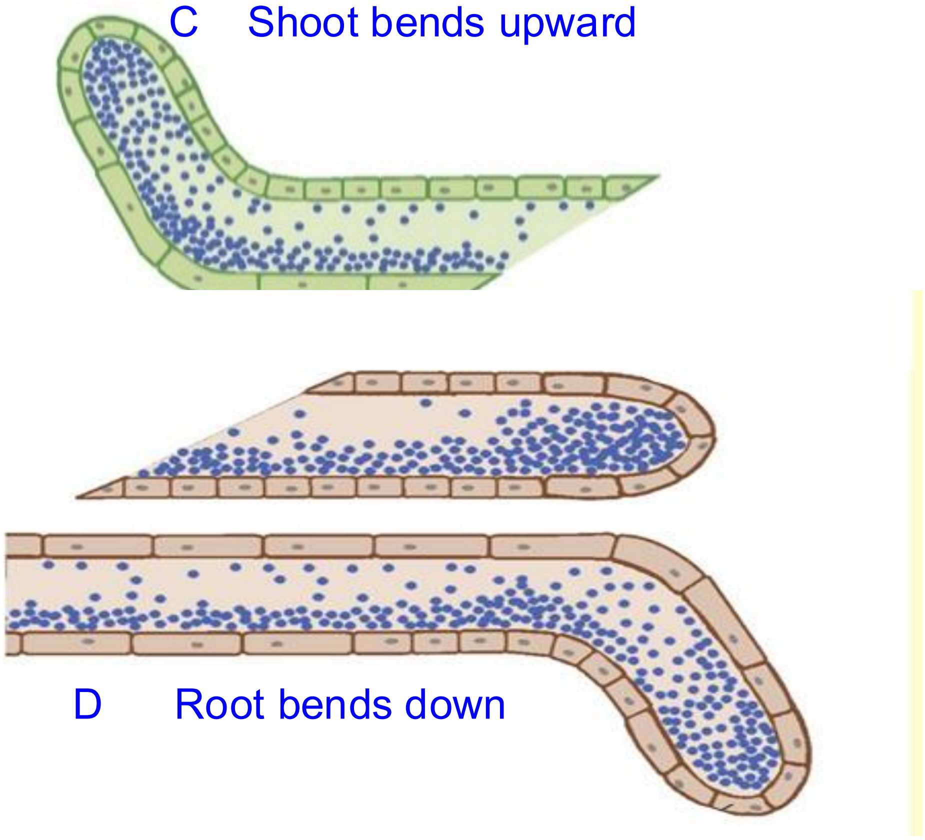
6. Auxin and Tropic Responses

Phototropism (向光性)

6. Auxin and Tropic Responses

Gravitropism (向重力性)





Other Physiological Effects of Auxin

- ❖ **Auxin (生长素) can promote female flower formation in some cucurbits (葫芦科植物), often through interaction with ethylene (乙烯).**
- ❖ **In pineapple (菠萝), auxin-like treatments can induce flowering, partly by increasing ethylene production.**
- ❖ **Auxin usually delays leaf abscission (叶片脱落) by reducing abscission zone sensitivity to ethylene.**
- ❖ **Auxin can increase sink strength (库强度) in developing fruits and seeds.**
- ❖ **…**

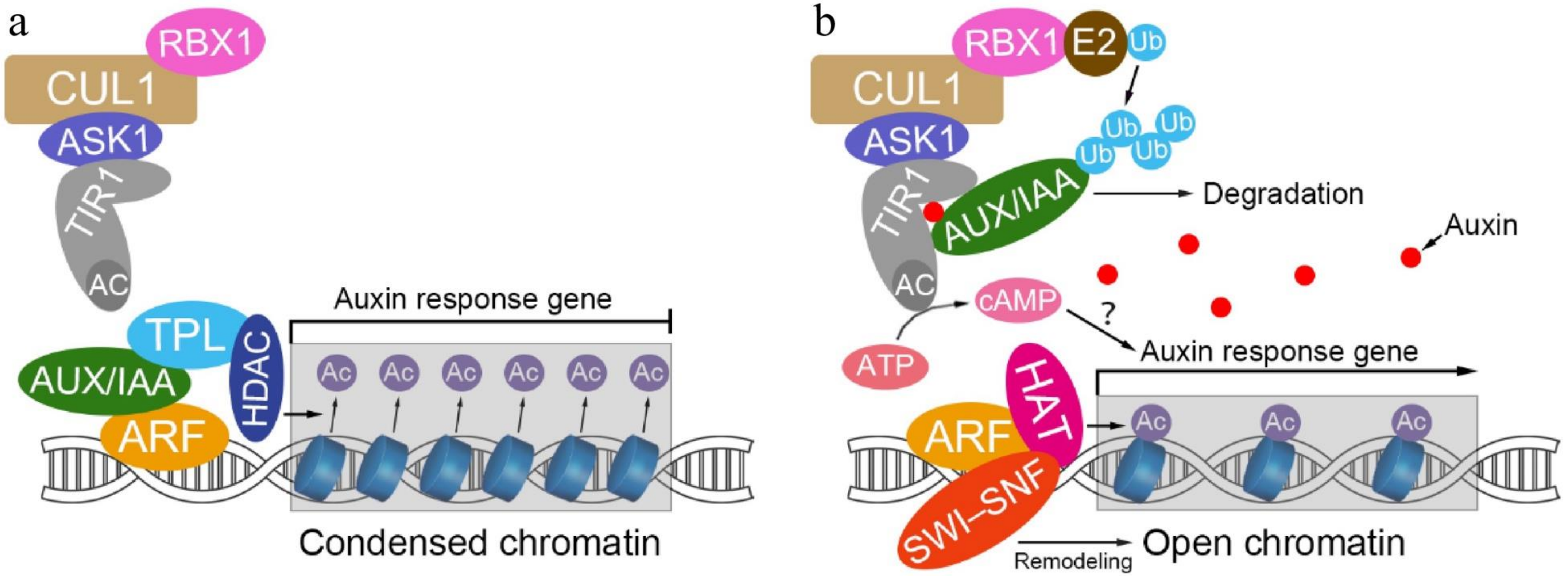
Auxins (生长素类)

1. Overview of Auxins
2. Biosynthesis, Catabolism, Transport, and Distribution
3. Physiological Functions
4. **Mechanisms of Action**

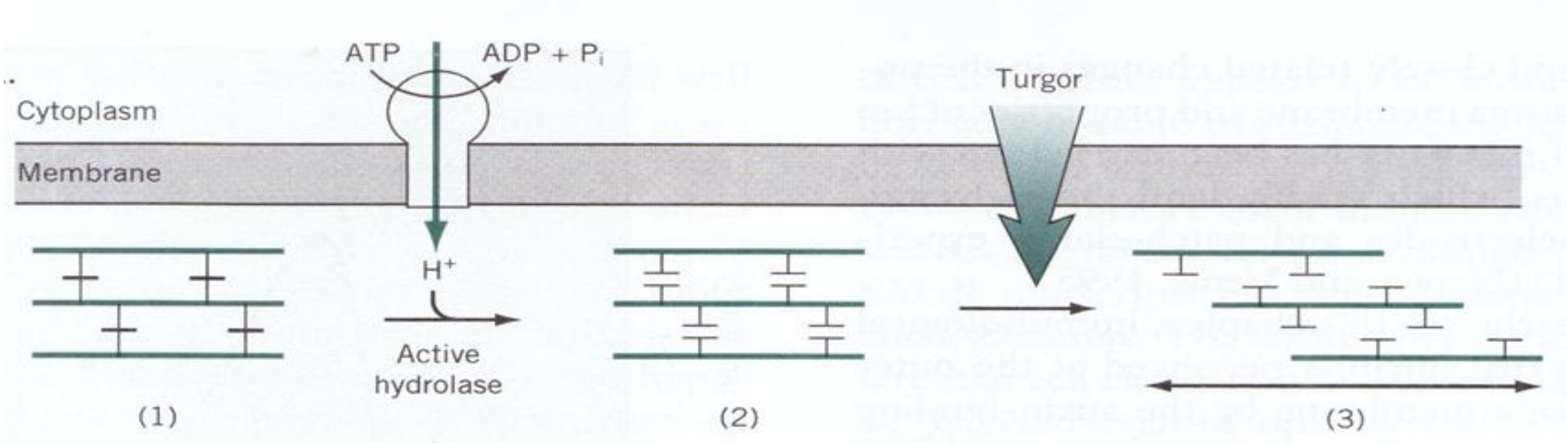
Mechanisms of Auxin Action: Overview

Auxin regulates growth through two major mechanisms:

- ❖ **Rapid cell expansion : explained partly by the acid growth hypothesis (酸生长假说).**
- ❖ **Gene regulation: controlled mainly by the TIR1/AFB–Aux/IAA–ARF pathway.**

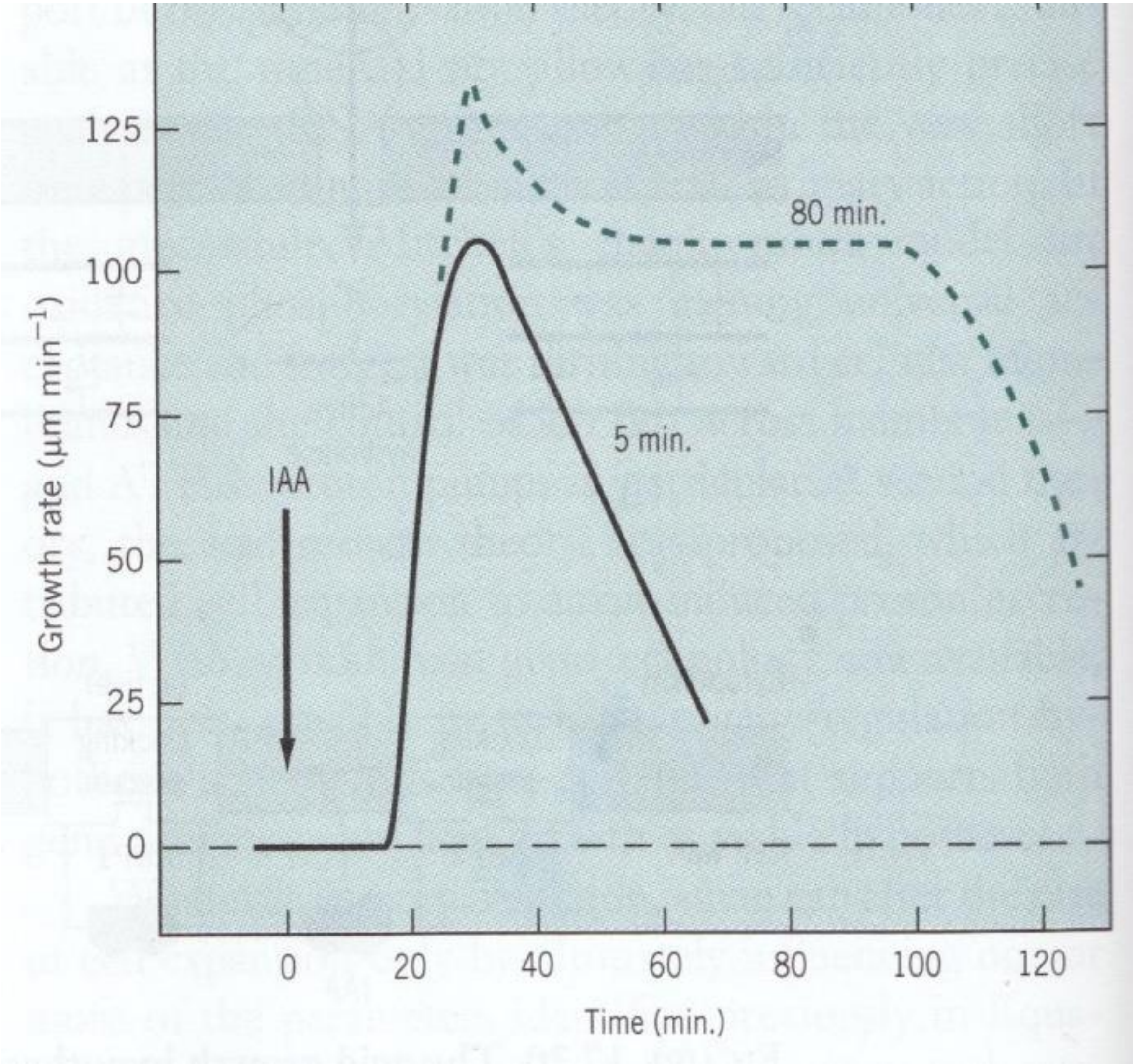


Mechanisms of Auxin Action: acid growth hypothesis



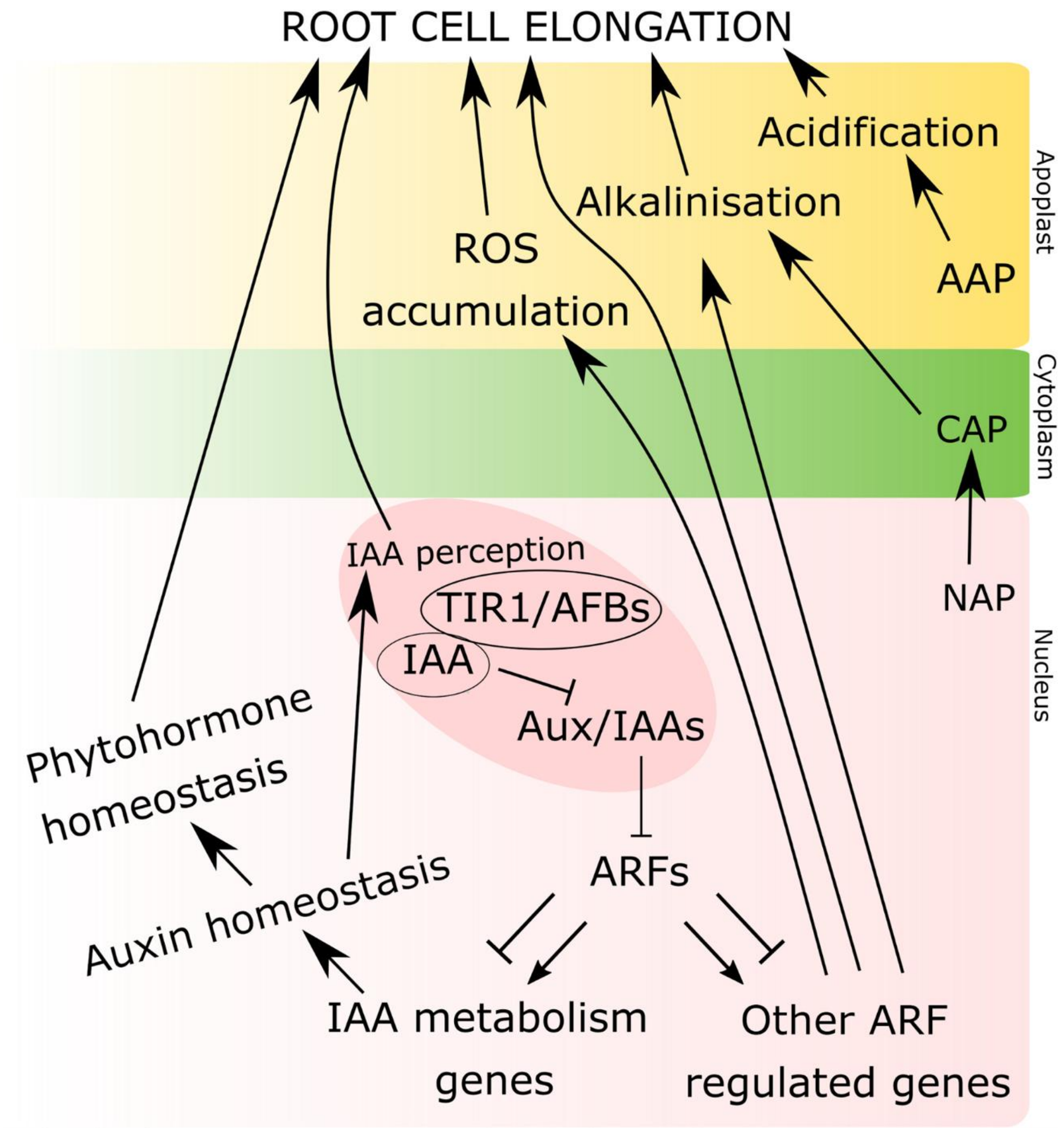
- ❖ Auxin activates plasma membrane H^+-ATPases
- ❖ Acidic pH activates expansins (扩展蛋白) and other wall-loosening processes.
- ❖ Water uptake and turgor pressure drive cell elongation

Mechanisms of Auxin Action: acid growth hypothesis



- 10^{-5}M IAA，
- Added at time = 0 min
- Removed after 5 or 80 min

Mechanisms of Auxin Action: Gene regulation



Auxin

TIR1/AFB

Aux/IAA degradation

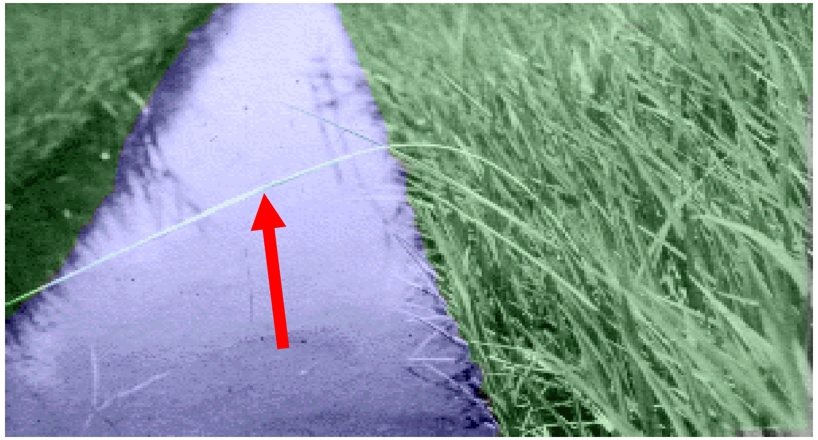
ARF activity

gene expression.

Gibberellins（GAs, 赤霉素）

1. GAs sources and fates
2. Biosynthesis
3. Physiological Functions

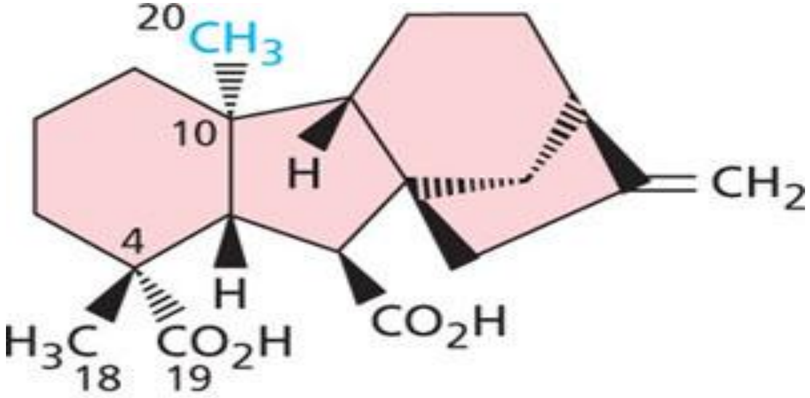
Discovery of Gibberellins



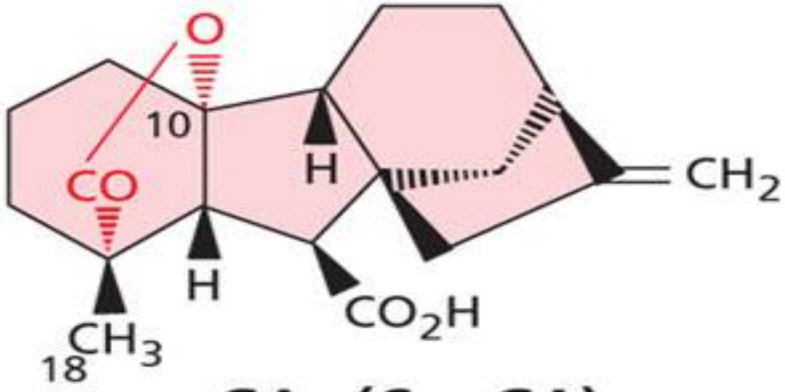
- In 1926, Eiichi Kurosawa showed that fungal extracts from *Gibberella fujikuroi* / *Fusarium fujikuroi* (藤仓赤霉菌/藤仓镰刀菌) caused excessive elongation in rice seedlings.
- In the 1930s, Teijiro Yabuta and colleagues isolated active substances from the fungus and named them gibberellins.
- In 1958, GA_1 was identified from immature seeds of higher plants.
- Today, many GAs are known, but only a few function as major bioactive plant hormones.

Chemical Structure of Gibberellins

- GAs are diterpenoid acids (二萜类酸).
- They share an ent-gibberellane skeleton (赤霉烷骨架).
- GAs are classified mainly as:
  - ✓ C_{20}-GAs (C_{20}赤霉素): usually biosynthetic precursors.
  - ✓ C_{19}-GAs (C_{19}赤霉素): often include bioactive forms.
- Structural differences in hydroxyl groups and oxidation state determine GA activity.
- Major bioactive GAs include GA_1, GA_3, GA_4, and GA_7.

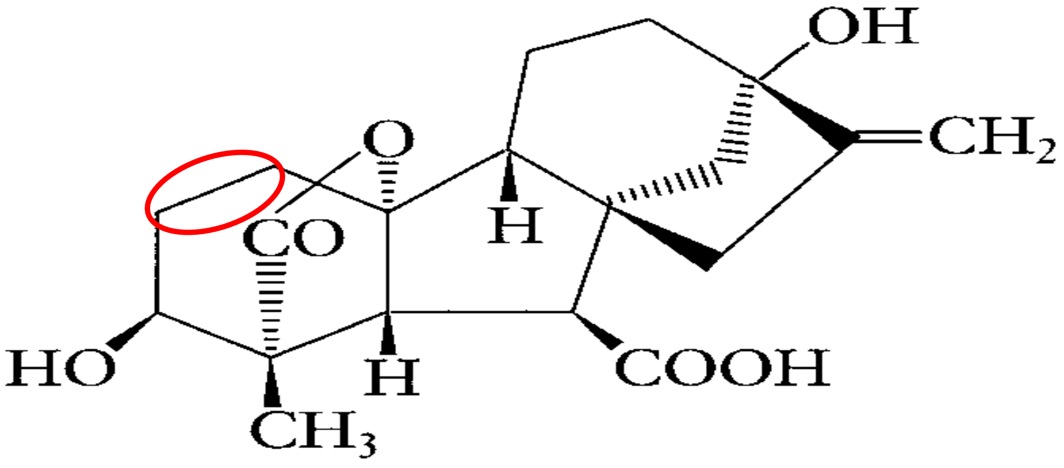


GA_{12} (C_{20}-GA)

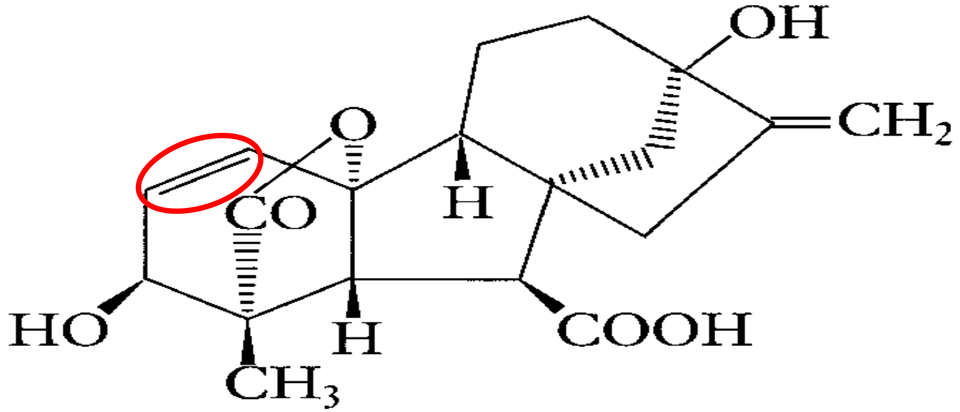


GA_9 (C_{19}-GA)

Chemical Structure of Gibberellins



GA_1



GA_3 Gibberellic Acid

- **GA_1 is an important endogenous bioactive GAs in many higher plants.**
- **GA_3，or gibberellic acid (赤霉酸), is widely used in agriculture and was originally isolated from fungi.**

Gibberellins（GAs, 赤霉素）

1. GAs sources and fates
2. Biosynthesis
3. Physiological Functions

Sites of GAs Biosynthesis

Gibberellins are synthesized mainly in young, actively growing tissues.

- ❖ Developing seeds and fruits (发育中的种子和果实)
- ❖ Shoot apical regions and young leaves (茎端区域和幼叶)
- ❖ Roots (根)

GA biosynthesis is especially active during seed germination, stem elongation, flowering, and fruit/seed development.

Gibberellin Biosynthesis

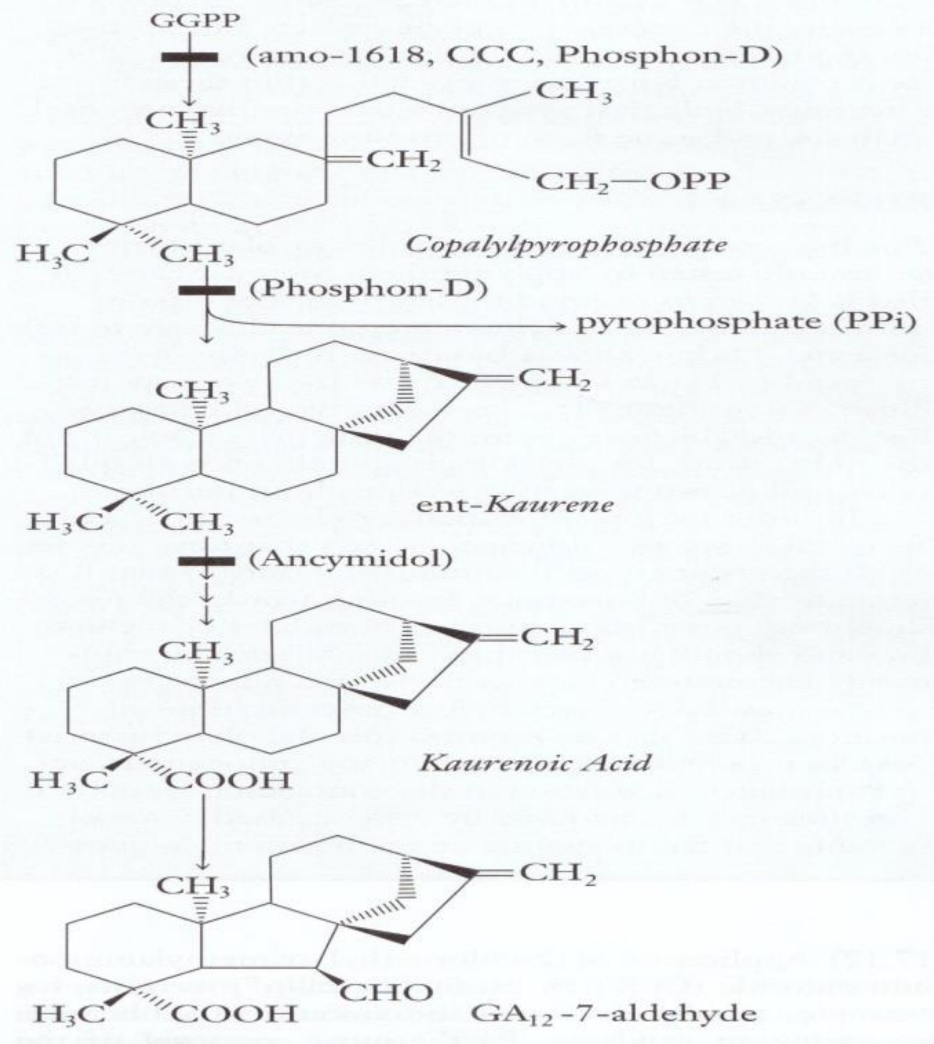
Derived from geranylgeranyl diphosphate (香叶基香叶基二磷酸, GGDP/GGPP).

Plastids (质体): early steps

- GGDP/GGPP → ent-copalyl diphosphate (内根-柯巴基二磷酸, ent-CPP)
- ent-CPP → ent-kaurene (内根-贝壳杉烯)
- Key enzymes: CPS (柯巴基二磷酸合酶) and KS (贝壳杉烯合酶)

Endoplasmic reticulum (内质网): middle steps

- ent-kaurene → ent-kaurenoic acid (内根-贝壳杉烯酸) → GA_{12}-aldehyde → GA_{12}
- Key enzymes: KO (内根-贝壳杉烯氧化酶) and KAO (内根-贝壳杉烯酸氧化酶)



Gibberellin Biosynthesis

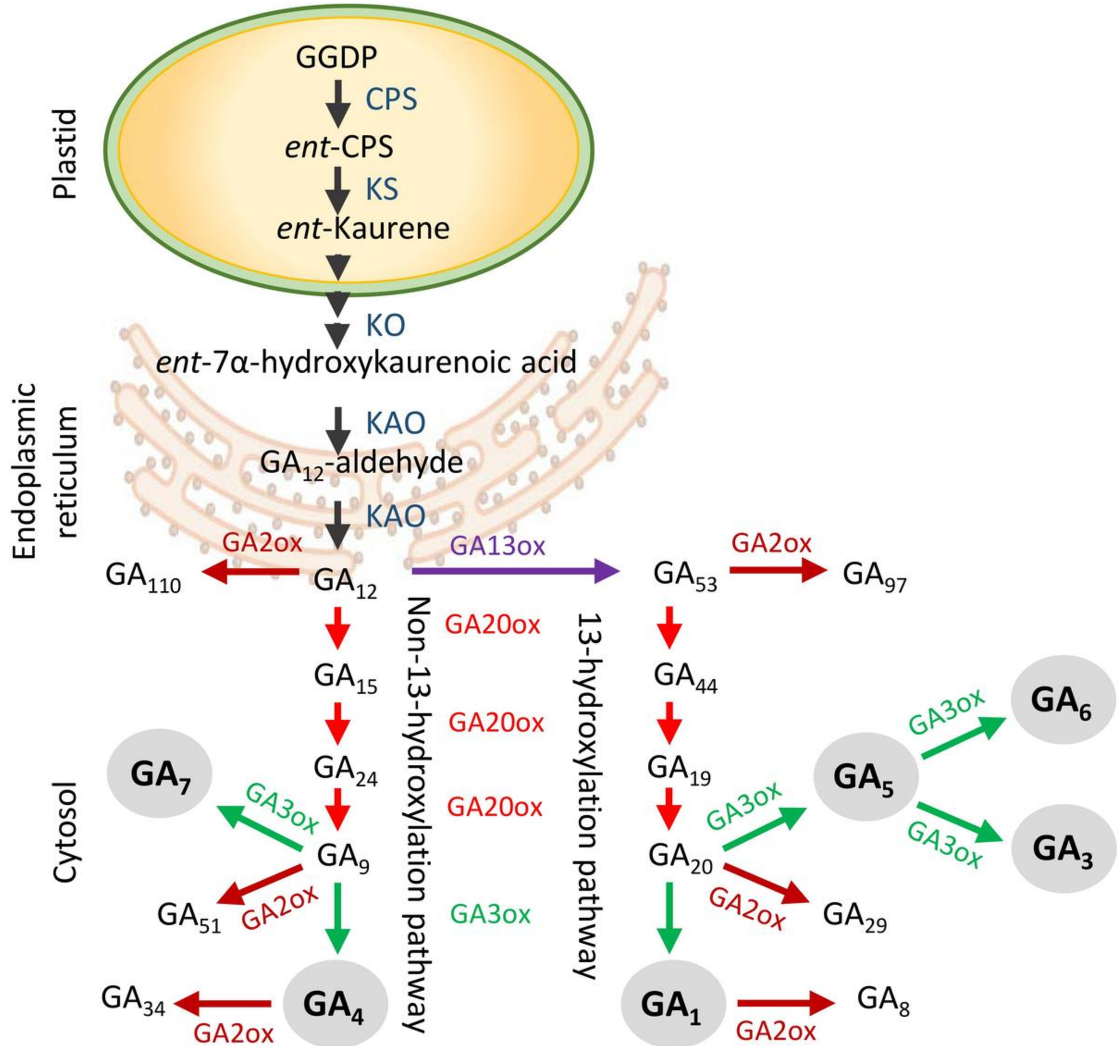
Cytosol (细胞质): late steps

- GA_{12} is converted into different GA intermediates and bioactive GAs.

Two major branches:

- **13-hydroxylation pathway (13-羟化途径):** produces GA_1 as a major bioactive GA.
- **Non-13-hydroxylation pathway (非13-羟化途径):** produces GA_4 as a major bioactive GA.

Bioactive GA levels are controlled by both biosynthesis and deactivation.



Gibberellin Deactivation

- ❖ Gibberellin metabolism regulates the level of bioactive GAs.
- ❖ **Activation (活化):** GA20-oxidase (GA20-氧化酶) and GA3-oxidase (GA3-氧化酶) produce bioactive GAs such as GA_1 and GA_4.
- ❖ **2β-hydroxylation (2β-羟化):** GA2-oxidase (GA2-氧化酶) converts active GAs into inactive forms.
- ❖ **Conjugation (偶联):** GA glycosides (赤霉素糖苷) and GA glucose esters (赤霉素糖酯) usually have reduced activity.

Transport and Distribution of Gibberellins

- GAs can move between plant organs through vascular tissues. GA transport occurs mainly through: Xylem (木质部): often from roots to shoots
- Phloem (韧皮部): from source tissues to growing sinks
- Both bioactive GAs and GA precursors can be transported.
- GA_{12} is a mobile precursor that can move long distances and be converted into bioactive GAs locally.

Gibberellins（GAs, 赤霉素）

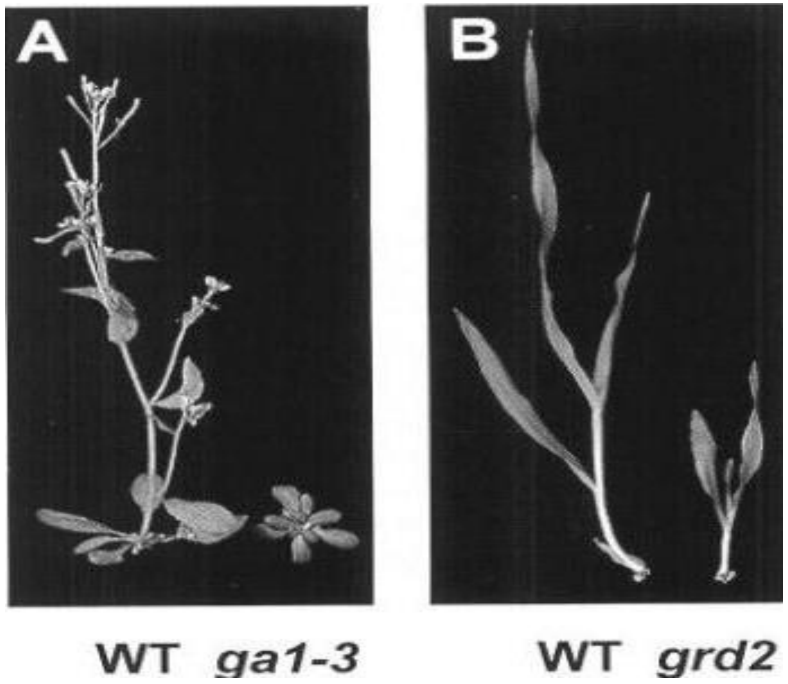
1. GAs sources and fates
2. Biosynthesis
3. Physiological Functions

1. Promote Stem and Internode Elongation

GAs) promote stem elongation and internode elongation (节间伸长).

dwarf pea seedlings

7d after treatment with GA_3



Phenotype of GA-deficient mutants in Arabidopsis and in barley

1. Promote Stem and Internode Elongation

GA treatments are used in some contexts to improve Stem or stalk elongation, Fruit growth, Malting quality in barley and Uniform growth in horticultural production

1. Promote Stem and Internode Elongation

Reducing GA Response: Semi-Dwarf Crops. the Green Revolution (绿色革命).

37 Regulation of Plant Growth

CHAPTER OUTLINE

AGRICULTURAL SCIENTISTS are constantly searching for ways to help farmers produce more food for a growing population. One way is to breed crop plants whose physiology allows them to produce more grain per plant (resulting in higher yields). The drawback of this approach is that the sheer weight of the load of seeds may cause the stem to bend over. The problem is made worse when fertilizer makes the plants grow taller. Harvesting seeds on the ground is very difficult; think of how hard it would be to pick up seeds one by one, when some have already sprouted.

During World War II, the island nation of Japan was blockaded and could not import food or other supplies. Food was rationed and many people were hungry, but there were no major famines in Japan during that period. How were the Japanese able to produce enough grain to feed their population? One answer to this question lay in the fields: the Japanese had bred genetic strains of rice and wheat with short, strong stems that could bear high yields of grain without bending over. An agricultural advisor to the occupying American army sent samples of the grains to the U.S.

A decade later, the American plant geneticist Norman Borlaug, who was working in Mexico at the time, began making genetic crosses between the Japanese wheat and other varieties that had genes conferring rapid growth, adaptability to varying climates, and resistance to fungal diseases. The results were "semi-dwarf" wheat varieties that gave record yields. The varieties were grown first in Mexico, and later in India and Pakistan during the 1960s. At about the same time and using a similar strategy, scientists in the Philippines developed semi-dwarf rice with equally spectacular results. People who had lived on the edge of starvation now produced enough food. Countries that had relied on food from other countries were now able to grow more than enough grain, and export the surplus. The development of these semi-dwarf grains began what was called the "Green Revolution." Borlaug was awarded the Nobel Peace Prize for his research on wheat, which is estimated to have saved a billion lives.

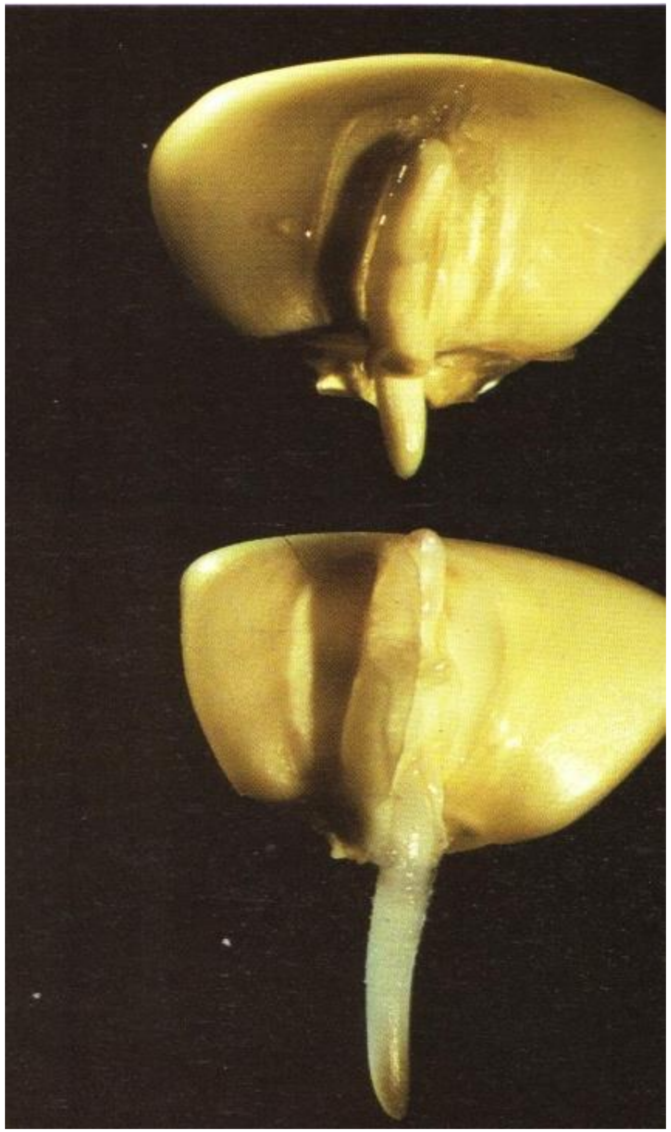
Norman Borlaug Seen here in a field of semi-dwarf wheat, plant geneticist Norman Borlaug carried out a program of genetic crosses that led to high-yielding varieties and saved millions from starvation.

What changes in growth patterns made the new strains of wheat and rice successful?

See answer on p. 775.

2. Promote Seed Germination

- GA helps break seed dormancy (种子休眠)
- In some dormant seeds, external GA treatment can stimulate germination.
- GA promotes embryo growth and weakening of seed-covering tissues.



2. Promote Seed Germination

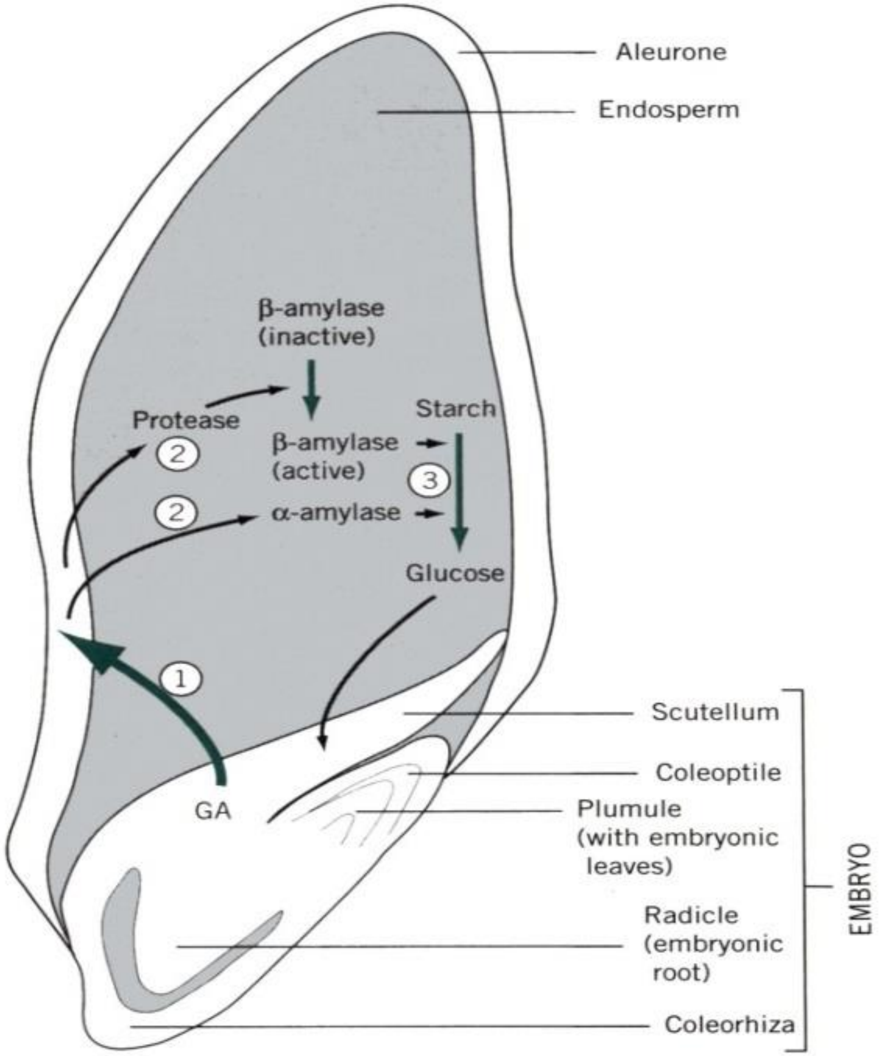
❖ During cereal seed germination, the embryo (胚) produces GA.

❖ GA moves to the aleurone layer (糊粉层).

❖ Aleurone cells produce hydrolytic enzymes (水解酶), especially α-amylase (α-淀粉酶).

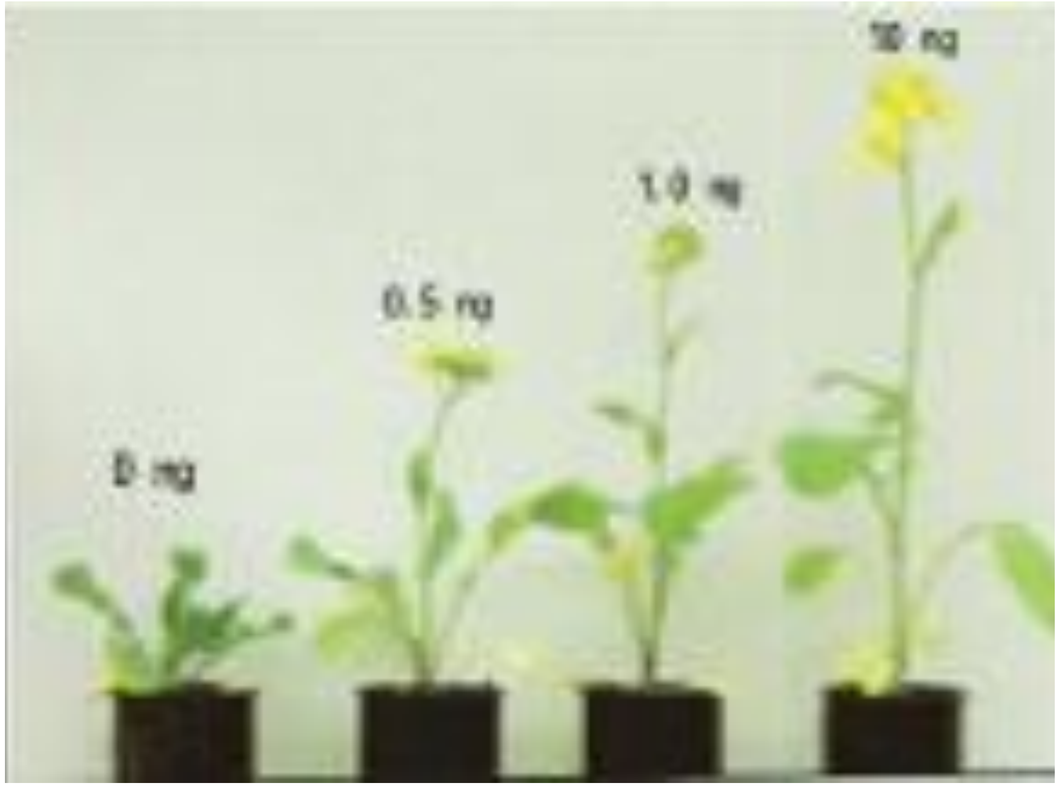
❖ α-Amylase breaks down starch (淀粉) in the endosperm (胚乳) into sugars.

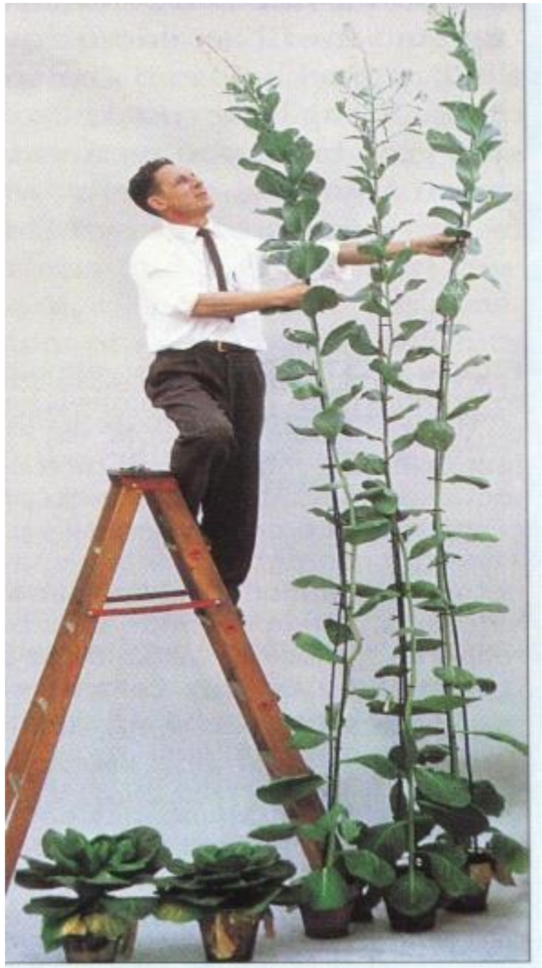
❖ Sugars provide energy and carbon for seedling growth.



3. Promote Bolting and Flowering

- ❖ GA stimulates internode elongation, producing visible stem bolting (抽薹) .
- ❖ The flowering response depends on species, developmental stage, photoperiod, and GA dose.



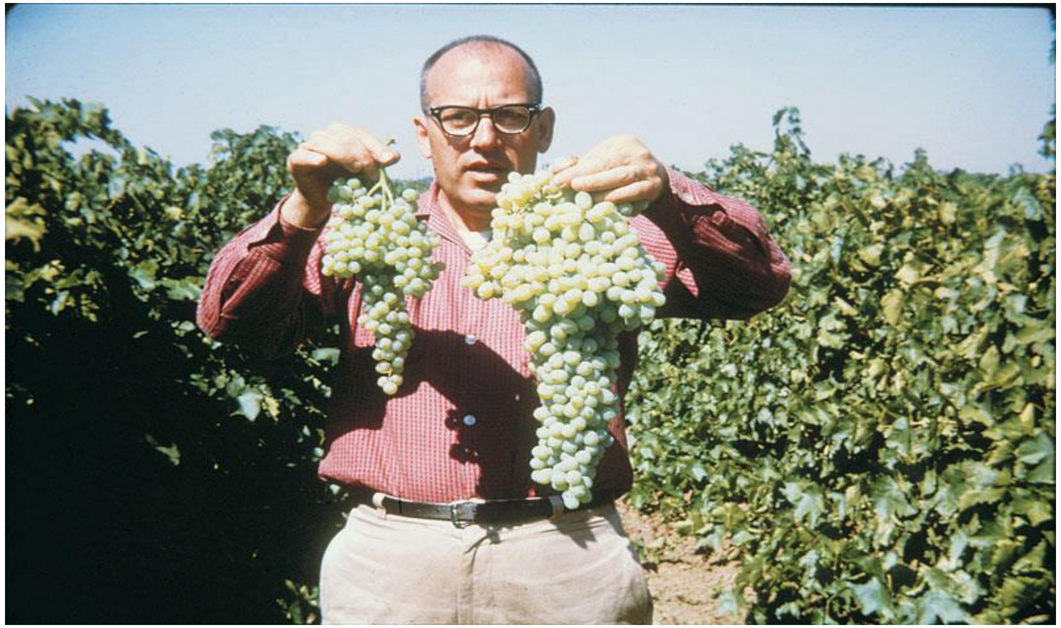


4. Modify Fruit Shape

Control

$GA_4 + GA_7$

5. Promote Fruit Set and Fruit Growth



Gibberellin induces growth in Thompson’s seedless grapes. The bunch on the left is an untreated control. The bunch on the right was sprayed with Gibberellin during fruit development.

6. Other Applications of Gibberellins

- ❖ Promote vegetative growth of leafy crops, such as celery (芹菜), spinach (菠菜), and tea plants (茶树).
- ❖ Improve fruit set (坐果) in some crops and reduce pre-harvest fruit drop (采前落果), depending on species and timing.
- ❖ Delay senescence (延缓衰老) and extend storage life in some fruits, such as citrus (柑橘).
- ❖ GA biosynthesis inhibitors (赤霉素生物合成抑制剂) are used to reduce excessive elongation and improve lodging resistance.

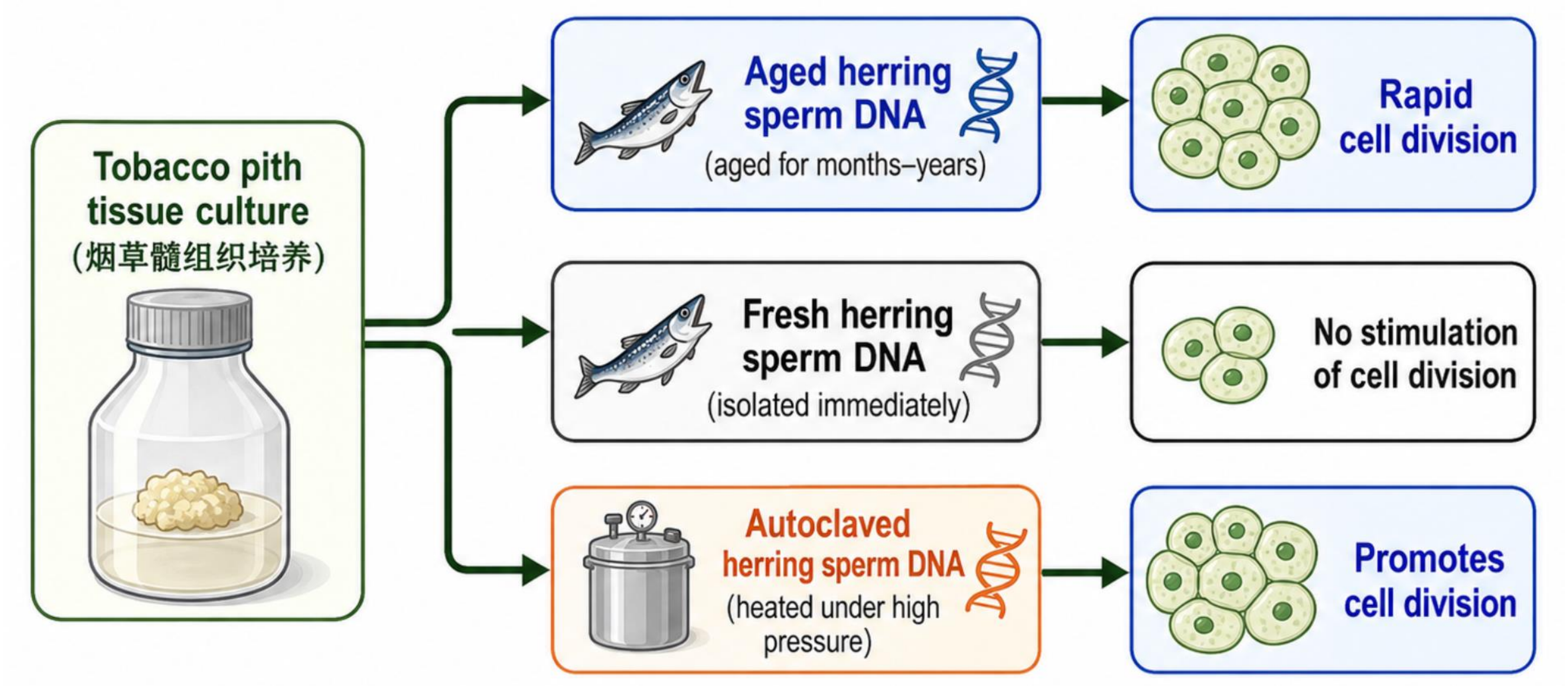
Cytokinins

1. What are Cytokinins
2. Biosynthesis
3. Physiological Functions

Discovery of Cytokinins

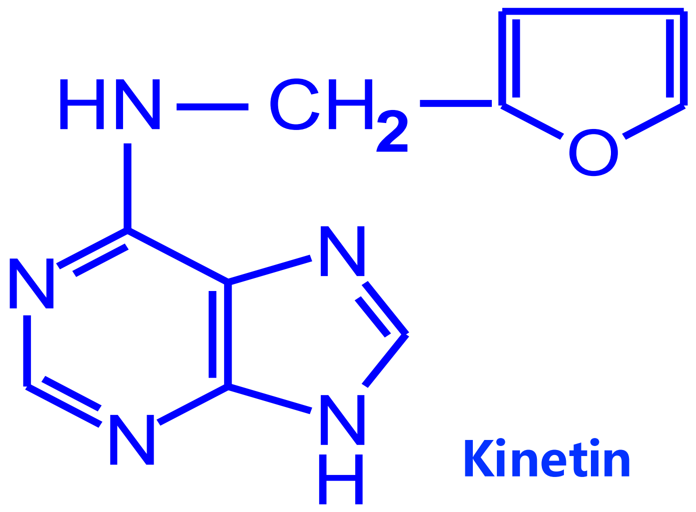
- ❖ Cytokinins (细胞分裂素，CTKs) were discovered through plant tissue culture studies.
- ❖ In the 1940s–1950s, Folke Skoog and colleagues used tobacco pith tissue culture (烟草髓组织培养) to study cell division.
- ❖ Coconut milk (椰乳), yeast extract (酵母提取物), and vascular tissue extracts stimulated cell division in culture.
- ❖ Carlos O. Miller, working in Skoog’s lab, identified kinetin (激动素), an adenine derivative with strong cell-division activity.

Discovery of Cytokinins

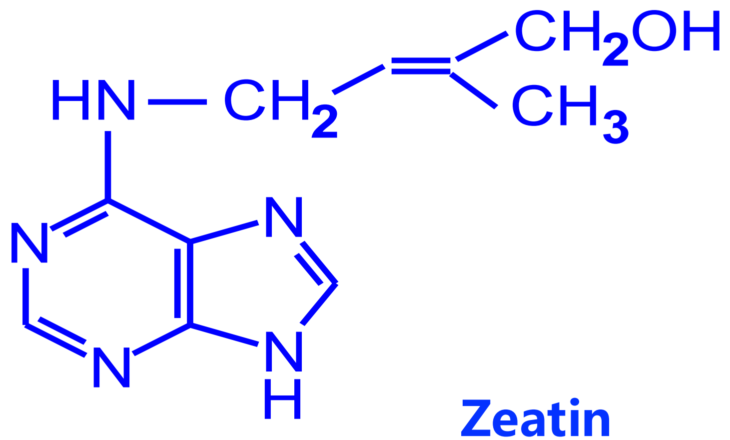


What are Cytokinins

- ❖ **1956 — Kinetin (激动素, KT)**
  - ✓ Miller and colleagues isolated kinetin from autoclaved herring sperm DNA.
  - ✓ Kinetin is **N^6-furfuryladenine (N^6-呋喃甲基腺嘌呤)**.
- ❖ **1963 — Zeatin (玉米素, Z)**
  - ✓ Miller isolated a cytokinin-like compound from maize kernels.
  - ✓ Letham independently isolated a similar active compound from plum fruit.
- ❖ **1965 — Cytokinins (细胞分裂素, CTKs)**
  - ✓ Skoog and colleagues proposed the term **cytokinins**.
  - ✓ Cytokinins are adenine derivatives substituted at the N^6 position.



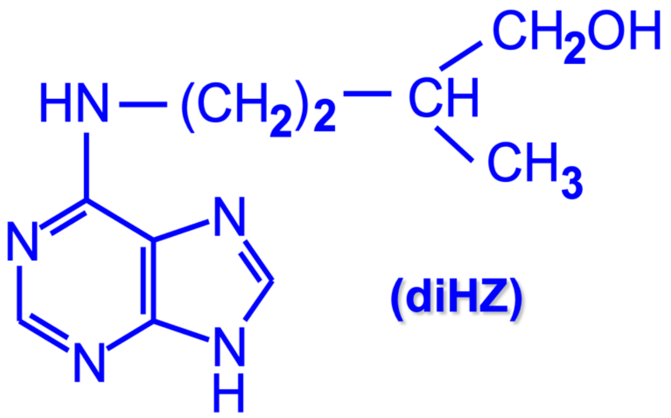
Kinetin



Zeatin

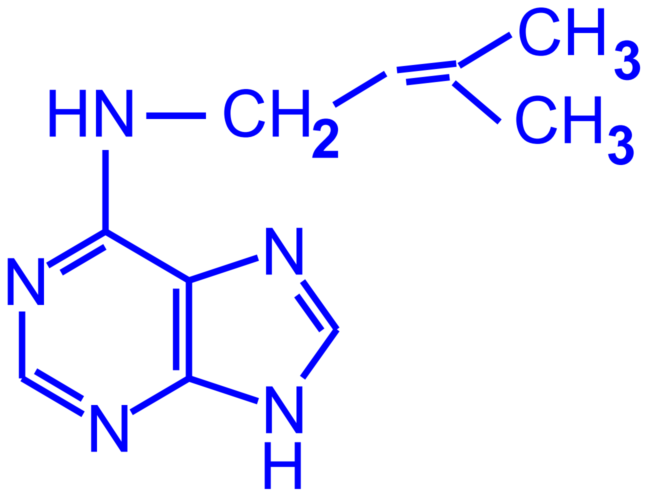
What are Cytokinins

Other Naturally Occurring Cytokinins



(diHZ)

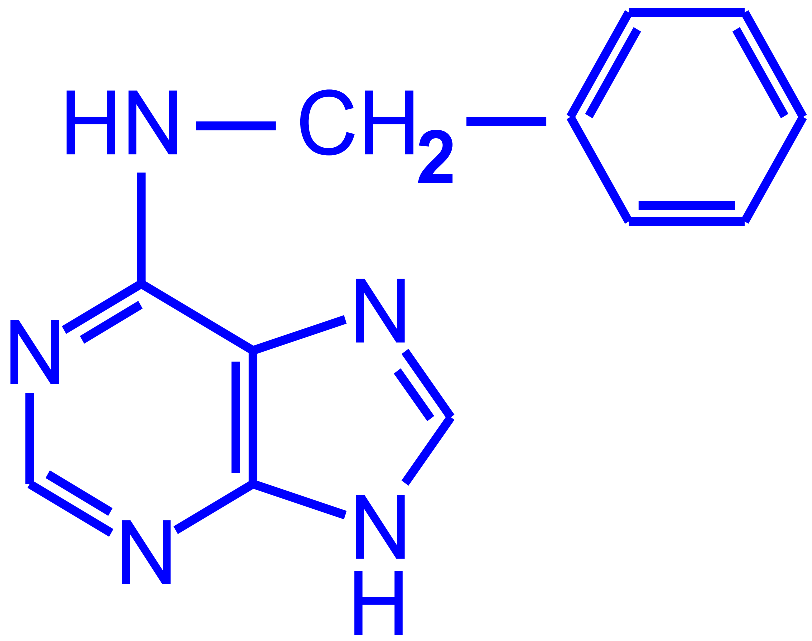
- **Dihydrozeatin (二氢玉米素, DHZ)**
  - ✓ A reduced form of zeatin (玉米素)
  - ✓ Found in many higher plants
- **N⁶-isopentenyladenine (异戊烯基腺嘌呤, iP)**
  - ✓ A major naturally occurring cytokinin precursor and active form
  - ✓ Important in cytokinin biosynthesis and transport



Cytokinins commonly share an adenine(嘌呤) ring with substitution at the N^6 position.

What are Cytokinins

Synthetic Cytokinin: 6-Benzylaminopurine (6-苄基腺嘌呤, 6-BA)



- ❖ It is widely used to induce shoot formation and delay leaf senescence.
- ❖ Compared with many natural cytokinins, 6-BA is relatively stable and effective in culture media.

Cytokinins

1. What are Cytokinins
2. Biosynthesis
3. Physiological Functions

Cytokinin Biosynthesis

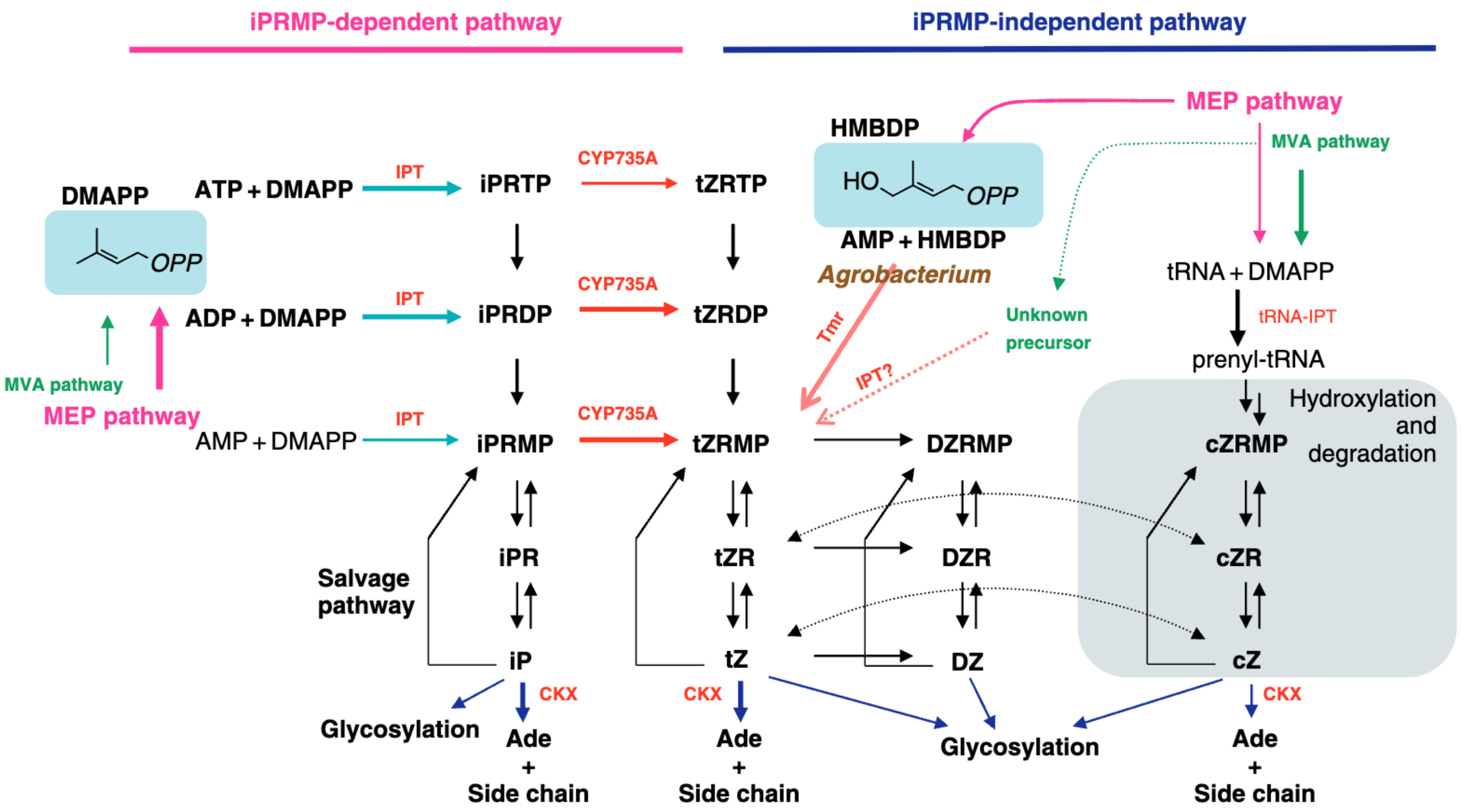
❖ **Cytokinins (细胞分裂素, CTKs) are mainly synthesized in:**

✓ **Root tips with active cell division**

✓ **Developing fruits and seeds**

✓ **Young growing tissues**

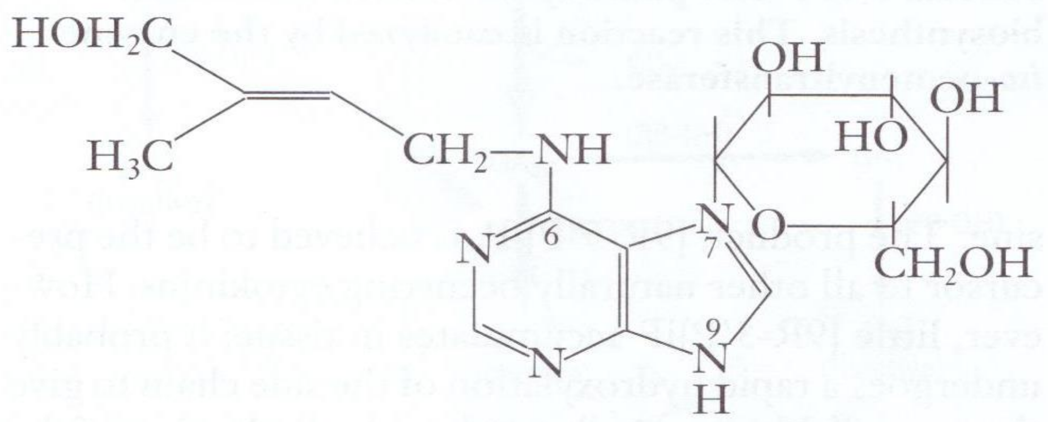
Core Pathway of Cytokinin Biosynthesis



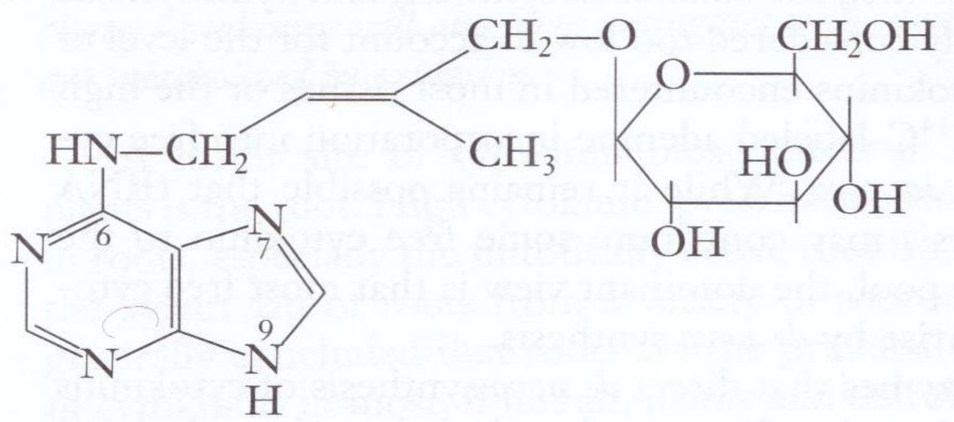
Cytokinin Conjugation and Degradation

CTKs are regulated by conjugation and oxidative degradation.

Sugar conjugation (糖基化):



trans-Zeatin-7-glucoside
([7G]Z)



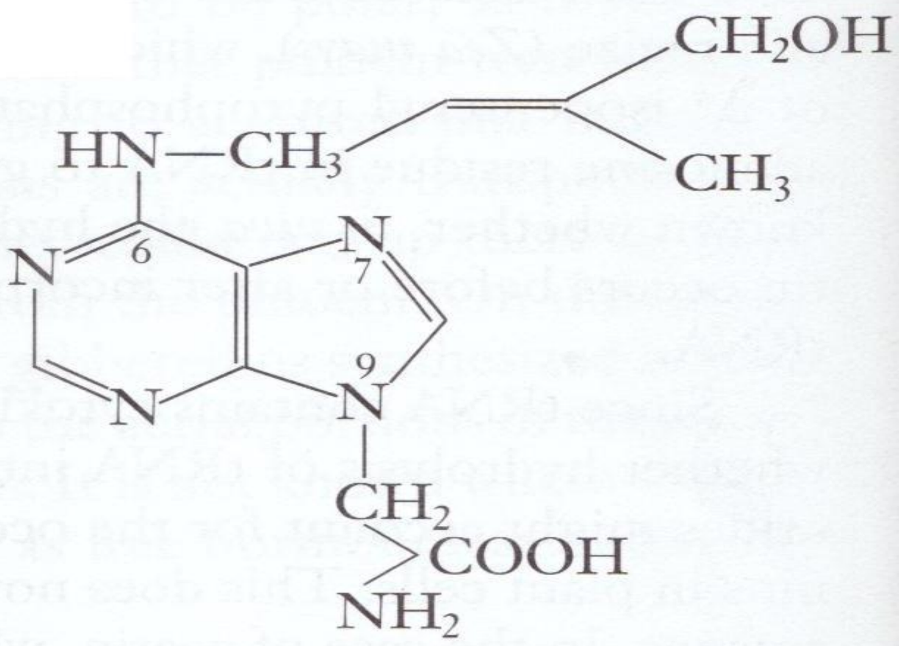
Zeatin-O-glucoside
([OG]Z)

反式-玉米素-7-葡糖苷

玉米素-*O*-葡糖苷

Cytokinin Conjugation and Degradation

CTKs are regulated by conjugation and oxidative degradation.



9-Alanyl Zeatin
([9Ala]Z)

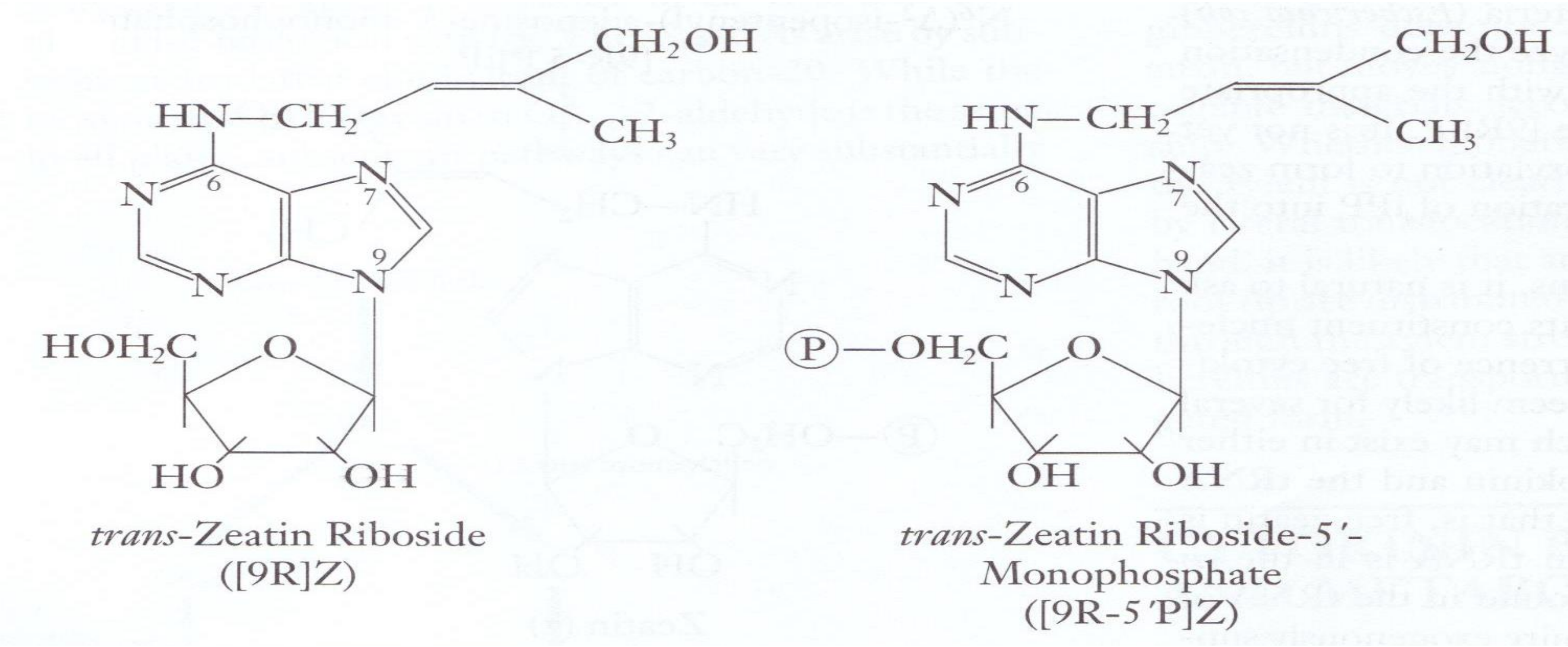
9-丙氨酰玉米素

Amino acid conjugation

Cytokinin Conjugation and Degradation

CTKs are regulated by conjugation and oxidative degradation.

Ribosides and nucleotides (核苷和核苷酸):

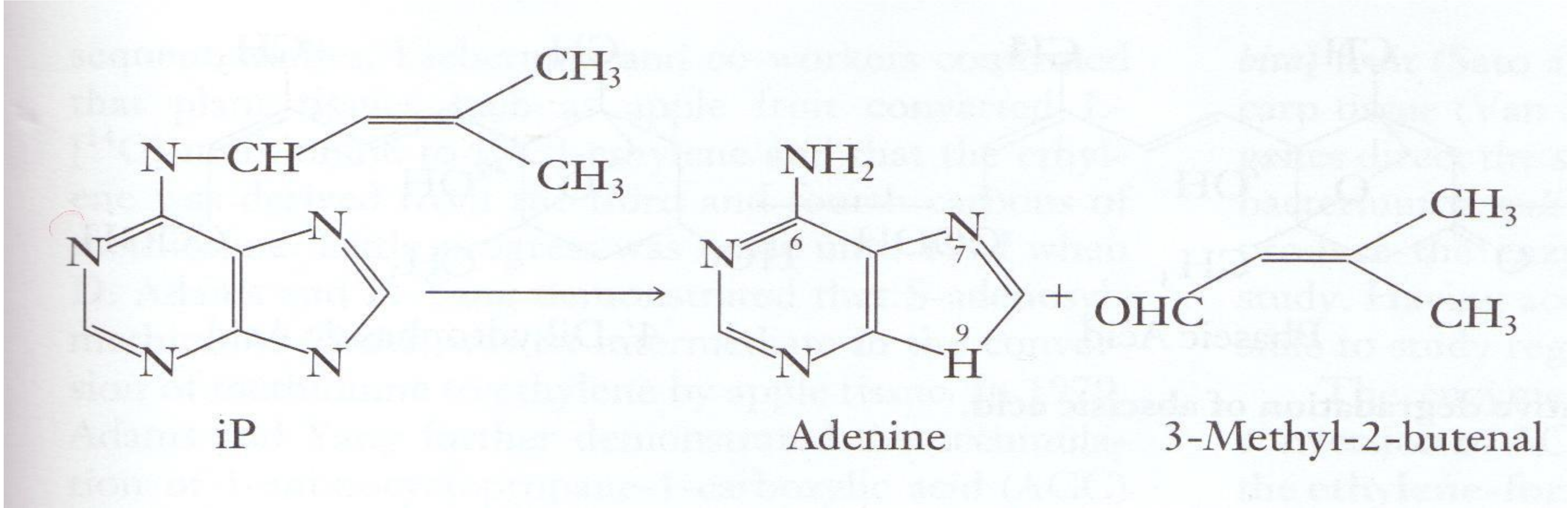


反式-玉米素核苷

反式玉米素核苷-5’-单磷酸

Cytokinin Conjugation and Degradation

CTKs are regulated by conjugation and oxidative degradation.



异戊烯基腺嘌呤 **腺嘌呤** **3-甲基-巴豆醛**

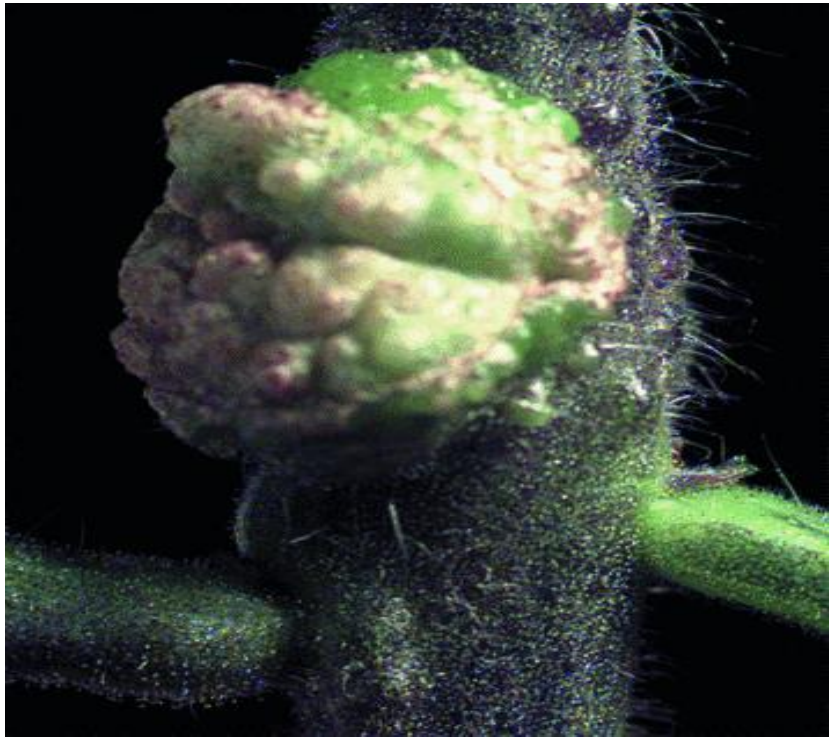
Cytokinin oxidase/dehydrogenase (细胞分裂素氧化/脱氢酶, CKX) irreversibly degrades many cytokinins.

Cytokinins

1. What are Cytokinins
2. Biosynthesis
3. **Physiological Functions**

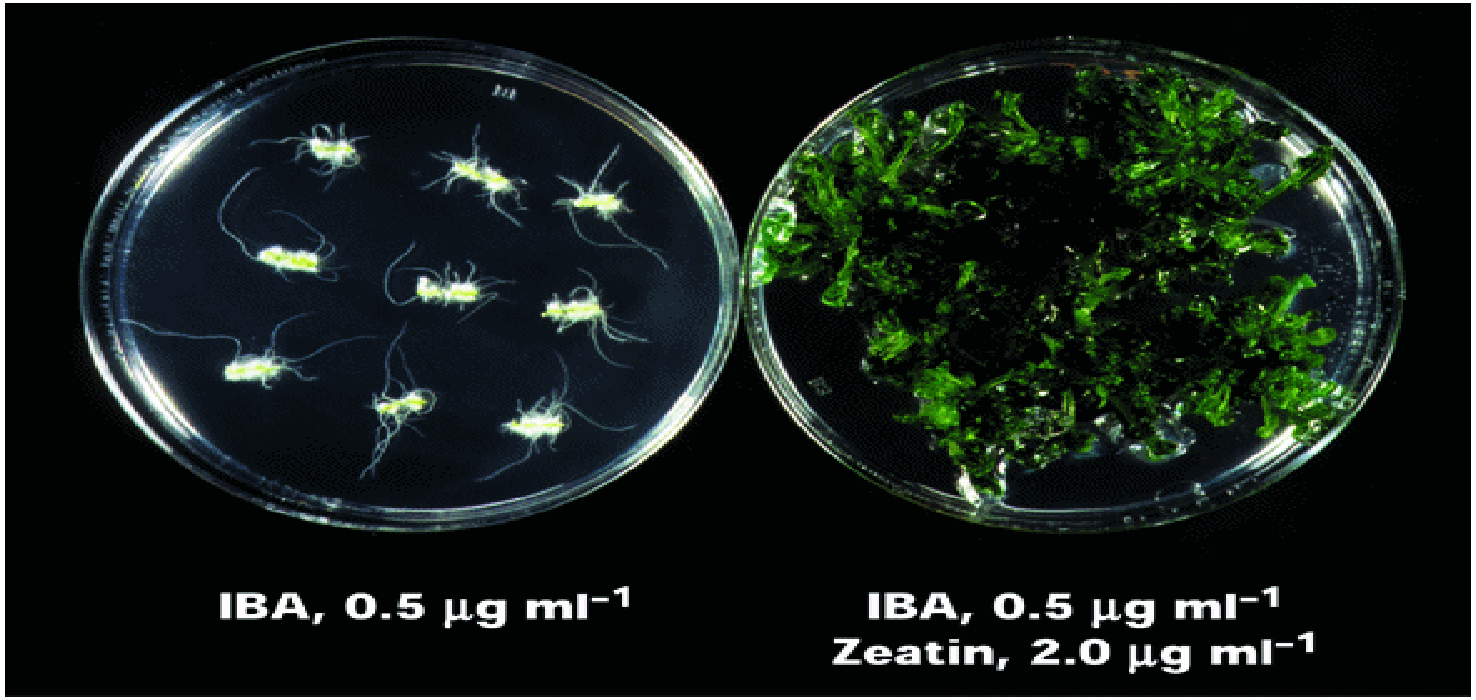
1. Promote Cell Division and Morphogenesis

- ❖ CTKs are enriched in actively dividing tissues, such as meristems and developing organs.
- ❖ Crown gall tumors (冠瘿瘤) show excessive cell proliferation.
- ❖ Increased auxin and cytokinin levels drive uncontrolled tissue growth.



1. Promote Cell Division and Morphogenesis

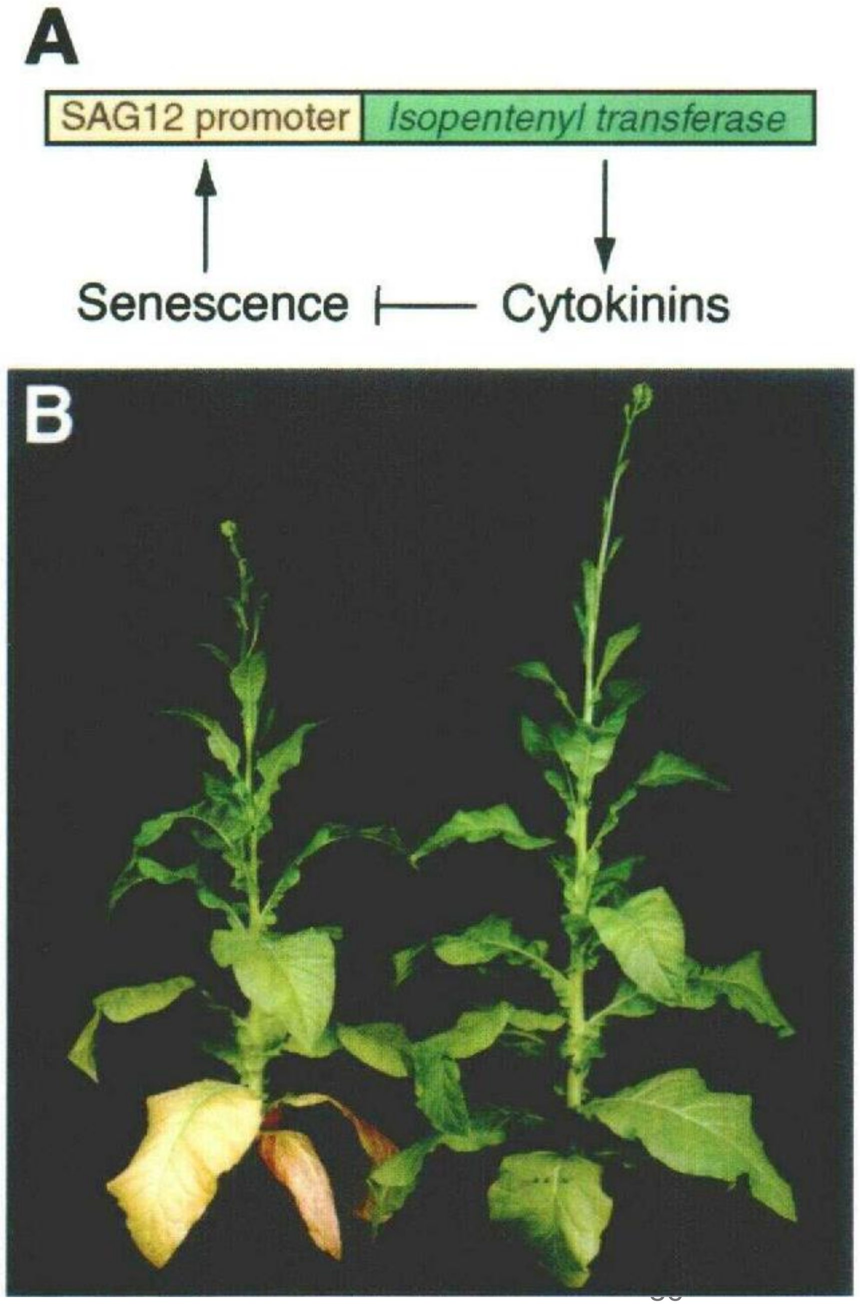
The cytokinin/auxin ratio (细胞分裂素/生长素比例) is a classic regulator of organogenesis in tissue culture.



High auxin / low cytokinin **High cytokinin / low auxin**

2. Delay Leaf Senescence

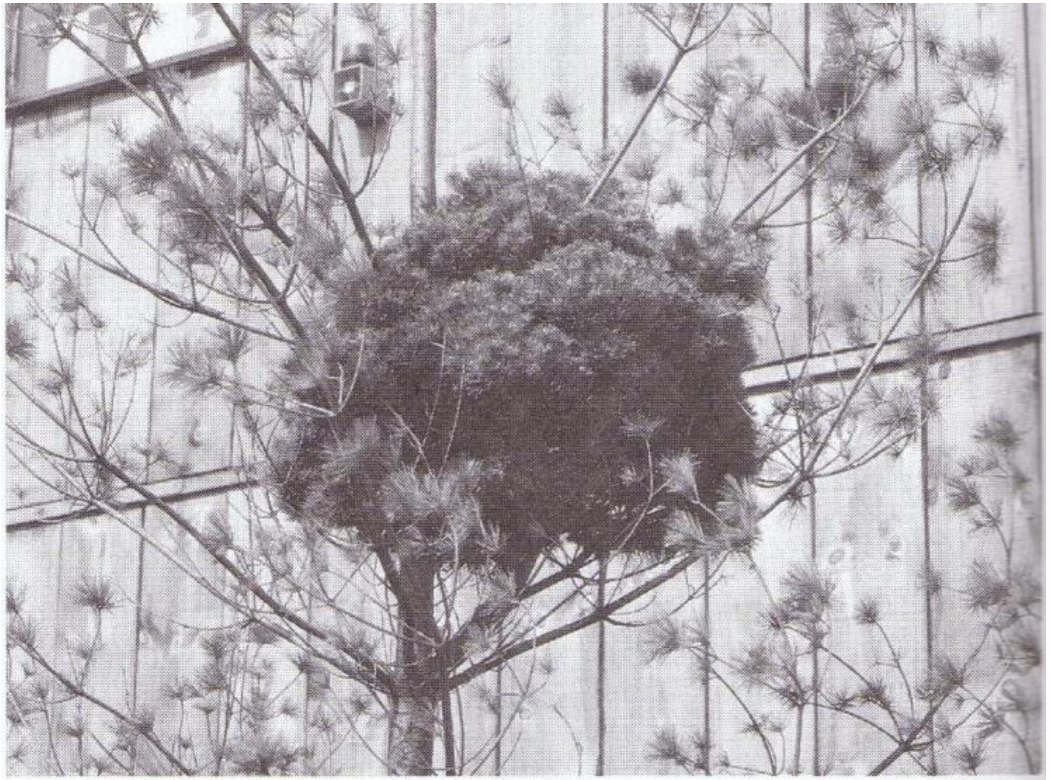
❖ Root-derived cytokinins are transported to leaves and help maintain leaf function.
❖ Removing roots reduces cytokinin supply and can accelerate leaf yellowing and senescence.
❖ Exogenous cytokinin treatment can keep detached leaves green for longer.
❖ Cytokinins delay senescence by maintaining chlorophyll, photosynthesis, and protein synthesis.



3. Release Lateral Buds from Apical Dominance

- CTKs promote axillary bud outgrowth.
- High cytokinin levels can stimulate lateral branching.

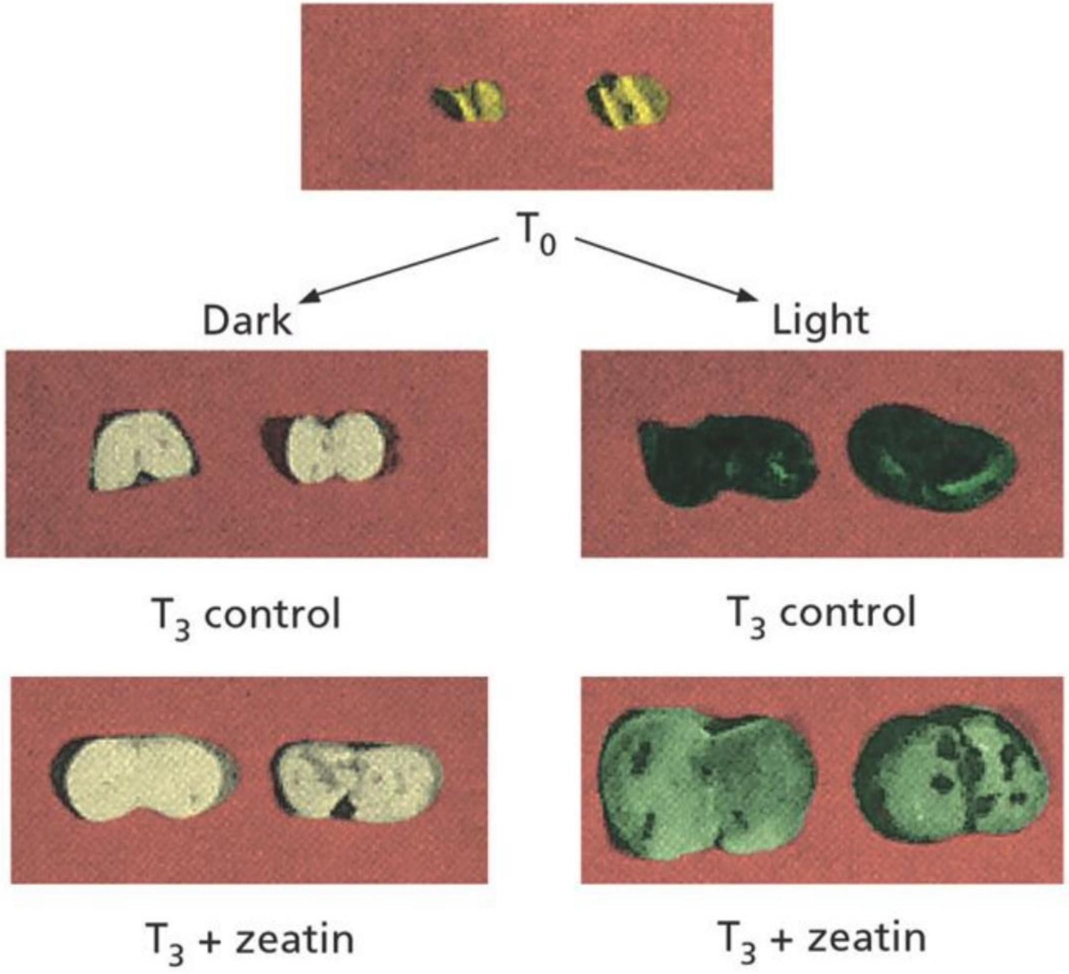
In azalea (杜鹃花), cytokinin-like compounds can be used to increase branching and improve plant form.



Witch' s broom (丛枝病) can result from abnormal cytokinin production by pathogens

4. Induce Cotyledon Expansion (子叶膨大)

Cytokinin-stimulated expansion of radish (萝卜）cotyledons is associated with an increase in the mechanical extensibility of the cell walls.



Other Physiological Functions of Cytokinins

- ❖ CTKs can promote fruit set (坐果) in some species.
- ❖ CTKs may stimulate stomatal opening (气孔开放), often by affecting guard cell ion transport.
- ❖ CTKs can help release light-requiring seeds from dormancy promoting germination.
- ❖ CTKs delay leaf senescence by maintaining chlorophyll and photosynthetic activity.
- ❖ ••••

Abscisic acid, ABA

1. What
2. Biosynthesis
3. Physiological Functions

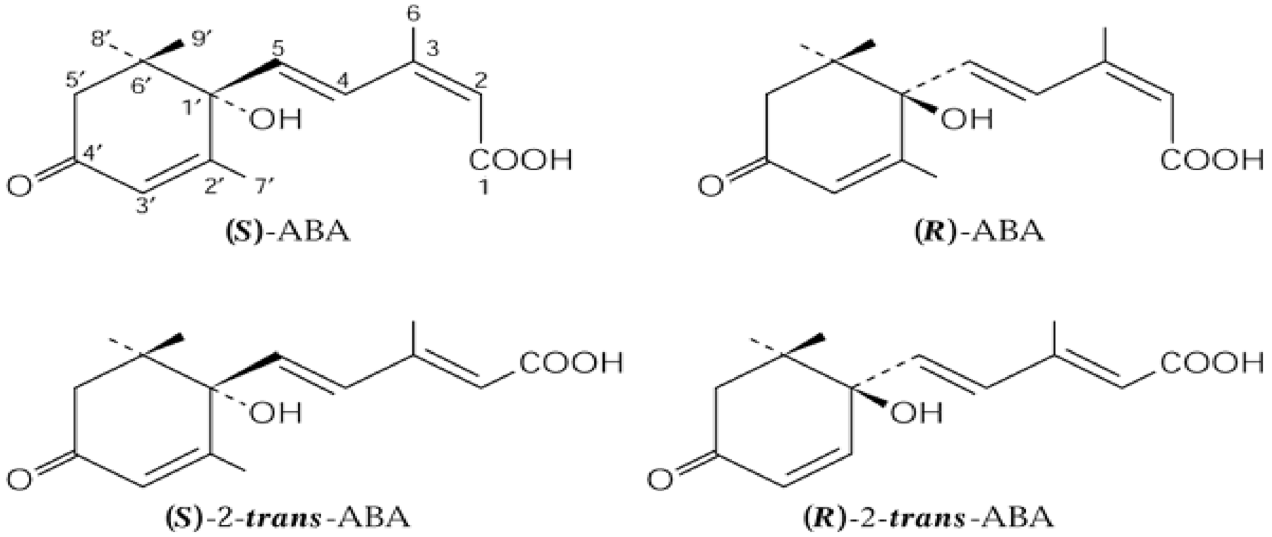
Discovery and Naming of Abscisic Acid

Abscisic acid (脱落酸, ABA) was identified through studies of senescence, abscission, and dormancy.

- **1955 — Osborne**
  - Isolated a substance from senescing bean leaves that promoted abscission.
  - It was called senescence factor (衰老因子, SF).
- **1963 — Ohkuma and Addicott**
  - Isolated an abscission-promoting substance from young cotton fruits.
  - It was named abscisin II (脱落素II).
- **1964 — Wareing**
  - Proposed dormin (休眠素) as a growth-inhibiting factor associated with bud dormancy.
  - These substances were later shown to be the same compound.
- **1967 — The name abscisic acid (脱落酸, ABA) was adopted.**

Chemical Forms of Abscisic Acid

- ❖ Abscisic acid (脱落酸, ABA) has both optical and geometric isomers.
- ❖ The major natural form in plants is **2-cis-(+)-ABA**, also called **S-ABA (S-脱落酸)**.
- ❖ A small amount of **2-trans-(+)-ABA** may also occur naturally.
- ❖ Chemically synthesized ABA is usually a racemic mixture containing both (+)-ABA and (−)-ABA.

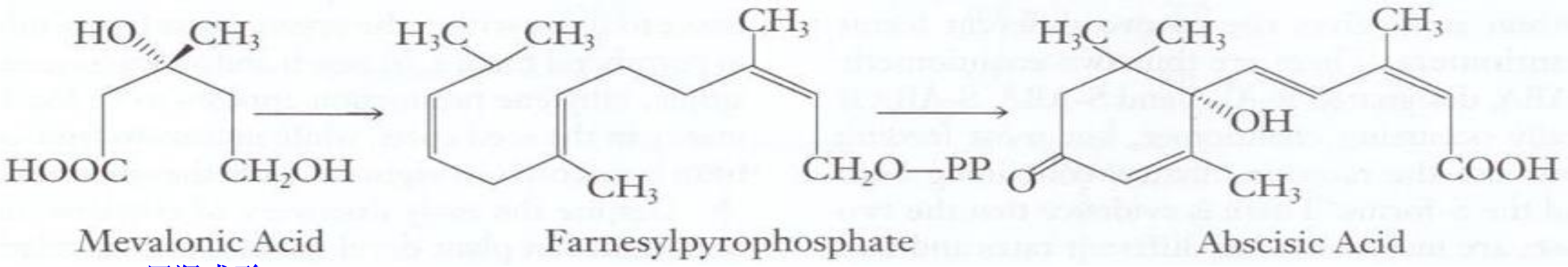


Several fungi, including *Botrytis cinerea* (葡萄灰霉菌), can also produce ABA.

Abscisic acid, ABA

1. What
2. Biosynthesis
3. Physiological Functions

ABA Biosynthesis: Direct Pathway in Microorganisms



甲羟戊酸

法尼基焦磷酸

- This route is mainly found in ABA-producing fungi, such as *Botrytis cinerea* (葡萄灰霉菌).
- It is **not** the major ABA biosynthetic pathway in higher plants.

ABA Biosynthesis in Higher Plants

❖ABA biosynthesis begins from carotenoids (类胡萝卜素) in plastids (质体).

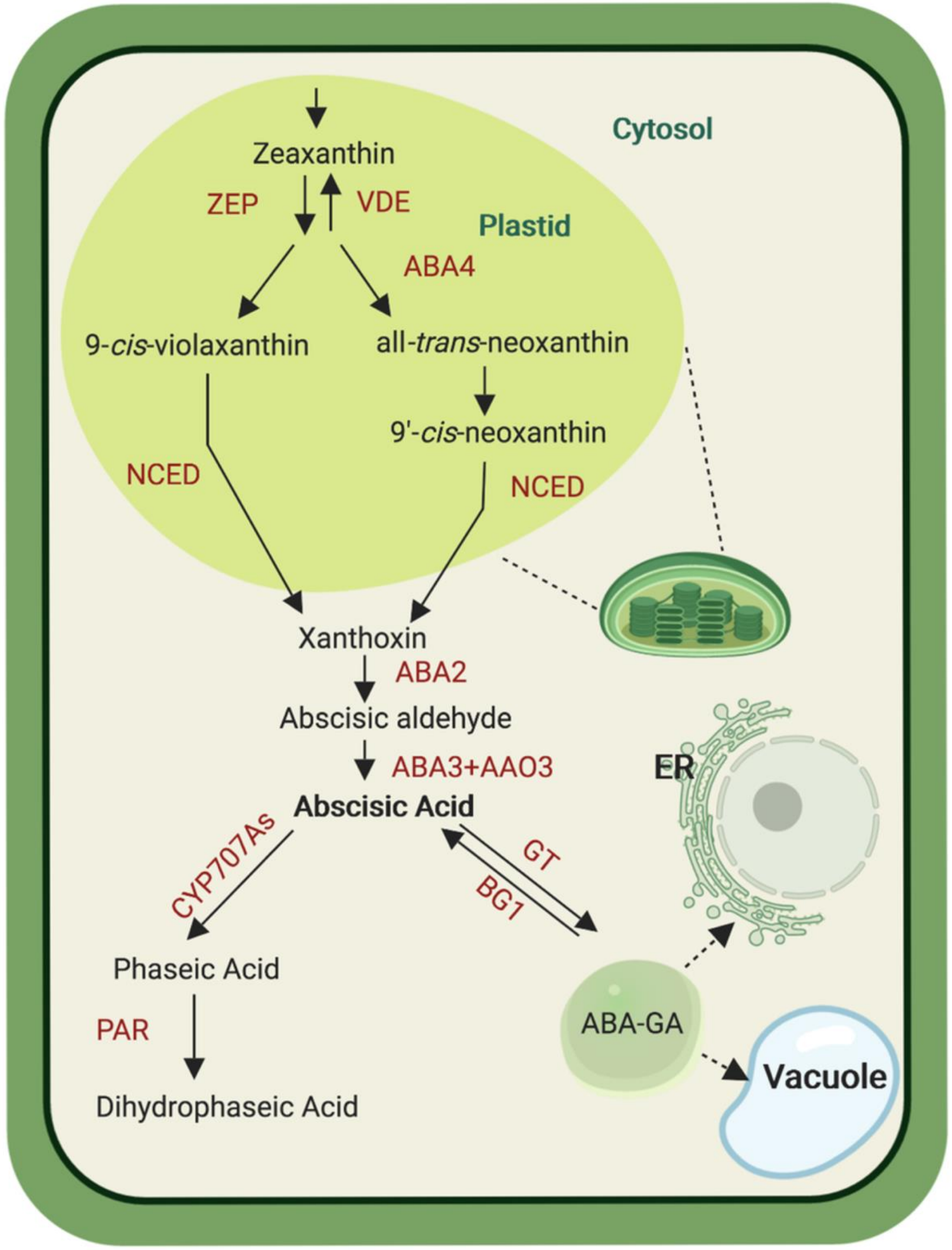
❖Key steps:

➢ Zeaxanthin (玉米黄质) → violaxanthin (紫黄质)

➢ Violaxanthin → 9-cis-violaxanthin / 9-cis-neoxanthin

➢ 9-cis-epoxycarotenoids are cleaved by NCED (9-顺式环氧类胡萝卜素双加氧酶).

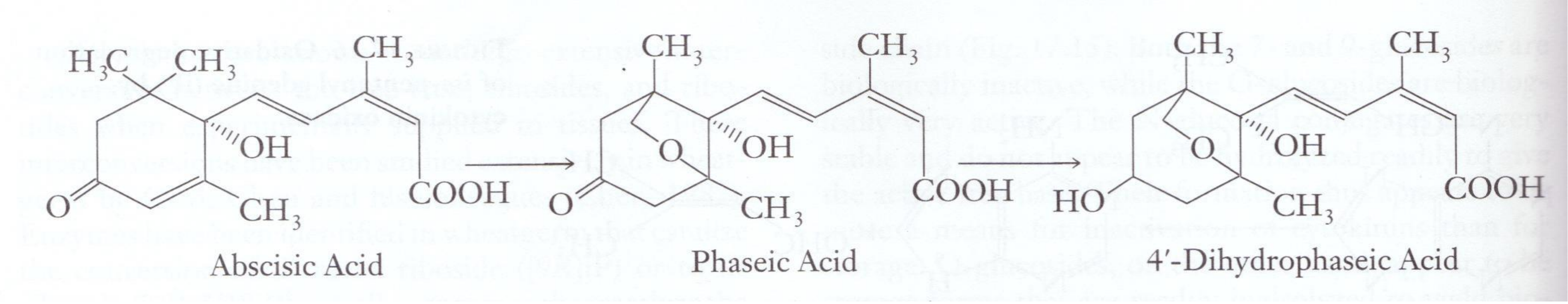
❖NCED produces xanthoxin (黄质醛), which moves to the cytosol (细胞质).



ABA Degradation and Conjugation

❖Oxidative degradation (氧化降解):

- ABA is converted to phaseic acid (红花菜豆酸, PA).
- PA is further reduced to dihydrophaseic acid (二氢红花菜豆酸, DPA).
- This pathway lowers active ABA levels.

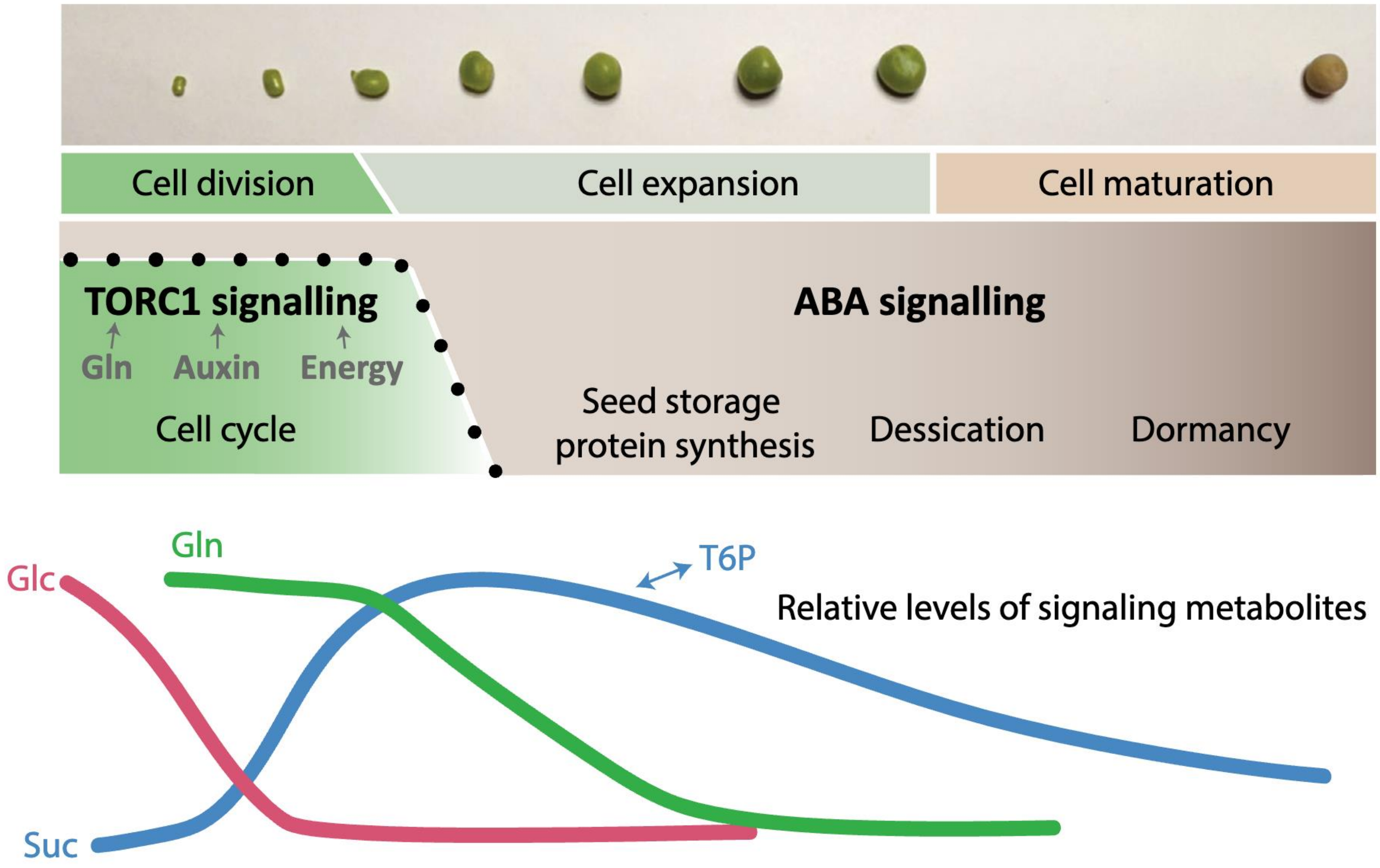


❖ABA can be conjugated with glucose (葡萄糖) to form ABA-glucose ester (ABA-葡糖酯, ABA-GE).

Abscisic acid, ABA

1. What
2. Biosynthesis
3. Physiological Functions

1. Promotes Seed Maturation and Dormancy



1. Promotes Seed Maturation and Dormancy

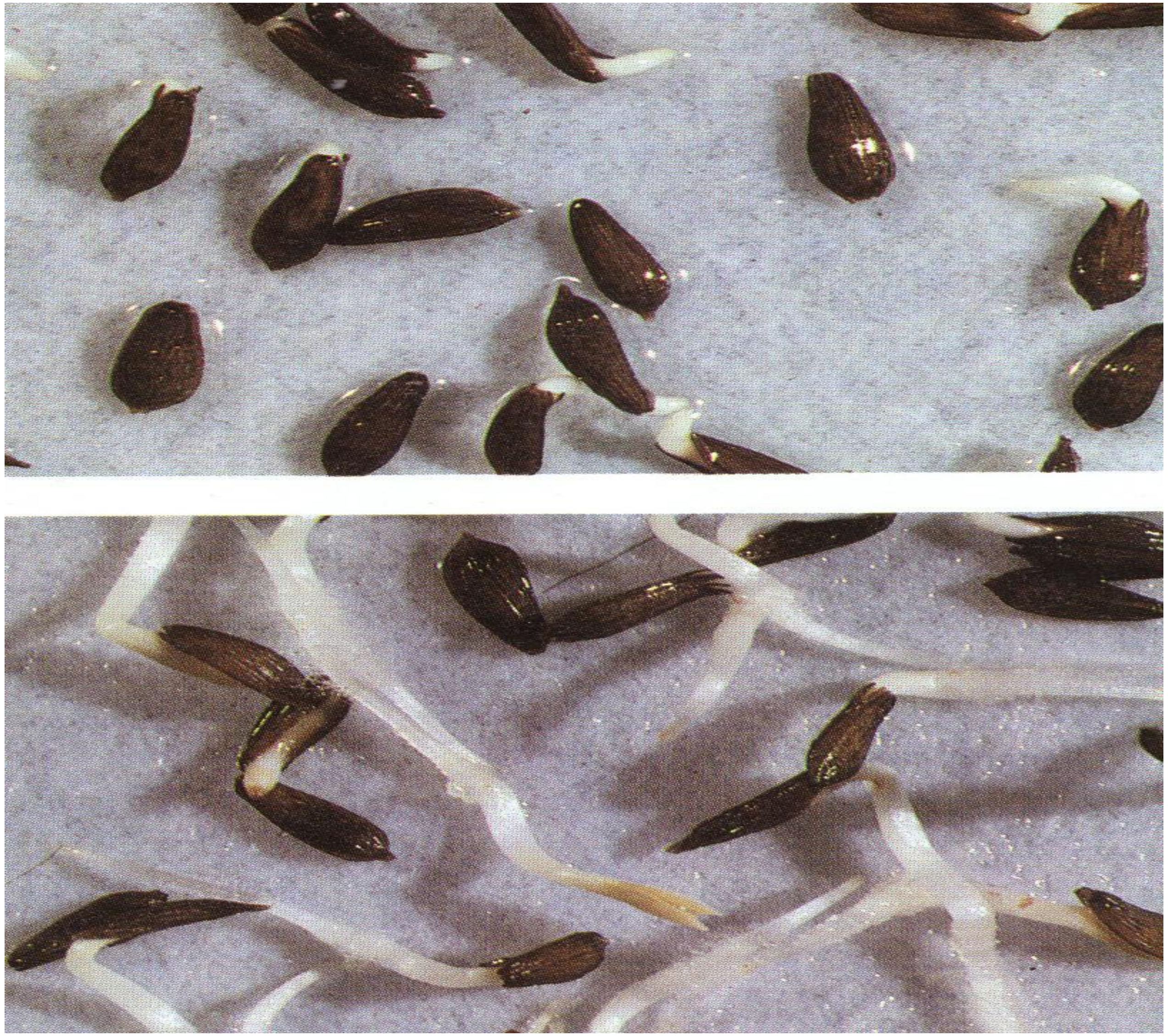
- ❖ **ABA accumulates during mid-to-late seed development.**
- ❖ **ABA promotes seed maturation and storage reserve accumulation.**
- ❖ **ABA induces seed dormancy, preventing premature germination.**
- ❖ **The ABA/GA balance is a key regulator of seed dormancy and germination.**
- ❖ **ABA promotes expression of LEA proteins (胚胎发育晚期丰富蛋白, LEA proteins).**

Low seed moisture is essential for safe storage and mechanical harvest.

1. Promotes Seed Maturation and Dormancy

+ ABA

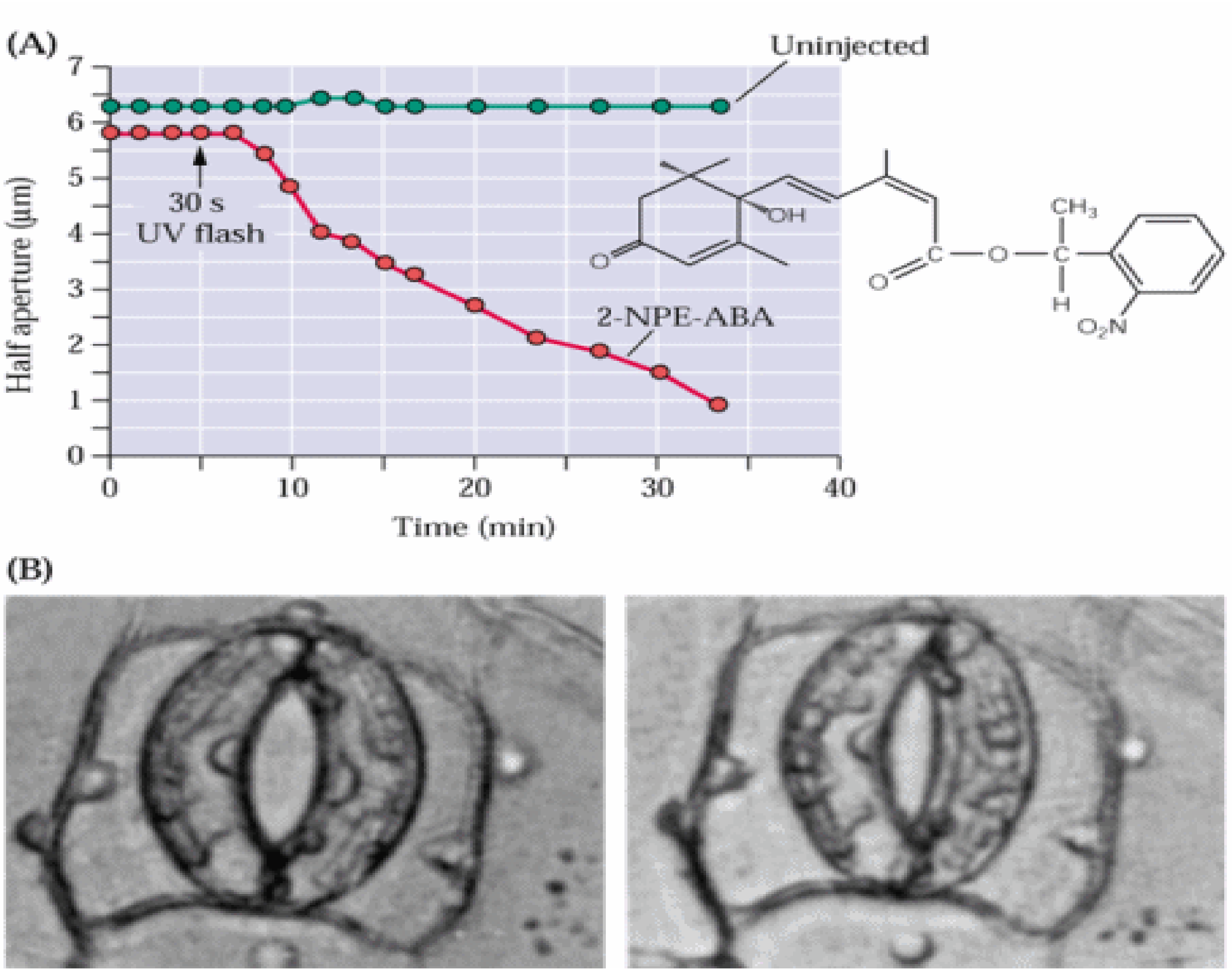
+ H_2O



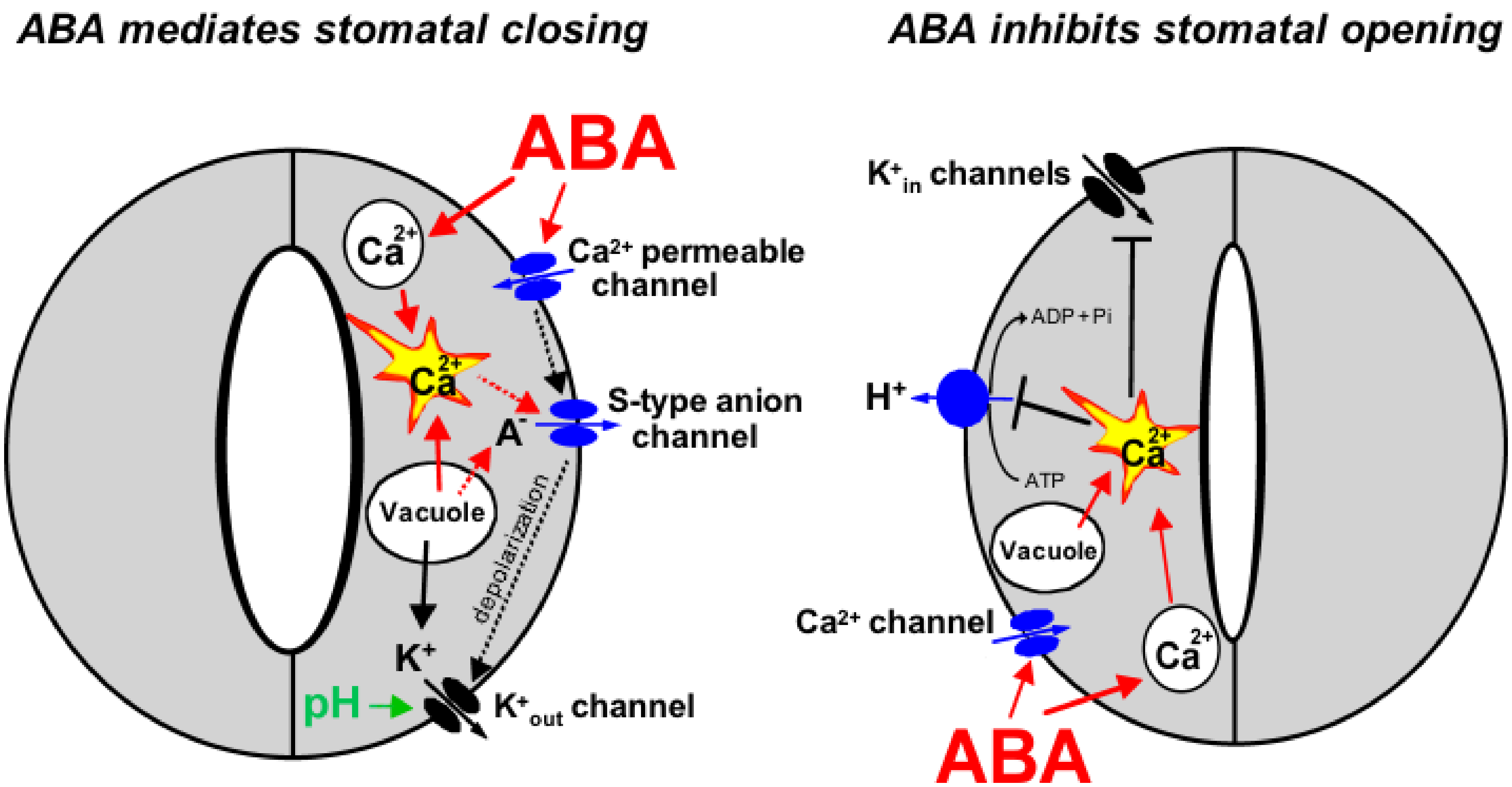
2. ABA Induces Bud Dormancy

ABA promotes bud dormancy (芽休眠) in woody plants.

3. ABA as a Drought Signal: Stomatal Closure



3. ABA as a Drought Signal: Stomatal Closure



Ethylene, ETH

Discovery of Ethylene

Ethylene (乙烯, ETH) was recognized through its effects on plant growth and fruit ripening.

- ❖ **1864 — Girardin:** gas leaking from street lamps promoted leaf abscission .
- ❖ **1901 — Neljubow**: illuminating gas affected pea seedling growth and ETH is the active component causing the “triple response” phenotype.
- ❖ **1910 — Cousins:** ripe oranges accelerated banana ripening.
- ❖ **1934 — Gane:** ethylene is naturally produced by ripening fruits.

By the late 1960s, ethylene was widely accepted as a plant hormone.

Key Features of Ethylene

ETH is the simplest alkene:

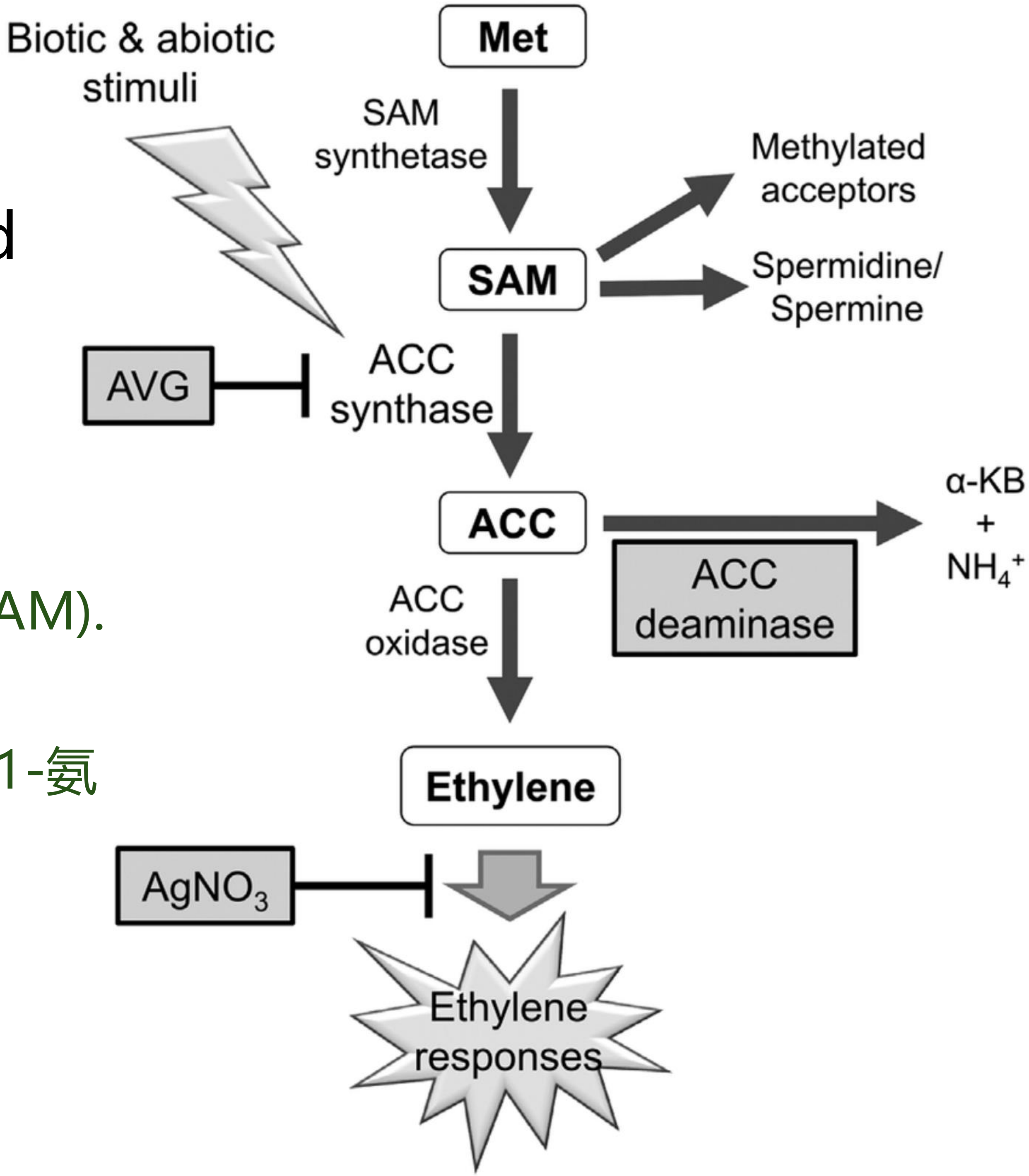
$$CH_2{=}CH_2$$

Because ethylene diffuses quickly, agricultural use often relies on ethylene-releasing compounds or inhibitors.

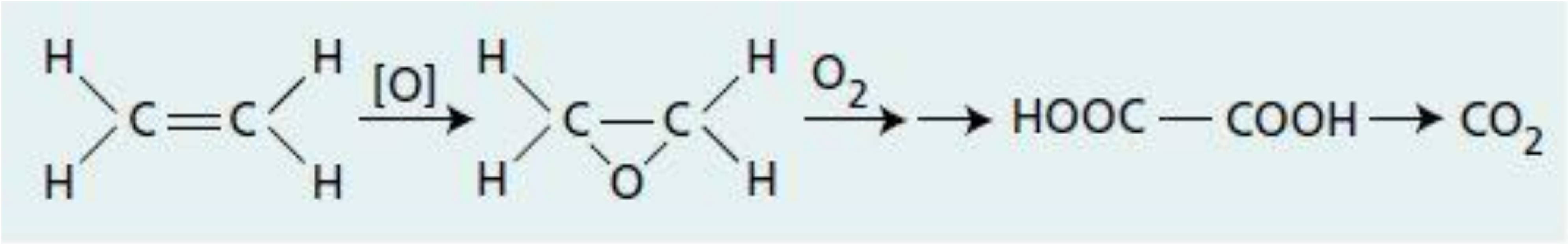
Ethylene Biosynthesis

Ethylene (乙烯, ETH) is synthesized from methionine (甲硫氨酸, Met).

- ❖ Methionine is converted to S-adenosylmethionine (S-腺苷甲硫氨酸, SAM).
- ❖ SAM is converted to 1-aminocyclopropane-1-carboxylic acid (1-氨基环丙烷-1-羧酸, ACC)
- ❖ ACC is converted to ethylene by ACC oxidase (ACC氧化酶, ACO).



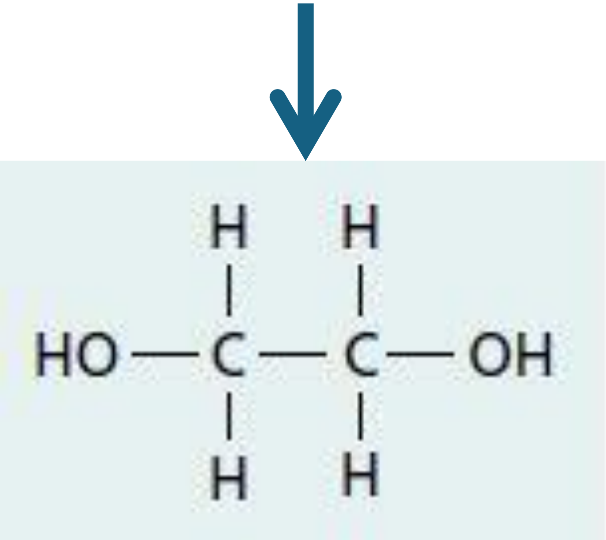
Ethylene Oxidative



Ethylene

Ethylene oxide

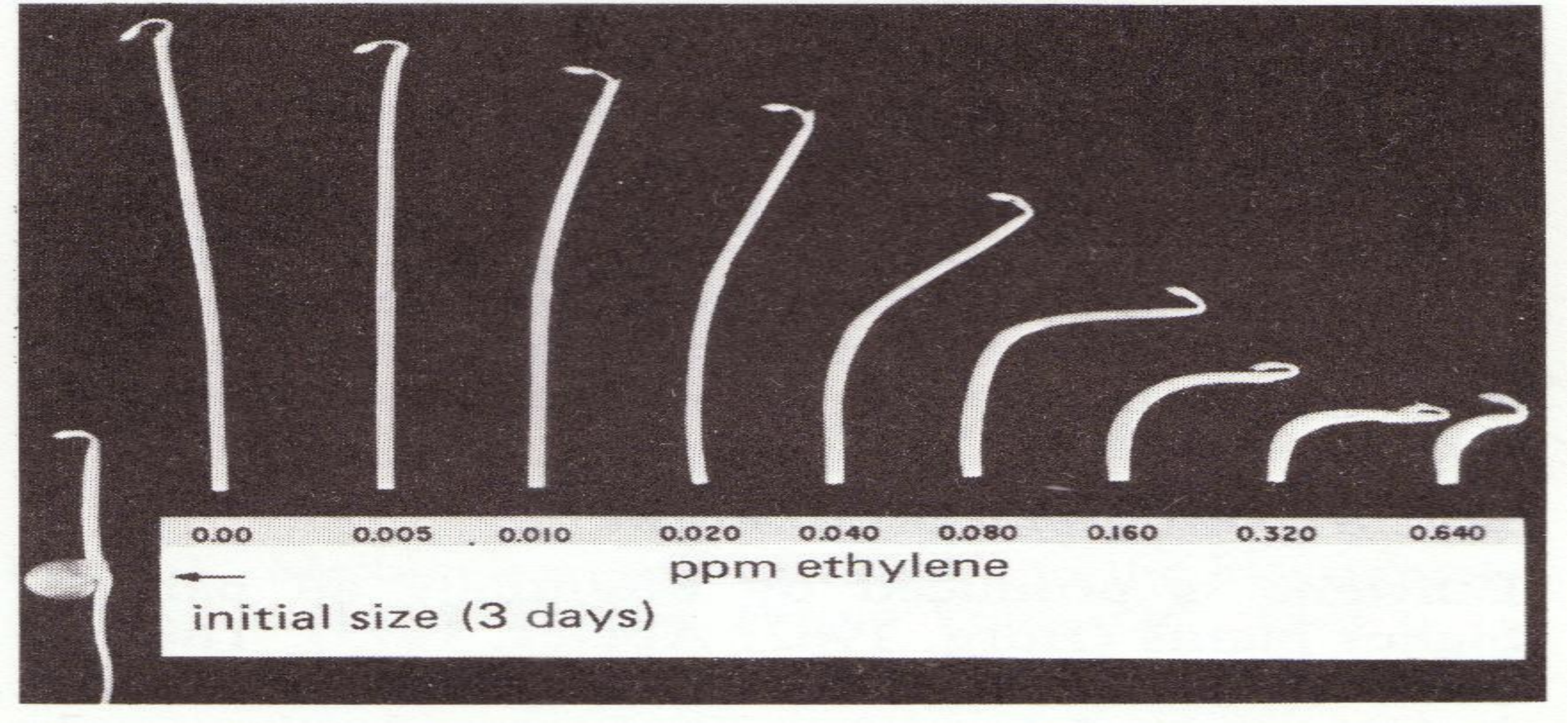
Oxalic acid



Ethylene glycol

1. Regulates Seedling Growth: Triple Response

The classic **triple response (三重反应)** in dark-grown seedlings: Inhibition of hypocotyl elongation (下胚轴伸长受抑) , Radial swelling of the hypocotyl (下胚轴横向膨大) , and exaggerated apical hook formation (顶端弯钩加剧)

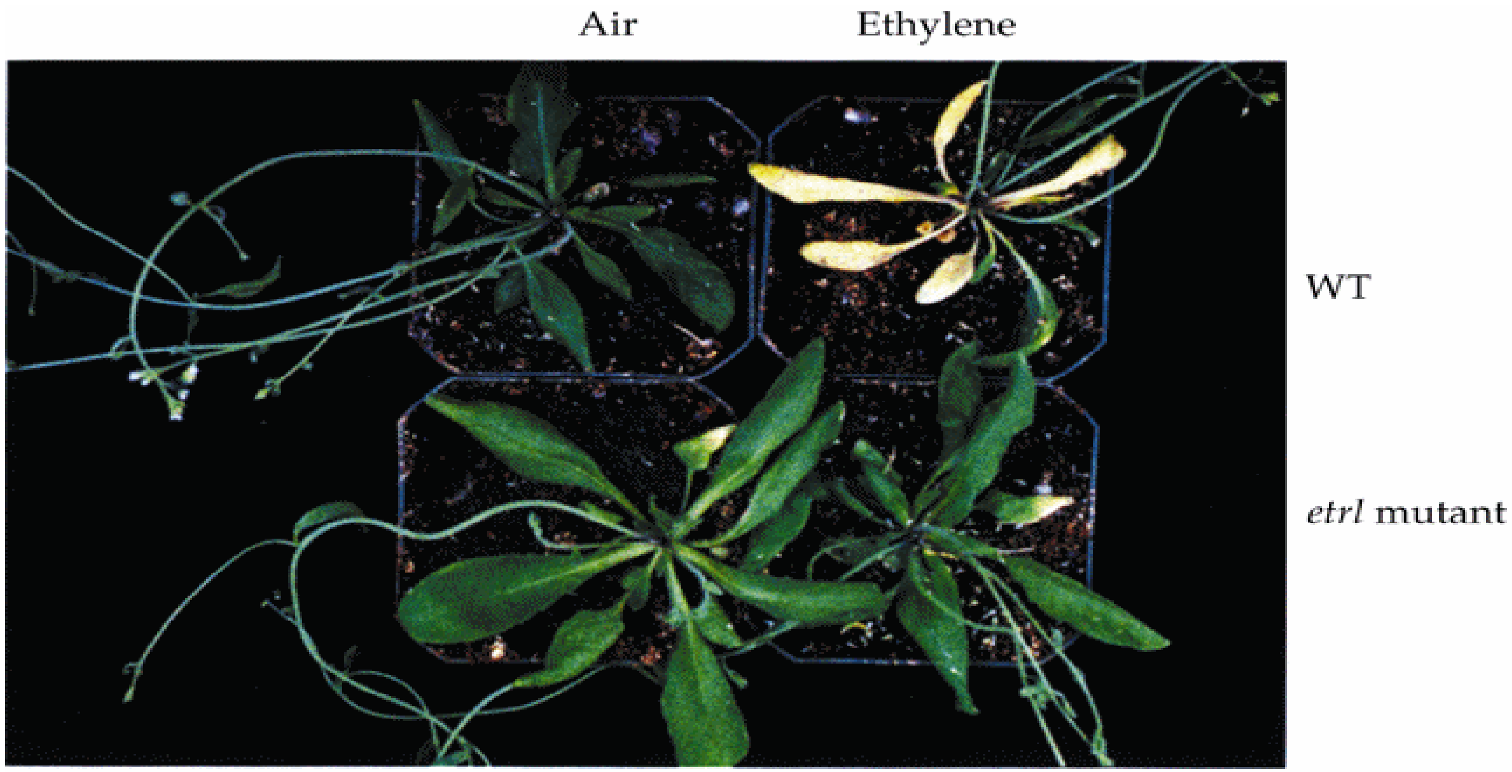


2. Ethylene Promotes Fruit Ripening

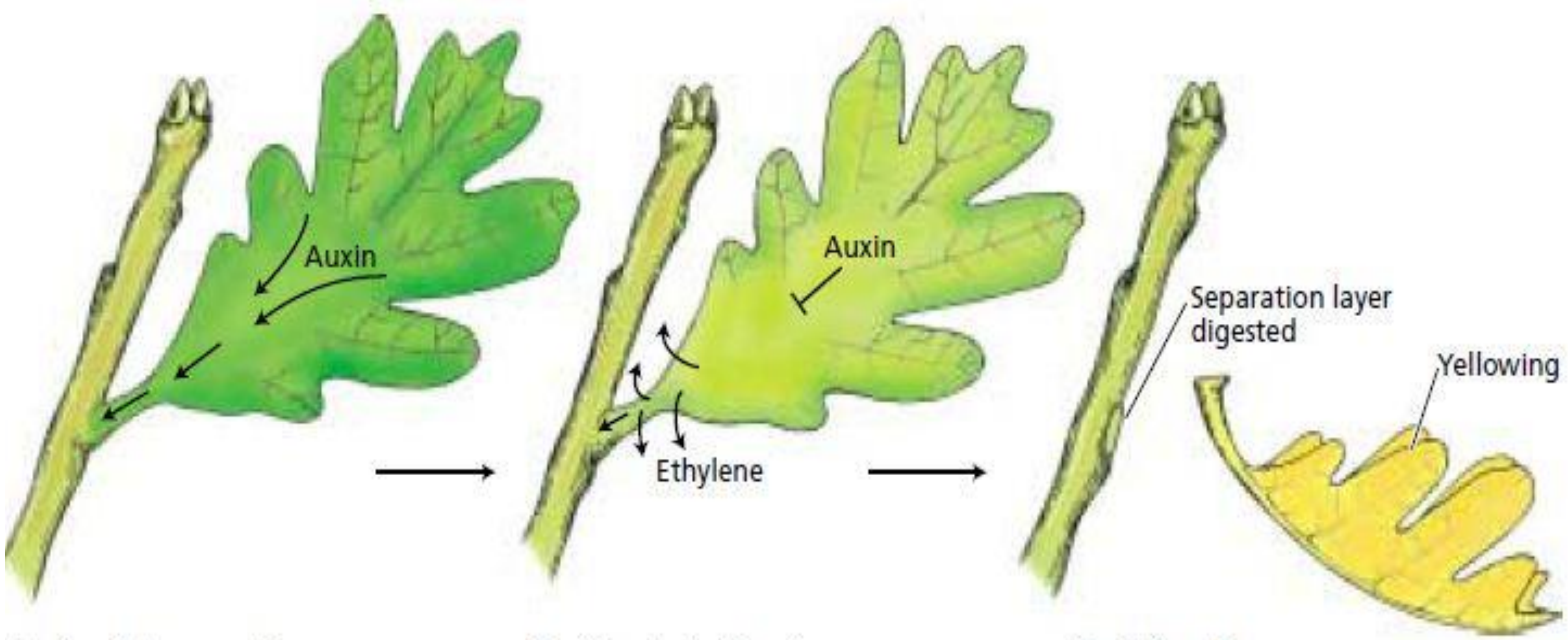
Ethylene (乙烯, ETH) promotes ripening in climacteric fruits (跃变型果实), such as banana, tomato, and apple.

- ❖**Starch-to-sugar conversion**
- ❖**Fruit softening**
- ❖**Color change**
- ❖**Aroma production**

3. Ethylene Promotes Senescence and Abscission



3. Ethylene Promotes Senescence and Abscission

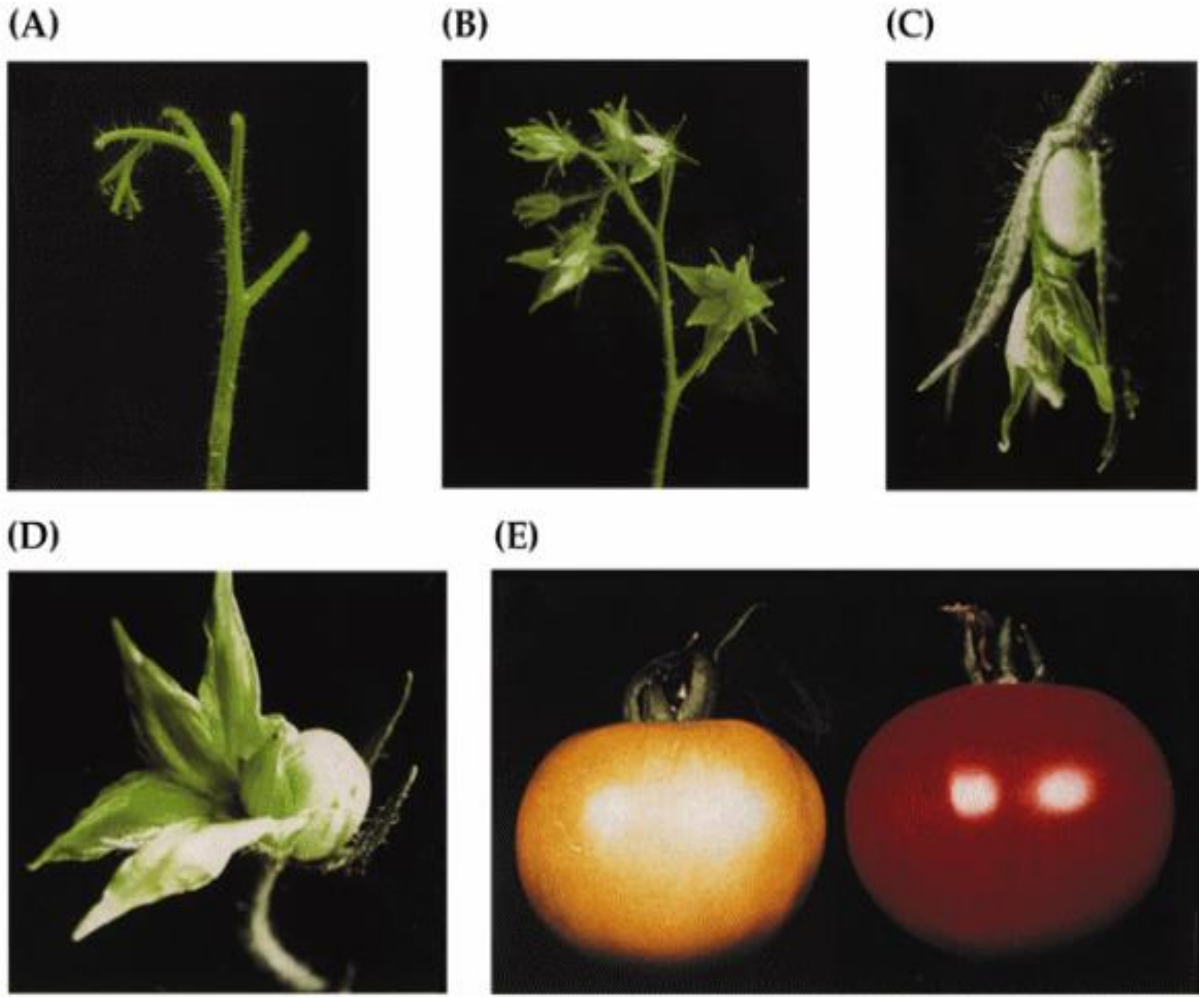


Leaf maintenance phase
High auxin from leaf reduces ethylene sensitivity of abscission zone and prevents leaf shedding.

Shedding induction phase
A reduction in auxin from the leaf increases ethylene production and ethylene sensitivity in the abscission zone, which triggers the shedding phase.

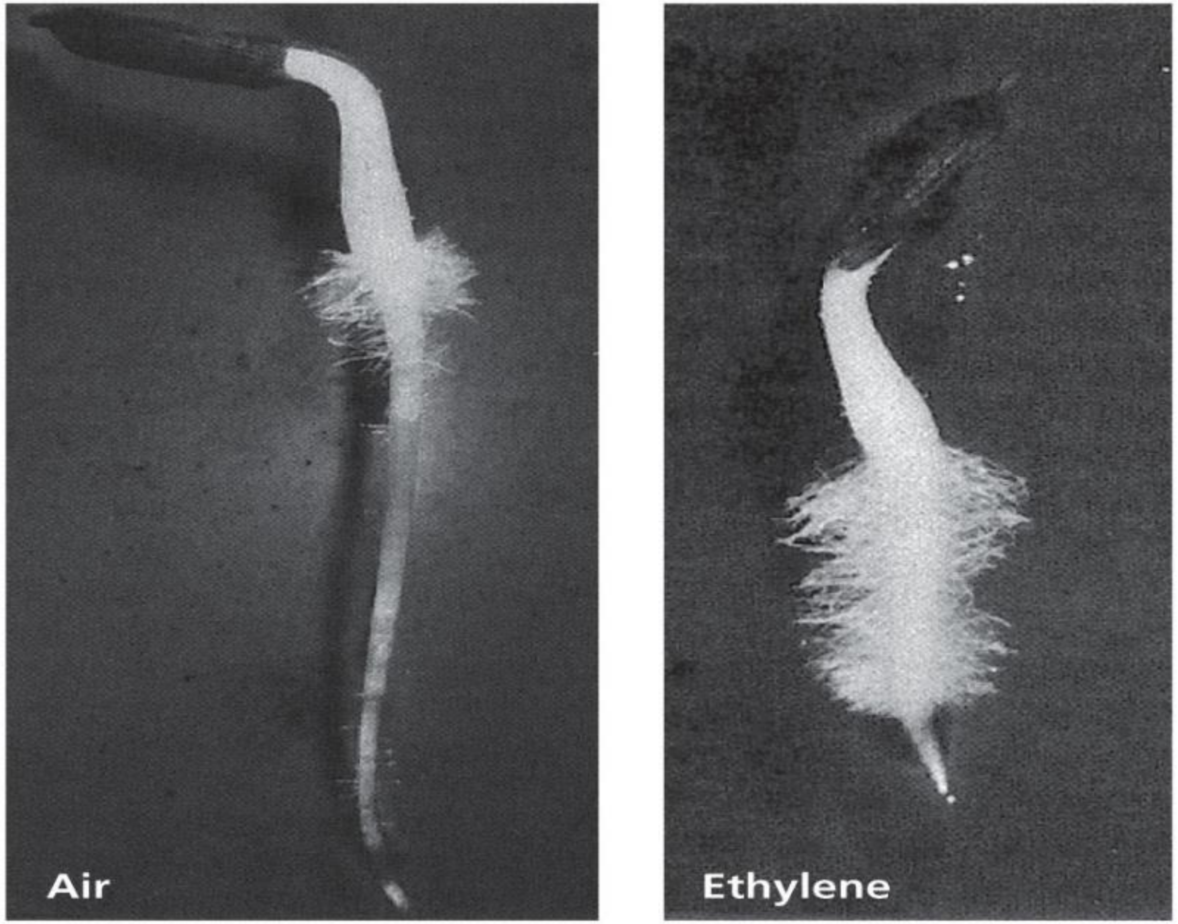
Shedding phase
Synthesis of enzymes that hydrolyze the cell wall polysaccharides, resulting in cell separation and leaf abscission.

4. Ethylene Signaling Affects Floral and Fruit Development



- ❖ Ethylene (乙烯, ETH) regulates flower senescence, fruit ripening, and organ abscission.
- ❖ The **never ripe** tomato mutant has reduced ethylene sensitivity.
- ❖ Ethylene-insensitive fruits fail to ripen normally.

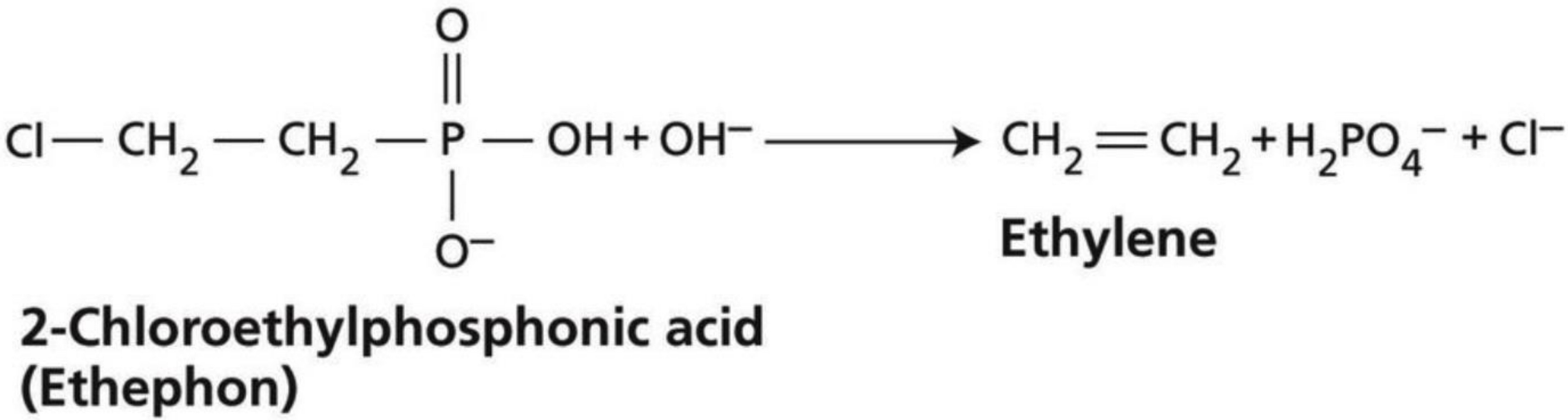
5. Promotes of root hair formation



Promotion of root hair formation by ethylene in lettuce seedlings. Two-day-old seedlings were treated with air (left) or 10 ppm ethylene (right) for 24 hours before the photo was taken.

Agricultural Use of Ethylene: Ethephon

Ethephon (乙烯利), or 2-chloroethylphosphonic acid (2-氯乙基膦酸), is an ethylene-releasing compound.



Hormone	Major active forms	Main biosynthesis sites	Key transport feature	Major physiological functions
Auxin	IAA, IBA, PAA	Shoot apex, young leaves, developing seeds/fruits, root tips	Strong **polar transport (极性运输)** via PIN, AUX1/LAX, ABCB proteins	Cell elongation, apical dominance, adventitious rooting, tropisms, fruit development, vascular differentiation
CTKs	trans-zeatin, iP, DHZ	Root tips, developing seeds/fruits, young tissues	Mainly transported through xylem and phloem as bases, ribosides, or nucleotides	Cell division, shoot formation, bud outgrowth, delayed leaf senescence, cotyledon expansion
GAs	GA_1, GA_3, GA_4, GA_7	Young shoots, developing seeds/fruits, roots	Mobile through vascular tissues; GA_{12} can act as a transportable precursor	Stem/internode elongation, seed germination, bolting, flowering in some species, fruit growth
ABA	2-cis-(+)-ABA / S-ABA	Leaves, roots, seeds; strongly induced under drought	Transported through xylem and phloem; ABA-GE can serve as storage/transport form	Seed maturation, dormancy, drought response, stomatal closure, bud dormancy, stress tolerance
ETH	Ethylene gas, $CH_2{=}CH_2$	Many tissues; high in ripening fruits, senescing tissues, wounded/stressed organs	Gaseous diffusion through tissues and air spaces	Triple response, fruit ripening, senescence, abscission, flower wilting, stress responses

	Germination	Growth to Maturity	Flowering	Fruit Development	Abscission	Seed Dormancy
Gibberellin	✓	✓	✓	✓	✗	✗
Auxin	✗	✓	✓	✓	✗	✗
Cytokinins	✗	✓	✓	✓	✗	✗
Ethylene	✗	✗	✓	✓	✓	✗
Abscisic Acid	✗	✗	✗	✗	✓	✓

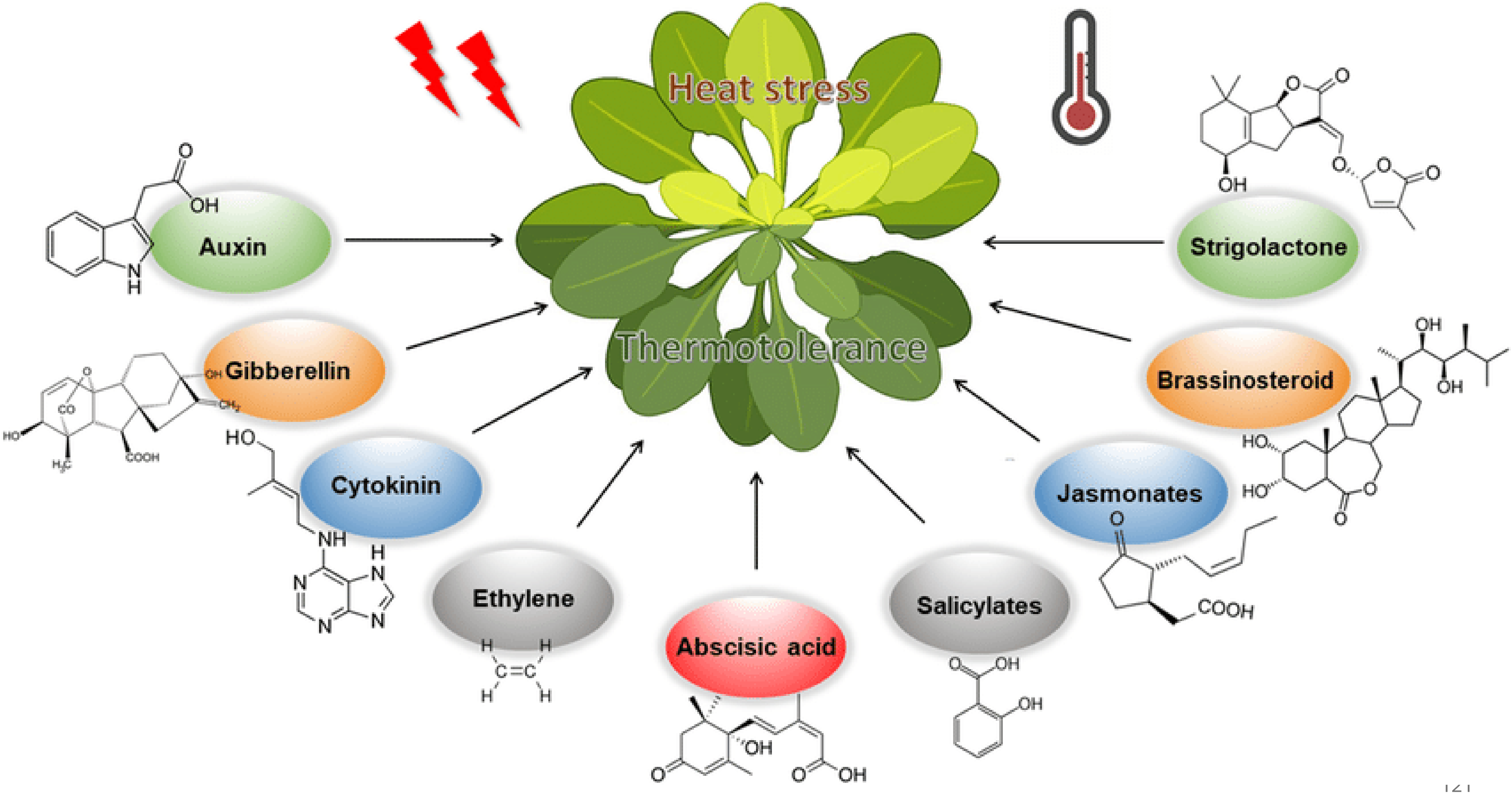
Other Endogenous Plant Growth Regulators

Self-study topic; included in course review/exam scope

- ❖Brassinosteroids (油菜素甾体类, BRs)
- ❖Polyamines (多胺, PAs)
- ❖Jasmonates (茉莉酸类, JAs)
- ❖Salicylic acid (水杨酸, SA)
- ❖Turgorins (膨压素)
- ❖Peptide hormones (植物肽激素)
- ❖Strigolactones (独脚金内酯, SLs)

Interactions Among Plant Hormones

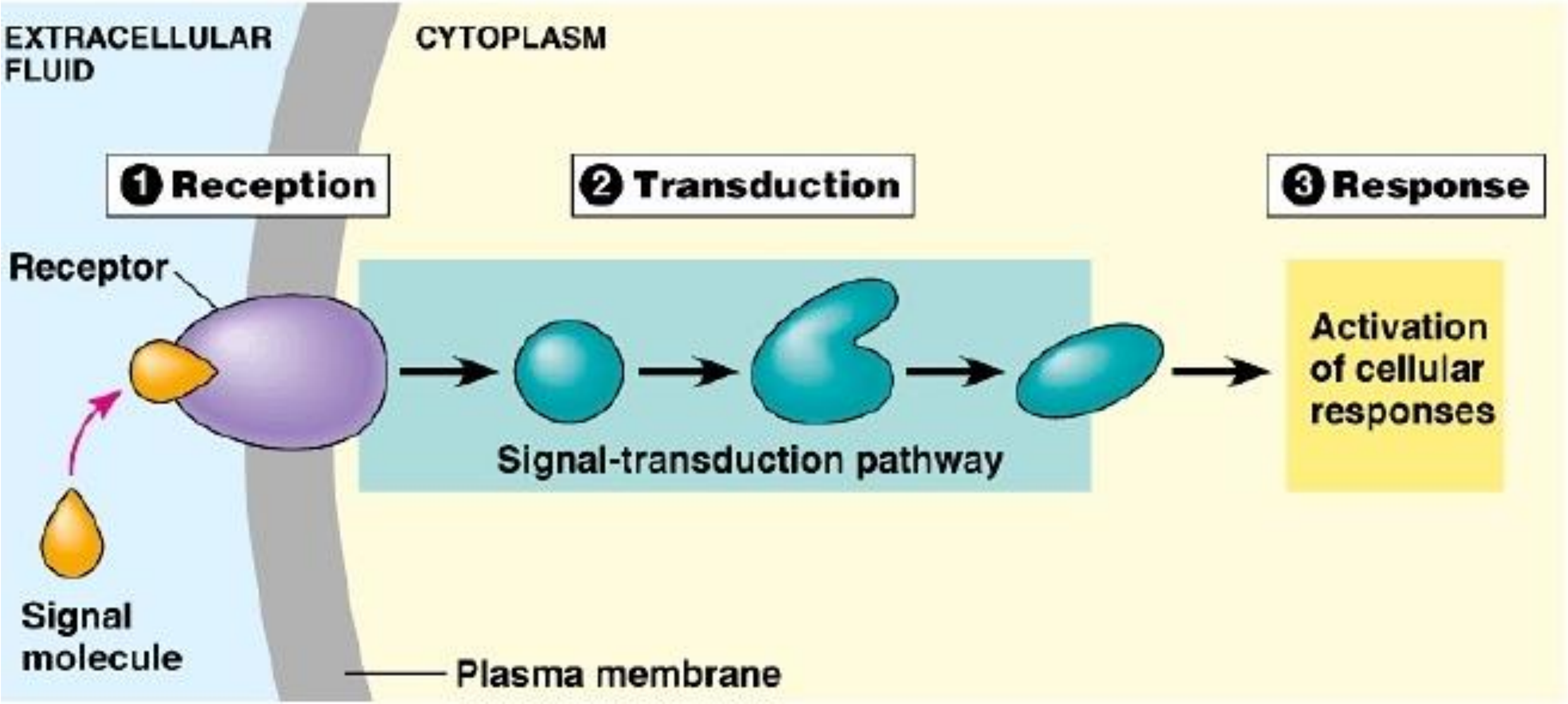
- **Plant hormones rarely act alone; growth and stress responses depend on hormonal balance.**
- **High auxin (生长素, IAA) can stimulate ethylene (乙烯, ETH) biosynthesis.**
- **Ethylene can modify auxin biosynthesis, transport, and sensitivity.**
- **Cytokinins (细胞分裂素, CTKs) can delay auxin degradation and promote shoot activity.**
- **Cytokinins and abscisic acid (脱落酸, ABA) can reduce active gibberellin (赤霉素, GA) levels by promoting GA deactivation.**
- **Ethylene and ABA often interact during stress responses, senescence, and abscission.**
- **Auxin can promote GA biosynthesis and reduce GA deactivation in some elongating tissues.**


Heat stress
Thermotolerance
Auxin
Gibberellin
Cytokinin
Ethylene
Abscisic acid
Salicylates
Jasmonates
Brassinosteroid
Strigolactone

Cell Signal Transduction

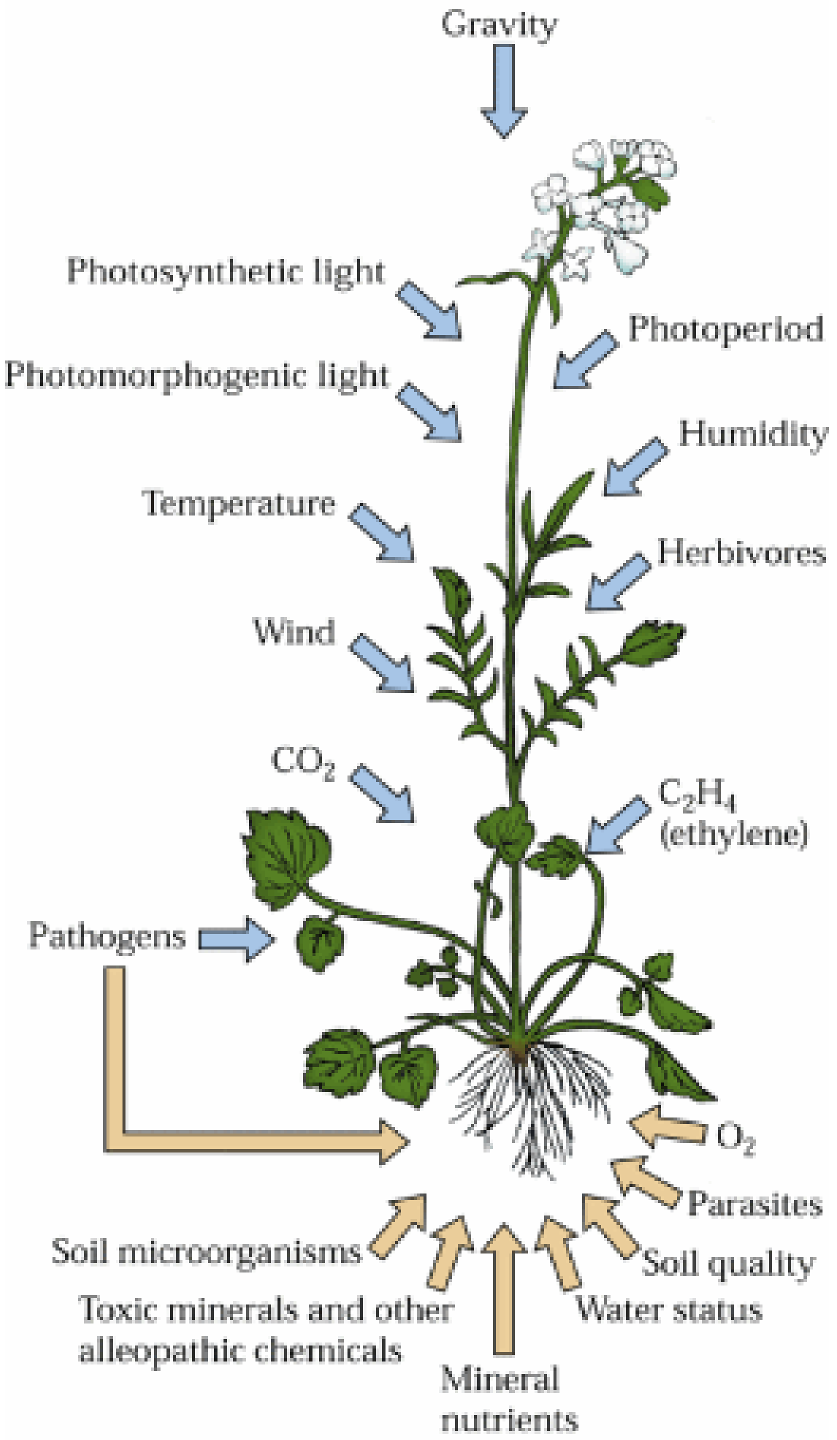
What is cell signal transduction?

Cell signal transduction (细胞信号转导) is the process by which a cell converts an external or internal signal into a specific physiological response.

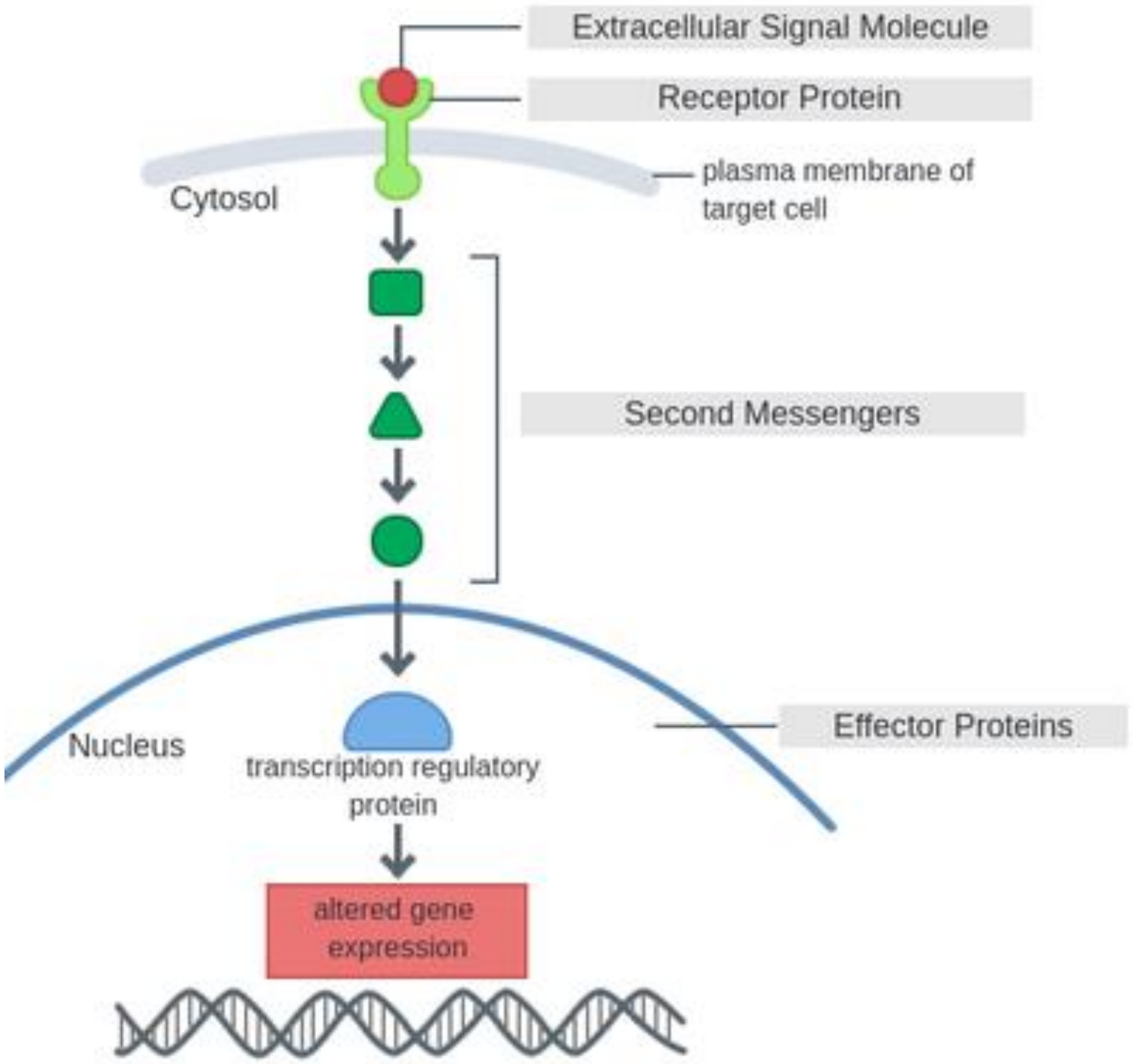


细胞信号转导与诺贝尔奖

Year	Recipient	Prize	Area of Research
1971	E.W. Sutherland	M&P	**激素作用机理，第二信使cAMP**
1992	E. Fischer, E. Krebs	M&P	**蛋白质的可逆磷酸化调节酶活性**
1994	A. Gilman, M. Rodbell	M&P	**G蛋白及其在信号转导中的作用**
1998	R. Furchgott, L. Ignarro, F. Murad	M&P	**NO在心血管系统中作为信号分子**
1999	G. Blobel	M&P	**控制细胞运输和定位的内在信号蛋白**
2000	A. Carlsson, P. Greengard, E. Kandel	M&P	**神经系统的信号转导**
2004	R. Axel, L. Buck	M&P	**嗅觉受体**
2012	R.J. Lefkowitz, B. K. Kobilka	C	**G蛋白偶联受体**



Cell Signal Transduction



Signal

↓

Receptor

↓

Second messengers / phosphorylation cascade

↓

Cellular response

External and internal signals

Major signal sources

- ❖ **Light**: energy source for photosynthesis and a developmental signal
- ❖ **Temperature, water, gases, minerals, and gravity**
- ❖ **Wounding, pathogens, and herbivores**
- ❖ **Chemical signals**, such as auxin, ABA, and GAs
- ❖ **Physical signals,** such as Electrical, Hydraulic, and Mechanical signals

First messengers (第一信使) are signals that are perceived by receptors and initiate signal transduction. Examples include hormones, light, stress signals, and cell-to-cell chemical or physical signals.

Transmembrane Conversion

Signal perception is the first committed step in signal transduction.

❖A **receptor (受体)** recognizes a specific signal or **ligand (配体)**.

❖Receptors determine the **specificity** of the cellular response.

Where Are Plant Receptors Located?

Plant receptors occur in several cellular locations.

- **Plasma membrane (质膜)**
  - ✓ Receptor-like kinases, RLKs (受体样激酶)
  - ✓ Receptor-like proteins, RLPs (受体样蛋白)
  - ✓ Ion channels and transporters
  - ✓ Some hormone and peptide receptors
- **Endomembranes**
  - ✓ Ethylene receptors are mainly associated with the endoplasmic reticulum.
  - ✓ Some stress and hormone signals are perceived on internal membranes.
- **Cytosol and nucleus**
  - ✓ Auxin, gibberellin, jasmonate, and ABA signaling involve intracellular receptors.
  - ✓ Many light and hormone responses directly regulate transcription.

Where Are Plant Receptors Located?

Plant cells use several receptor mechanisms.

- **Receptor-like kinases, RLKs**
  Detect peptides, brassinosteroids, pathogen signals, and developmental cues.
- **Receptor-like proteins, RLPs**
  Often function with kinases in immunity and development.
- **Ion-channel-linked signaling**
  Regulates Ca^{2+}, K^+, Cl^-, H^+, and membrane potential.
- **Two-component / histidine kinase-related receptors**
  Important in cytokinin and ethylene signaling.
- **Intracellular hormone receptors**
  Auxin, GA, JA, ABA, and strigolactone signaling often involve ligand-dependent protein degradation.

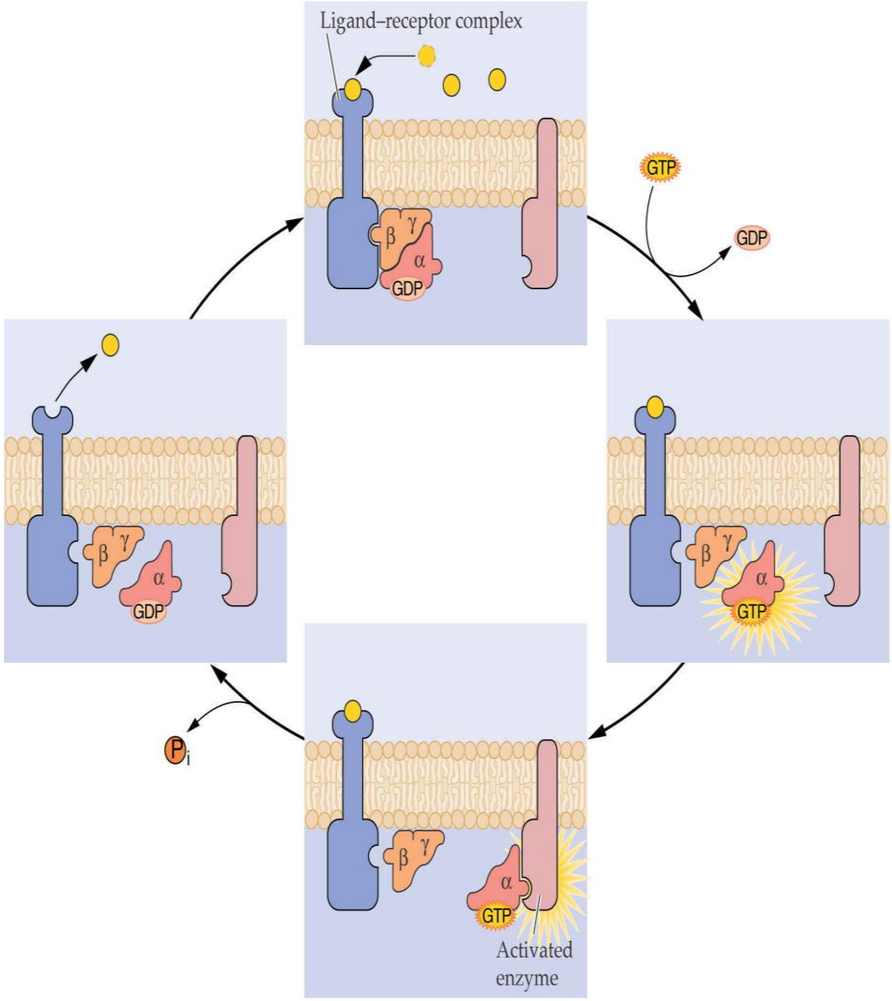
Ion Channels and Rapid Early Signals

Some signals rapidly change ion flux across membranes.

- ❖ Opening or closing of ion channels
- ❖ Changes in membrane potential
- ❖ Cytosolic Ca^{2+} elevation
- ❖ pH changes in the cytosol or apoplast
- ❖ ROS production and downstream kinase activation

Heterotrimeric G Proteins in Plants

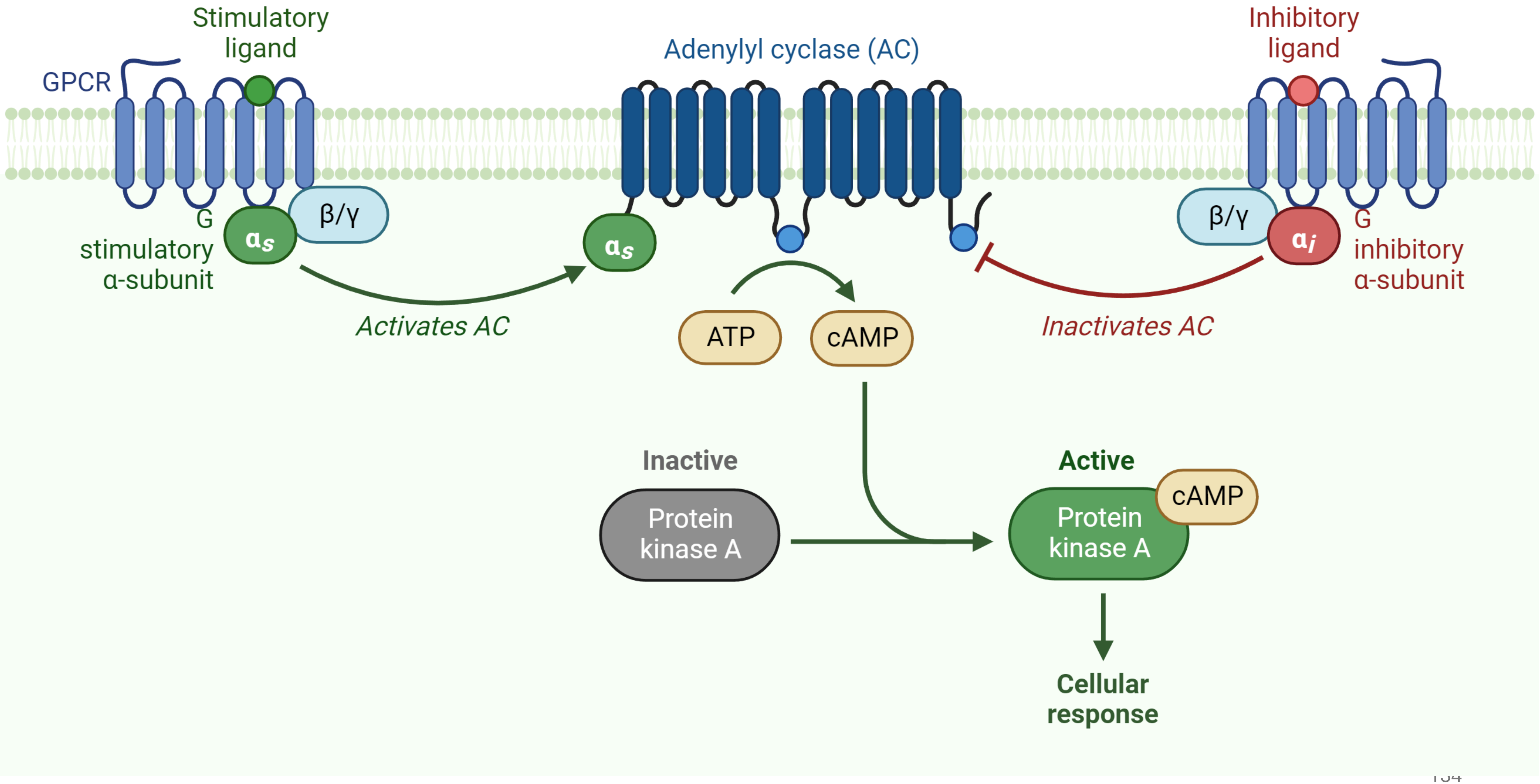
Heterotrimeric G proteins (异源三聚体G蛋白) are molecular switches involved in plant signaling.



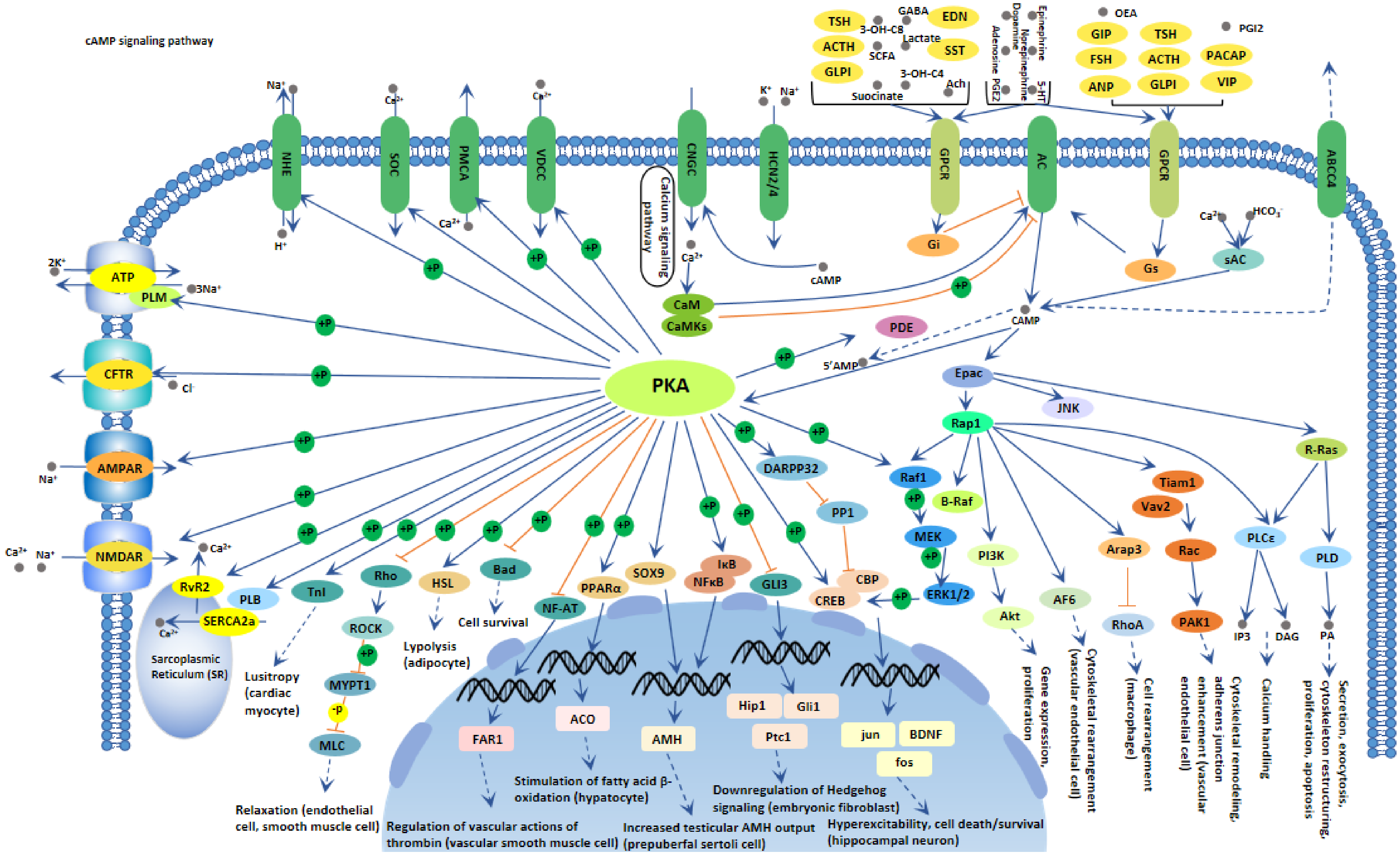
Intracellular Signal Transduction: Second Messengers

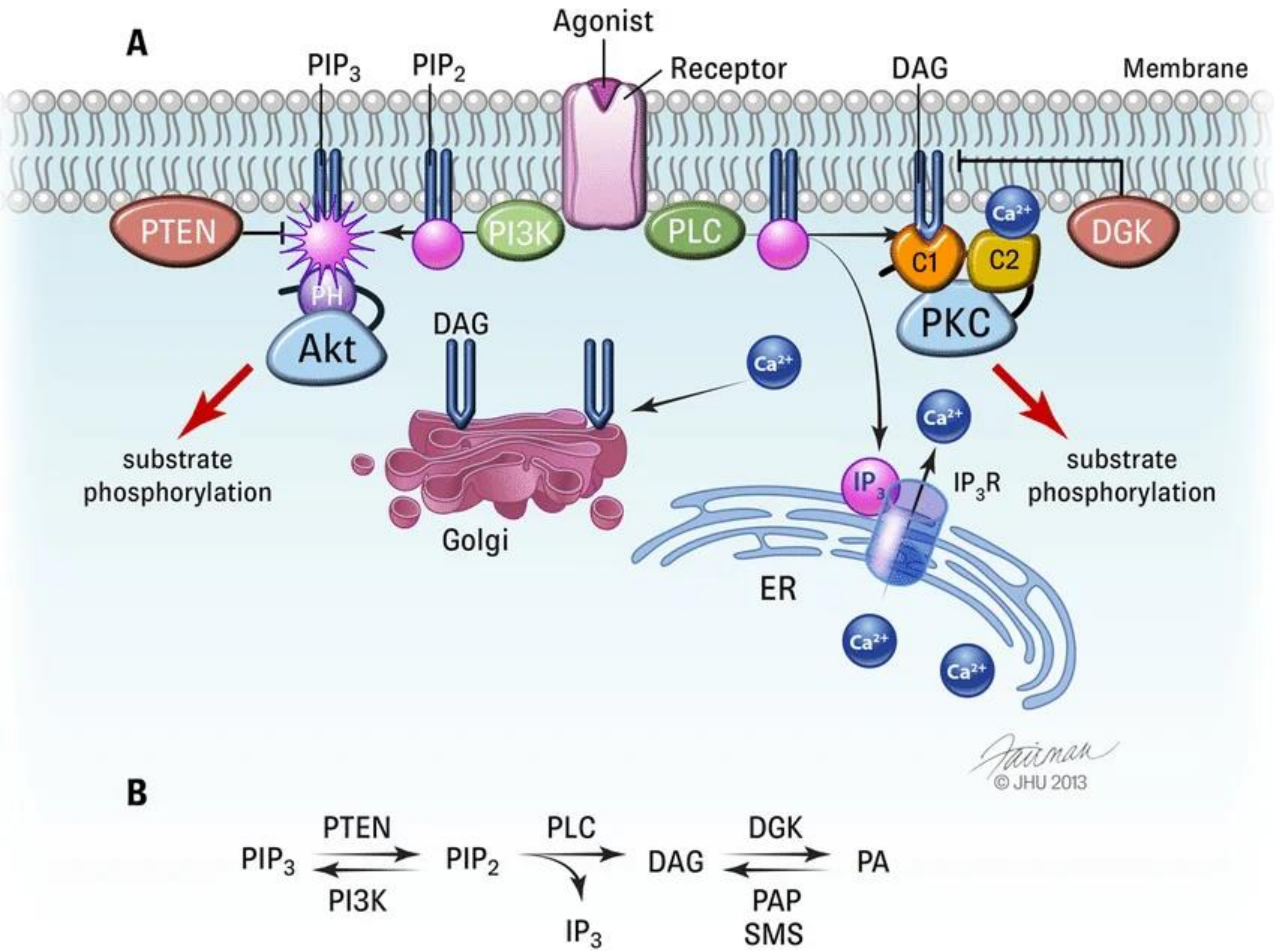
Second messengers (第二信使) are intracellular signaling molecules or ions that change rapidly after a receptor perceives a signal.

- **Ca^{2+} signals**: encode information through changes in concentration, location, and duration
- **ROS and NO**: reactive signaling molecules involved in stress, defense, and development
- **pH and membrane potential**: regulate ion transport and enzyme activity
- **Phospholipid-derived signals**: phosphatidic acid (PA), inositol phosphates, and phosphoinositides
- **Cyclic nucleotides**: cAMP and cGMP may participate in some plant signaling pathways


Stimulatory ligand
GPCR
G stimulatory α-subunit
$α_s$
β/γ
Activates AC
Adenylyl cyclase (AC)
$α_s$
ATP
cAMP
Inhibitory ligand
β/γ
$α_i$
G inhibitory α-subunit
Inactivates AC
Inactive
Protein kinase A
Active
Protein kinase A
cAMP
Cellular response

cAMP signaling pathway




A
Agonist
Receptor
PIP3
PIP2
DAG
Membrane
PTEN
PI3K
PLC
DGK
Ca2+
C1
C2
PKC
PH
Akt
DAG
substrate phosphorylation
substrate phosphorylation
IP3
IP3R
Golgi
ER
© JHU 2013
B
PIP3
PTEN
PI3K
PIP2
PLC
IP3
DAG
DGK
PAP
SMS
PA

Homework Assignments

Choose ONE phenomenon and explain it using plant hormones:

- Seed dormancy or germination
- Fruit ripening
- Drought-induced stomatal closure
- Pruning-induced branching
- Rooting of stem cuttings

Your task:

1. Identify the key hormone(s).
2. Explain the mechanism, not just the function.
3. Discuss one hormone interaction, such as ABA–GA or auxin–cytokinin.
4. Propose one simple agricultural or experimental application.

Challenge:

Design a simple experiment: treatment, control, predicted result.