Contents

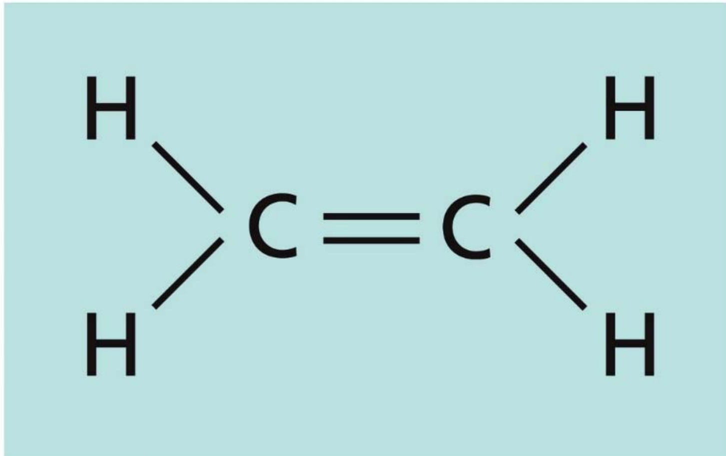
- **Ethylene ; The gaseous hormone**

  ① **Structure, biosynthesis, and Measurement of ethylene**

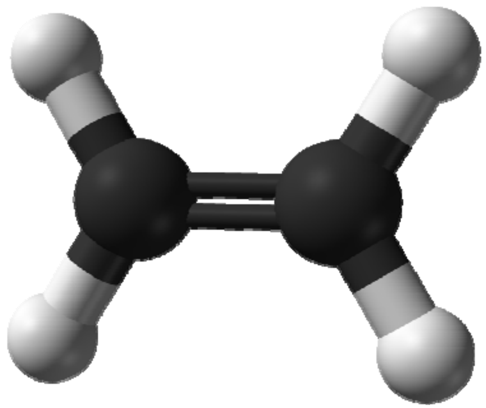
  ② **Ethylene signal transduction pathway**

Structure of ethylene

- **The simplest <u>olefin</u>**
  at least one carbon-carbon double bond
- **M.W. 28**
- **Lighter than air, gaseous hormone**
- **Ethylene can be produced by almost all parts of higher plants**
- **Ethylene production increases during**
  ① Leaf senescence
  ② Fruit ripening
  ③ Wounding
  ④ Pathogen infection
  ⑤ Physiological stresses (flooding, disease, drought stress)



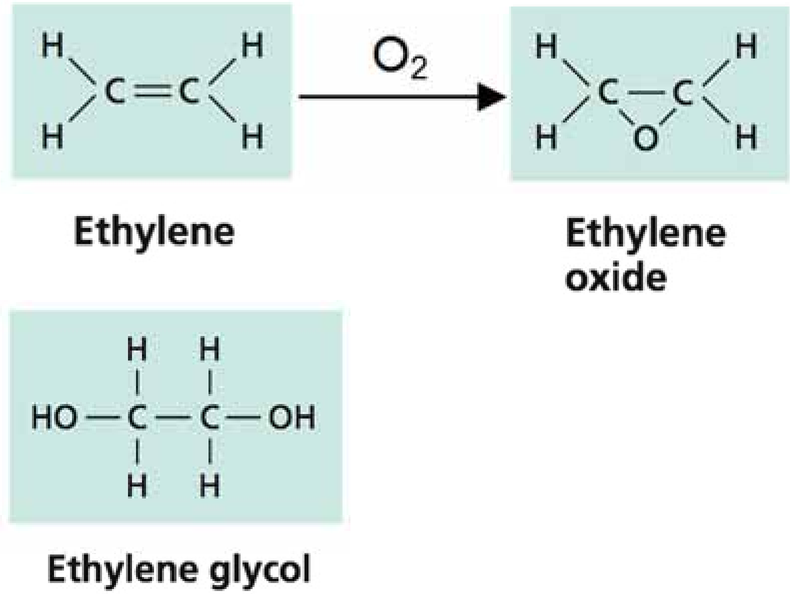
Ethylene



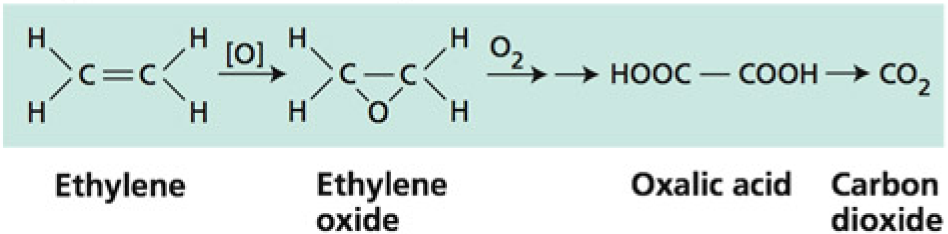
Ethylene Readily Undergoes Oxidation

Ethylene is a flammable gas and readily undergoes oxidation to ethylene oxide:
Ethylene oxide can then be hydrolyzed to ethylene glycol:

In most plant tissues, ethylene can be completely oxidized to CO_2, in the following reaction:

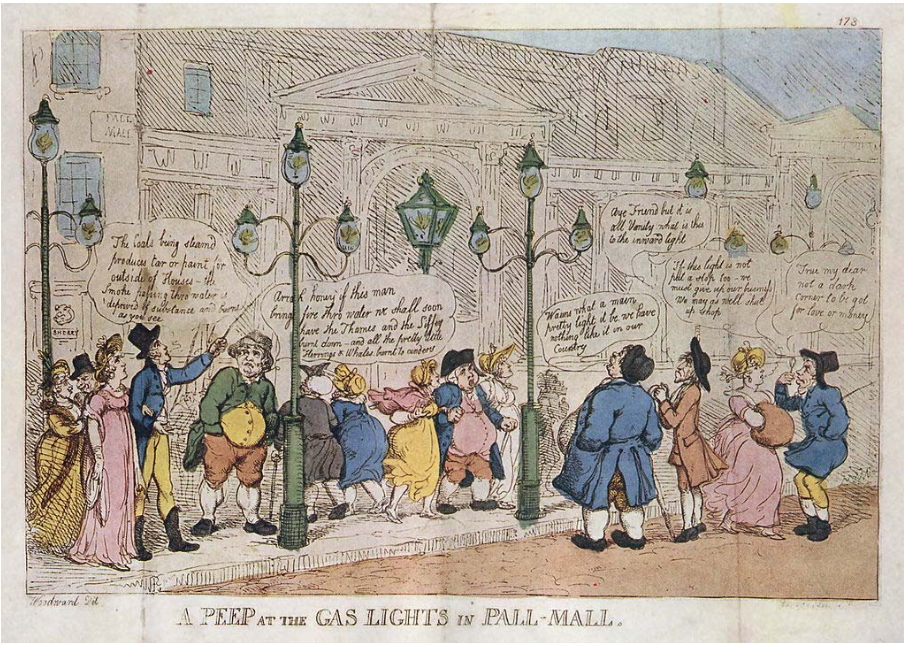


Complete oxidation of ethylene



Discovery of ethylene

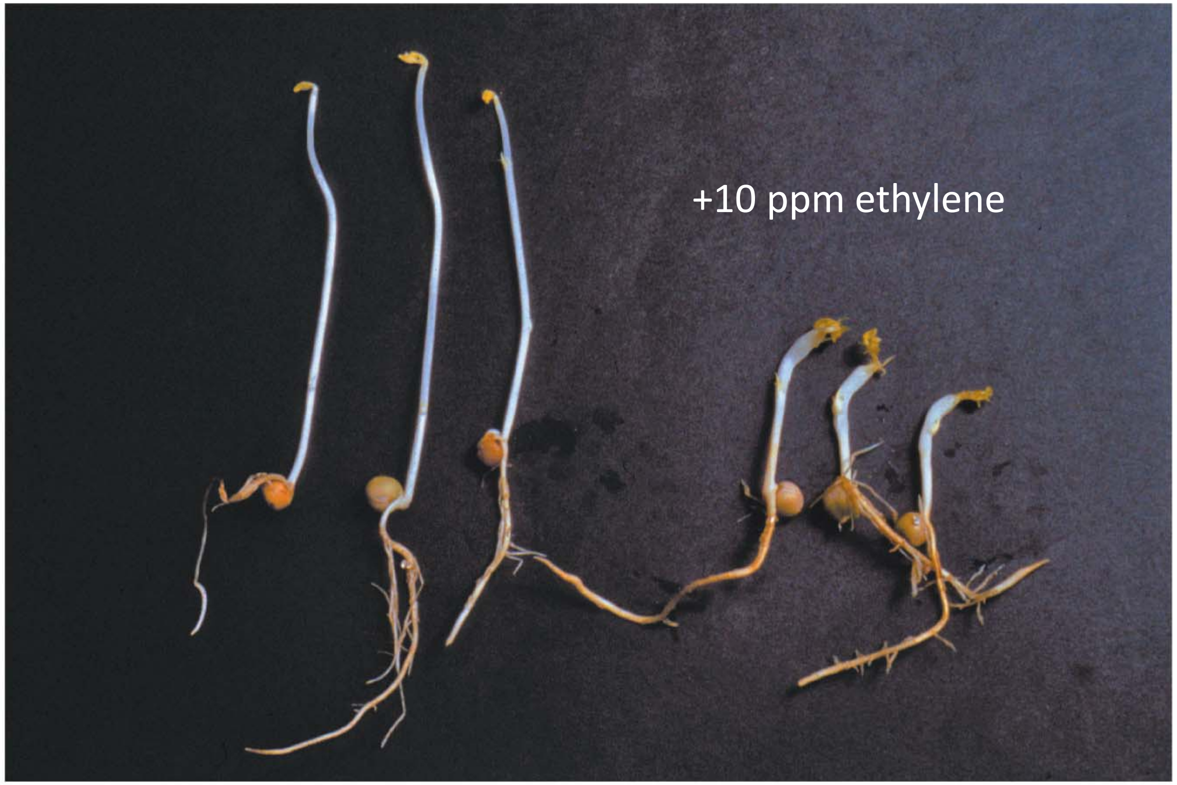
- **During 19th century , coal gas was used for street illumination**
- **Studies of the defoliant effect of leaking gas pipes led to the discovery of ethylene** (1901, Dimitry Neljubov)



http://www.wikiwand.com/en/Gas_lighting

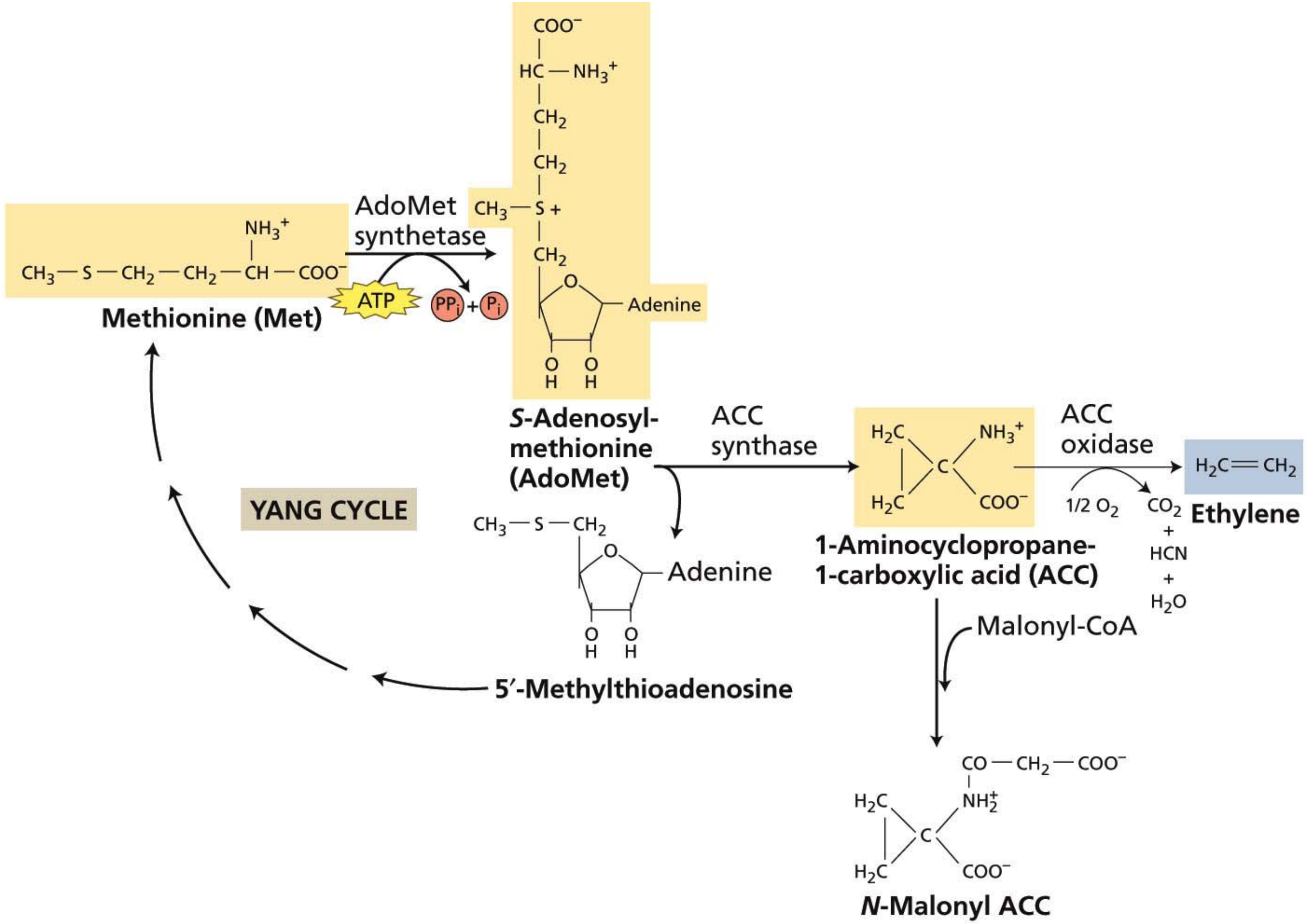
Triple response of etiolated pea seedlings

- **1910, Dimitry Neljibov : etiolated pea seedlings exhibited 'triple response'**
  ① Reduced stem elongation
  ② Increased lateral growth (swelling)
  ③ Abnormal, horizontal growth (diagratropism, 횡지성)



***PLANT PHYSIOLOGY,* 5e, Figure 22.1**

Ethylene biosynthetic pathway



PLANT PHYSIOLOGY, 5e, Figure 22.2

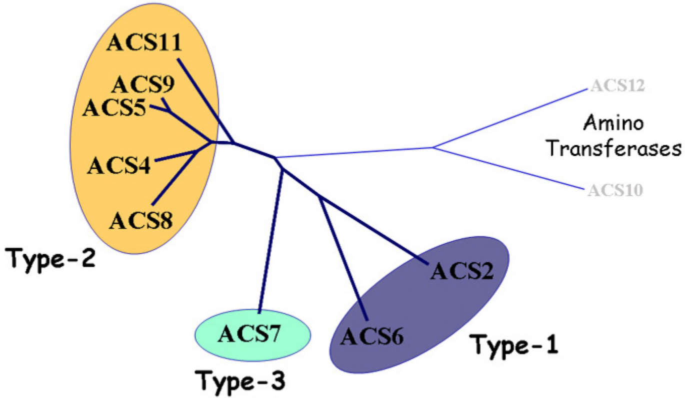
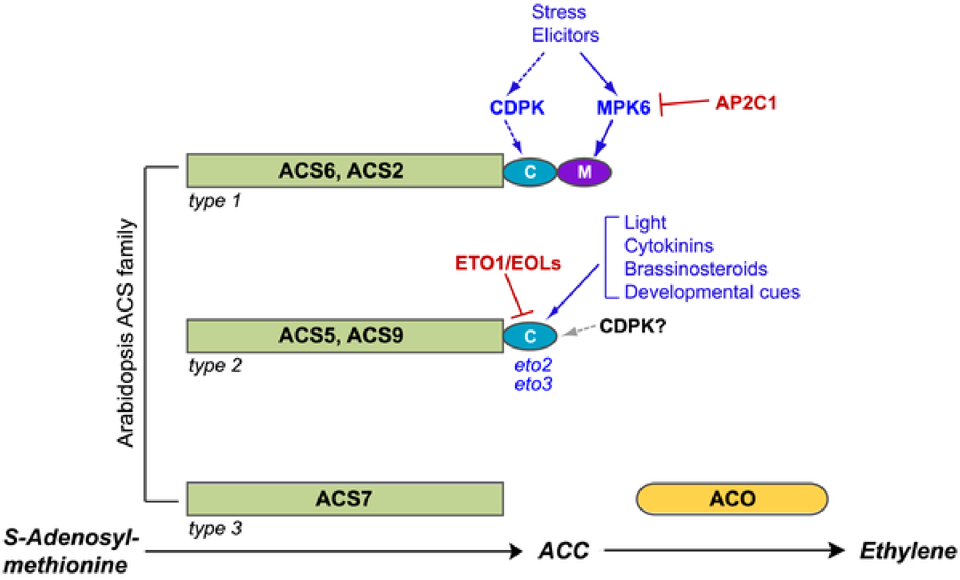
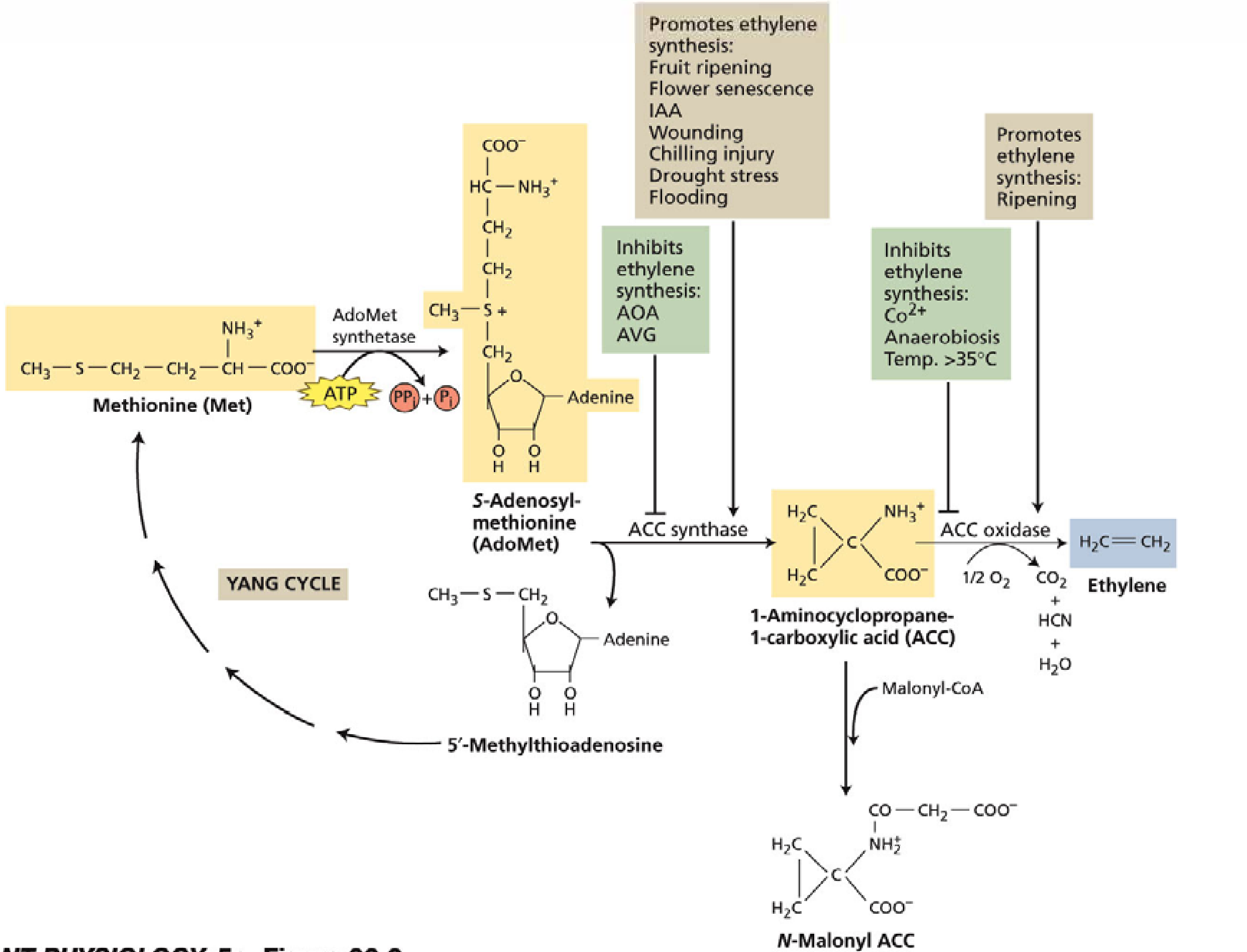

ACS11
ACS9
ACS5
ACS4
ACS8
Type-2
ACS12
Amino
Transferases
ACS10
ACS2
ACS7
ACS6
Type-1
Type-3

Figure 1. Post-translational modifications of ACS proteins regulate ethylene synthesis.



Skottke KR, Yoon GM, Kieber JJ, DeLong A (2011) Protein Phosphatase 2A Controls Ethylene Biosynthesis by Differentially Regulating the Turnover of ACC Synthase Isoforms. PLoS Genet 7(4): e1001370. doi:10.1371/journal.pgen.1001370
http://www.plosgenetics.org/article/info:doi/10.1371/journal.pgen.1001370

Figure 22.2 Ethylene biosynthetic pathway and the Yang cycle



PLANT PHYSIOLOGY, 5e, Figure 22.2

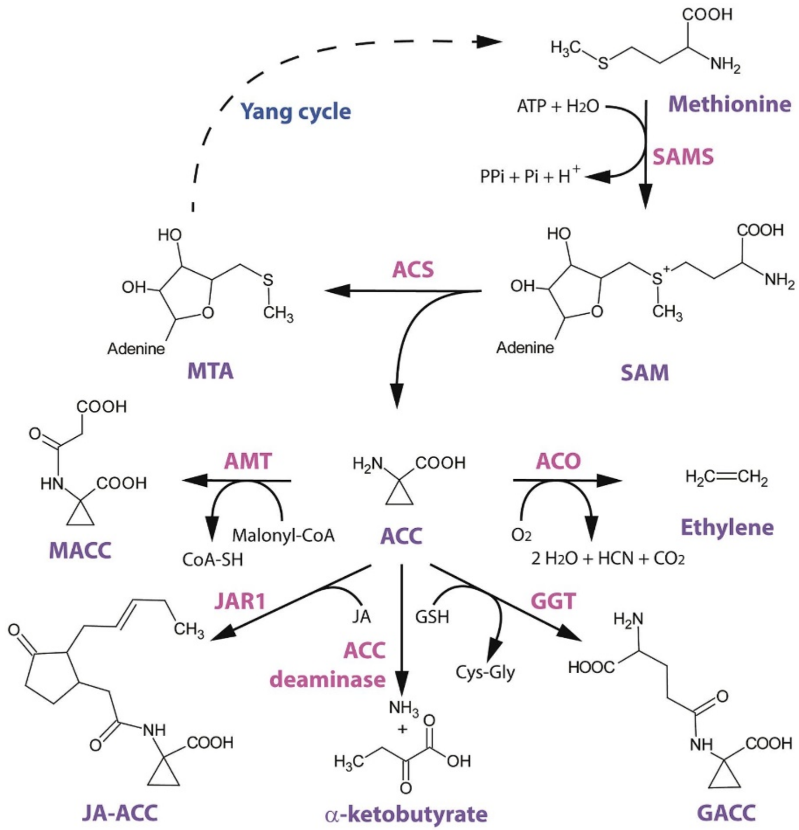
Ethylene catabolism, conjugation and deamination

- **Mechanisms regulating the level of the ethylene**

1. Catabolism
- ✓ Metabolic breakdown products
- ✓ Carbon dioxide, ethylene oxide, ethylene glycol…

2. Conjugation
- ✓ Not all the ACC is converted to ethylene
  - ① N-malonyl ACC
  - - Accumulates primarily in the vacuole
  - ② 1-(γ-L-glutamylamino) cyclopropane-1-carboxylic acid (GACC)
  - - Minor conjugated form of ACC

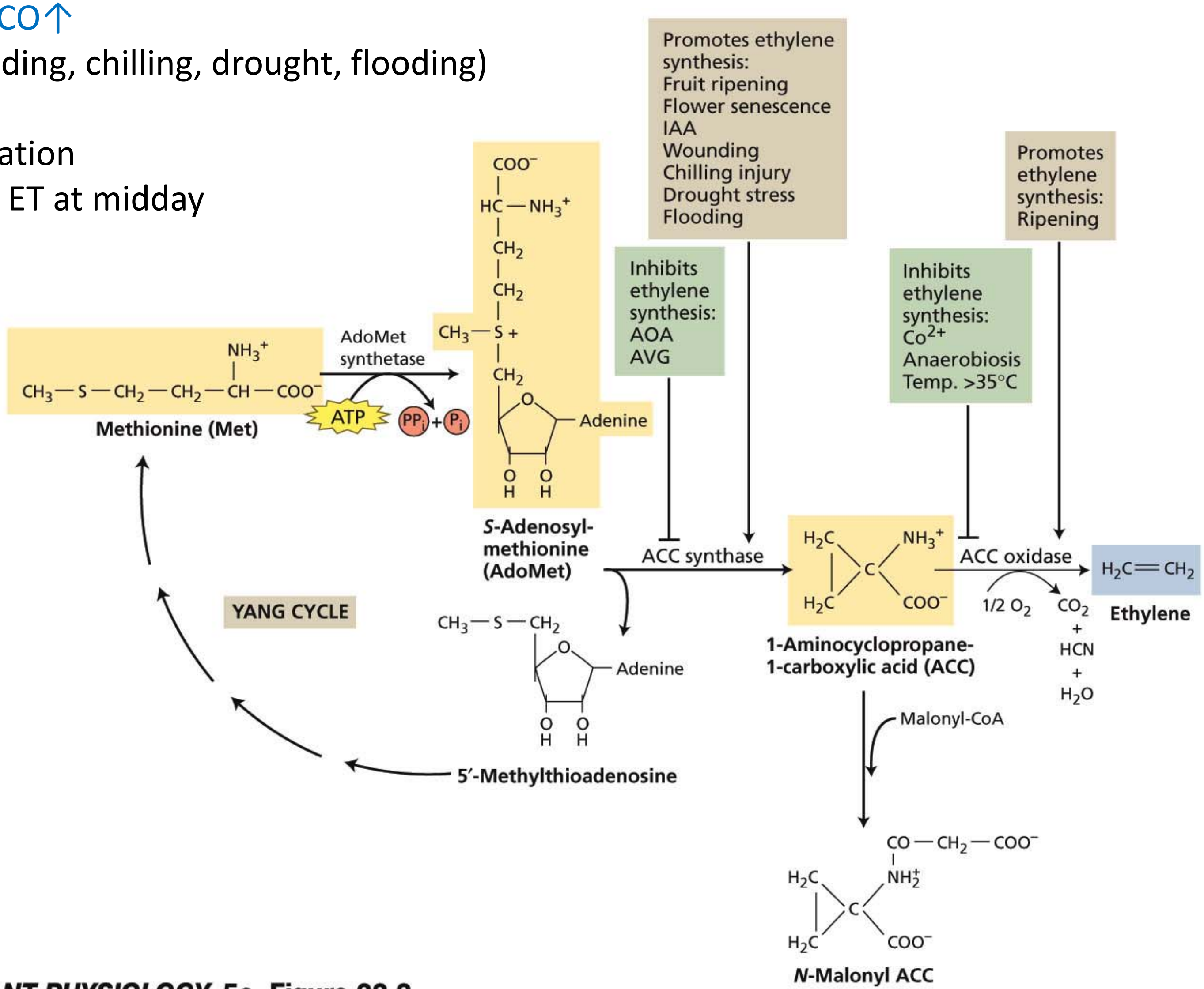
3. Deamination
- ✓ ACC deaminase
- ✓ ACC→ Ammonia, α-ketobutyrate



http://journal.frontiersin.org/article/10.3389/fpls.2014.00640/full

Ethylene biosynthesis is promoted by several factors

- Fruit ripening
  - ✓ ACS ↑, ACO↑
- Stresses (wounding, chilling, drought, flooding)
  - ✓ ACS ↑
- Circadian regulation
  - ✓ A peak of ET at midday
  - ✓ ACS
- Auxin
  - ✓ ACS ↑



PLANT PHYSIOLOGY, 5e, Figure 22.2

Figure 2

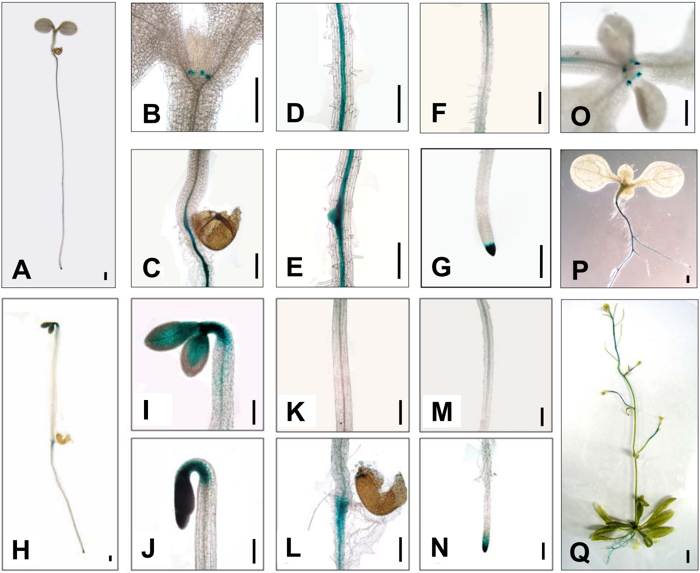


Figure 1

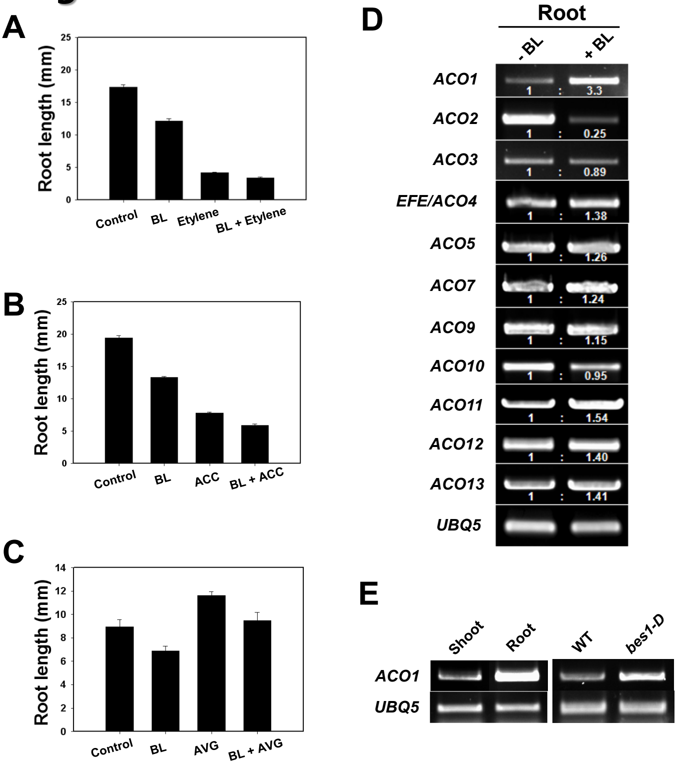

A
Root length (mm)
Control
BL
Etylene
BL + Etylene
B
Root length (mm)
Control
BL
ACC
BL + ACC
C
Root length (mm)
Control
BL
AVG
BL + AVG
D
Root
- BL
+ BL
ACO1
1 : 3.3
ACO2
1 : 0.25
ACO3
1 : 0.89
EFE/ACO4
1 : 1.38
ACO5
1 : 1.26
ACO7
1 : 1.24
ACO9
1 : 1.15
ACO10
1 : 0.95
ACO11
1 : 1.54
ACO12
1 : 1.40
ACO13
1 : 1.41
UBQ5
E
Shoot
Root
WT
bes1-D
ACO1
UBQ5

Figure 3

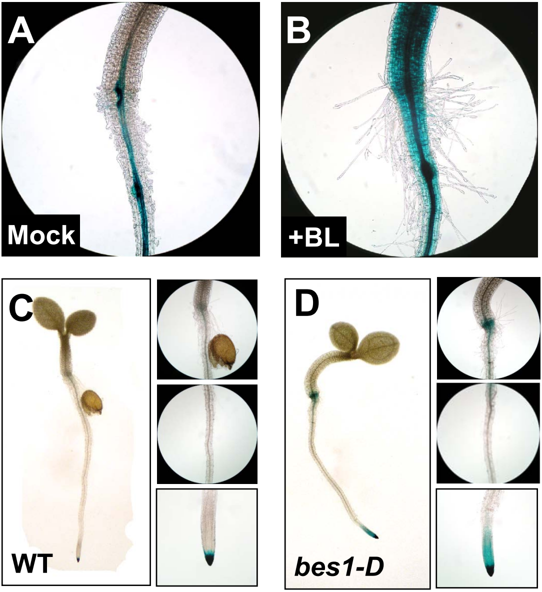
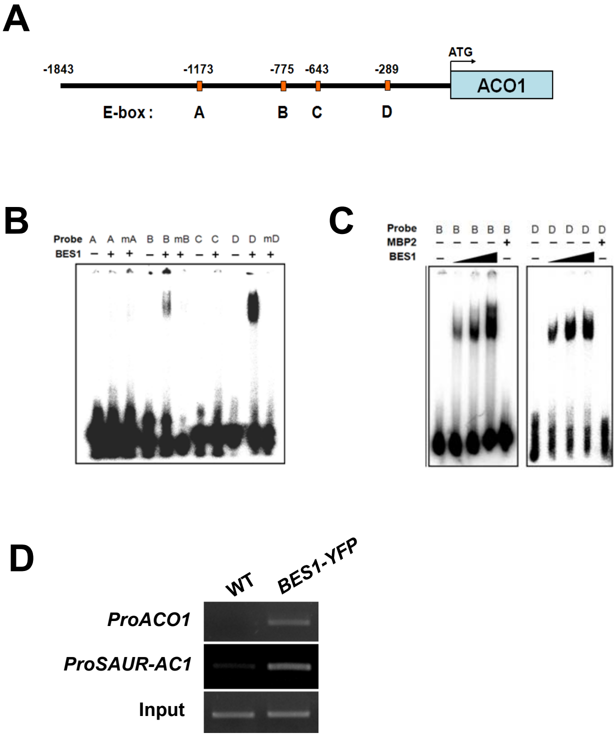


Figure 4



A
ATG
-1843
-1173
-775
-643
-289
ACO1
E-box :
A
B
C
D
B
Probe A A mA B B mB C C D D mD
BES1 – + + – + + – + – + +
C
Probe B B B B B
MBP2 – – – – +
BES1 – –
D D D D D
– – – – +
– –
D
WT
BES1-YFP
ProACO1
ProSAUR-AC1
Input

Figure 5

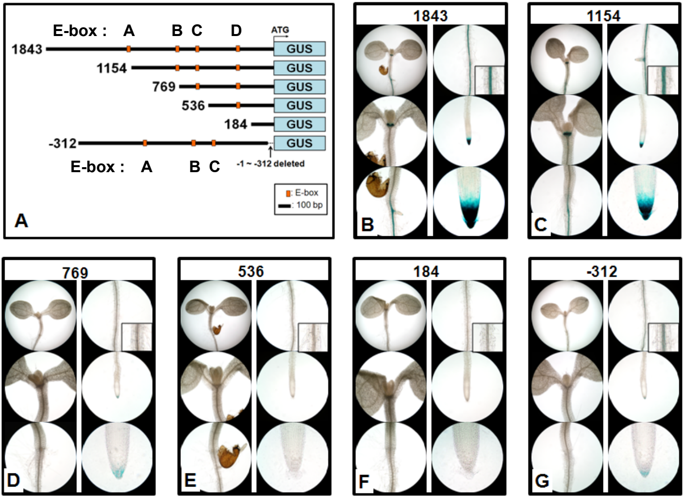
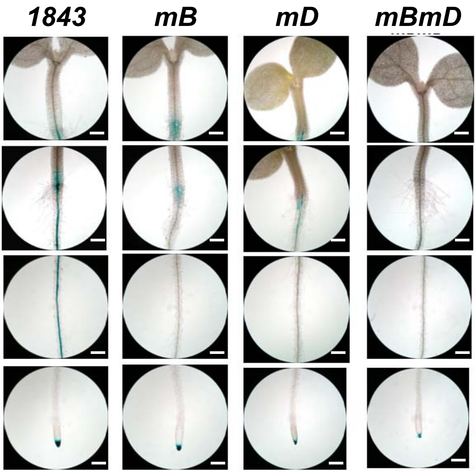

E-box : A B C D
ATG
1843
1154
769
536
184
-312
GUS
-1 ~ -312 deleted
E-box : A B C
: E-box
: 100 bp
A
1843
B
1154
C
769
D
536
E
184
F
-312
G

Figure 6

A


1843
mB
mD
mBmD

B

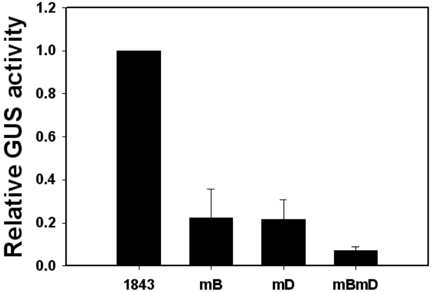
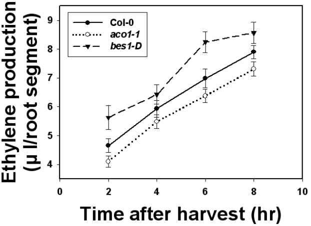
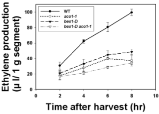

Relative GUS activity
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1843
mB
mD
mBmD

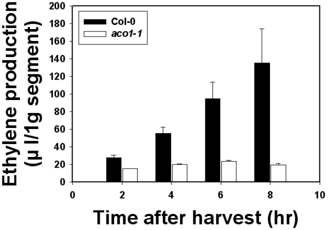
Figure 7

A

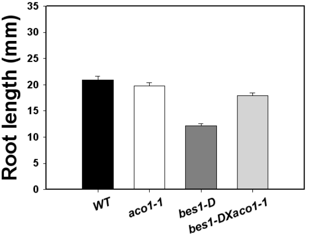


B

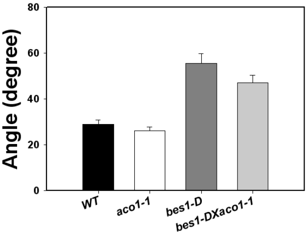




C

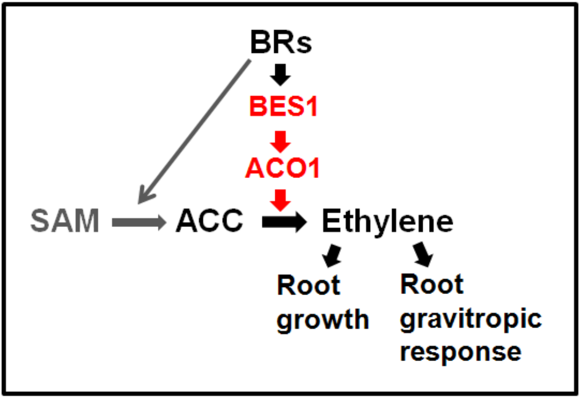


D



E

F


BRs
BES1
ACO1
SAM
ACC
Ethylene
Root growth
Root gravitropic response

Various inhibitors can block ethylene biosynthesis

- (ex) Ethylene mimics high concentrations of auxins
  → by inhibiting stem growth and causing epinasty

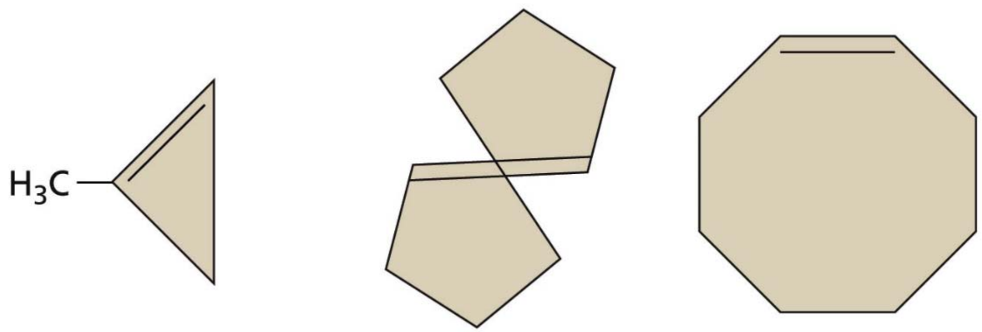
- **Use of specific inhibitors of ethylene**
  → discrimination between the actions of auxin and ethylene

1. **Inhibitors of ethylene synthesis**
   - ✓ AVG, AOA : Inhibition of ACS
   - ✓ AIBA, Co^{2+} : Inhibition of ACO
2. **Inhibitors of ethylene action**
   - ✓ Ag^{+}, CO_2, trans-Cyclooctene, MCP (irreversibly)
3. **Ethylene absorption (for extending fruit storage)**
   - ✓ $KMnO_4$

Select PURAFIL®

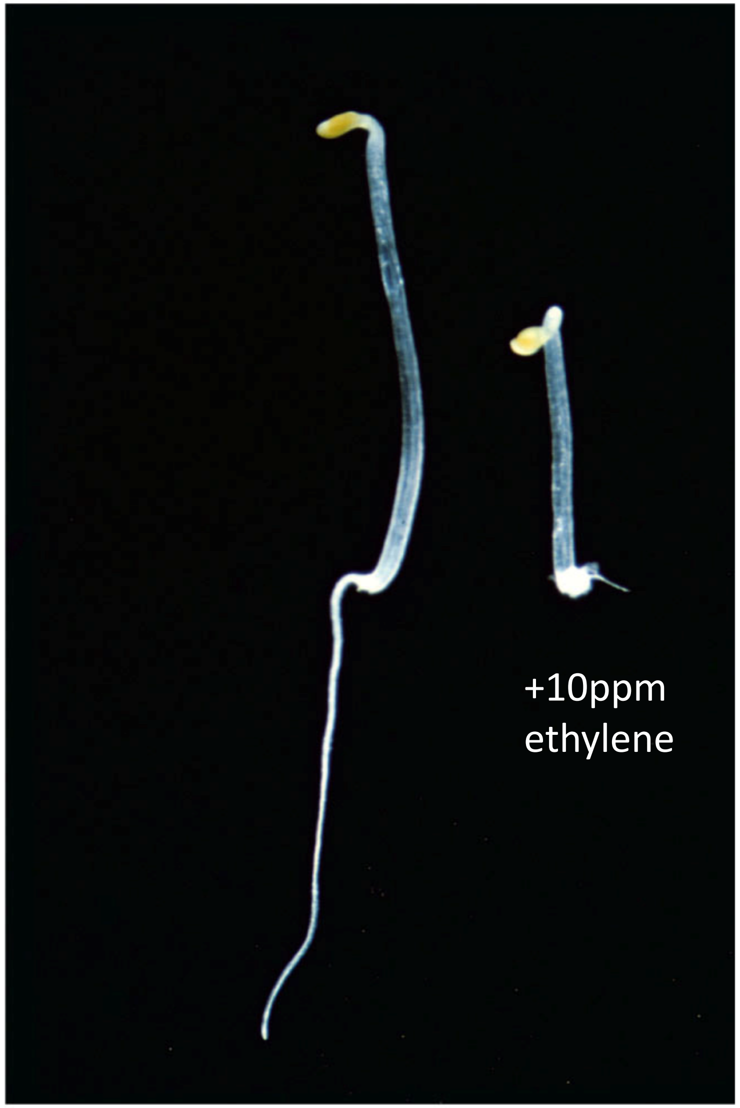
Removes sulfur oxides and other odorous pollutants from makeup air.

Purafil Select is also recommended for the preservation of fruits, vegetables, and flowers because of its effectiveness at removing ethylene, a ripening agent. Contains 8% of potassium permanganate.



1-Methylcyclopropene (MCP) **_trans_-Cyclooctene** **_cis_-Cyclooctene**

The triple response in Arabidopsis



- **The triple response in Arabidopsis**

① Shortened hypocotyl
② Reduced root elongation
③ Exaggeration of the curvature of the apical hook

- The triple response morphology
  → has been used as a screen to isolate
  mutants affected in their response to ethylene

  ✓ **Class I (ET-resistant or ET-insensitive)**
  - Mutants that fail to respond to exogenous ethylene

  ✓ **Class II (Constitutive)**
  - Mutants that display the response even in the absence of ethylene

Ethylene receptors are related to bacterial histidine kinase

- **The first ethylene-insensitive mutant,**
  - ✓ *ethylene-response 1 (etr1)*
- **5 ethylene receptors in Arabidopsis**
  - ✓ Bind to ethylene
  - ✓ Missense mutations in the gene
    → analogous to the *etr1* mutation

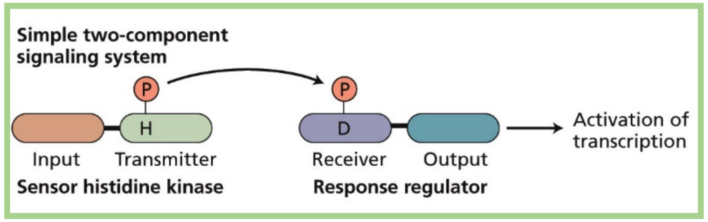
- ✓ Subfamily I
  - ETR1
  - ERS2
- ✓ Subfamily II
  - *EIN4*
  - *ETR2*
  - *ERS2*

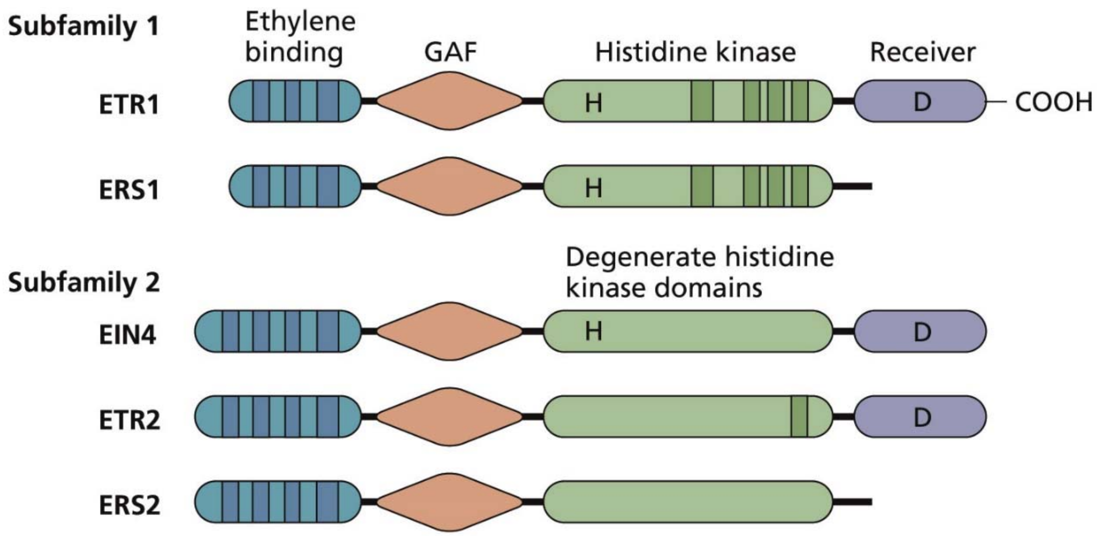
- **5 ethylene receptors have been shown to interact with each other, forming large multisubunit complexes**
- **5 ethylene receptors are located on the ER.**
  (ETR1 may also be localized to the Golgi apparatus)

Schematic diagram of ethylene receptors and their functional domains

- **All of 5 ethylene receptor proteins share at least 2 domains**

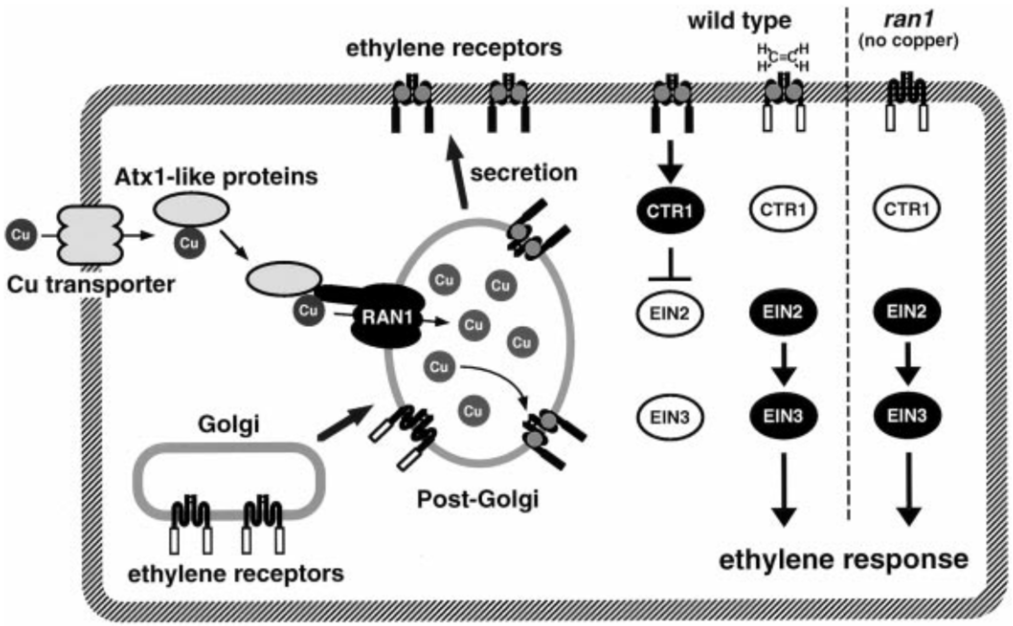
1. **N' terminal**
   - Spans the membrane at least 3 times
   - Contains the ethylene-binding site
   - Ethylene can readily access this site because of its hydrophobicity
2. **C' terminal**
   - Contains a domain homologous to histidine kinase catalytic domains





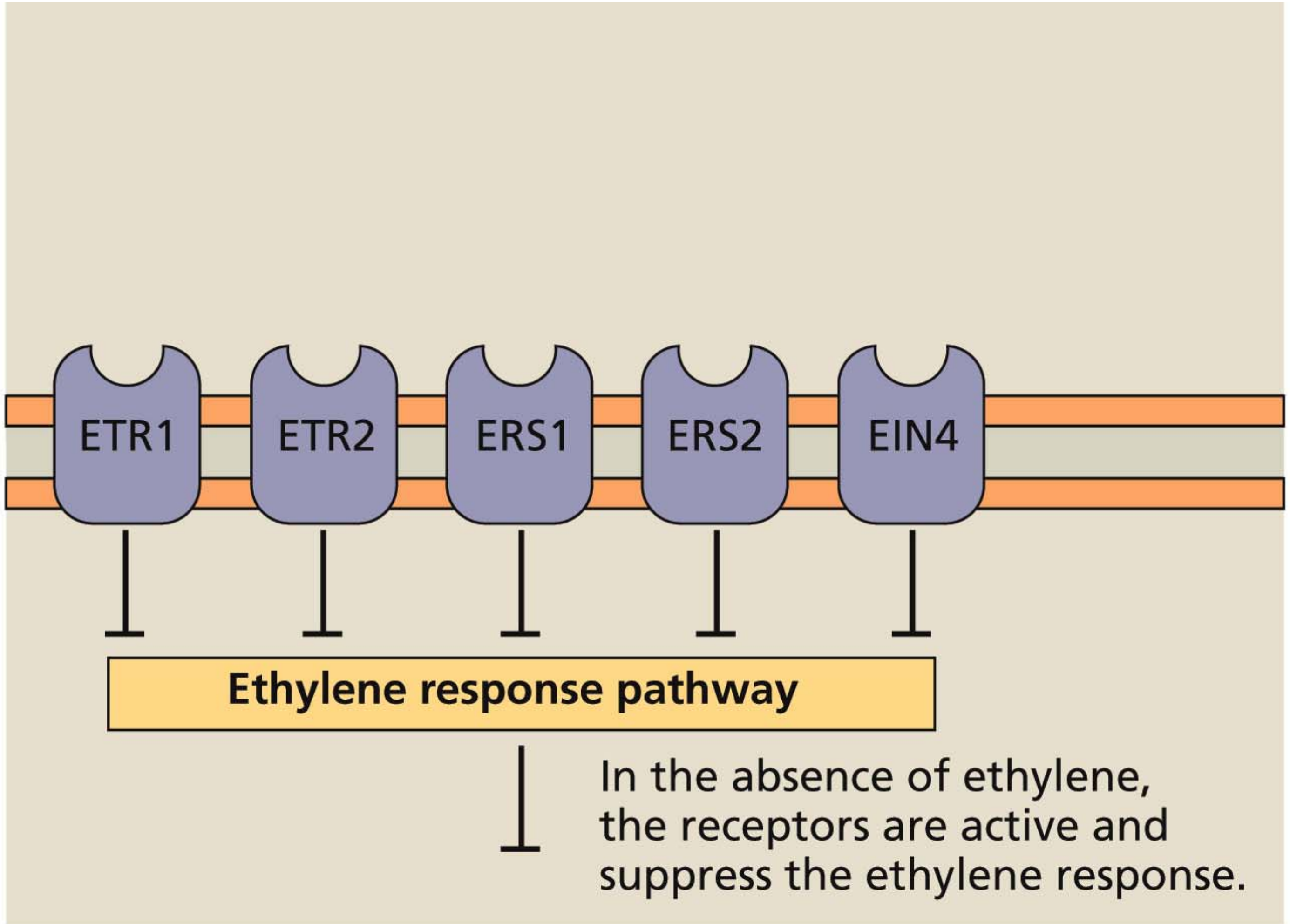
High-affinity binding of ethylene to receptor requires a copper

- **Ethylene binds to receptor via a transition metal, 'copper (Cu)'**
- **RAN1 (RESPONSIVE-TO-ANTAGONIST1)**
  - ✓ Analogous to yeast Ccc2p (protein required for the transfer of copper to an iron transporter)
  - ✓ Copper ions received from Atx1-like proteins may be transported by RAN1 into a post-Golgi compartment, delivering the metal to membrane-targeted ethylene receptor.
- **After the incorporation of a copper ion(s), the receptors are able to coordinate ethylene.**
  - ✓ In the absence of the hormone, the receptors are active and function to negatively regulate downstream signaling pathway.
  - ✓ Ethylene is expected to inactivate the receptors upon binding.



Hirayama et al., 1999

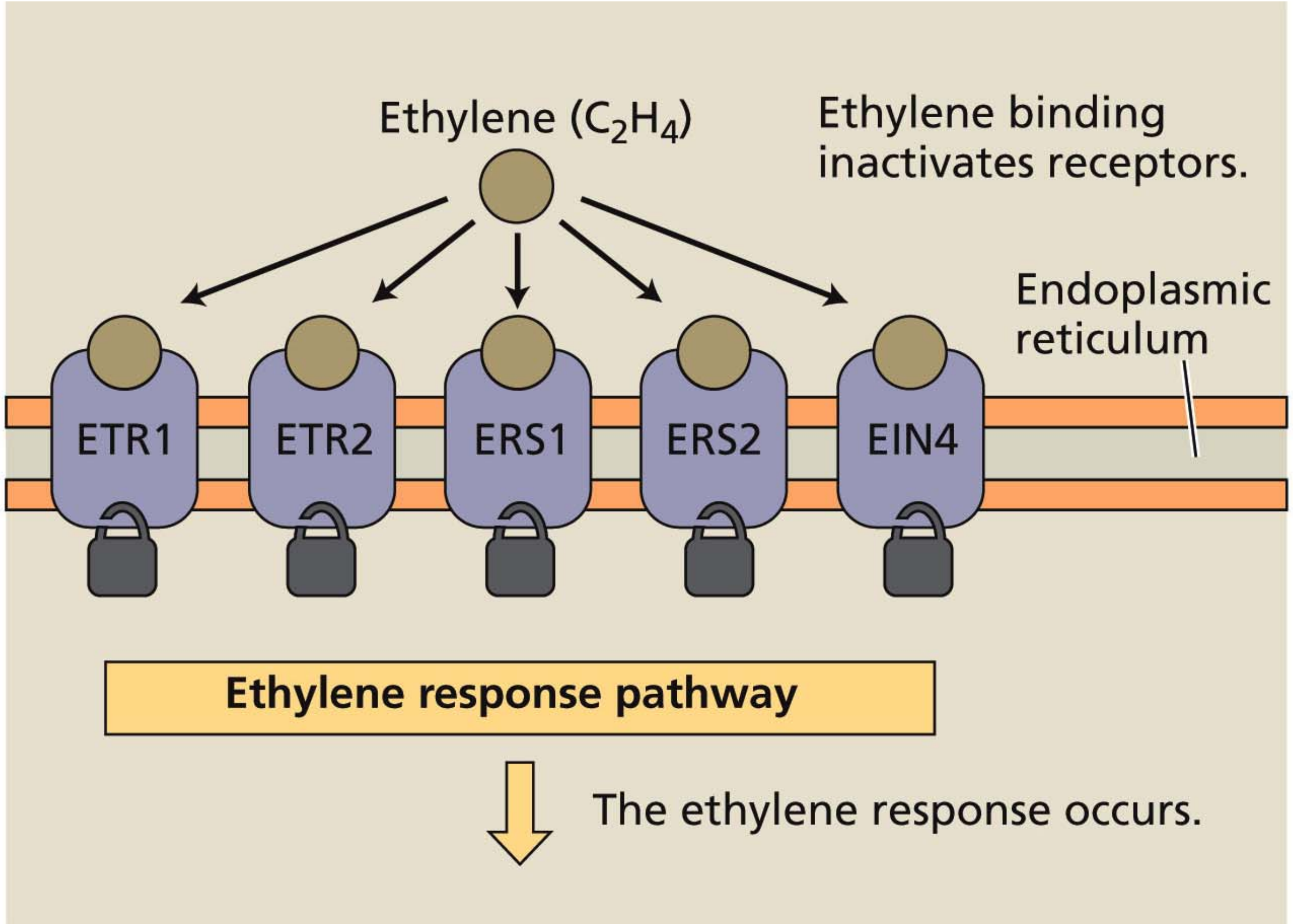
Unbound ethylene receptors are negative regulators



PLANT PHYSIOLOGY, 5e, Figure 22.8 (Part 2)

Unbound ethylene receptors are negative regulators

- A decrease in the level of ethylene receptors actually makes a tissue more sensitive to ethylene.
  → The level of functional ethylene receptors is an important mechanism regulating ET sensitivity.

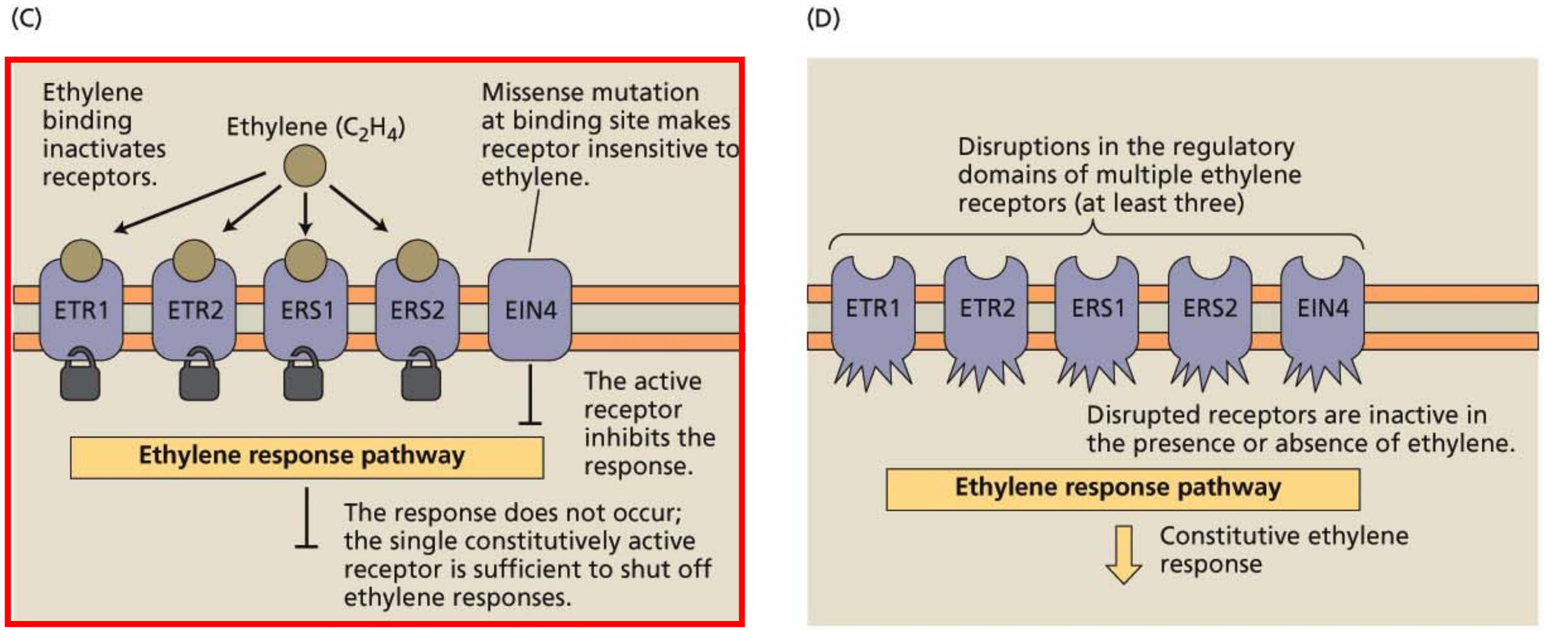


PLANT PHYSIOLOGY, 5e, Figure 22.8 (Part 1)

Unbound ethylene receptors are negative regulators

- **5 receptors in Arabidopsis → Functionally redundant !**
- **Disruption of any single gene has no effect, but a plant with disruptions in multiple receptors exhibits a constitutive ethylene response phenotype.**
- **Receptors with missense mutations at the ethylene binding site are unable to bind ethylene but are still active as negative regulators of the ethylene response**

  → Receptors that can no longer be turned off by ethylene
  (Dominant ethylene-insensitive phenotype)



(ex) Tomato, 'never-ripe' mutation

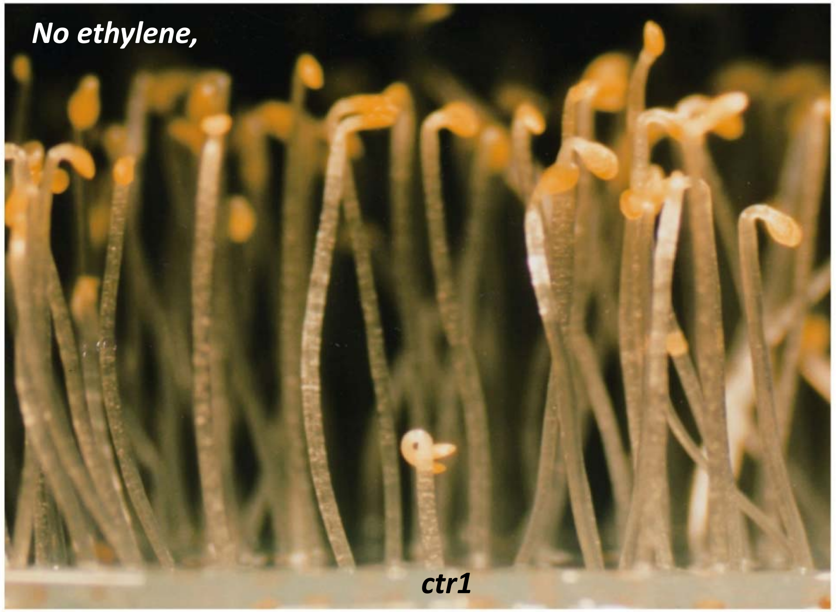
A serine/threonine protein kinase & transmembran

- ***ctr1*** **(*constitutive triple response 1*)**
  - ✓ Constitutively displayed the triple response
  - ✓ Recessive mutation→ activation of ET response
  - ✓ Wild-type CTR1 acts as a negative regulator of ET response

- **CTR1**
  - ✓ Serine/threonine protein kinase
  - ✓ MAPKKK (mitogen-activated protein kinase kinase kinase)
    - Involved in the transduction of various external signals and developmental signals in organisms ranging from yeast to humans
  - ✓ CTR1 directly interacts with the ethylene receptors

- ***ein2*** **(*ethylene-insensitive 2*)**
  - ✓ Blocks all ethylene responses in both seedling and adult Arabidopsis

- ***EIN2***
  - ✓ 12 membrane-spanning domains
  - ✓ Most similar to the N-RAMP (natural resistance-associated macrophage protein) cation transporters family



PLANT PHYSIOLOGY, 5e, Figure 22.9

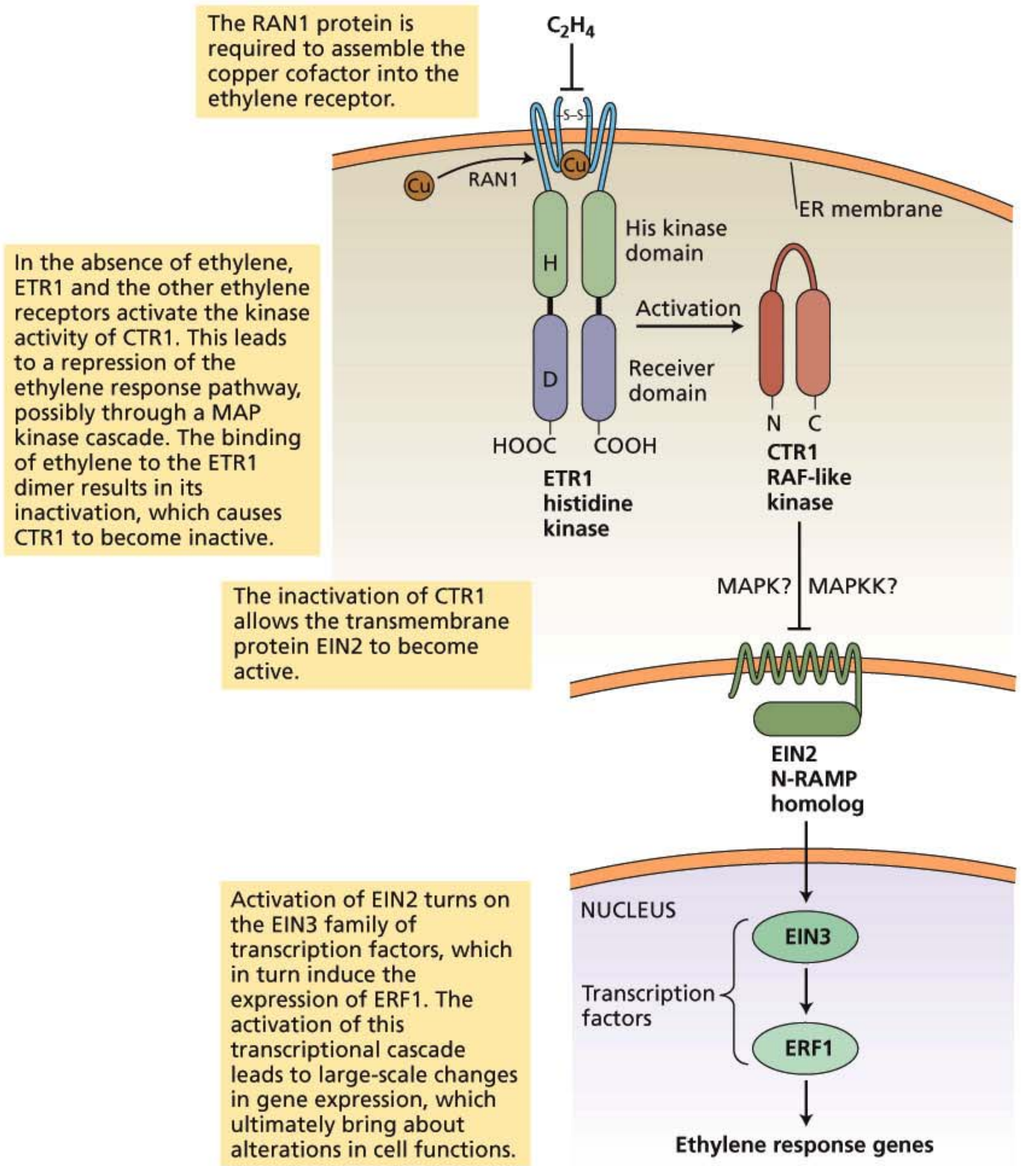
Transcription factors are involved in ethylene-regulated gene expression

- **EIN3 family of transcription factors**
  - ✓ 4 EIN3-like genes genes in Arabidopsis
  - ✓ In response to an ET signal, homodimers of EIN3 or related proteins bind to the promoters of genes that are rapidly induced by ethylene
    (ex) ERF1 (ETHYLENE RESPONSE FACTOR 1)

- **The regulation of EIN3 protein stability plays a important role in ethylene signaling.**
  - ✓ F-box proteins (EBF1, EBF2) promotes ubiquitination.
  - ✓ Ethylene inhibits this EBF1/EBF2-dependent degradation of EIN3,
    (possibly through phosphorylation of EIN3 by MAP kinase)
    → Accumulation of EIN3 and subsequent expression of ethylene regulated genes

- **ERF1**
  - ✓ Ethylene response element (ERE) have been identified among the ethylene-regulated genes
  - ✓ ERE-binding protein family (EREBP)
  - ✓ The EREBP genes exist in Arabidopsis as a very large gene family,
    but only a few of the genes are inducible by ethylene

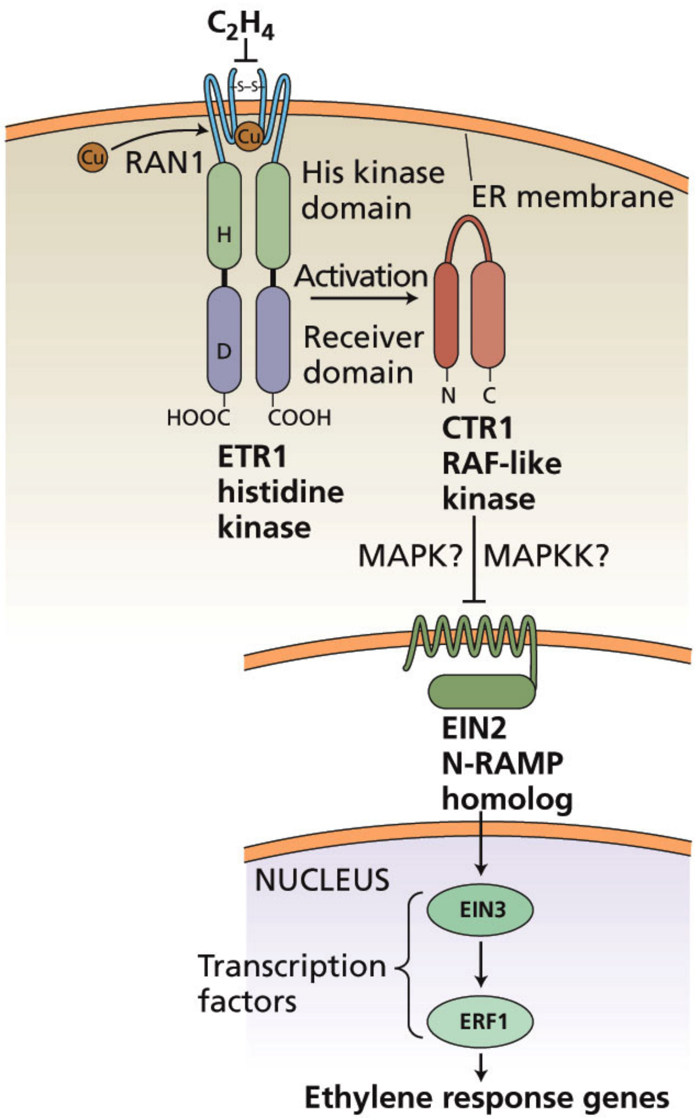
Ethylene signal transduction pathway



MAPK

PLANT PHYSIOLOGY, 5e, Figure 22.10

Genetic epistasis reveals the order of the ethylene signaling components



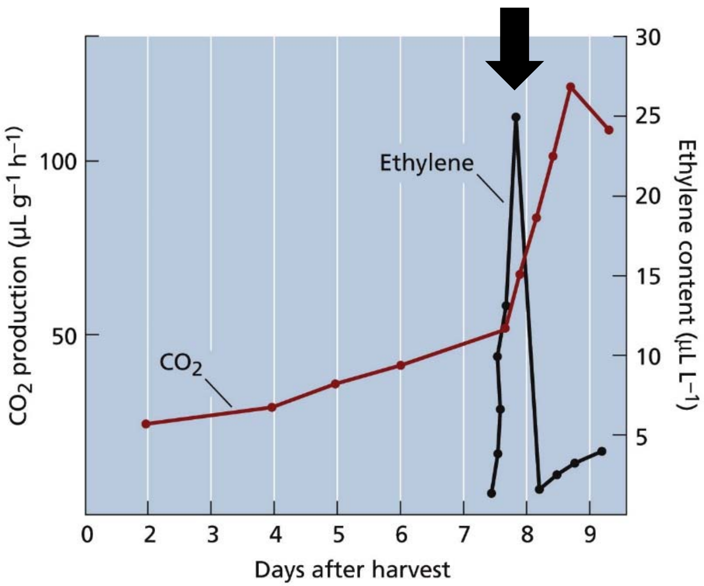
- **Epistasis , 상위**
  - ✓ 대립유전자가 아닌 두 개의 유전자가 같이 있을 때 표현형으로 나타나는 형질을 지배하는 유전자를 상위유전자(epistatic gene)라 하고, 표현되지 않은 쪽을 하위유전자(hypostatic gene)라고 함
  - ✓ (ex) *etr1ctr1* double mutant displays a *ctr1* mutant phnotype

    → *ctr1* is said to be epistatic to *etr1*

Ethylene promotes the ripening of some fruits

- **Climacteric**
  - ✓ A rise in cellular respiration of fruits that ripen in response to ethylene before the ripening phase
  - ✓ Noted by carbon dioxide production

- **Climacteric fruits + Ethylene**
  - ① Additional production of ethylene
  - ② Accelerate ripening



PLANT PHYSIOLOGY, 5e, Figure 22.11

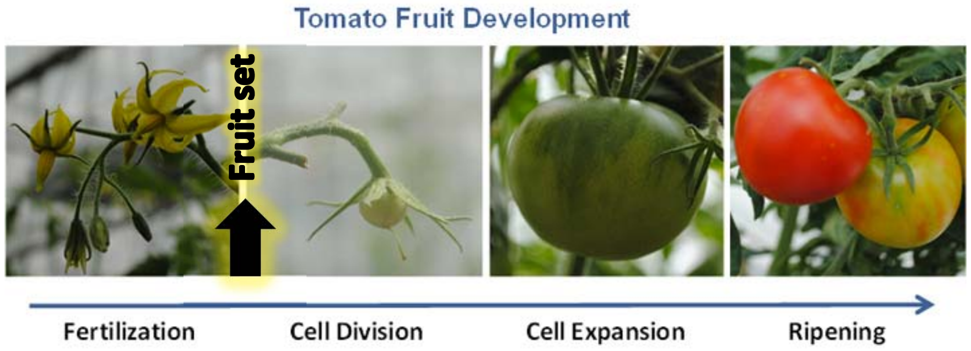
TABLE 22.1
Climacteric and nonclimacteric fruits

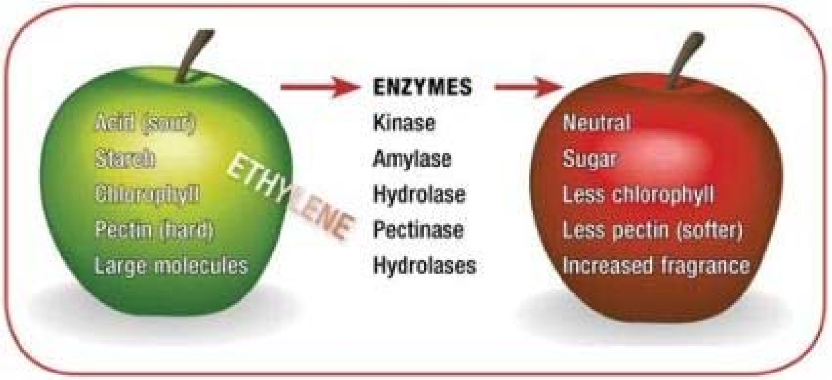
Climacteric		Nonclimacteric
Apple	Olive	Bell pepper
Avocado	Peach	Cherry
Banana	Pear	Citrus
Cantaloupe	Persimmon	Grape
Cherimoya	Plum	Pineapple
Fig	Tomato	Snap bean
Mango		Strawberry
		Watermelon

PLANT PHYSIOLOGY, 5e, Table 22.1

Ethylene promotes the ripening of some fruits

- **Fruit set**





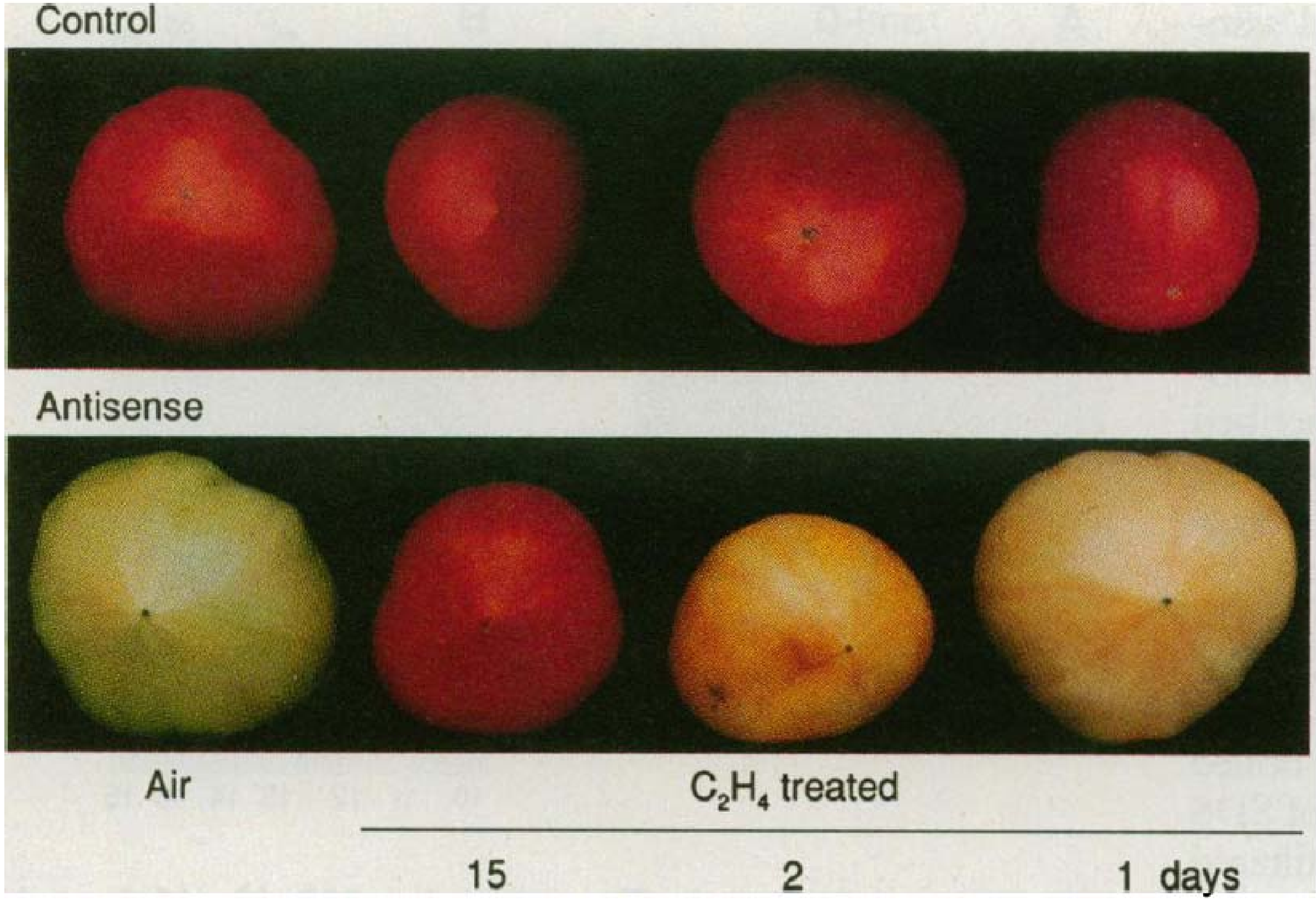
- **'Fruit ripening'**
  ① In everyday usage ; 'Ready to eat'
  ② From the perspective of the plant ; 'Ready for dispersal'
    - For seeds whose dispersal depend on animal digestion : 'Ripeness and edibility'
    - For seeds that rely on other means for dispersal : 'Drying'

- **3 steps of fruit ripening**
  1) Accumulation of sugars, organic acids and volatile organic compounds influencing flavor
  2) Conversion of chloroplasts to chromoplasts ,accumulation of carotenoid pigments
  3) Softening of the fruit

- **Ethylene has long been recognized as the hormone that accelerates the ripening of edible fruits.**
  Ethylene exposure → Ethylene production ↑ + Initiation of fruit ripening

Ethylene promotes the ripening of some fruits

- **Elimination of ethylene biosynthesis in transgenic tomatoes completely blocked fruit ripening, and application of exogenous ethylene restored ripening.**



Oeller et al., 1991

Ethylene promotes the ripening of some fruits

- **In climacteric fruits, two systems of ethylene production operate.**

① **System 1**– Negative feedback loop
  ✓ Acts in vegetative tissue
  ✓ Ethylene inhibits its own biosynthesis

② **System 2** – Positive feedback loop
  ✓ Occurs in ripening climacteric fruit and in the senescing petals
  ✓ Ethylene stimulates its own biosynthesis (Autocatalytic)

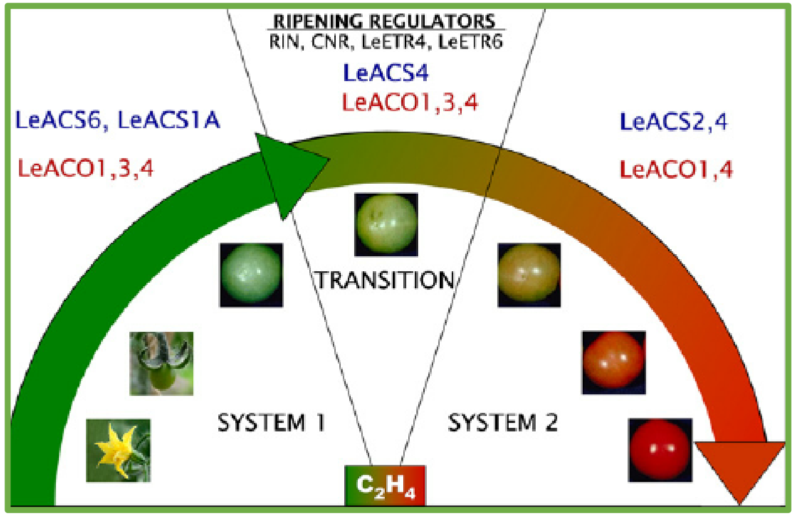


Fig. 1. Regulation of ethylene biosynthesis in tomato fruit development and ripening. During development (System 1) lower and auto-inhibitory ethylene is synthesized by LeACS1A,6 and LeACO1,3,4. At the transition stage, the ripening regulators indicated play critical roles. LeACS 4 is induced and a large increase of auto-catalytic ethylene starts, resulting in negative feedback on System 1. LeACS2,4 and LeACO1,4 are then responsible for the high ethylene production through System 2.

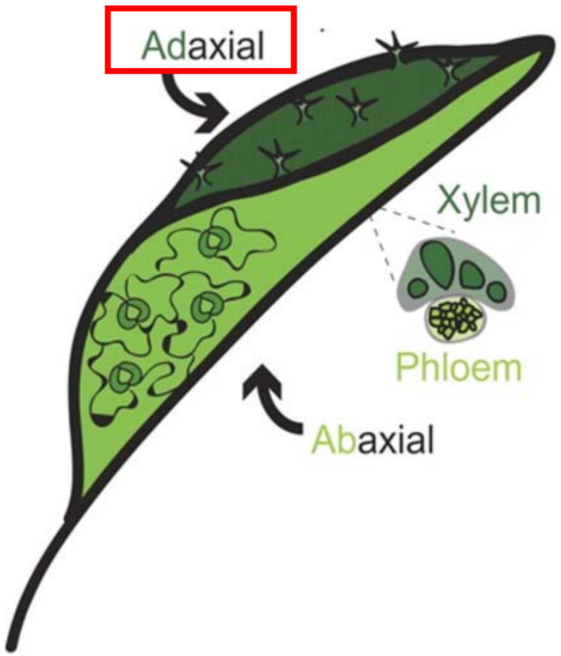
- **Nonclimacteric fruits + Ethylene**

  Respiration rate increases as a function of ethylene

Leaf epinasty results when ACC from the root is transported to the shoot

- **Epinasty, 상편생장**
  - ✓ Downward bending of leaves and floral organs (ex) Tomato
  - ✓ The cells on the upper side (adaxial) of the petiole grow faster than those on the bottom side (abaxial).
  - ✓ In unfavourable ambient conditions; Waterlogging, salinity stress, drought, pathogen attack

- Ethylene and high concentrations of auxin induce epinasty.
  (Auxin acts indirectly by inducing ethylene production).



PLANT PHYSIOLOGY, 5e, Figure 22.12

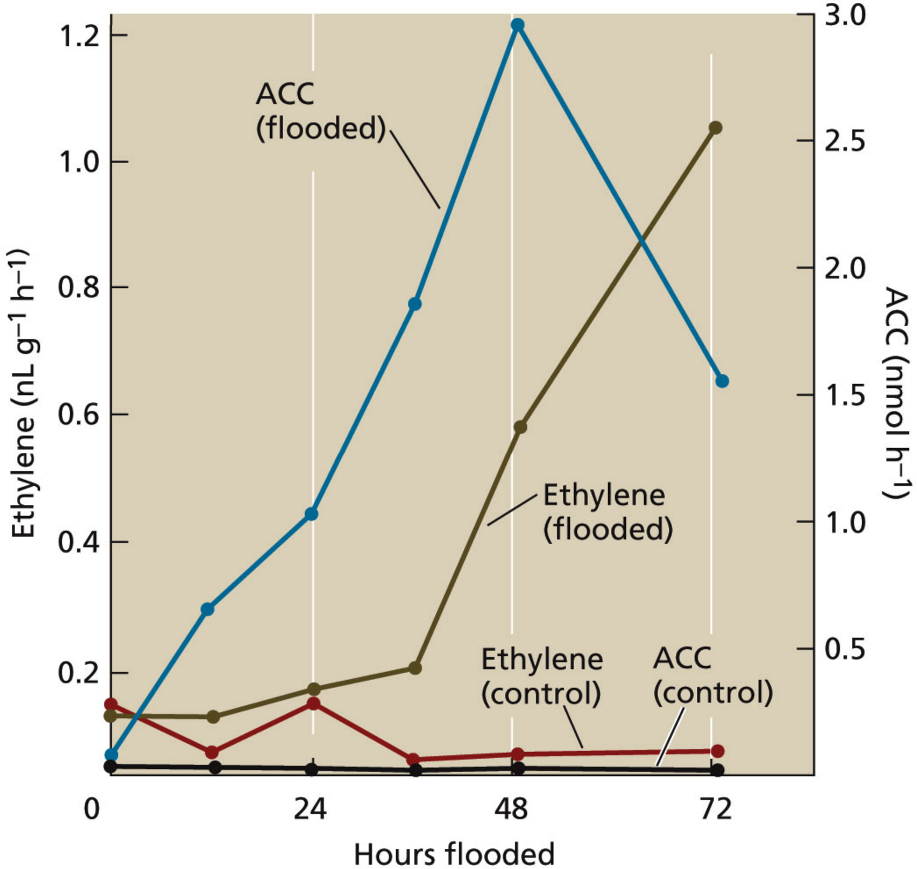
Leaf epinasty results when ACC from the root is transported to the shoot

- **Flooding or anaerobic conditions around the roots** (Sensed by the roots)
  → Enhance the synthesis of ethylene in the shoot (Response displayed by the shoots)
  → Leading to the epinastic response

- **Signal : ACC**

  In tomato,
  after flooding stress for 1-2 days

  ① ACC accumulates in roots
  ② Transported to shoots
  via the transpiration stream
  ③ Readily converted to ethylene
  in the presence of oxygen

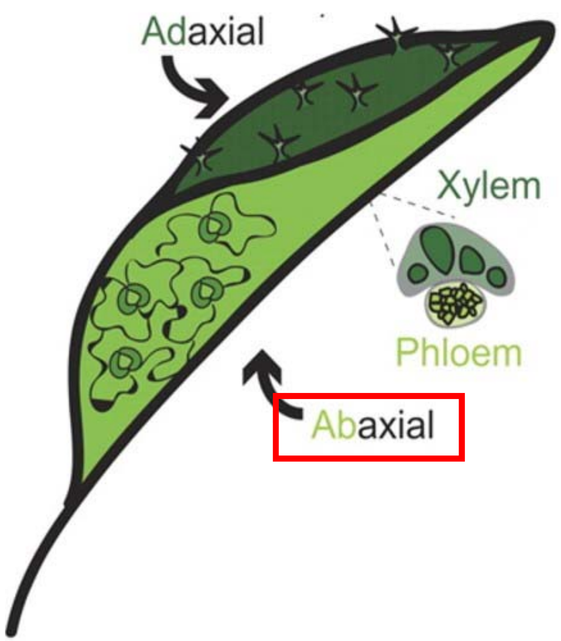


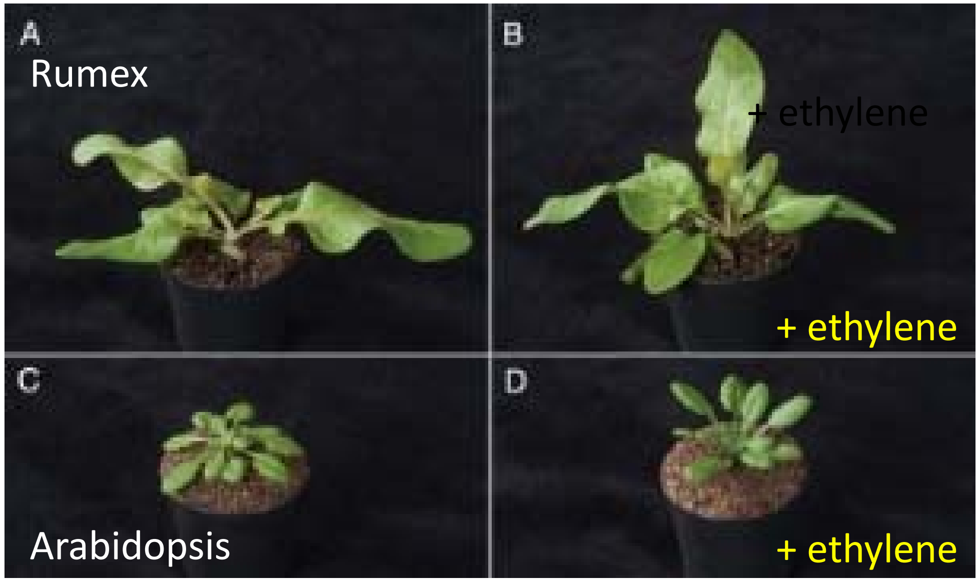
PLANT PHYSIOLOGY, 5e, Figure 22.13

Leaf epinasty results when ACC from the root is transported to the shoot

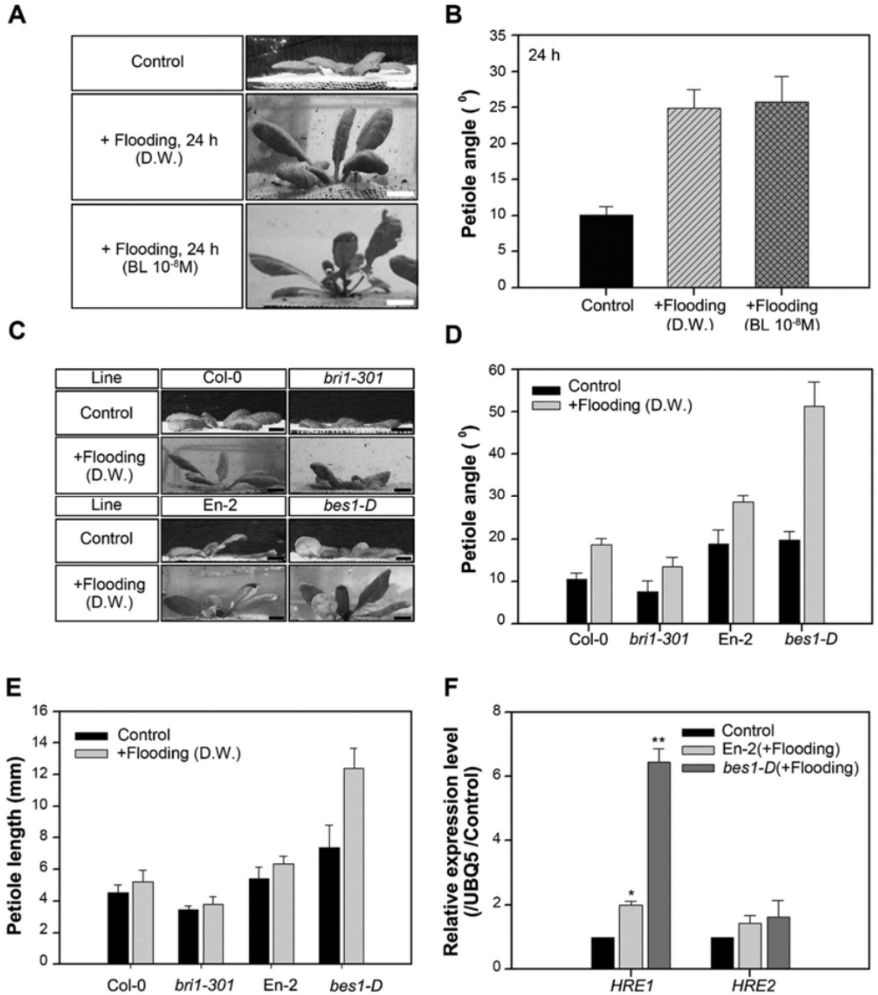
- **Hyponasty, 하편생장**
  - ✓ Upward bending of leaf blades and petioles (ex) Arabidopsis, Rumex
  - ✓ The cells on the bottom side (abaxial) of the petiole grow faster than those on the upper side (adaxial).
  - ✓ In abiotic types of stresses ; Flooding, shade, elevated temperatures

- Ethylene is regarded as a key factor regulating hyponastic growth in submerged.





BR modulates submergence-induced hyponastic growth in Arabidopsis

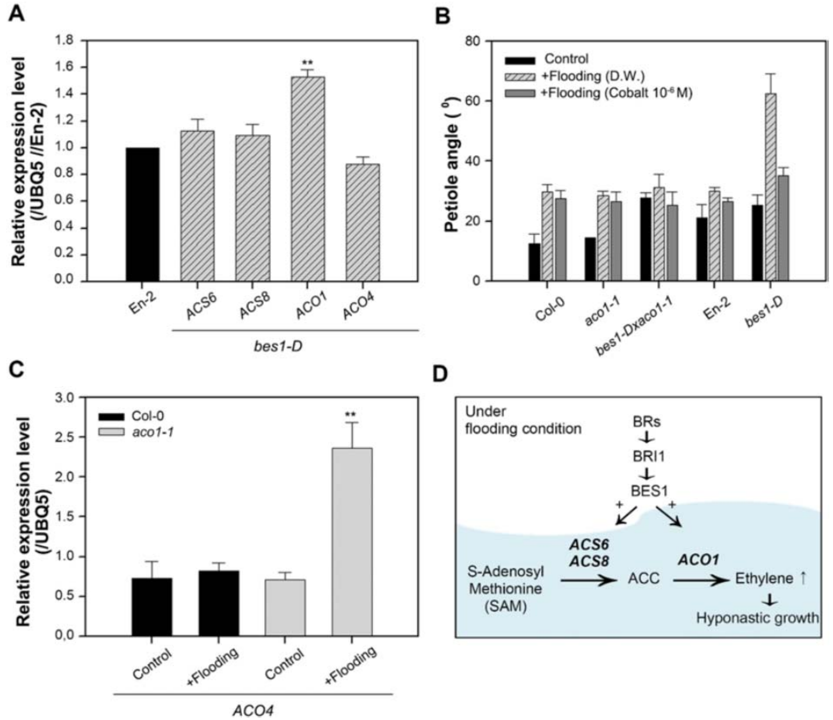


ORIGINAL ARTICLE

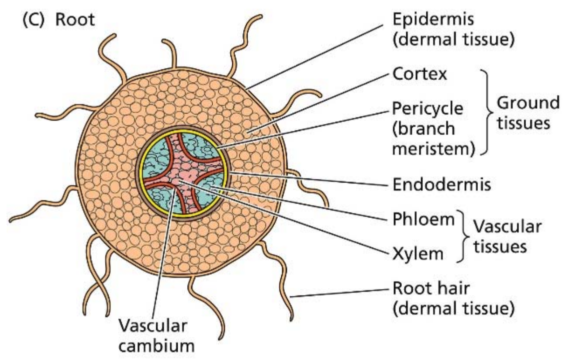
Brassinosteroid Signaling Modulates Submergence-induced Hyponastic Growth in *Arabidopsis thaliana*

Ji Hyun Youn[†], Seung Hye Kang[†], Jeehee Roh, Ji Eun Lee, Hyeon Soong Yeom and Seong-Ki Kim[*]

Department of Life Science, Chung-Ang University, Seoul, 156-756, Korea



Ethylene induces lateral cell expansion



PLANT PHYSIOLOGY, 5e, Figure 1.1 (Part 4)

- **Ethylene changes the growth pattern of seedlings by reducing the rate of elongation and increasing lateral expansion, leading to swelling of the hypocotyl.**

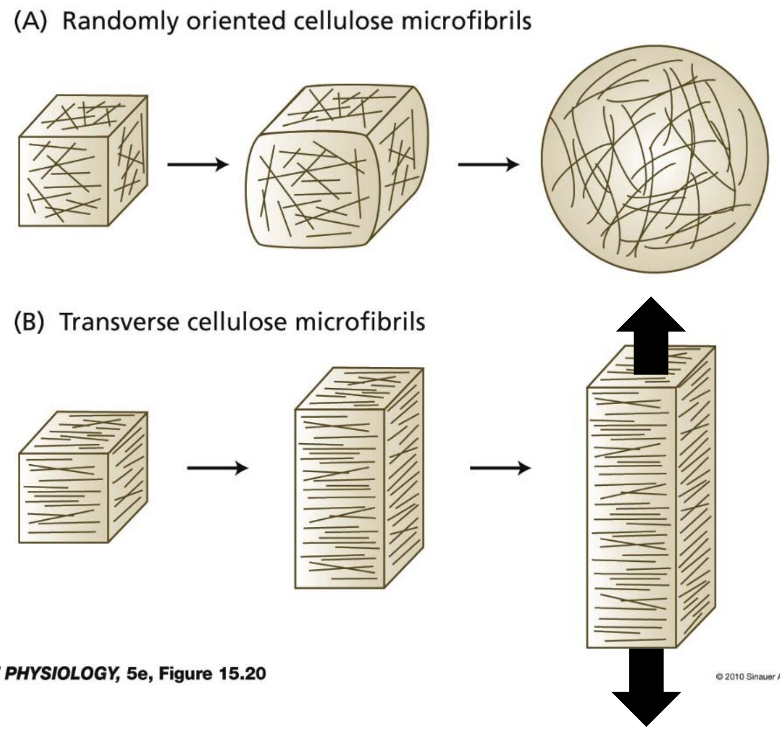
  ✓ Triple response (in Arabidopsis)

  ① Hypocotyl swelling
  ② Inhibition of root elongation
  ③ Exaggeration of the curvature of the apical hook

- **In typical elongating plant cells, the cortical microtubules are arranged transversely.**

- **Plant cell expansion is determined by the orientation of the cellulose microfibrils in the cell wall.**

- **Transverse microfibrils reinforce the cell wall in the lateral direction.**



PLANT PHYSIOLOGY, 5e, Figure 15.20

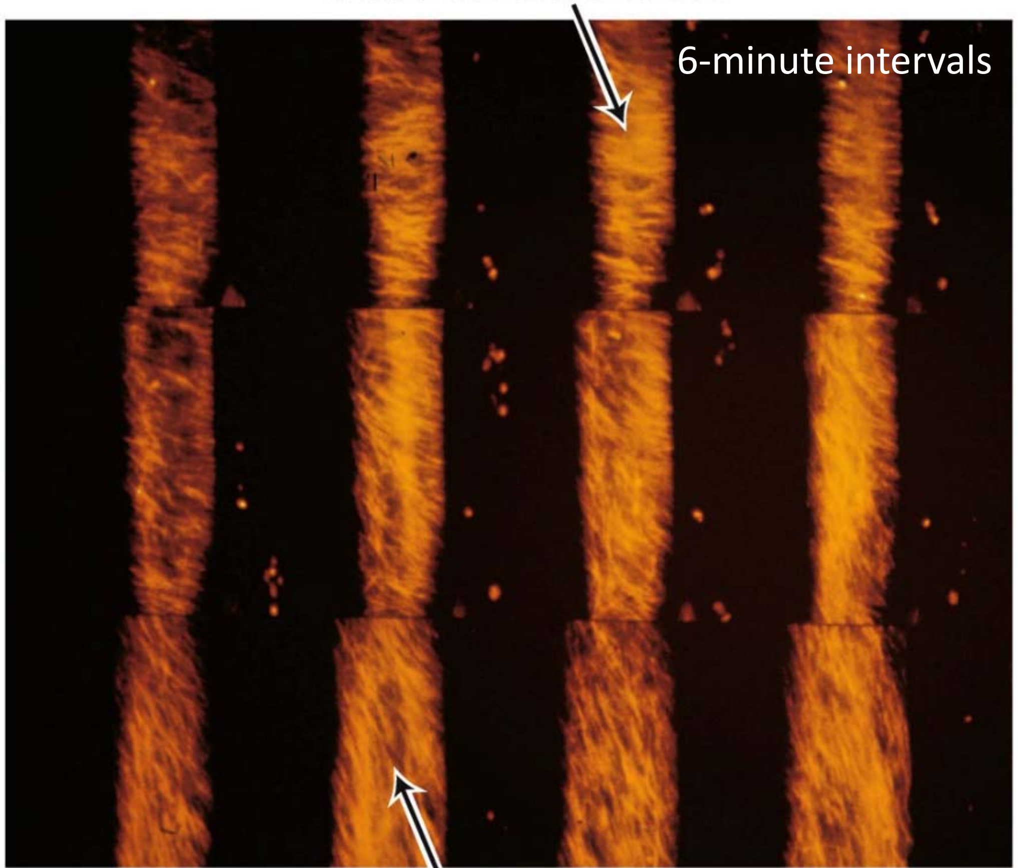
Ethylene induces lateral cell expansion

- **During the seedling triple response to ethylene, the transverse pattern of microtubule alignment is disrupted, and the microtubules switch over to a longitudinal orientation.**

✓ Microtubules do not reorient from the transverse to the longitudinal direction by complete depolymerization and repolymerization.

✓ Increasing numbers of nontransversely aligned new microtubules appear.

✓ Neighboring microtubules then adopt the new alignment.



The hooks of dark-grown seedlings are maintained by ethylene production

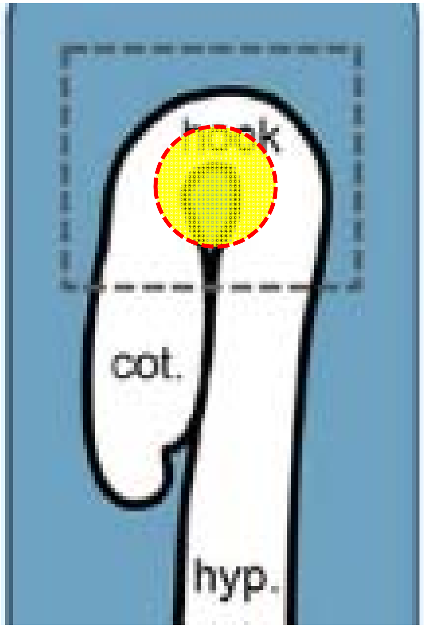
- **Hook shape of etiolated dicot seedlings facilitates penetration of the seedling through the soil, protecting the tender apical meristem.**

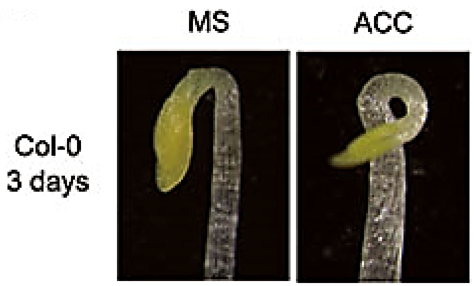
- **Hook formation and maintenance result from ethylene-induced asymmetric growth.**

  ✓ More rapid elongation of outer side of the stem compared with the inner side.

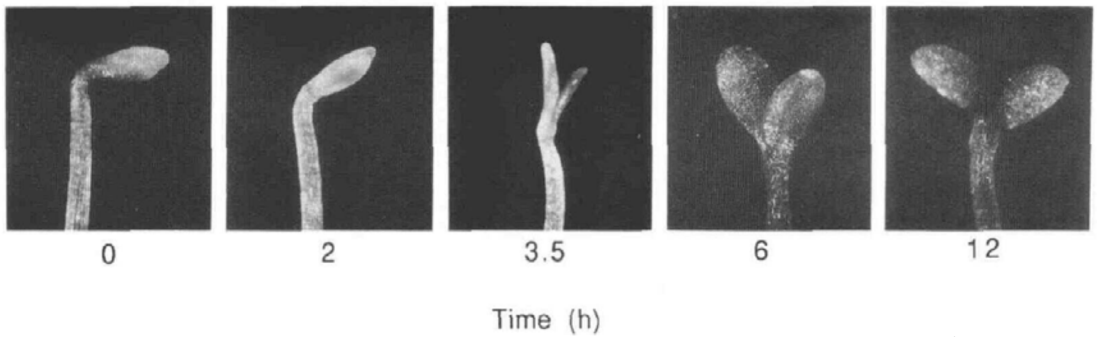
- **Ethylene is produced by the hook tissue in the dark, elongation of the cells on the inner side is inhibited.**

- **When the hook is exposed to white light, it opens, because the elongation rate of the inner side increases.**





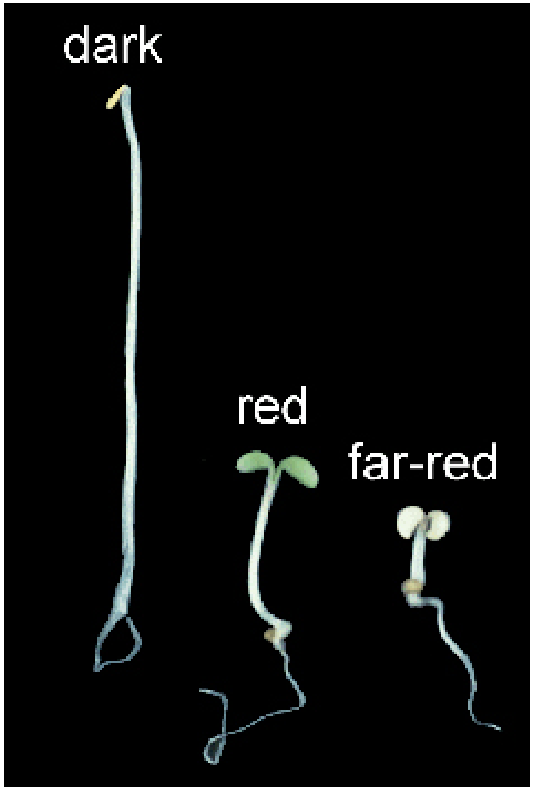
An et al., 2012

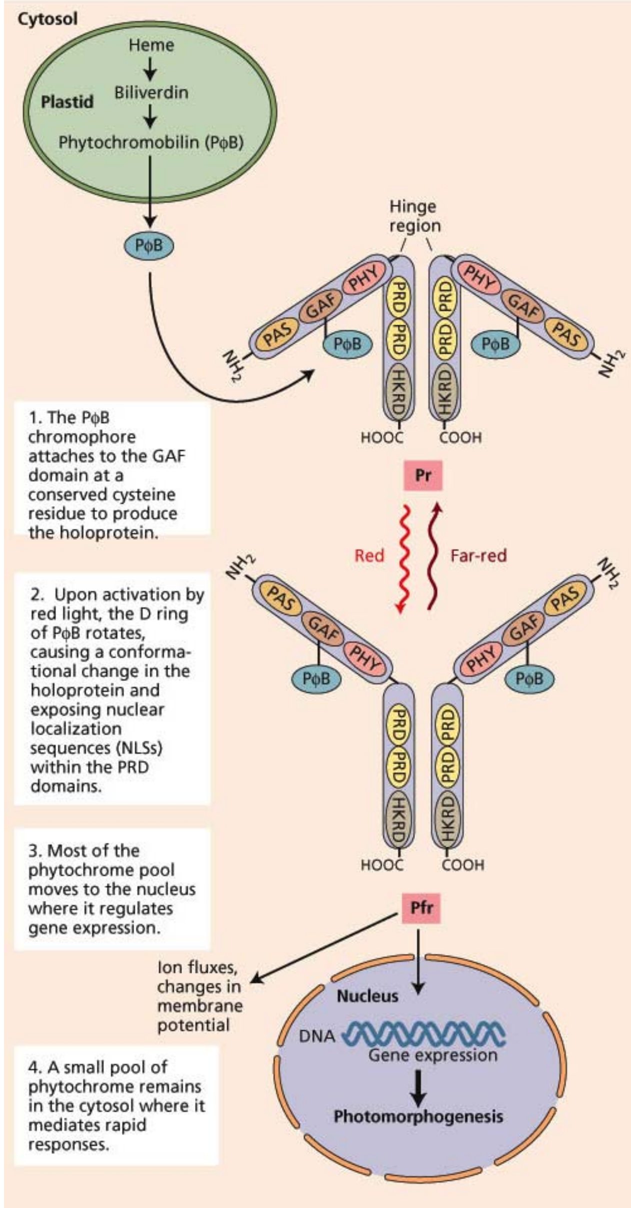


Liscum and Hangarter 1993

The hooks of dark-grown seedlings are maintained by ethylene production

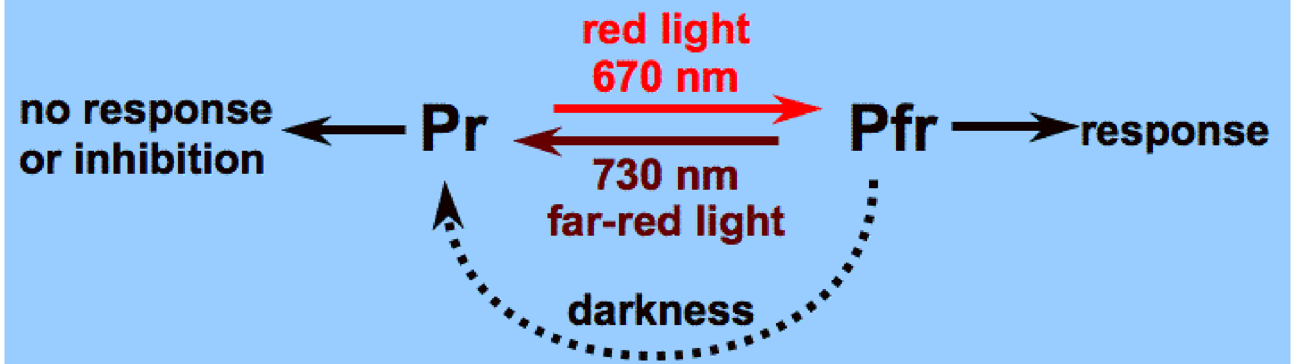
- **Phytochrome is the photoreceptor involved in hook opening.**
  - ✓ Red light induces hook opening, and far-red light reverses the effect of red.
  - ✓ Red light inhibits ethylene formation, promoting growth on the inner side, thereby causing the hook to open.
  - ✓ Pr vs Pfr (active form)



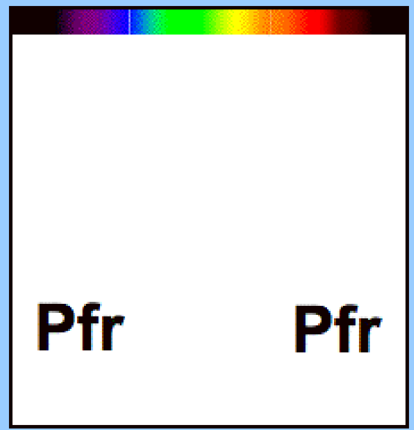


http://www2.mcdaniel.edu/Biology/appliedbotany/reponsetoenv/response.htm

Phytochrome is a Pigment with Two interconvertible forms
The two forms elicit different responses



Be sure you understand the difference between red and far-red light and the two different forms of phytochrome!



Be sure you understand which form of phytochrome is present when red or far-red light is on!

Figure 17.3 Absorption spectra of purified oat phytochrome in the Pr and Pfr forms overlap

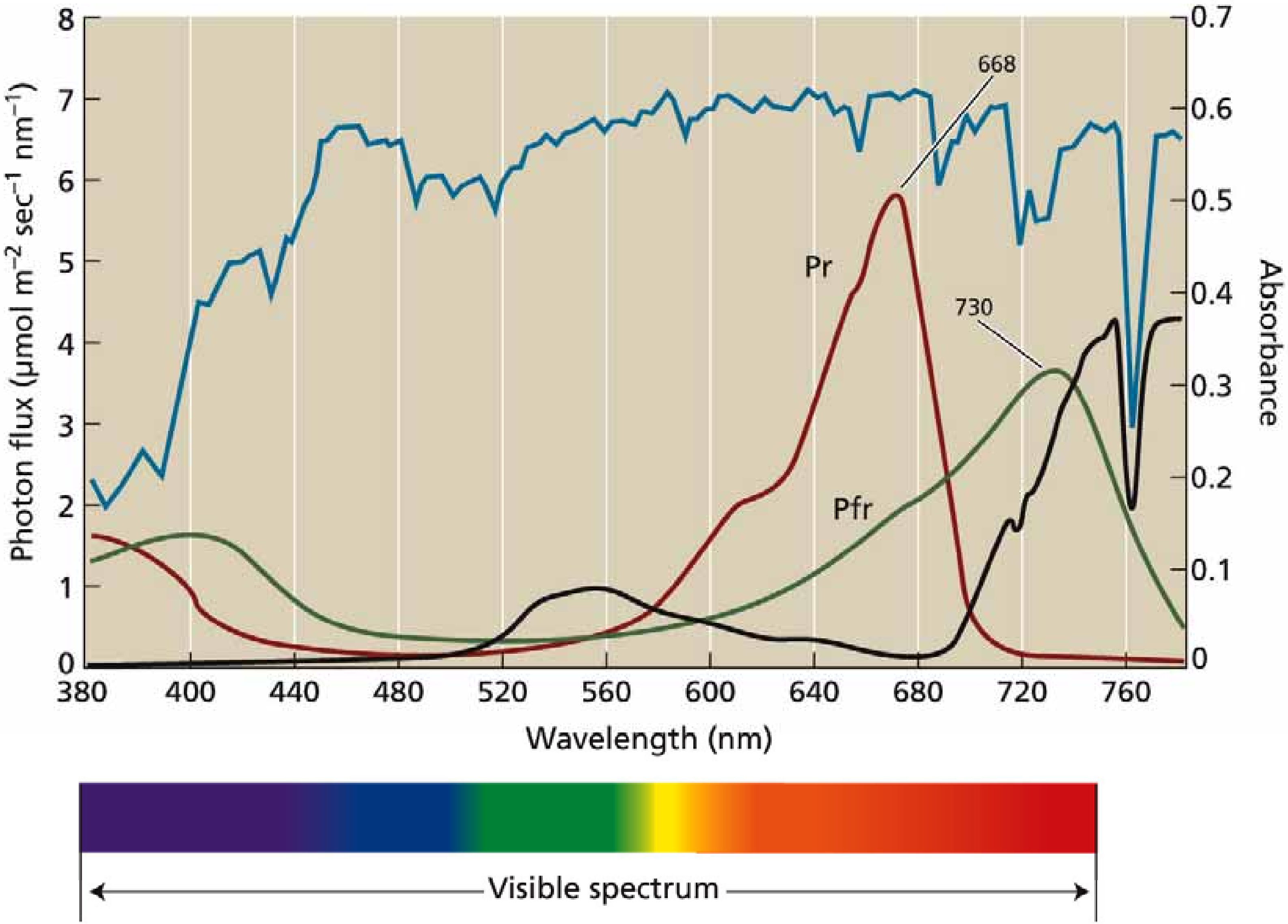
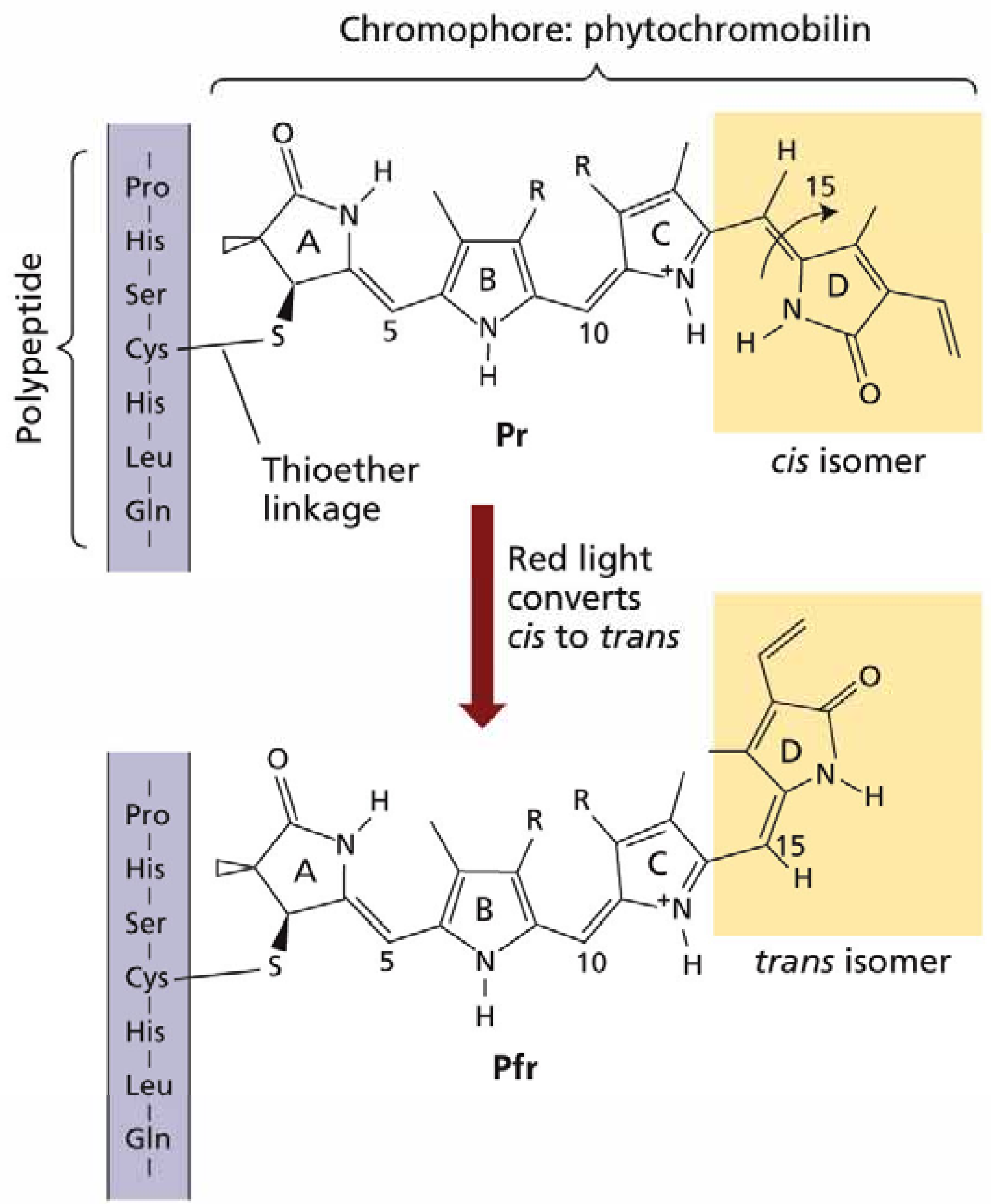
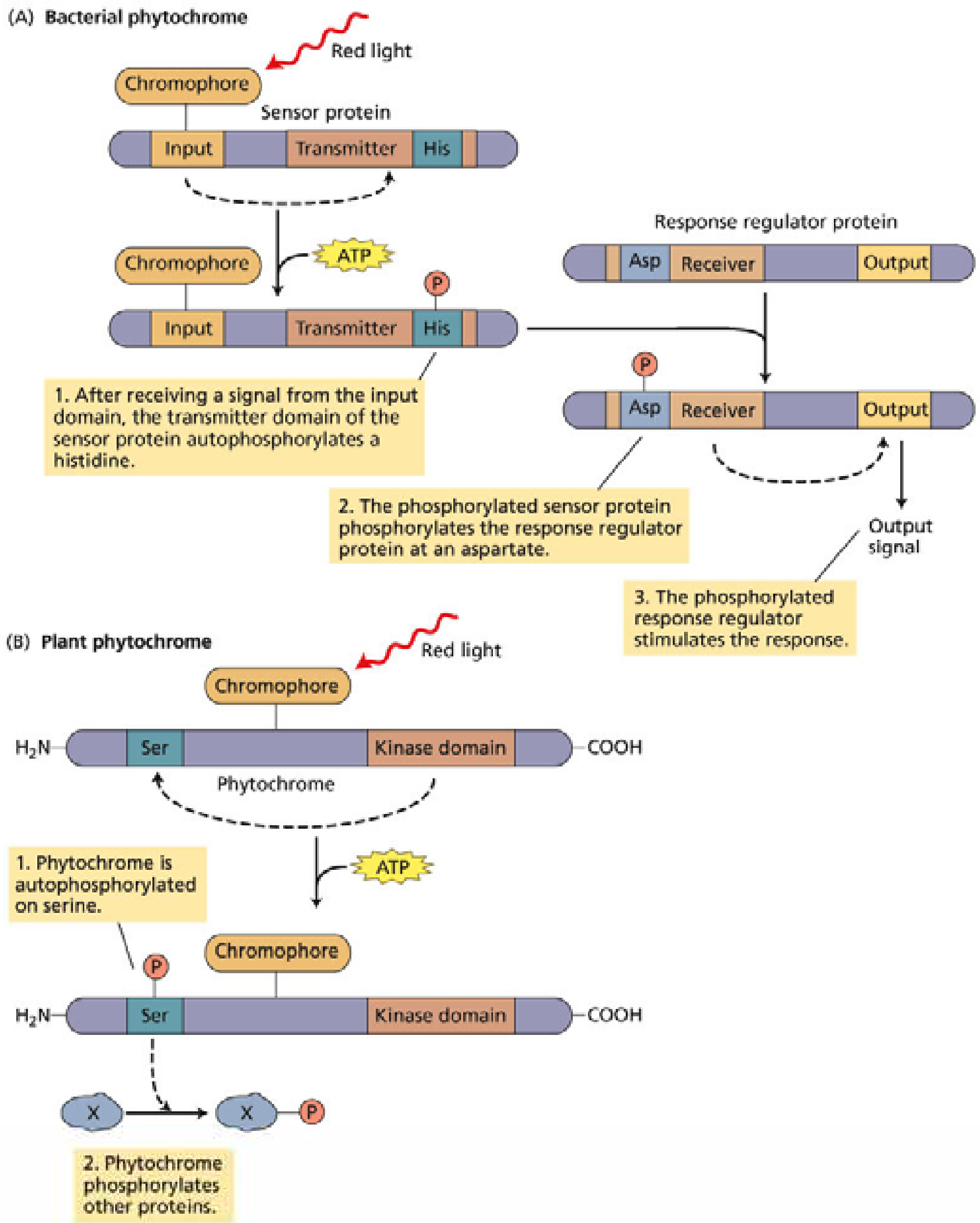


Figure 17.6 Structure of the Pr and Pfr forms of the chromophore



PLANT PHYSIOLOGY, 5e, Figure 17.6

Figure 17.9 Phytochrome is an autophosphorylating protein kinase



PLANT PHYSIOLOGY, 5e, Figure 17.9

Figure 17.2 Lettuce seed germination is a typical photoreversible response

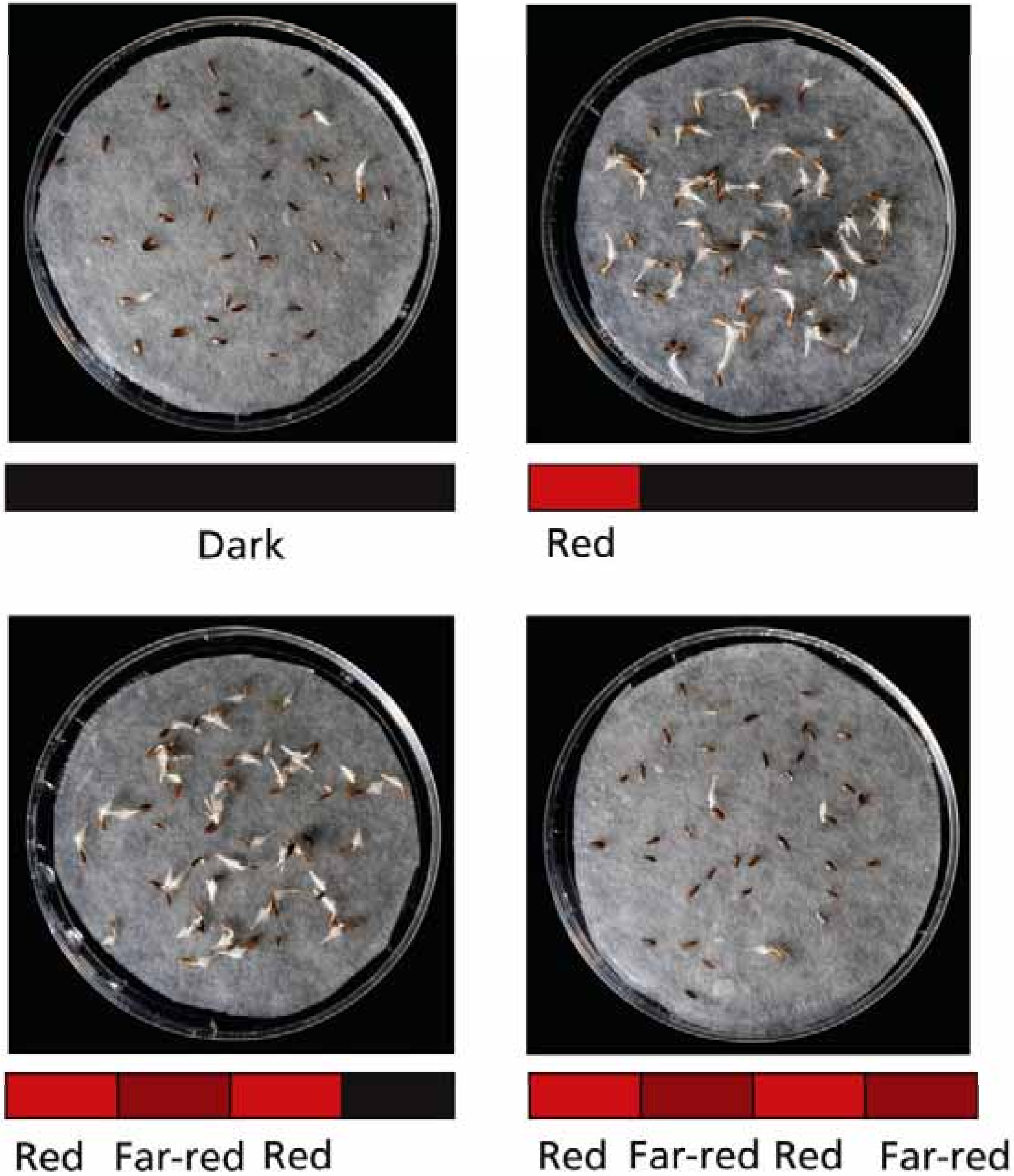
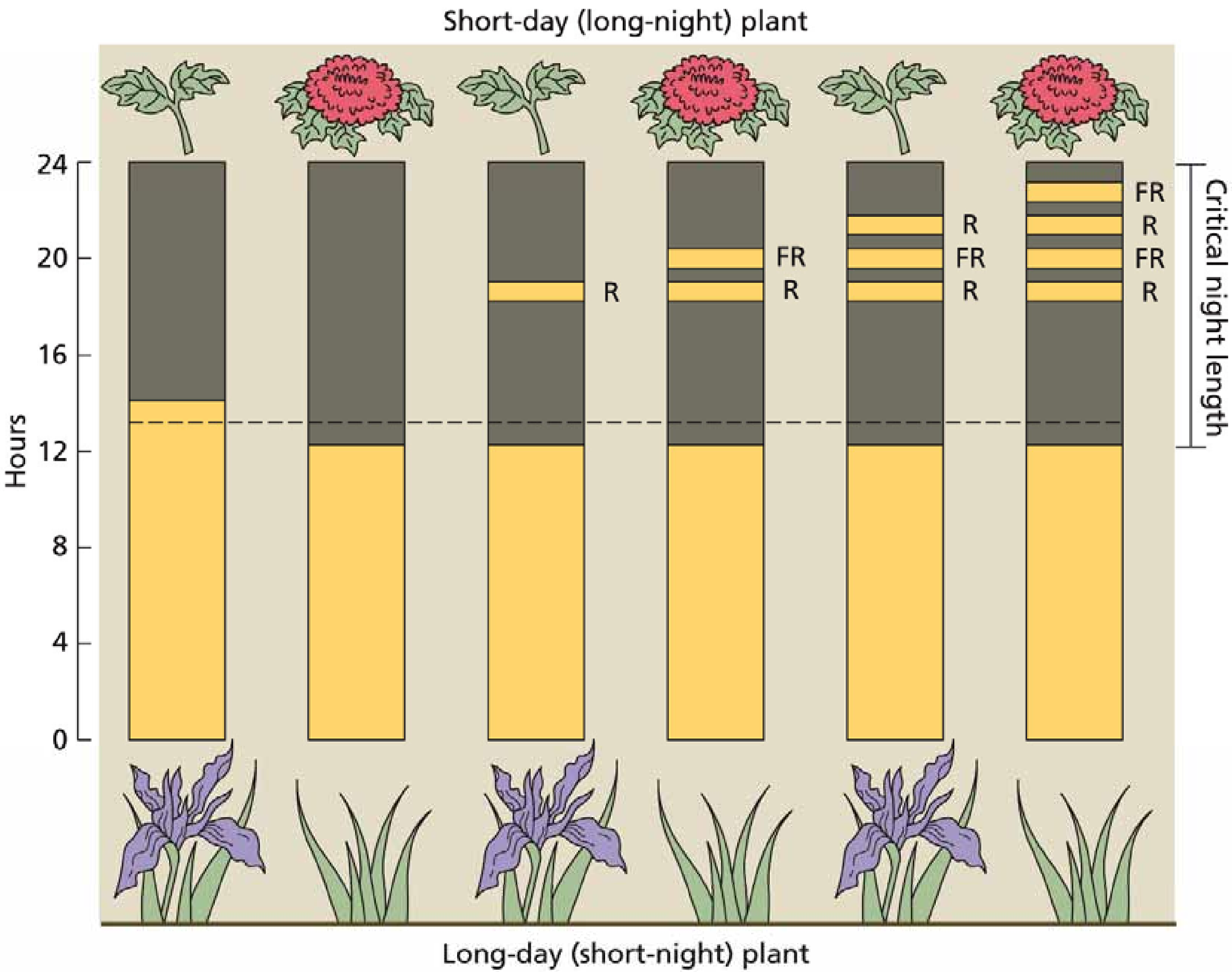


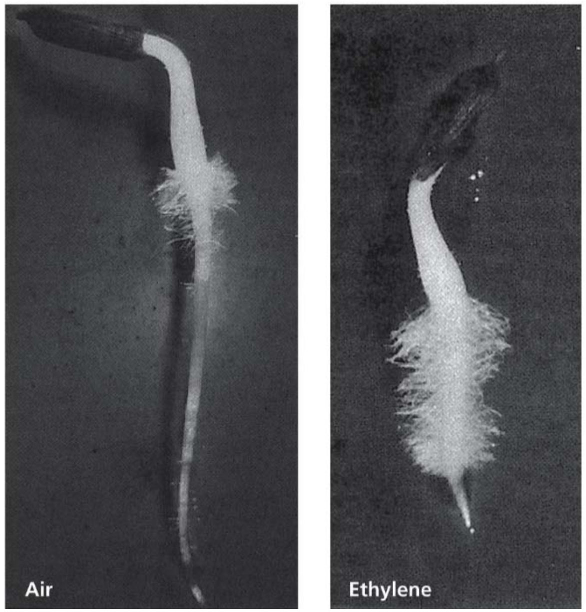
Figure 25.23 Phytochrome control of flowering by red (R) and far-red (FR) light

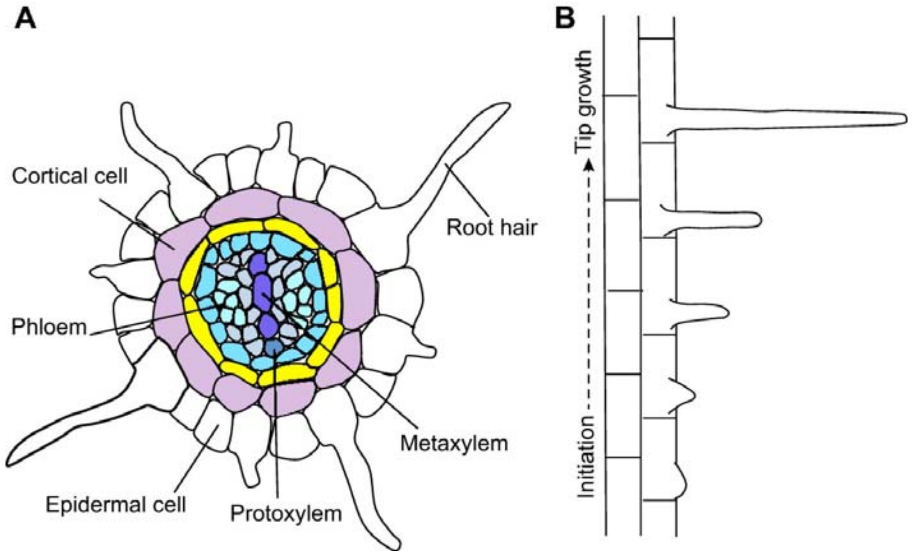


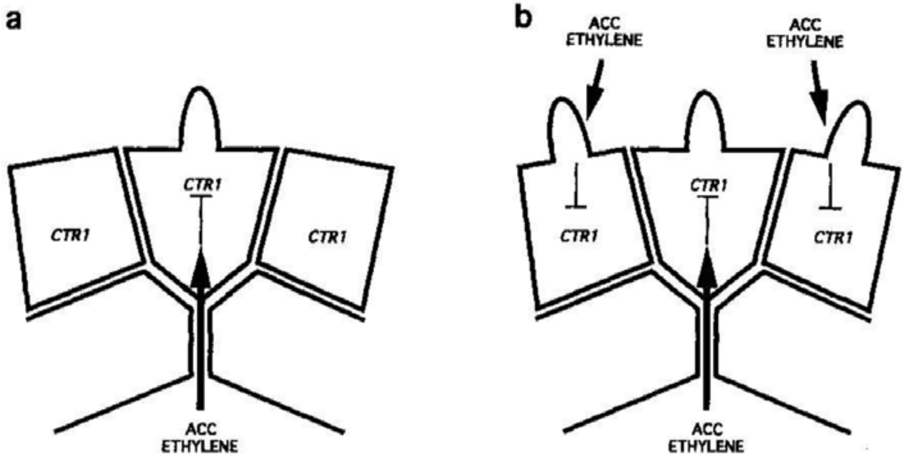
PLANT PHYSIOLOGY, 5e, Figure 25.23

Ethylene induces the formation of roots and root hairs

- Ethylene acts as a positive regulator in the differentiation of root hairs.
- Root hairs normally are located in the epidermal cells that overlie a junction between the underlying cortical cells.
- In ethylene-treated roots, cells not overlying a cortical cell junction differentiated into hair cells, and produce root hairs in abnormal locations.







Ethylene enhances the rate of leaf senescence

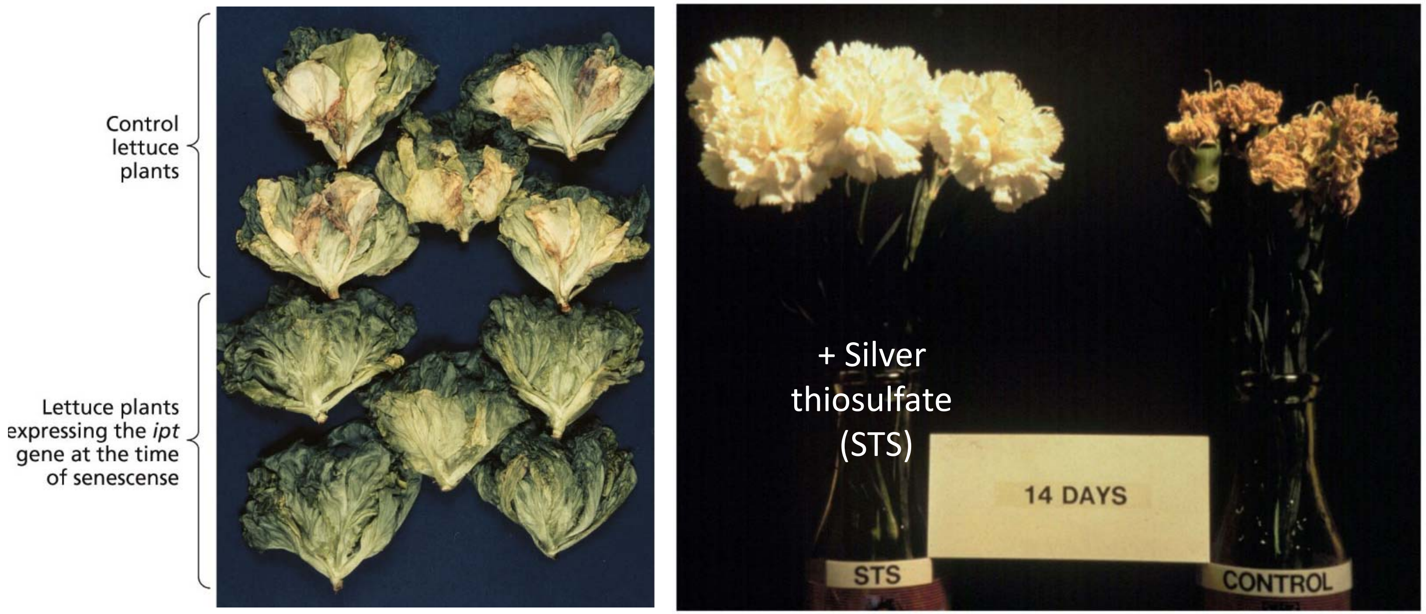
- **Senescence is regulated by the balance of ethylene and cytokinin.**

- **Physiological evidences ;**

  ✓ Exogenous applications of ethylene or ACC accelerate leaf senescence, and treatment with cytokinins delays leaf senescence.

  ✓ Enhanced ethylene production is associated with chlorophyll loss and color fading.

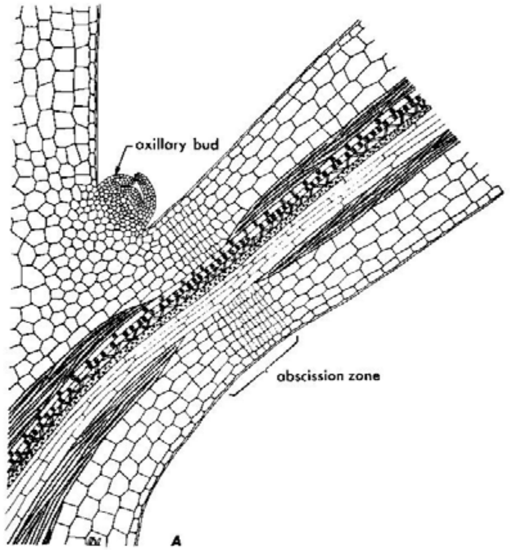
  ✓ Inhibitors of ethylene synthesis (AVG or Co^{2+}) and action (Ag^{+} or CO_2) retard leaf and flower senescence.



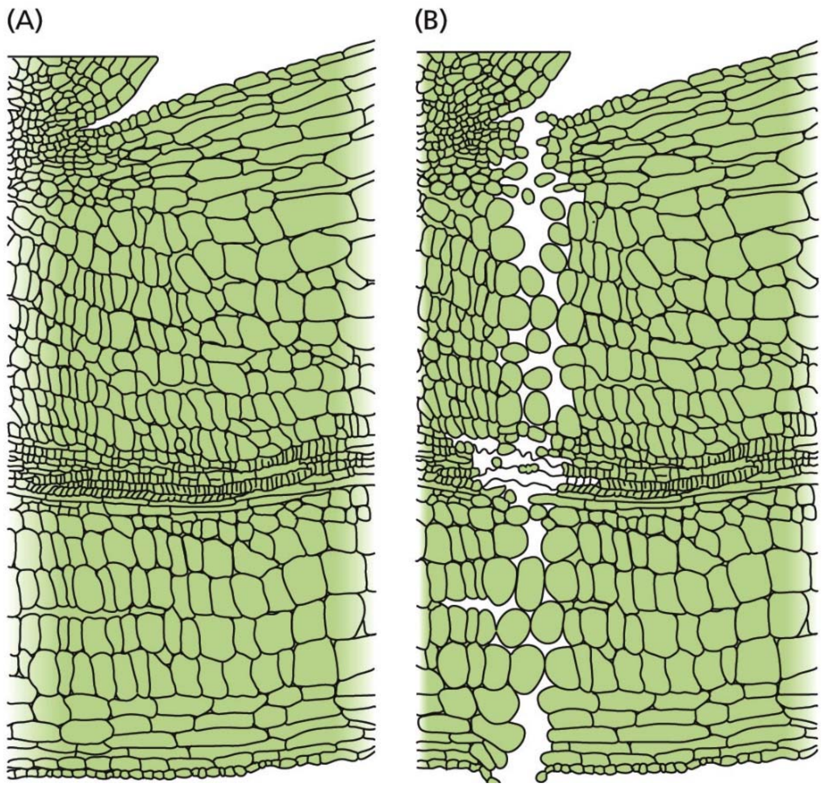
PLANT PHYSIOLOGY, 5e, Figure 22.17

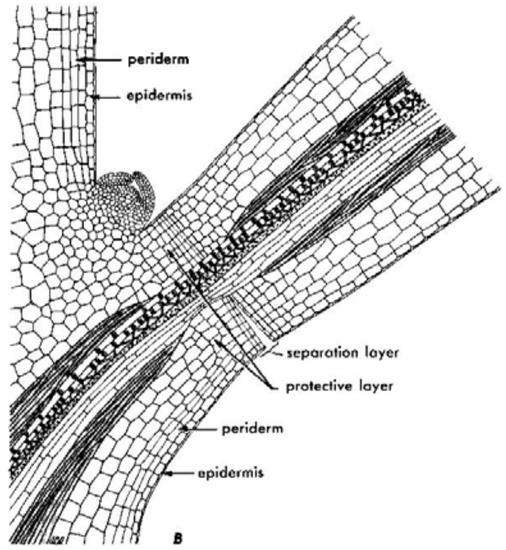
Ethylene acts on the abscission layer

- **Abscission** : The shedding of leaves, fruits, flowers, and other plant organ.
- **Abscission takes place in specific layers of cells called abscission layers.**
- **Weakening of the cell walls at the abscission layer depends on cell wall-degrading enzymes such as cellulose and polygalaturonase.**



During leaf abscission, two or three rows of cells in the abscission zone undergo cell wall breakdown





The protoplast expand and push apart the xylem cells, facilitating the separation of the leaf from the stem.

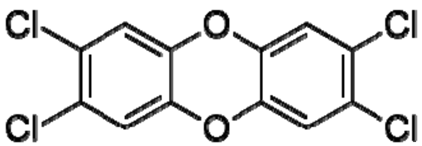
Ethylene acts on the abscission layer

- **Ethylene appears to be the primary regulator of the abscission process.**

- **Supraoptimal auxin concentrations stimulate ethylene production, which has led to the use of auxin analogs as defoliants.**

- **'Agent Orange'**

  - ✓ Mixture of equal parts of two herbicides, 2,4,5-T and 2,4-D
  - ✓ Contained traces of 2,3,7,8-tetrachlorodibenzo-p-dioxin (TCDD)
  - ✓ Increase ethylene biosynthesis, thereby stimulating leaf abscission
  - ✓ Widely used as a defoliant during the Vietnam War
  - ✓ Caused enormous environmental damage in Vietnam



TCDD

+ 50 ppm ethylene, for 3 days

Wild-type

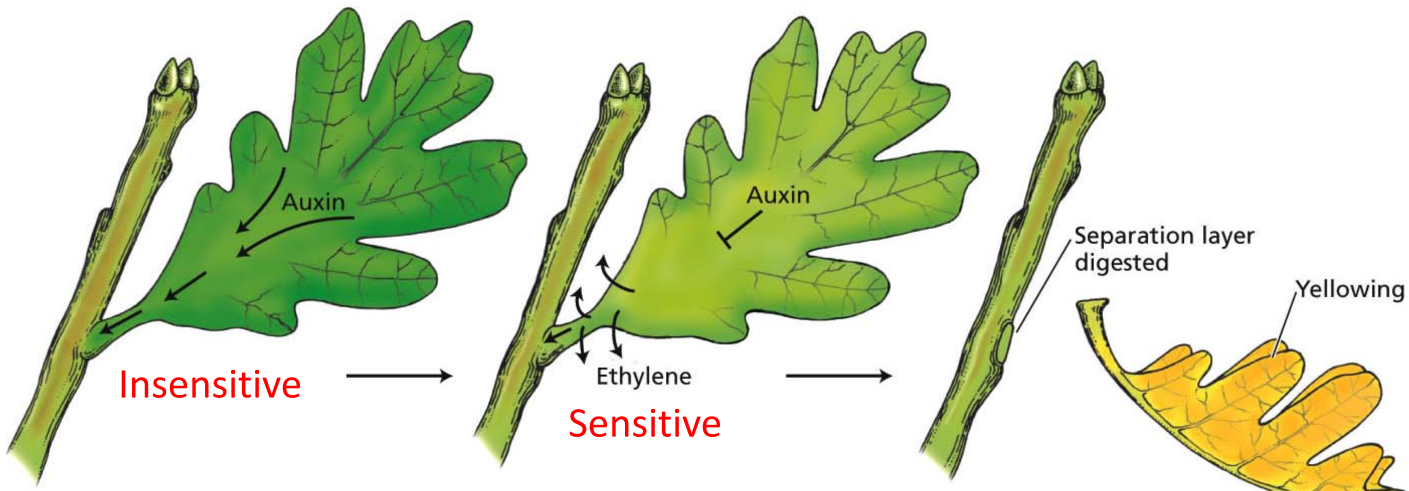
etr1

A model of the hormonal control of leaf abscission

- **Leaf maintenance phase**
  - ✓ High auxin levels in equilibrium with ethylene production
  - ✓ A gradient of auxin from blade to the stem maintains the abscission zone in a nonsensitive state.

- **Shedding induction phase**
  - ✓ The amount of auxin from the leaf decrease and ethylene level rises.
  - ✓ A reduction or reversal in auxin gradient from the leaf, causes the abscission zone to become sensitive to ethylene.

- **Shedding phase**
  - ✓ The sensitized cells of the abscission zone respond to low concentrations of endogenous ethylene by synthesizing and secreting cellulase and other cell wall-degrading enzymes.



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

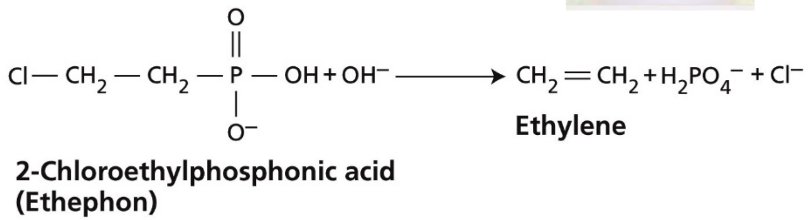
Shedding induction phase
A reduction in auxin from the leaf increases ethylene sensitivity in the abscission zone, which triggers the shedding phase.

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

Ethylene has important commercial uses

- **High diffusion rate, ethylene is very difficult to apply in the field as a gas, but this limitation can be overcome if an ethylene-releasing compound is used**

  (ex) Ethephon (or 2-Chloroethylphosphonic acid)
  - ✓ Hasten fruit ripening of apple and tomato
  - ✓ Degreening of citrus fruits
  - ✓ Synchronizes flowering and fruit set in pineapples
  - ✓ Accelerates abscission of flowers and fruits



- **Storage facilities developed to inhibit ethylene production and promote preservation of fruits.**
  - ✓ Low O2 concentration
  - ✓ Low temperature
  - ✓ High CO2 concentration (3-5%)
  - ✓ Low pressure

- **Ethylene binding inhibitor, 'EthylBloc'**

EthylBloc.

Treated with EthylBloc™ Technology *Control (no EthylBloc™ Technology)*

Summary

- **Structure, biosynthesis, and Measurement of ethylene**
  - ✓ Structure of ET
  - ✓ Physiological effects of ET
  - ✓ Discovery of ET
  - ✓ Skotomorphogenesis, etiolation
  - ✓ Triple response
  - ✓ Biosynthesis : ACS, ACO
  - ✓ Several promoting factors, Inhibitors

- **Ethylene signal transduction pathway**
  - ✓ Receptors
  - ✓ Domain structure
  - ✓ RAN1, copper
  - ✓ CTR1, MAP kinase kinase kinase
  - ✓ EIN2, Serine/threonine kinase
  - ✓ EIN3, ERF1, transcription factors
  - ✓ Epistasis

Summary

- **Developmental and physiological effects of ethylene**

  ① Fruit ripening
  ② Cell expansion / orientation of the cellulose microfibrils
  ③ Two mechanistically distinct phases to ethylene inhibition of hypocotyl elongation
  ④ Submergence / ET stimulates rapid internode elongation
  ⑤ Root hair formation
  ⑥ Leaf and flower senescence
  ⑦ Leaf abscission